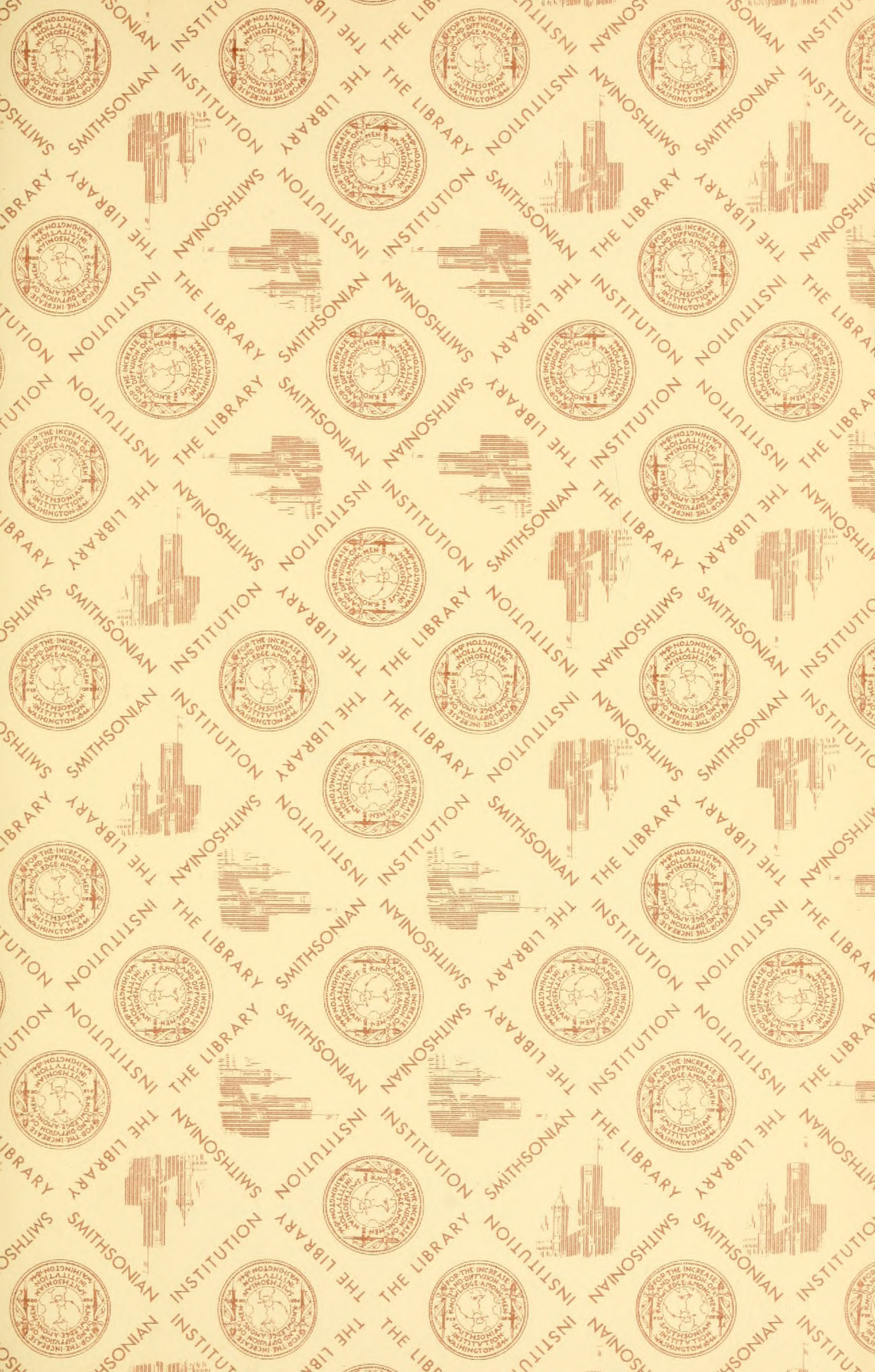
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LEONARD CARMICHAEL,
Secretary, Smithsonian Institution.

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INTRODUCTION

Ornithological literature abounds in descriptions of the habits and activities of birds, while anatomical studies are less common and are related mostly to taxonomy. Attempts to correlate structure with function in birds are few, yet this is a very intriguing subject for study since birds are among the most active members of the animal kingdom. This is reflected in their high rate of metabolism and elevated temperature. Their versatility is great; they can fly, run, or swim, some performing all these activities, while others are limited to one or two. However, certain species excel in locomotion in the air, on the land, or in the water.

We note the explosive flight of the grouse, the graceful glide of the swallow, the soaring of the vulture, the poise of the hummingbird, the racing of the roadrunner, and the diving of the loon. Their skill can be seen, their speed can be measured, but the relative power involved escapes us.

Actual measurement of these activities is necessarily limited, since the confinement required would defeat its goal, but the muscles can be weighed as an indication of their potential capacity. The flight muscles can serve as a measure of power in the air. Likewise muscles of the lower extremities represent the power for terrestrial or aquatic locomotion, while heart weights bear a direct relation to the ability to sustain activity. The areas of the wings, tail, and total gliding surface are measures of the airlift, and the relation of length to breadth of the wing shows the adaptation for lift or glide. The superficial and deep layers of the pectoralis, which constitute 48 to 68 percent of all flight muscles, are most essential in depressing the wing or lifting the body, while the supracoracoideus raises the wing. The remainder of the flight muscles (grouped in the master list, table 1 (pp. 38-87), under the heading "Rest") play their part in controlling wing movement.

Little accurate information about the relative size of muscles has been available. General statements have been made such as that by

Aymar (1935, p. 57): "a pigeon's pectoral muscles which raise and lower the wing are as much as 50 percent of the entire bird." However, Fisher (1946) made careful comparisons of the volumes of the individual locomotor muscles of vultures preserved in alcohol. For the present study I selected certain groups of muscles used in locomotion and weighed them in the fresh condition. In addition, the areas used in lift or glide have been determined.

METHODS

All specimens were kept in waterproof plastic bags to prevent drying until weighed at the field station. Small birds were weighed on a torsion balance of 120 grams' capacity. Larger ones were weighed on Chatillon spring balances, the most sensitive one for the weight involved being used: 6,000 grams' capacity with 24 grams' sensitivity; 500 grams' capacity with 10 grams' sensitivity; and 250 grams' capacity with 5 grams' sensitivity.

The bird was spread out on a sheet of paper tacked to a drawing board. A careful outline of the spread wings, tail, and body was traced. The length and median width of the wing were also determined for the calculation of the aspect ratio $\left(\frac{\text{L}}{\text{W}}\right)$. Areas were obtained later by a compensating polar planimeter. The buoyancy index was calculated by the formula, $\frac{\sqrt[2]{\text{wing area}}}{\sqrt[3]{\text{body weight}}}$, since area is two-dimensional and weight is three-dimensional (George and Nair, 1952). After skinning the areas involved, the pectoralis superficialis, supracoracoideus, the rest of the flight muscles (called "rest") except those along the carpus, metacarpus, and phalanges, and finally all the muscles of the lower extremities were removed by means of scalpel and scissors and then weighed. (If there was any delay before weighing, the dissected muscles were kept in a moist chamber.) These muscles were weighed on both sides from at least 200 birds, but thereafter the muscles on one side only were weighed, since the two sides proved to be identical within the limits of error of dissection. The weights of smaller muscle groups have been determined in a few species. Thus the shoulder, upper and lower arm, and upper and lower leg muscles have been separated. Doubling these values gave the totals used in calculations.

Heart vessels were trimmed close to the organ and both sides cut open, any remaining blood being removed by contact with blotting paper. Weighing was carried out on the torsion balance or on a

Roller-Smith balance with a capacity of 1,500 milligrams and a sensitivity of 0.02 milligram. Only healthy adult birds were used, except for a few immature specimens which are mentioned in the text. Nomenclature is based largely on Peters' check list (1931-1951) and on the check list of the American Ornithologists' Union (1957) for North American passerine species. The values obtained were listed in tables. In our earlier work some of the muscles were not weighed, which accounts for the lack of complete data in some species. The text figures make comparison of typical values in each family, those preceded by an asterisk in the table being represented.

Material for this work was collected in Florida, Maine, Ohio, and Panamá. Panamanian birds were collected during the period January through March at the following stations: Juan Mina, Canal Zone, on the Río Chagres; Río La Jagua in the Pacora marshes, in the Province of Panamá east of Panama City; Cerro Copete (elevation 7,000 ft.) above Boquete, and the finca "Palo Santo" near the village of El Volcán (4,250 ft. above sea level), in the Province of Chiriqui. Florida birds were collected at different seasons on Lake Okeechobee, around the islands of the Gulf Coast, and on the prairies and hammocks of the peninsula. Ohio birds were obtained from the central part of the State, and Maine birds were collected at or near Lake Kezar in the southwestern part of the State. Most specimens were obtained in the morning before 11 o'clock.

ACKNOWLEDGMENTS

I am very much indebted to Richard Archbold, of the Archbold Biological Station, Florida, for his personal assistance in the collection of material, and for the use of the facilities of the Station. In Panamá the studies in the Canal Zone were based at the Juan Mina Field Station of the Gorgas Memorial Institute through the good offices of Dr. Carl Johnson, the director. The La Jagua Hunt Club permitted the use of their facilities for work in the open country near the Río La Jagua. Pablo Brackney kindly granted our party the use of a cottage at "Palo Santo," and the late Tollef Mönniche aided us on our expeditions on Cerro Copete above Boquete. Alois Hartmann also permitted us to stay at his place in western Chiriquí. The late Dr. James Zetek, then Resident Manager of the Canal Zone Biological Area on Barro Colorado Island, was very helpful at all times with advice. I wish to thank Dr. Alexander Wetmore for the identification of some of the Panamanian birds and for a critical reading of the manuscript. Many of the measurements and calculations were carried

out by Carl Albrecht, Kent Bruno, Barbara Caldwell, David Gillespie, Elmer E. Hartman, Donald Neal, and Kenneth Teague. This study was aided by grants from the Comly-Coleman Fund and the Graduate School of the Ohio State University.

RESULTS

Data on more than 360 species in 70 families are included in this report. The muscle weights are calculated as percent of body weight. The wing and other areas are given as cm.^{2} per gram of body weight. Glide area is the area included in wings, tail, and body.

In the master list (table 1, pp. 38-87) the number of individuals in a species is shown in parentheses, with the mean values and standard error of the means, or the individual values are given if less than three. Sexes are separated for body weights and for other determinations where the differences between sexes are significant; otherwise the data of the two sexes are combined. Although the data from a single individual may not be representative of a species, they have been included if the species is sufficiently interesting.

Before embarking on a consideration of the muscles I wish to call attention to certain species in which there is a significant difference in body weight between the sexes. Those in which males are larger are: *Podiceps dominicus, Casmerodius albus, Gallus gallus, Aramus guarauna, Porphyrula martinica, Columba speciosa, Brotogeris jugularis, Crotophaga major, Crotophaga ani, Crotophaga sulcirostris, Nyctidromus albicollis,* many trochilids, *Centurus rubricapillus, Centurus chrysauchen, Dendrocincla homochroa, Sittasomus griseicapillus, Xiphorhynchus guttatus, Anabacerthia striaticollis, Manacus vitellinus, Fluvicola pica, Cyanocitta cristata, Parus carolinensis, Parus bicolor, Parula pitiayumi,* many icterids, and *Arremonops conirostris.* In the following species the females are larger: *Jacana spinosa, Tyto alba, Speotyto cunicularia, Cotinga ridgwayi, Corapipo leucorrhoa, Thryothorus modestus,* and *Selasphorus scintilla.*

Let us now consider the distinctive values in each family and their possible relation to habits (table 1).

Tinamidae.—The tinamous are most unusual birds, possessing extremely large flight muscles (37 to 40 percent of the body weight, of which the pectoralis is 63 percent) and large leg muscles (13 to 17 percent) but the smallest heart (0.19 to 0.25 percent) of all birds. The pectorals are so large that they extend beyond the keel of the sternum. In *Crypturellus* the sternum is submerged 7 to 8 mm. below the bulging pectorals. The same condition is present in *Nothocercus* and in *Tinamus,* where the submergence may reach 9 to 10 mm. The wings are small (buoyancy index, 2.86 to 3.14) and broad (aspect ratio, 1.49 to 1.62). The wing area per gram of flight muscles is 19 cm.^{2} in *Tinamus* and 36 cm.^{2} in *Crypturellus. Nothocercus* possesses smaller pectoralis muscles ($P<0.01$) but larger lower-extremity muscles than *Tinamus* and *Crypturellus.* The muscles are in keeping with the habits—these birds run along the ground or fly explosively for short distances, the small heart preventing more prolonged effort.

Podicipedidae.—Grebes are most proficient in swimming and diving, using their feet in the process (Van Tyne and Berger, 1959). Their flight muscles are very small, being only 14 percent of the body in *Podiceps dominicus.* This species, which weighs only a little more than one-third as much as *Podilymbus podiceps,* possesses almost double the wing area of the latter. *Podiceps dominicus* also has a lower aspect ratio (2.51 compared to 2.91). The tails are insignificant in both species. The leg muscles are large, being 16 percent in *Podiceps* and 18 percent in *Podilymbus.* The leg position is ideal for swimming but causes an awkward waddling gait in walking. The heart is moderate in size in both species (1.00 to 1.05 percent).

Pelecanidae.—The clownish brown pelican starts rather awkwardly with slow, sweeping wing strokes, continuing with frequent soaring and sailing or, on a gentle breeze, gliding gracefully just above the water. The male has relatively larger flight and leg muscles than does the female, but compared to the cormorant, the flight muscles are but a little larger while the legs are less than half the size. His wings are moderately large (1.34 cm.^{2} per g. of body; buoyancy index, 4.38) but very long (aspect ratio, 3.75), enabling him to skim over the water with ease.

Phalacrocoracidae.—The cormorant prefers to dive and swim, since that is his method of obtaining food. He is a rapid swimmer, using only his feet according to Selous (see Bent, 1922), holding his wings motionless. In the air he is a heavy flier (flight muscles, 17 percent; buoyancy index, 3.27), slowly flapping his wings after the manner of a heron. His legs are large (muscles are 11 percent of the body), but because of their position, on land he is awkward, though less helpless than the grebe.

Anhingidae.—The anhinga, like the cormorant, obtains his food by diving and swimming, using his feet only, with wings slightly folded or slightly expanded and steering with his tail, which can be spread as a rudder (Bent, 1922). However, unlike the cormorant he is a graceful, rather powerful flier, having somewhat larger flight muscles (19 percent) and wings (buoyancy index, 3.7) but smaller legs (8.6 percent).

Fregatidae.—The man-o'-war, one of the most graceful birds in the air, soars much of the time, steering by his scissors tail, but he can also fly rapidly to overtake another bird. His wings are very large (buoyancy index, 5.55) and extremely long (aspect ratio, 3.5 to 4.4), but his pectoralis plus supracoracoideus muscles are moderate (13 to 17 percent).

Ardeidae.—The large leg muscles of the herons are useful for wading and stalking prey. The members of this family show a considerable range in equipment, but the wings of all are rather long (aspect ratio, 2.00 to 2.66) and large (buoyancy index, 3.68 to 5.28), and all have large flight muscles (20 to 25 percent) except *Ixobrychus* (13.89 percent).

They vary as much in flight as in muscular equipment. Some, like the great blue heron, make an awkward start on the takeoff by vigorous wing strokes, but once underway the long, slow strokes carry them majestically through the air. The black-crowned night heron differs from other herons in having a flight more gull-like, being stronger and swifter with quicker wing strokes. This is not due to the size of the wing muscles, since they are no larger. The least bittern has an awkward fluttering flight for a short distance, preferring to escape by walking or climbing. However, on long flights he appears strong and rather swift despite small flight muscles. The hearts of all herons are rather small (0.57 to 0.83 percent).

The hearts of the Florida subspecies of *Butorides virescens* are heavier ($P<0.05$) than those of the same species collected in Panamá. This is also true for individuals of *Florida caerulea* and *Ixobrychus exilis* from the two localities. The hearts ($P<0.01$) and pectoral and supracoracoideus muscles ($P<0.05$) of *Tigrisoma lineatum* are larger than the same features in *Heterocnus mexicanus*.

Cochleariidae.—The boat-billed heron is similar to the true herons in the size of its flight equipment. It is interesting to note that in an immature *Cochlearis,* at a time when the body had almost attained adult weight, the flight muscles were less than half the weight of those in the adult, while the leg muscles were nearly the weight of the adult's. The heart of the immature was also very much smaller than that of the adult. The early development of the leg muscles was also shown in a young *Heterocnus mexicanus* (250 g.). In this bird the legs were half-grown (muscles 5.88 percent of the body) while the flight muscles were little more than one-tenth the value of those of the adult (2.28 percent). Likewise, an immature male *Podilymbus podiceps* that had attained the weight of the adult (450 g.) possessed flight muscles (7.58 percent) somewhat less than those of the adult, while the legs were the size of those of the adult (18.9 percent). The wing feathers were just emerging.

Ciconiidae.—The wood ibis springs powerfully into the air and flies higher and higher until almost out of sight, when he sails gracefully on motionless wings in wide circles. His flight muscles are somewhat larger (27 percent of body) and his wings narrower (aspect ratio, 2.85) than in most herons, but his legs are about the same size (10.9 percent).

Threskiornithidae.—The white ibis walks and climbs nimbly and swims well. He flies with strong, rapid strokes, varied with occasional periods of sailing. There is nothing unusual about his measurements.

Anatidae.—Both the pintail (*Anas acuta*) and blue-winged teal (*Anas discors*) are fast fliers with fairly large hearts (1.23 and 1.15 percent respectively) and large flight muscles (31.36 and 29.2 percent). They spring upward from the water and get underway at once. The whistling of the teal's wings is probably due to the rapid wing beats, since the wings are small for the weight (buoyancy index, 2.84). The lesser scaup (*Aythya affinis*), a rather laborious but steady flier, has a buoyancy index of 2.62. Its heart is smaller than that of *Oxyura dominica* ($P<0.05$) and *Anas acuta* ($P<0.01$). The heart of *Cairina,* in the domesticated form, is smallest of all. The flight muscles of the male *Cairina* are smaller ($P<0.01$) than those of the female, while the reverse is true for the legs. The supracoracoideus in ducks is about one-third that of the "rest" group. *Cairina* possesses the largest legs of all ducks studied.

Cathartidae.—The flight of *Coragyps* is inferior to that of *Cathartes.* He has smaller wings ($P<0.01$) and flight muscles ($P<0.05$) a larger heart and legs ($P<0.01$,), and broader wings. Differences are also shown between Panamá and Florida vultures. The hearts of Florida *Coragyps* ($P<0.05$) and *Cathartes* ($P<0.01$) are larger than those of the Panamá species.

Accipitridae.—Among the hawks, *Elanoïdes* is unsurpassed in beautiful maneuverings. With his long wings (aspect ratio, 3.40) and forked tail he soars aloft to sport among the clouds. The speedy accipiters fly by a series of quick flappings followed by short periods of rapid sailing. In contrast the *Buteo* flight is heavy but powerful and graceful. *Buteogallus anthracinus* is similar in flight.

The hearts of the Accipitridae are relatively small, ranging from 0.40 to 0.81 percent. The flight muscles of most of them are of moderate size, *Chondrohierax* and *Spizaëtus* being exceptions. The most striking finding is the relatively small size of the supracoracoideus (only 0.39 to 0.56 percent of the body). The legs, except in *Elanoïdes,* are fairly large, and the wings are fairly long. These characteristics indicate good fliers but little ability to sustain activity for long periods, unless by soaring. The muscles of the lower extremities of many hawks are relatively large, and those of the upper extremities are not small. Several hawks are strong fliers, although they frequently soar.

Pandionidae.—The muscles of the osprey resemble those of the Accipitridae, but the legs are smaller and the heart is larger than in most of the latter.

Falconidae.—The hearts of falcons are a little larger than those of hawks, ranging from 0.53 percent (*Micrastur*) to 1.11 percent (*Polyborus*). The supracoracoideus is also somewhat larger than in hawks. The wings are narrower in species that are fast fliers. The flight and leg muscles of *Micrastur semitorquatus* are larger than those of *Micrastur ruficollis,* while the wings are much smaller; yet the buoyancy index is about the same.

Cracidae.—In the Cracidae, represented in our study by the chestnut-winged chacalaca (*Ortalis garrula*) and the black guan (*Chaemepetes unicolor*), the flight muscles are moderately large (23 to 26 percent), with the supracoracoideus of fair size (2 to 3 percent). These birds are heavy fliers with wings rather moderate in size (buoyancy index, 3.66) and broad (aspect ratio, 1.38 to 1.51); the leg muscles are large (15.7 to 20 percent), while the heart is small (0.48 to 0.62 percent).

Phasianidae.—The phasianids are very interesting. Three species of quail, natives of widely different parts of the world, possess very large flight muscles (*Coturnix,* 25.6 percent; *Odontophorus,* 29.4 percent; *Colinus,* 34.3 percent) and large supracoracoideus (5.66 percent; 5.89 percent; 7.16 percent), with a "rest" nearly the size of the latter (4.46 percent; 6.17 percent; 5.53 percent). But the heart of *Coturnix* is about three times the size of that of the other two species (1.00 percent compared to 0.34 percent and 0.38 percent). The lower extremities are large (muscles 12.16 percent, 16.38 percent, and 14.6 percent), but the wings are small (buoyancy indices, 2.38, 3.10, 2.62). It should be noted that the aspect ratio of *Coturnix* is higher than that of other phasianids (2.15 as compared with 1.56 and 1.74). The powerful musculature for flight indicates great bursts of speed although the species with small hearts would have limited endurance. *Coturnix,* with a larger heart, can sustain the flight required in its long migrations. In the domesticated *Gallus gallus* (white leghorn) the flight muscles and wings are much smaller than in the quail; otherwise the values are similar. However, the males are much larger than the females and have larger legs ($P<0.01$) and hearts ($P<0.01$). Our specimens of *Coturnix* were raised in captivity, but they have not been subjected to selective breeding as has *Gallus.*

Numididae.—*Numida meleagris,* although domesticated, has values similar to those for some of the quails except that the heart is about twice the size and the wings are somewhat smaller.

Aramidae.—The limpkin (*Aramus guarauna*), a slow and infrequent flier, alternating wing beats with sailing, has fairly large flight muscles (21 to 24 percent), wings with a buoyancy index of 3.59, and large leg muscles (16 percent). Like the rail, he can travel rapidly on the ground. His wings are fairly long (aspect ratio, 2.2 to 2.9).

Rallidae.—Many rails dive and swim readily but fly feebly, and after a short flight, drop to the ground and run swiftly. Thus their flight muscles are small (12 to 17 percent), and their hearts are moderate in size, ranging from 0.58 to 0.65 percent. In most species the legs are large, especially so in *Aramides cajanea* (24.8 percent). An immature *Laterallus albigularis* weighing 20.75 grams possessed a heart 0.70 percent of body, a pectoralis of only 0.61 percent (adult 7.0 percent), and lower extremity muscles of 2.51 percent (adult 17.4 percent). The flight of the purple gallinule (*Porphyrula martinica*) ordinarily seems weak and labored, but on long flights it is fairly swift. Both gallinules run with great speed. The coot (*Fulica americana*) is a more vigorous flier than the gallinules.

Heliornithidae.—The finfoot (*Heliornis fulica*) resembles the rail in all his proportions. He swims much and dives to escape, although he is a fairly strong flier for short distances. A young female weighing 76.05 grams possessed a heart 0.68 percent of the body, flight muscles only 8.07 percent compared to 17.64 percent for the adult, and lower extremities 9.31 percent of body (adult, 15 percent).

Jacanidae.—The jaçana, which spends much time running over lily pads, swimming if need be, has leg muscles somewhat smaller than those in rails (10 to 12 percent). He hovers much in flying, using his rather large wings (buoyancy index, 3.64).

Charadriidae.—The plovers are swift runners and strong fliers. Such activity is supported by a large heart (1.36 percent), large flight muscles (29 percent), and lower extremities of moderate size (7.88 percent).

Scolopacidae.—Likewise, the sandpipers, as they run up and down the beach or fly swiftly to new hunting grounds, use a fairly large flight apparatus (flight muscles, 23 to 32 percent and hearts, 1 to 1.54 percent) and small to moderate lower extremities (4.5 to 9 percent).

Recurvirostridae.—The birds in this group are similar to the other shore birds, being equipped for strong flight.

Laridae.—The flight apparatus of gulls and terns differs in conformity with their respective habits. The slow-flying gulls, which soar much, possess rather small hearts (0.85 percent), moderate flight muscles, and moderate lower extremities (5 to 6 percent), while the more active terns, which dash about and dive for fish, have larger hearts (0.84 to 1.08 percent), flight muscles about the same, and lower extremities only half the size of those in gulls.

Rynchopidae.—Skimmers are almost identical with terns with respect to their equipment; they are swift and dextrous as they plow the surface of the water for food.

Columbidae.—Doves and pigeons can be divided into two groups according to heart size. In one group hearts range from 0.28 to 0.56 percent of the body; in the other, from 0.93 to 1.29 percent. Those of the first group are *Leptotila cassini, Leptotila rufinucha, Geotrygon costaricensis* and *Geotrygon chiriquensis,* while all other species including *Leptotila verreauxi,* are in the second group. We are unable to explain the differences between the two species of the genus *Leptotila.* The contrast in muscle values between *Leptotila cassini* and *Leptotila verreauxi,* both collected at sea level, is striking. The heart of *verreauxi* is larger ($P<0.01$), while the pectoral muscles of *cassini* are larger ($P<0.01$). The heart of *Columbigallina passerini* of Florida is larger than that of *Columbigallina talpacoti* ($P<0.05$) of Panamá; the heart of *Claravis pretiosa* is larger ($P<0.01$) than that of *Claravis mondetoura.* The flight muscles of all pigeons are almost as large in proportion (31 to 44 percent) as those in tinamous, and the supracoracoideus is as large or nearly as large as the "rest" group. The wings are quite large (buoyancy ratio, 3.0 to 3.65), the legs small to moderate (4.5 to 7.8 percent). Both the wild and domesticated species of *Columba* are powerful long-range fliers, while *Columbigallina* flies but short distances.

Psittacidae.—Parrots are usually strong fliers and make good use of their legs. The female *Brotogeris* is larger than the male. All have fairly large hearts (1.03 to 1.52 percent) and large flight muscles (25 to 28 percent). The supracoracoideus is one-third to one-half of the "rest" group. Wings of fair size give them a buoyancy index of 3.2 to 3.7, and the lower extremities are of medium size (5.5 to 7.8 percent). The proportions of domesticated *Melopsitticus* are similar to those of the wild forms except that the buoyancy index is lower (2.84).

Cuculidae.—Some cuckoos fly very little, and we have studied only those that do more flying. In these, the power of flight varies considerably. The hearts (0.50 to 0.94 percent) indicate little staying power. The flight muscles are very moderate (14 to 20 percent), supporting wings of a high buoyancy index (3.7 to 4.4) and a low aspect ratio (1.3 to 1.8), enabling them to fly only slowly. The tails are large, and the lower extremities are of considerable size (muscles, 7 to 15 percent). Anis fly with a series of steady wing beats alternating with short sails. The flight resembles somewhat that of the Florida jay, being slow and gliding and rather labored. The hearts and flight muscles are smaller in *Piaya cayana* ($P<.01$) and *Crotophaga ani* ($P<0.01$) in specimens collected at sea level than in the same species collected at 4,300 feet elevation.

Tytonidae.—The barn owl (*Tyto alba*) may be grouped with the typical owls with respect to muscle values, although he has a larger wing than most of the others.

Strigidae.—Owls are able to fly quietly, as their wings are soft, very large (buoyancy index, 4.24 to 5.11), and broad (aspect ratio, 1.8 to 2.7). The flight muscles are moderately powerful (19 to 27 percent), and the hearts are small to medium (0.31 to 0.89 percent), the largest being found in the burrowing owl (*Speotyto cunicularis*).

Nyctibiidae.—The wings of the Nyctibiidae and Caprimulgidae are as large as, or larger than (buoyancy index, 4.36 to 5.19), those of owls but with a very high aspect ratio (2.20 to 3.4). The smaller heart (0.58 percent) of the potoo (*Nyctibius griseus*) is in keeping with his more limited activity, since he makes but short flights in his forays for insects, in contrast with the caprimulgids (0.78 to 1.12 percent), which sweep the air in sustained flight.

Caprimulgidae.—The pauraque (*Nyctidromus albicollis*), with a longer tarsus and larger leg muscles (8.28 percent) than some other caprimulgids, is more active on its feet and can run swiftly.

Trochilidae.—The hummingbird is the acrobat among birds—none equals him in speedy maneuverability. He hovers and flies forward or backward at will. Of his large flight muscles, the pectoralis plus the supracoracoideus constitute a large proportion. Many species show sex differences, and in these species the muscles of the male are always larger than those of the female. Never has the reverse been found in the 25 species that I have examined. This sex difference applies to the heart in several species, and in *Amazilia edward, Amazilia tzacatl, Lampornis castaneoventris,* and *Selasphorus scintilla* it applies to the heart and pectoralis-supracoracoideus. Hearts range from 1.65 to 3.25 percent of the body, pectoralis-supracoracoideus from 21.7 to 33.1 percent. The supracoracoideus, ranging from 6.6 to 12.2 percent, is the largest of all birds studied. The "rest" is small, ranging from 1.75 to 4.79 percent, and leg muscles are very small, being only a little more than 1 percent. Wings range from 3.11 to 5.70 cm.^{2} per gram; tail from 1.57 to 2.95 cm.^{2} per gram; and buoyancy index from 1.31 to 3.09.

Trogonidae.—Trogons make short, rapid flights among the trees to catch insects. Their flight muscles (29 to 32 percent) are slightly larger than those of nightjars. Their hearts are also larger (1.05 to 1.29 percent), but the wings are smaller (buoyancy index, 3.68 to 3.91) and much wider (aspect ratio, 1.9 to 2.1) for flight among foliage. Like the nightjars, their legs are small (2.4 to 3.1 percent). The wings and glide areas of *Pharomachrus, Trogon massena,* and *Trogon melanurus* are smaller than those of the other three species of trogons measured.

Alcedinidae.—The fairly large wings (buoyancy index, 3.09 to 3.68) enables the kingfisher to fly swiftly in short flights. The hearts of these birds are large, especially in the smaller species (1.02 to 1.35 percent). The flight muscles (24.5 to 26 percent) are about the size of those in the nightjars, and the legs are small (2.48 to 3 percent).

Momotidae.—Motmots perch for long periods in one place (lower extremities 6 percent). Their flight is undulating, their wings are large (buoyancy index, 3.85) and broad (aspect ratio, 1.70), and they have long, ornamental tails. The small hearts are indicative of limited activity (0.39 to 0.49 percent).

Bucconidae.—Although most species of puffbirds are sedentary, they sally forth occasionally to capture insects (flight muscles, 24 to 28 percent; buoyancy index, 3.4 to 3.56). Their lower extremities are of moderate size (4 percent), and their hearts are small 0.45 to 0.58 percent).

Capitonidae.—Barbets are weak fliers (flight muscles, 18.7 percent) but have large lower extremities (9.4 percent) and larger hearts (0.74 percent) than do the puffbirds, although they also remain in one spot for a long time.

Ramphastidae.—The restlessly active toucans are weak fliers (flight muscles, 20 to 23 percent; hearts, 0.62 to 0.81 percent), but they have large lower extremities (9 to 12 percent). Specimens of *Pteroglossus torquatus* found at sea level are smaller ($P<0.05$ for males, and $P<0.01$ for females) and have a smaller heart ($P<0.01$) than those of *Pteroglossus frantzii* obtained at 4,300 feet above sea level. Pectoralis plus supracoracoideus muscles show corresponding proportions in the two species.

Picidae.—The woodpecker, aptly called "carpintero" by Spanish-speaking natives, devotes much of his time to chiseling holes in tree trunks for food or nest. His legs (6 to 11 percent) and his heart (0.81 to 1.41 percent) are fairly large. Sizable flight muscles (22 to 29 percent) and large and broad wings (buoyancy index, 3.39 to 4.25; aspect ratio, 1.62 to 2.07) give him the power for his characteristic undulating flight marked by a series of graceful dips. The largest woodpeckers studied, of the genus *Phloeoceastes,* possessed the smallest wing and glide areas but the largest legs. The downy woodpecker flies rapidly, the pileated woodpecker, slowly but vigorously, at times, like a crow, otherwise in short swings and dips like other woodpeckers.

Dendrocolaptidae.—Woodhewers, like the woodpeckers, climb trees in search of food, frequently making short, strong flights to a new tree, where the quest is repeated. The hearts are large (1.10 to 1.48 percent) in the smaller species and of medium size (0.65 to 0.93 percent) in the others. The pectoralis plus supracoracoideus muscles are larger in the male than in the female in *Xiphorhynchus guttatus and Lepidocolaptes affinis* ($P<0.01$). The legs are similar in size to those of the woodpeckers. The buoyancy index is large (3.65 to 4.20).

Furnariidae.—In the ovenbirds there is a wide variety of habits, ranging from those of terrestrial species to those of species that climb trees, bracing with the tail. Flight is weak to strong (flight muscles, 16 to 30 percent), and the wings are large (buoyancy index, 3.0 to 4.0). As might be expected, the muscles of the lower extremities are large (8 to 13 percent). The heart muscles are moderate (mostly 1.0 to 1.16 percent) except in *Anabacerthia* (1.49 percent) and *Automolus* (1.48 percent).

Formicariidae.—Like the ovenbirds, antbirds may be arboreal or terrestrial. All have large muscles in the lower extremities (8 to 14 percent) but small to medium flight muscles (16 to 23 percent) except for *Formicarius* (30.5 percent). As in other birds that fly among close vegetation, their wings are large (buoyancy index, 3.15 to 3.75) and broad (aspect ratio, 1.45 to 1.59). Hearts range from 0.58 to 1.26 percent.

Pipridae.—Among the manakins, *Corapipo* and *Schiffornis* have a high heart value of 1.50 percent, compared to 1.06 percent for *Manacus* and 1.11 percent for *Pipra.* In view of the practice of dancing on the part of the male, larger leg muscles than in the female might be expected. In *Corapipo* we found no great difference, but in *Manacus* the leg muscles of the male were larger than those of the female (11.91 percent compared to 8.42 percent). Moreover, the leg muscles of *Manacus* were larger than those of other manakins. Lowe (1942) mentions that the pectoralis and thigh muscles of the male are very well developed.

Cotingidae.—The cotingas, birds of the forest, are peculiar to the warmer parts of the Americas. Arboreal in habit, they possess strong flight equipment for movement among the tree tops (22 to 33 percent flight muscles; buoyancy index, 3.28 to 4.83; aspect ratio, 1.65 to 2.00). The hearts are large (1.11 to 1.45 percent) and the legs moderately so (5.15 to 8.18 percent).

Tyrannidae.—The tyrant flycatchers constitute one of the largest families of American birds (365 species, according to Van Tyne and Berger). Those found south to Panamá are mostly arboreal, darting from a strategic perch to capture insects. There is great variation in their musculature, heart size ranging from 0.71 to 1.88 percent and flight muscles from 16 to 33 percent. Large and broad wings (buoyancy index, 3.39 to 4.71; aspect ratio, 1.46 to 2.05) give great maneuverability. The muscles of the lower extremities show considerable range (3 to 7.35 percent). Their adaptations for catching prey or for bold attacks in defense of territory are quite varied. The genus *Todirostrum* in proportion to its size has much larger muscles of the lower extremities and smaller flight muscles than do other members of the family.

Hirundinidae.—As swallows spend much time in the air, their legs are very small, being used only for perching (lower extremity muscles, 1.80 to 2.84 percent), yet their flight muscles are not unusually large (19.7 to 25 percent). All except *Progne* have very large, narrow wings (buoyancy index, 4+; aspect ratio, 2.3 to 2.6) and fairly large tails.

Corvidae.—The jay family contains the largest passerine birds and some of the most aggressive ones. Although fairly strong fliers (flight muscles, 20 to 25 percent; buoyancy index, 3.4 to 4.7), they use their feet extensively in walking and manipulating food (lower extremity muscles, 10 to 15 percent). Their hearts are of moderate size (0.85 to 1.0 percent).

Paridae.—Titmice display restless, acrobatic activity; they use their feet to hold prey. Their hearts are large (1.35 to 1.49 percent), the flight muscles (23 to 27 percent) and leg muscles (7 percent) fairly so. They are weak fliers, and the wings are typical of perchers.

Sittidae.—The nuthatches are similar to the titmice in muscular proportions but somewhat different in habits. They not only hop over the bark looking for food, but the red-breasted nuthatch also catches insects in the air like a flycatcher.

Certhiidae.—The creepers are good fliers, possessing large hearts (1.48 percent) and large wings (buoyancy index, 4.22) and tails (2.35 $cm.^2$ per g.)

Troglodytidae.—The members of the fairly large family of wrens are weak fliers and do much running around in exploring for food and in other activities; as might be expected, their leg muscles are large (10 to 13 percent). Hearts (0.86 to 1.19 percent), flight muscles (16 to 20 percent), and wings (buoyancy index, 3 to 3.39) are moderate in size.

Mimidae.—Mockingbirds and thrashers show values much like those of wrens but have smaller leg muscles (8.0 to 9.7 percent). Although partly arboreal, they also do much feeding on the ground.

Turdidae.—The above remarks concerning the Mimidae apply also to the thrushes, except that the latter possess large flight muscles (20 to 36 percent).

Sylviidae.—The smaller gnatcatchers may also be described in much the same way as the wrens, above.

Motacillidae.—Although the pipits are terrestrial in their habits, running about rapidly, their leg muscles are of only moderate size (6 percent). They are powerful and swift fliers, having fairly large flight muscles (28 percent), large, broad wings (buoyancy index, 3.66; aspect ratio, 1.77), and large hearts (1.57 percent).

Bombycillidae.—Waxwings have flight power similar to that of the pipits, but their wings are somewhat smaller (buoyancy index, 3.29) and narrower (aspect ratio, 2.13). Their hearts are large (1.54 percent).

Ptilogonatidae.—The silky flycatcher (*Ptilogonys caudatus*) has a large heart (1.33 percent) and a high buoyancy index (3.80).

Laniidae.—The loggerhead shrike (*Lanius ludovicianus*) makes brief, swift flights through the air to seize a victim, but his muscles are moderate in size.

Sturnidae.—The common starling (*Sturnus vulgaris*) is a very active bird with rather small, narrow wings (buoyancy index, 3.17;

aspect ratio, 2.19) and fairly large legs (7.76 percent). In short flights he appears slow and feeble, but on long journeys he flies strongly and swiftly.

Cyclarhidae.—Concerning peppershrikes it need only be noted that they have large leg muscles (9.46 percent) and that their flight is deliberate and weak.

Vireonidae.—Vireos, feeding mostly among the leaves, are moderately endowed with muscles: heart, 1.06 to 1.43 percent; flight muscles, 21 to 25 percent; leg muscles, 5.89 to 7.63 percent. They do, however, have large wings (buoyancy index, 3.44 to 3.88).

Coerebidae.—Honeycreepers, being quick in the air, have flight muscles ranging from 23 to 34 percent and large hearts (1.25 to 1.44 percent). Their wings are large (buoyancy index, 3.37), but their legs are only moderate in size (muscles, 5 to 8 percent).

Parulidae.—Although the wood warblers range from the treetops (black-throated green warbler) through lower levels of the forest (magnolia warbler) to the ground (Kentucky warbler), their flight muscles do not differ greatly, as their activities in the air are similar. These muscles are not large, ranging mostly from 20 to 25 percent of the body, with many around 22 percent. The wings (buoyancy index, 3.27 to 4.16) and tails are large, making the glide area as high as 10 $cm.^2$ per gram in some species. The muscles of the lower extremities are largest in *Basileuterus* (9 to 10 percent) and as low as 5 percent in others. The hearts range from 0.95 to 1.39 percent.

Ploceidae.—The house sparrow (*Passer domesticus*) is typical of many small perchers; large heart (1.39 percent) and flight muscles (25.4 percent); wings designed for quick takeoff (buoyancy index, 3.05; aspect ratio, 1.88); and moderate lower extremities (muscles, 6.47 percent).

Icteridae.—Icterids show characteristics similar to those given above: hearts, 0.85 percent in *Sturnella magna* to 1.2 percent in *Icterus galbula;* flight muscles, 19 percent in *Amblycercus* to 28 percent in *Leistes;* buoyancy index, 3.13 for *Sturnella* to 4.4 for *Cacicus;* aspect ratio, 1.31 for *Amblycercus* to 2.03 for *Psarocolius;* lower extremities, 7.46 percent for *Icterus spurius* to 15.2 percent for *Amblycercus.*

Thraupidae.—Thraupids show a greater range in heart size than the fringillids, *Rhodinocichla* possessing the smallest (0.63 percent), the male *Habia rubica* the largest (1.46 percent). Flight muscles also show a somewhat greater range: 1 percent in *Chlorospingus* and 29 percent in *Thraupis.* Buoyancy index likewise runs from 2.82 in

Tanagra to 3.98 in *Habia,* while the aspect ratio is only 1.47 in *Rhodinocichla* but reaches 1.89 in *Piranga rubra.* The muscles of the lower extremities are from 5.19 percent in *Tanagra luteicapilla* to 11.36 percent in *Rhodinocichla.*

Fringillidae.—This almost worldwide group of birds, feeding everywhere that seeds are to be found from the ground to the treetops, shows a great range of locomotor equipment. Their hearts vary from 0.60 percent in *Pezopetes* to 1.57 percent in the male *Saltator maximus,* and flight muscles show as great a range (19.5 to 29 percent). The buoyancy index of the wings ranges between 3.09 and 3.72, the aspect ratio between 1.42 to 1.88. The highest values for muscles of the lower extremities are more than twice as high (13.2 percent) as the lowest (5.43 percent).

After this survey of the variations in the families, let us compare the locomotor organs individually.

HEARTS

Since the heart limits the activities of a bird, it is proper to consider it first. Whatever the size of a musculature, it cannot act for long without an adequate circulation. Thus the tinamou, with its tremendous breast muscles but very small heart, can make only short flights. On the other hand, birds with only a moderate equipment of muscles can fly for long periods if they possess large hearts. It is this relationship between the heart and the locomotor muscles that we wish to deal with primarily, but there are other factors which also must be considered, namely, sex, season, latitude, and altitude.

Sex.—Whenever there is evidence of sex difference in the relative weight of the heart, the sexes are separated for consideration. In the following species the hearts are heavier in the male than in the female: *Gallus gallus, Phaethornis guy, Anthracothorax nigricollis, Chlorostilbon canivetii, Damophila julie, Amazilia edward, Amazilia tzacatl, Elvira chionura, Lampornis castaneoventris, Selasphorus scintilla, Sittasomus griseicapillus, Cranioleuca erythrops, Anabacerthia striaticollis, Mitrephanes phaeocercus, Thryothorus modestus, Habia rubica, Habia fuscicauda, Saltator maximus,* and *Pipilo erythrophthalmus.* Heavier hearts in males may also hold for other species, but the number of individuals available is not always sufficient to settle the question.

Seasonal variation.—A difference in relative heart size is noted in certain Florida birds collected in June as compared with those obtained in the winter months, as shown in table 2 (p. 88).

Latitude.—A difference in heart size is noted in a few species collected in Florida compared with the same or closely related species obtained in Panamá, the hearts of Florida birds being larger. These species are *Butorides virescens, Coragyps atratus, Cathartes aura,* and *Sturnella magna.*

Altitude.—Larger hearts are present in some species at higher altitudes when compared with other species of the same family at lower altitudes. Specimens of *Crotophaga ani* and *Piaya cayana* obtained at 4,500 feet have larger hearts than those of the same species obtained at sea level ($P<0.01$).

In general the smaller birds have relatively larger hearts than large birds. The lowest values appear for the tinamids, followed by the strigids, nyctibiids, momotids, and bucconids, with others of lesser deviations from the mean. The highest values emerge for the trochilids, hirundinids, motacillids, and bombycillids. Comparison of the heart weight with the habits of the bird leads one to the conclusion that heart weight is directly related to the ability to sustain power flight.

The muscles of locomotion show even greater variation. I shall consider first the muscles used in flight. As already indicated, we weighed all the muscles involved except the small muscles along the carpals, metacarpals, and phalanges.

FLIGHT MUSCLES

Sex, latitude, and altitude appear to have some influence in muscle size in a few species.

Sex.—In *Cairina moschata* (domestic) the female possesses flight muscles that are larger than those of the male, while in *Micrastur ruficollis, Phaethornis guy, Amazilia amabilis,* and *Manacus vitellinus* flight muscles are larger in the male. In other species our data are insufficient to determine the sex differences in the more inclusive flight muscles, but in the more limited combination of pectoralis plus supracoracoideus, where we have more data, these muscles are larger in the male than in the female of *Pelecanus occidentalis, Micrastur ruficollis, Amazilia amabilis, Amazilia edward, Amazilia tzacatl, Lampornis castaneoventris, Selasphorus scintilla, Pharomachrus mocinno, Sittasomus griseicapillus, Xiphorhynchus guttatus, Lepidocolaptes affinis, Anabacerthia striaticollis, Myiarchus tuberculifer, Empidonax flavescens, Mitrephanes phaeocercus, Thryothorus modestus, Tangara ic-*

terocephala, Thraupis espicopus, Piranga leucoptera, Habia fuscicauda, and *Saltator maximus.* In only two species, *Jacana spinosa* and *Vireo philadelphicus,* were the pectoralis plus supracoracoideus larger in the female than in the male.

Latitude.—The pectoralis plus supracoracoideus muscles were relatively heavier in Panamá specimens of *Florida caerulea* and *Cathartes aura* than in birds of the same species collected in Florida.

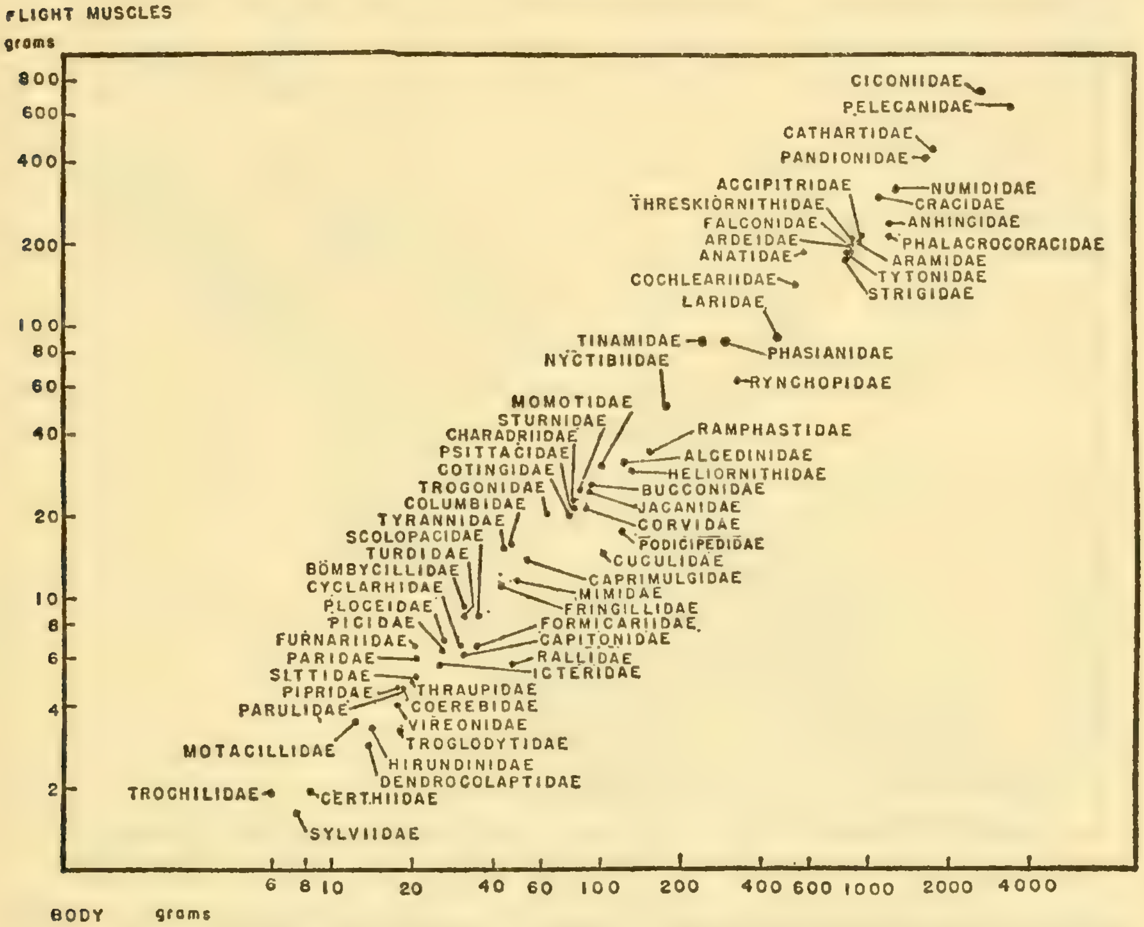

FIG. 1.—Selected plottings (see asterisks in table 1) of upper extremity muscle weights against body weights (log scales).

Altitude.—In *Piaya cayana* and *Crotophaga ani* both flight muscles and pectoralis plus supracoracoideus were relatively heavier in high-altitude birds (4,300 ft.) than in these species collected on the Río Chagres. Likewise the pectoralis plus the supracoracoideus were heavier in *Pteroglossus frantzii* (collected at 4,300 ft.) than in *Pteroglossus torquatus* obtained on the Río Chagres.

For an overall comparison of the flight muscles, selected species from each family have been plotted on a logarithmic scale (fig. 1). If one draws a line through the values for the heavier birds, it will be seen that many of the birds less than 200 grams in weight are decidedly above this line, only the Rallidae, Cuculidae, and Podicipedidae falling below.

Since the pectoralis (pectoralis superficialis or p. major) is the most important muscle in depressing the wing, it was also treated separately (fig. 2). It will be seen that the divergences from a straight line are not only different, but sometimes greater than those observed for the flight muscles as a whole. Those with a large pectoralis also have large flight muscles, and vice versa. Examples of those with a relatively large pectoralis are found in the tinamids, threskiornithids, anatids, phasianids, charadriids, columbids, psittacids, trochilids, trogonids, cotingids, motacillids, coerebids, and thraupids. Those with a relatively small pectoralis are the podicipedids, phalacrocoracids, some ardeids, some accipitrids, rallids, heliornithids, cuculids, formicariids, and troglodytids.

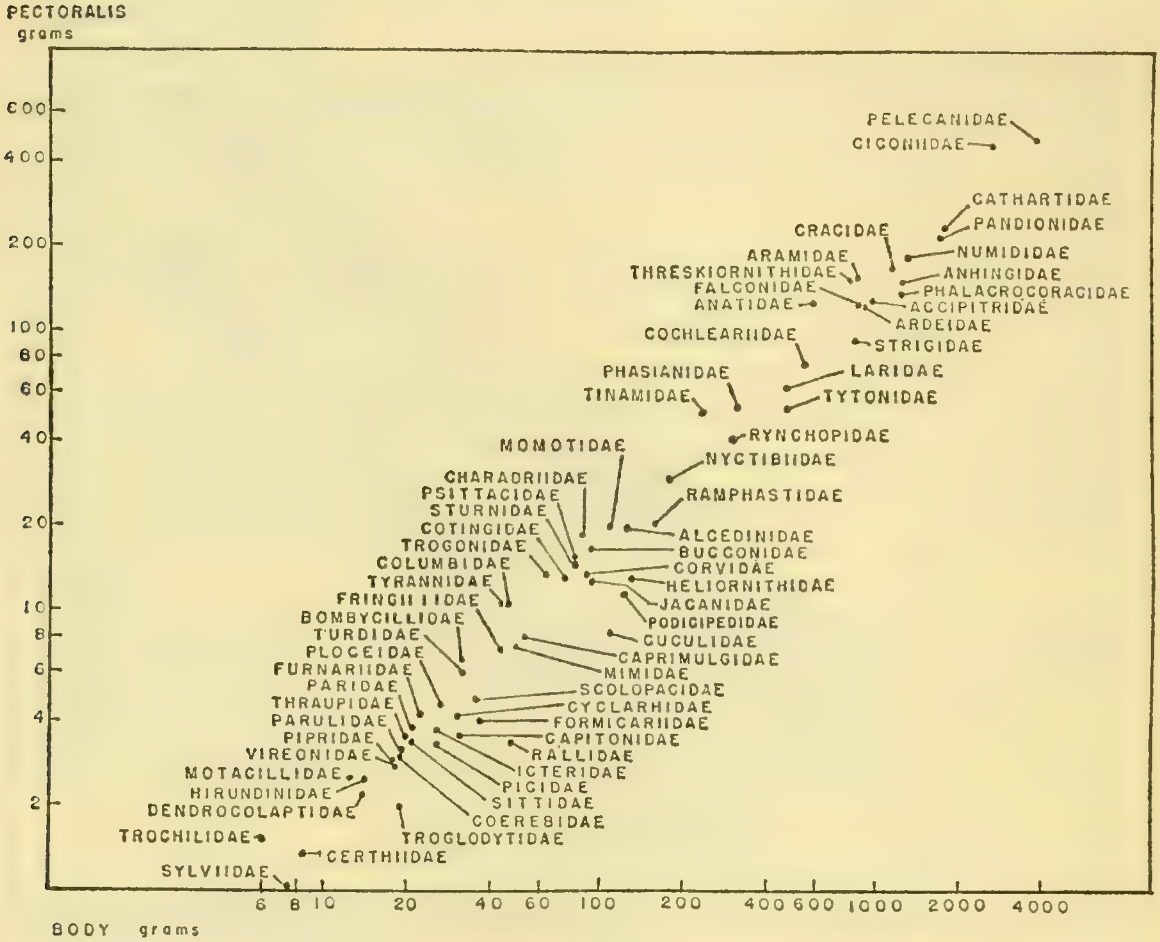

FIG. 2.—Selected plottings of pectoralis superficialis muscle weights against body weights (log scales).

Although there is a tendency toward similarity among different species in the same family, it will be recalled that there are some exceptions. In the herons the range of the pectoralis is from 10 to 17 percent of the body weight; in the flycatchers, from 12 to 22 percent; in the swallows, from 14 to 21 percent.

Supracoracoideus.—The supracoracoideus, one of the principal levators of the wing, appears to be of little importance in many birds, judging from its size. In our studies it ranged from about 0.40 percent of the body in species of the genus *Buteo* to 11.5 percent of the body in the trochilids, or 1.8 to 30 percent respectively of the flight muscles. High values (table 1) are found in *Crypturellus, Chamaepetes, Odontophorus, Numida, Capella,* trochilids, doves, *Pyrrhura,* and *Manacus.* Low values appear in *Phalacrocorax, Buteo, Pandion, Caracara, Piaya, Tyto,* and *Pulsatrix.* The supracoracoideus of *Nyctibius* (3.18 percent of the flight muscles) is much smaller than that of *Nyctidromus* (6.9 percent of the flight muscles). There is a great difference in this muscle in *Manacus* (14.2 percent of flight muscles) as compared to that in *Chiroxiphia* (6.0 percent of flight muscles). Likewise, this muscle is larger in *Cotinga ridgwayi* (7.76 percent of flight muscles) than in *Querula* (4.56 percent of flight muscles).

The range of supracoracoideus among different families is shown in figure 3. It will be noted that the greatest differences are to be found in the larger birds, the muscle being largest in those birds that make a quick takeoff. It is especially small in cuculids, tytonids, and strigids.

"Rest."—The combined muscles of the shoulder, brachium, and forearm (except those noted above), which appear in the table under the heading "Rest," are shown in figure 4. With fewer exceptions than in the other muscle groups, they tend to follow a straight line. Among the lowest are the grebes, rallids, certhiids, and sylviids.

Division of this group of muscles into shoulder, brachium, and forearm shows variations among the different families and among some species of the same family. This has been done for 67 species distributed among 32 families. Typical examples have been chosen in table 3 (p. 89). The shoulder group shows low values in *Anhinga* (1.04 percent), *Ardea* (1.47 percent), *Polyborus* (1.60 percent), *Ereunetes mauri* (1.13 percent), *Thalasseus* (1.37 percent), *Columba livia* (1.26 percent), and *Crotophaga* (1.60 percent). It was high in *Tinamus* (3.44 percent), *Heterocnus* (3.07 percent), *Chondrohierax* (3.30 percent), *Ortalis* (3.34 percent), *Colinus* (3.42 percent), *Columba speciosa* (3.15 percent), *Megaceryle* (3.25 percent), and *Mniotilta* (4.46 percent). These muscles were larger in *Colinus* (3.42 percent) than in *Odontophorus* (2.05 percent) and *Gallus* (1.61 percent).

The muscles of the brachium are usually heavier than those of the forearm, especially in the anatids, *Coragyps, Megaceryle,* picids, *Synallaxis, Muscivora, Iridoprocne,* corvids, parulids, icterids, and fringillids.

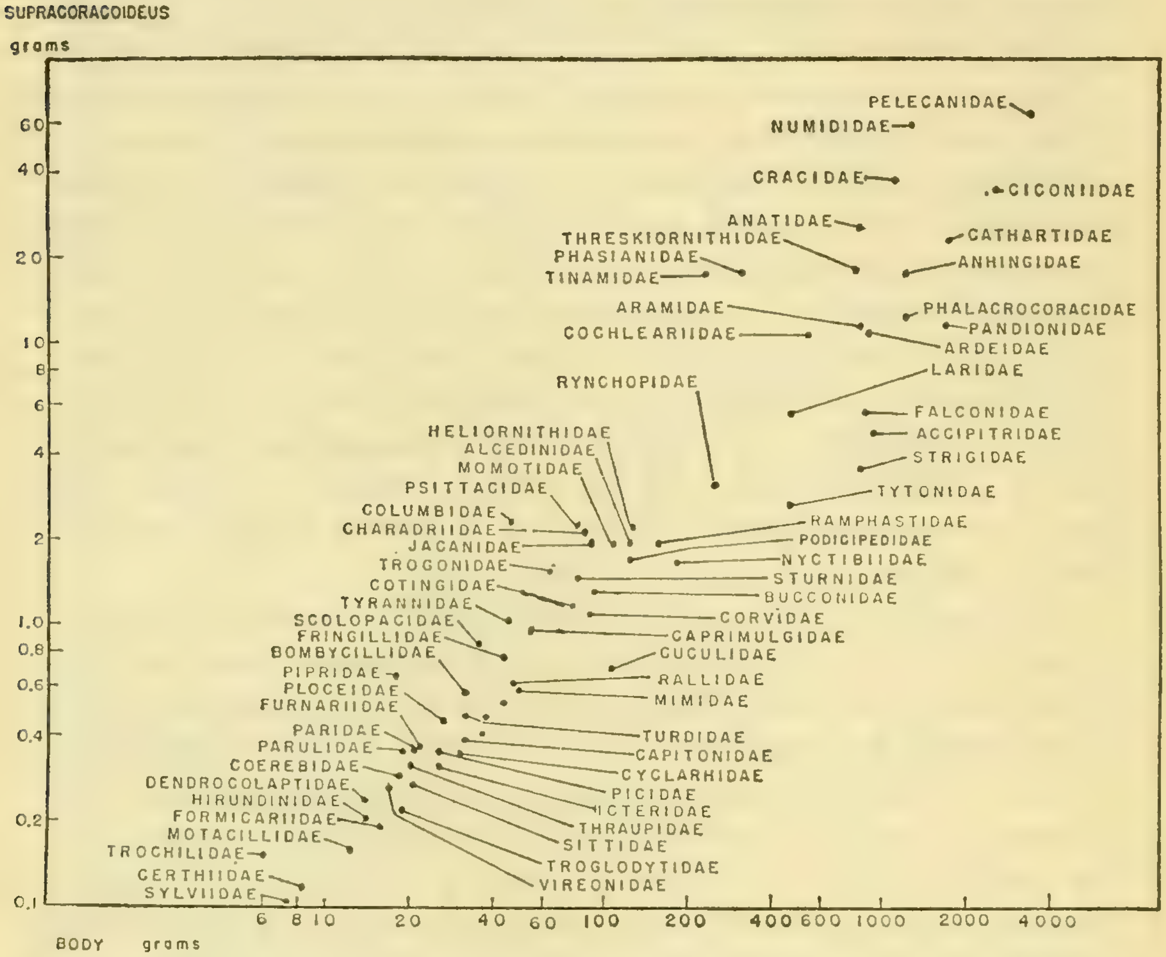

FIG. 3.—Selected plottings of supracoracoideus muscle weights against body weights (log scales).

LOWER-EXTREMITY MUSCLES

Muscles of the lower extremities vary much in size because of the great difference in degree of activity. In some birds they are used little, even for perching, while in others they may be the essential means of locomotion or may serve as important tools in obtaining food. Examples of typical species in the various families are shown in figure 5. The smallest muscles (1.2 to 3 percent) are found in trochilids, nyctibiids, alcedinids, and hirundinids; the largest are found in the tinamids, podicipedids, cathartids, cracids, phasianids, and rallids (14 to 23 percent). They are larger in the male than in the female in *Cairina* and *Gallus* (table 1).

Separation of the lower extremity into thigh and leg was done in the same specimens in which the muscles of the upper extremity were separated. The variation of the proportion of thigh to leg muscles is usually not great (table 4, p. 90). In many birds the thigh muscles are nearly equal to those in the lower leg; when they are unequal, it is usually the thigh that is larger. Exceptions are *Phalacrocorax,* some ardeids, and *Buteo lineatus,* in which the thigh muscles are smaller. Comparison of a domesticated phasianid, *Gallus,* with a wild species, *Odontophorus,* is interesting. The lower extremity muscles that are

FIG. 4.—Selected plottings of "rest" muscle weights against body weights (log scales).

still used by the domestic form are the same size as in the wild form, but the pectoralis and supracoracoideus muscles are less than half the size of those of the wild form, as is also the wing area.

FIG. 5.—Selected plottings of lower-extremity muscle weights against body weights (log scales).

BODY AREAS INVOLVED IN FLIGHT

The surface areas involved in flight are the wings used in propulsion, the tail and wings for steering, and the tail and body for gliding or soaring. The wing and glide areas for typical examples of each family are shown in figure 6.

WINGS

In general, the smaller birds show less divergence and have larger wings than the heavier birds. Exceptionally small wing areas are present in rallids, podicipedids, tinamids, anatids, cracids, scolopacids, and phalacrocoracids. Large wing areas are found in several small tyrannids, especially *Mitrephanes;* in other families in *Sittasomus, Xenops,* and *Myrmotherula,* hirundinids, *Sitta,* and several parulids.

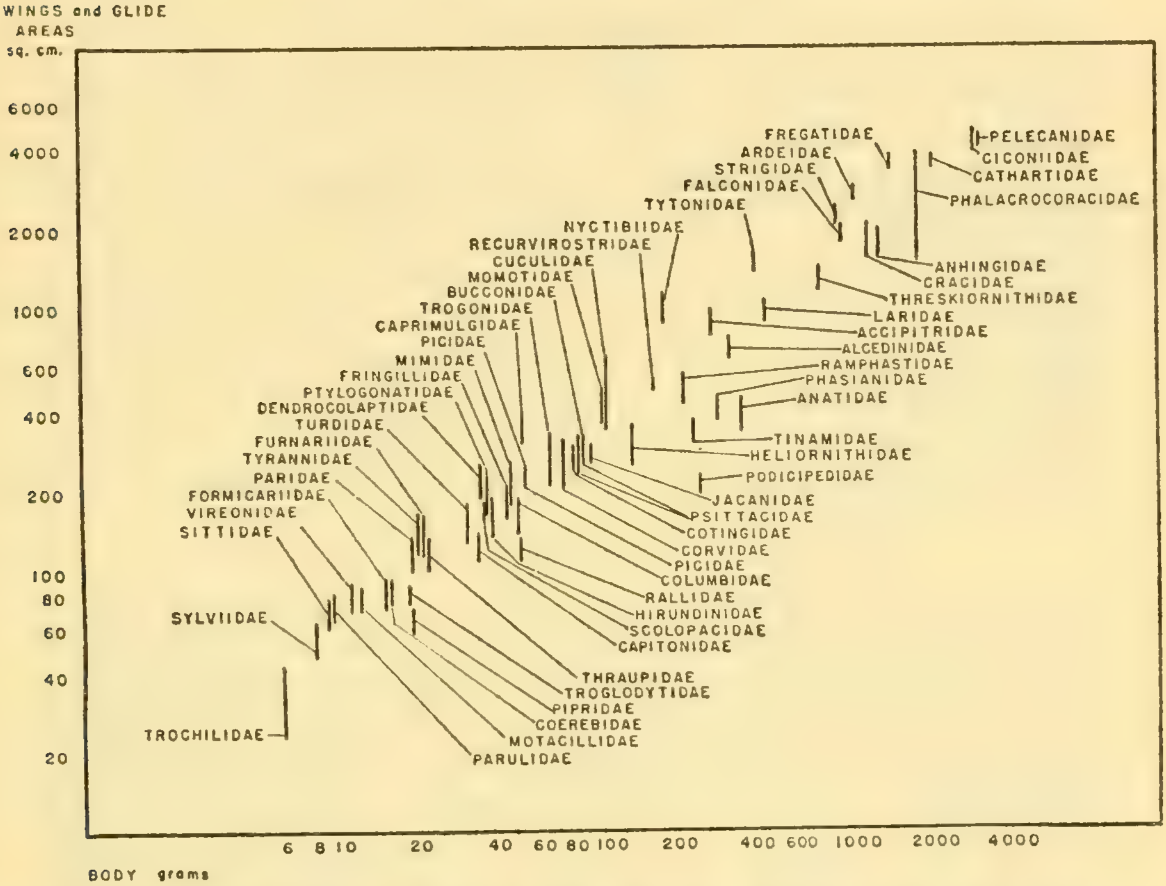

FIG. 6.—Selected plottings of areas for wings (low end of vertical lines) and glide (high end of vertical lines) against body weights (log scales).

Sex.—The wings of the males in the following species are significantly larger than those of the females: *Buteo lineatus* ($P<0.05$), *Tanagra icterocephala* ($P<0.01$), *Tanagra guttata* ($P<0.01$), *Tanagra gyrola* ($P<0.05$), *Saltator maximus* ($P<0.01$), and *Pipilo erythrophthalmus alleni* ($P<0.01$). In *Cassidix mexicanus* the wings are larger in the female than in the male ($P<0.05$).

Altitude.—*Momotus momota* collected at sea level has larger wings than the same species collected at 4,500 feet above sea level ($P<0.01$). Among the piprids, *Corapipo* collected at 4,500 feet elevation has wing and glide areas nearly twice those of *Manacus* collected at sea level, but this may not be an altitude effect.

Ratio of buoyancy index.—Values for the buoyancy index are shown in table 1. *Cathartes* tops the list with 5.86. *Nyctibius* and *Casmerodius* tie for second place, and *Pandion* is third, *Tyto* fourth, *Coragyps* fifth, and *Cochlearius* sixth. The lowest is *Manacus* (2.79).

ASPECT RATIO

The ratio of the length to the width of the wing, or aspect ratio, indicates the adaptation for soaring or quick takeoff—the long, narrow wing (high ratio) for soaring, and short, broad wing (low ratio) for prompt takeoff. Most small birds possess a low ratio, the cuckoo being the lowest. Exceptions are goatsuckers, trogons, potoo, shore birds, swallows, and hummingbirds, which are high, the last three being the highest. Of the heavier birds. *Chaemepetes* is the lowest, while the gull, frigate-bird, and pelican are the highest of all birds studied. The barn owl has a longer wing than the other owls that we have studied. *Corvus* has a much larger aspect ratio than the other corvids observed.

TAIL AREAS

The relative size of the tails is shown in figure 7. The tails in grebes were so small that they were not measured. They are small in shrikes, rails, jaçanas, and tinamous, and large in *Fregata, Anhinga,* falconids, cracids, cuculids, some strigids, the nyctibiids, caprimulgids, trogons, dendrocolaptids, furnariids, tyrannids, corvids, parids, mimids, turdids, sylviids, *Ptilogonys,* and fringillids. Hummingbird tails are relatively the largest of all. The tail of the turkey vulture is larger than that of the black vulture.

The size of a tail does not necessarily indicate its effectiveness, since it may be an ornament as in the male quetzal. However, in most instances it can be a factor in steering, gliding, or soaring.

GLIDE AREAS

The combined areas of wings, tail, and body make what we have called the glide area. An examination of table 1 will show that these areas tend to parallel the wing areas (see fig. 6). This is to be expected, since the wings constitute a large proportion of the total, the tail being relatively small in most instances. In those birds in which glide areas are much larger than the wing areas, the large tails usually account for the increase, as in trogons and cuckoos. In a few birds the wings are largely responsible for the glide area. This is true for wrens, tinamids, the stilt, grebes, herons, and some others.

DISCUSSION

All values in this study are based on body weights, which, of course, vary with the state of nutrition, hydration, and food content. By using only healthy, well-nourished birds and collecting them during the morning hours, the conditions are standardized as well as could be expected. In a few species that have large capacity and gorge themselves periodically, food contents should be considered. By having a sufficient number of individuals in a species, these variables are reduced. When values are far from the mean, as occurs occasionally, they have not been included.

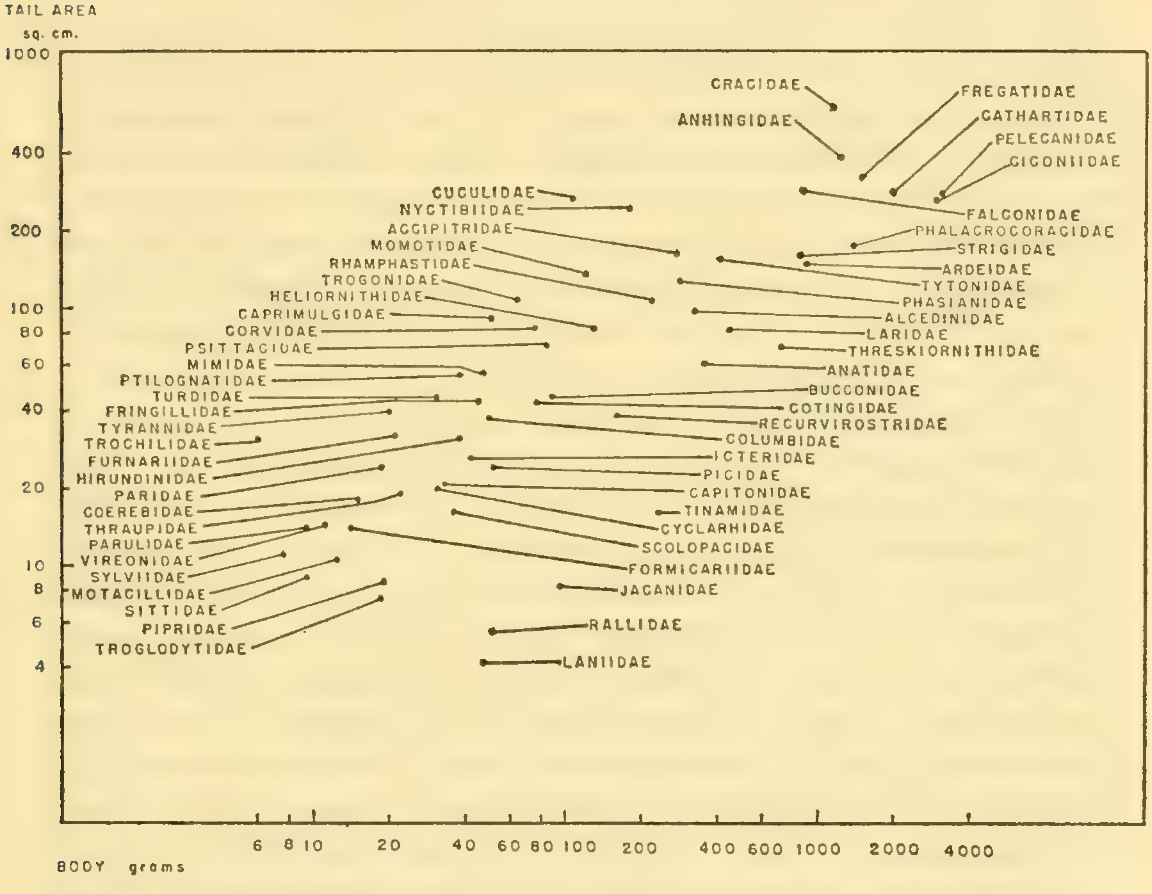

FIG. 7.—Selected plottings of tail areas against body weights (log scales).

Our observations show that muscle weights are related to activity. Muscles represent potential power but do not indicate the extent of their use. A large muscle may produce powerful contractions, either brief or sustained depending upon the heart that supports it. A small muscle, while not powerful, can continue contraction for a considerable period if supplied with oxygen and fuel. The flight muscles tend to parallel the performance in the air, while the muscles of the lower extremities are related to their use for locomotion or for acquiring food. Most important of the muscles is the heart, since it is the driving force that circulates oxygen and nutrients and removes waste products. A small heart limits activity, while a large one can maintain it much longer.

We had previously found no difference between the sexes in the relative heart weight (Hartman, 1955), but in the present survey we observed that in 19 species the heart in the male was relatively heavier than in the female; if more data were available the list might be increased. This difference occurred in small or relatively small birds, with the single exception of *Gallus*. In some species the males are more active than the females, but we cannot say whether this was so in the 19 species in which a difference was observed. Groebbels (1932) noted a difference in heart size between the sexes in some species.

In my earlier paper (Hartman, 1955) evidence suggesting a seasonal difference in heart weight was presented, but the number of individuals was too small to make the findings significant. This shortcoming was obviated in the present work in the case of a few species by the inclusion of a sufficient number of individuals. Birds collected in January and February possessed hearts larger than those obtained during June, a finding contrary to the suggestive evidence in the former paper. Such a difference could be explained by the higher rate of metabolism in the cooler weather. In keeping with this interpretation we find that certain species living in Florida possess larger hearts than the same species from Panamá. Since many *Cathartes aura* migrate to the south in winter, the season when our Panamá birds were collected, the question has been raised as to the identity of some of these birds. Whether they were migrants or not, there were very significant differences in the hearts and pectoralis plus supracoracoideus muscles between the two groups.

If altitude is a factor in increasing the heart size, why do not more species show the effect? Some of those that have larger hearts at the higher altitude are not very active (e.g., cuckoos). Perhaps additional data would extend the difference to more species. Stieve (1934) compared heart size in *Lagopus mutus mutus* and *L. lagopus lagopus*, both from the same altitude (400 to 700 m.). The alpine grouse (*L. m. mutus*) at this low level has a distinctly larger heart than the moor grouse. Therefore in these instances it is a species difference rather than an altitude effect. Stieve also compared hearts of *Lyrurus lyrurus tetrix* from different altitudes. Birds from higher levels (1,800 to 2,000 m.) possessed definitely smaller hearts than those living at 50 meters. The same could be shown in other species. Several authors (e.g., Parrot, 1893, and Rensch, 1948) have concluded that birds flying great distances or living in northern latitudes or high altitudes possess larger hearts than those less active or living in warmer climates.

A thorough study of the muscles used in locomotion should include the weight of each individual muscle because of the variation from species to species. Since this is impossible in an extensive survey, only the larger muscle groups have been weighed. The pectoralis superficialis is the most important in flight, as it depresses the wing, while the supracoracoideus is the principal levator of the wing. The remainder of the flight muscles (called "rest" in our study) also play an important role in the flight, whether it be in maneuvering or "setting" the wing for the action of the "power" muscles.

The flight muscles constitute a considerable proportion of many birds, varying from 14 to 40 percent. The percentage is lowest in those birds that use them least, but on the other hand, large size does not always indicate extensive use. The tinamou has very large flight muscles but makes only short flights. The flight muscles of the hummingbird, which spends much time in the air, are also relatively large, but not to be compared with those of the tinamou. The muscles of *Colinus, Chaemepetes,* and some trogons are relatively just as large as those of the hummingbird but are used much less.

The pectoralis superficialis, much the largest of the flight muscles, has received the most attention, but some authors have exaggerated its size. Stillson (1954) says, "In good fliers the pectoral muscles account for a large part of the total bird." Although Shufeldt (1890) said that in all the birds possessed of the power of flight, the pectoral muscles are second to none in importance, this is not true for grebes and some of the rails. In the former the leg muscles range from 15 to 18 percent, whereas the whole flight musculature is 14 percent or less. In *Aramides* the leg muscles are 24 percent, while the flight muscles are less than 17 percent.

Calculated from Fisher's (1946) data, the combined volume of all muscles that may aid in depressing the wing constitute 62.7 percent of the wing musculature in *Cathartes* and 56.2 percent in *Coragyps.* Of these the pectoralis superficialis is 60.5 percent of the total in *Cathartes* and 54.1 percent in *Coragyps.* The volume of all muscles that may aid in raising the humerus is 15.9 percent of wing musculature in *Coragyps* and 12.3 percent in *Cathartes,* while the supracoracoideus is only 6.50 percent of all wing muscles in *Coragyps* and 4.40 percent in *Cathartes.* In our studies we did not determine the weight of all muscles used in raising the humerus, singling out the supracoracoideus because it was the most important and was easily dissected.

It has been reported by Owen (see Shufeldt, 1890, p. 73) that the supracoracoideus is almost the largest of the breast muscles in penguins, guillemots, and gulls. It was pointed out that more effort was required to raise the wings in the water than in the air. Divers such as the grebe (*Podiceps dominicus*) that use their feet for propulsion under water possess a small supracoracoideus. According to experiments of Convreur and Chapeaux (1926), all birds that fly require the muscles that raise the wings. After these muscles were severed in pigeons, it was not possible for the birds to launch themselves into the air or, when released from a height, to attain any semblance of sustained flight.

As was to be expected, the largest pectoralis was found in powerful fliers, either those accustomed to long sustained flight or those that fly for short distances at high speed. The pectoralis does its heaviest work when taking off.

Many more examples have been observed of heart differences in relation to altitude than of flight muscle differences. The heart must work almost continuously, being inactive only during diastolic pause, while the flight muscles work intermittently. Why the altitude difference occurs in cuckoos and not in more active fliers is difficult to understand.

While the supracoracoideus appears to be of little importance in many birds, it is largest in those birds that make quick takeoffs and fly rapidly, such as tinamous, quail, hummingbirds, and doves.

The remainder of the flight muscles, those of the shoulder, brachium, and forearm, constitute only a small part of the total, and therefore variation in these muscles, which is not great, may not be very significant as a factor in flight. The muscles of the brachium are usually heavier than those of the forearm, which would seem to indicate that they do more work.

Although the size of the muscle may determine the work that can be accomplished, the continuance of the performance depends upon the contained fat or other fuel, together with that which may be brought to it by the blood. The amount of fat in the pectoralis superficialis is lower in nonflying or poor-flying birds than in long-distance fliers such as the parakeet, pigeon, and crow, while the percentage of carbohydrate is higher in short-distance fliers such as the sparrow (Nair, 1952). The distribution of this fat has been shown by George and Jyoti (1955), who observed that in birds such as the pigeon, *Columba livia,* the pectoralis superficialis contained two types of fibers, a narrow type in which the sarcoplasm was interspersed with fat globules as well as opaque granules appearing to be liproprotein, and another broader, clearer type in which these inclusions were fewer. When the pigeons became exhausted from flying, the narrow fibers lost their fat globules. In the kite (*Milvus migrans*) the pectoralis superficialis contained fewer narrow fibers and less fat. The leg muscles of both species consisted only of the broad fibers with less fat. The leg of the fowl, however, contained a high percentage of fat. Continuous excitation of pectorals or leg muscles reduced their content of free lipid (George and Jyoti, 1957). These authors concluded that the muscle lipid supported prolonged activity.

The muscles supply the power for flight, while the wing and other areas are the foils with which the muscles operate. These surfaces are difficult to measure accurately because their artificial expansion may not duplicate exactly their natural expansion. Our values represent an approximation of the maximal expansion and, to that degree, the possible area available, but this does not tell us how these areas are used or how the areas are distributed in actual performance. In action there is frequent change in areas as well as in shape. Aspect ratio tells us a little but fails to give the shape, camber, or potential slots of the wing. The shape, stiffness, and character of the tail are also needed to complete the picture. These are all factors in flight and maneuverability. The combined action of the flight muscles and feather "blades" and "planes" determine the performance.

This combined mechanism is used either in flapless flight in which gravity is the factor, as in gliding, or in flapping flight in which muscular contraction overcomes the pull of gravity. In gliding, the bird may take advantage of winds or thermal currents, or it may dive.

The size of glide areas is not always an indication of the amount of gliding or soaring done by particular species. For example, *Mycteria* with a glide area of 1.76 $cm.^2$ per gram is a good soarer, while *Phaethornis* with a glide area of 7.14 $cm.^2$ per gram does not glide. Compare also the glide area of *Parus* (9.42 $cm.^2$ per g.) with that of *Stelgidopteryx* (9.55 $cm.^2$ per g.), two birds whose activities are very different.

Flapping flight may be in the form of "sculling" as in the gull, hovering as in the hummingbird, or rocketing as in the pheasant (Jack, 1953).

Although we have employed the ratio, wing area per gram of body weight, for comparisons, the wing loading $\left(\frac{\text{body weight}}{\text{wing area}}\right)$ could be used, as was done by Jack (1953). Perhaps buoyancy index is to be preferred.

It is interesting that when a sex difference is shown in wing areas, as in the case of sex differences in heart and flight muscles, it is the male that shows the larger values, except in *Cassidix mexicanus,* in which the reverse is true.

In some manakins, as well as in the motmot, larger wing areas occur in specimens collected at high altitudes than in those collected at sea level. Traylor (1950) reported that some species from a high altitude possessed longer wings than those from lower elevations.

We have reported 39 of the species discussed by Poole (1938), many of whose values are from single specimens. Seven of his species possessed a smaller wing area per gram of body weight than ours. In the following comparisons, his values are given first and ours second: *Dendroica pensylvanica,* 5.45–7.0 cm.^{2} per gram; *Centurus carolinus,* 3.00–3.79; *Cyanocitta cristata,* 2.65–3.39; *Falco sparverius,* 2.74–3.50; *Sturnella magna,* 1.83–2.16; *Buteo lineatus,* 2.11–2.90; and *Cathartes aura,* 1.81–2.98. In all these species his specimens had larger body values than ours. In addition, three species with about the same body values had smaller wing values. They are *Dendroica virens,* 6.35–7.30; *Mniotilta varia,* 6.13–6.85; and *Stelgidopteryx ruficollis,* 6.79–7.54. Finally, his specimens of three species with smaller body values than ours possessed larger wing areas. They are: *Fulica americana,* 1.37–1.00; *Strix varia,* 3.59–2.49; and *Ardea herodias,* 2.33–2.06. These differences might be due to individual variation or to seasonal changes.

The tail is so variable in size, shape, and character that it may or may not be generally a factor in aerial locomotion. In many instances it has been observed to be useful in maneuvering. However, if the tail is small, the wings take over its function, as in the swift or duck. In the latter, on the other hand, because of the small wings together with the speed, the course of flight cannot be changed quickly.

The speed at which a bird flies is determined by the shape, size, and rate of beat of the wing and the angle of attack. Of course, the speed at which a bird can fly when pressed is not necessarily the speed that is customary. The greater the wing loading, the faster the bird must fly to prevent stalling. A long, narrow, pointed, flat wing is faster than a broad, curved one of the same area. Camber is greatest in slow fliers. Short wings are for bursts of speed. Wing areas are larger than absolutely necessary, especially in small birds, as can be shown in partial molts of wing feathers.

For sustained fast flying a low buoyancy index is best, while for soaring and gliding a higher index is an advantage (George and Nair 1952). *Coturnix* migrates considerable distances. Its aspect ratio is 2.15, its buoyancy index, 2.38, compared with a nonmigratory phasianid, *Colinus,* whose aspect ratio is 1.74 and buoyancy index 2.6.

Some birds are so equipped and so skilled that they have great control. The sparrow hawk, the kingfisher, and the hummingbird can hover, and the last mentioned can fly in any direction. The outer wing serves as propeller, while the inner wing, like that of a plane, gives "lift." In the hummingbird the wing is mostly propeller, giving great maneuverability but less efficiency. While this is satisfactory for a small bird, in a larger one greater efficiency is needed because weight increases by three dimensions while lift increases by only two dimensions (Storer, 1948).

In general, as has been stated by others, the small birds have relatively large, broad wings which give great maneuverability. This wing size is usually accompanied by tails that assist materially in quick change of direction or in landing. Small birds take off essentially by the same process as that used in free flight, the functions of lift and propulsion being common to a wing undifferentiated on the long axis and unadapted for kite-surface action (Demoll, 1930).

If the various species were arranged according to the size of the most important flight muscles (pectoralis superficialis plus supracoracoideus) we find that other values bear no relation to this arrangement. In table 5 (p. 91) typical examples are shown. Those species with 30 percent pectoralis plus supracoracoideus possessed wings ranging from 3.67 to 0.95 cm.^{2} per gram (buoyancy index, 3.31 to 2.91), glide areas from 6.71 to 1.16 cm.^{2} per gram, and hearts from 2.10 to 0.20 percent of the body. What does this indicate? The small wing would require a more rapid beat for the same performance. Large leg muscles suggest greater activity on the ground. The behavior of the birds listed bears this out. The hummingbird is a powerful sustained flier with little use for his legs. The tinamou is a ground bird and an explosive flier that spends little time in the air.

Consider the three birds with the smallest pectoralis plus supra-coracoideus in the table. None are especially good fliers. *Podiceps* has large legs which it uses in swimming. *Aramides* has the largest legs of all, which it can use in stalking through the swamps. *Crotophaga* spends much time on foot. Among the other birds in this table, the trogons, swallows, and kingfishers use their legs very little.

Let us examine the master table (table 1) with both the muscle size and flight areas in mind to see whether these values are related to the habits and activities of the bird. There appears to be a correlation; some illustrations may serve as examples. In the stork, *Mycteria,* the large legs indicate much ground work, yet the pectorals suggest medium flying power, the heart suggests ability to sustain activity, while the moderate wing area together with a high aspect ratio mean efficient flying and gliding once the bird is airborne. In the duck, *Aythya,* a medium-sized leg indicates moderate use, the pectoralis is fairly powerful, but the wings are small, thereby requiring a faster beat. An interesting comparison may be made in the two vultures. *Cathartes* has a much larger wing area and a greater aspect ratio than *Coragyps,* indicating more soaring and gliding, while the heart of *Cathartes* is small so that less sustained effort is possible. This agrees with the performance. *Coragyps* soars much less and flaps frequently in flight.

In the hawks large legs are useful in capturing prey, while large wings and high aspect ratio go with easy flight and soaring, but a medium-sized heart prevents long sustained effort.

All the rails have large legs but vary much in wing area. Their hearts can support moderate activity. The jaçana could be more active than the rails, having a larger heart, larger pectoralis, and very large wings, but medium-sized legs. Therefore, it could be in the air longer and fly with slower strokes. Likewise, the shore birds, with moderately large hearts and pectoralis and large wings with high aspect ratio, would be good fliers.

The large wings, high aspect ratio, but rather moderate pectoralis and fair-sized heart of larids suggest soarers. In the columbids, large pectoralis, large wings, but moderate aspect ratio and fair-sized hearts, with good tails, indicate good flying. Parrots as well as some columbids have fair-sized legs and good flight mechanisms. Cuckoos could not use their wings as much as some birds do, since they possess small pectoral muscles and small hearts. With their large wings, the beat need not be fast. The large wings of owls, moderate hearts and pectoral muscles, together with large legs, enable them to pounce noiselessly and seize prey. The large wings and fairly large pectoral muscles of the goatsuckers, together with rather small legs, suggest a life in the air for the capture of prey.

In the hummingbird, with tiny legs, large pectoralis, supracoracoideus, and heart, and wings with a high aspect ratio, together with large tail and glide area, we have the most capable and most active of the airborne birds. It possesses both speed and maneuverability. It hovers, flies in any direction, flies like an arrow or, on long trips over water, describes an undulating course (Murphy, 1913). Trogons, with somewhat broader but large wings and moderate hearts, would be good fliers, while kingfishers, with smaller pectoral muscles than the trogons, would be less powerful. The small heart of the motmot indicates little sustained activity, which would also be true for the puffbird. Barbets, with large legs and small pectoral muscles, suggest more footwork. Toucans likewise possess less powerful pectoral muscles and large legs.

In the woodpecker large, broad wings and a moderately powerful pectoralis enable it to flap and glide alternately. Its sizable legs suggest active use. The woodhewer is similar, except that a somewhat smaller heart could support less activity. In the ovenbird, the larger heart and a smaller pectoralis, together with larger legs, go with greater activity in the form of less flying and more footwork. In similar fashion the antbird seems to be adapted to ground activity. The cotingas and flycatchers have large, powerful wings, with medium to small legs and moderate hearts.

Large wings with a high aspect ratio and a very large heart are found in the very active swallow. The various values for the crows and jays suggest moderate activity. Many of the small perchers can be included in the classification of the large, broad-winged kinds but with varied pectoral muscles and leg power. The wrens have large legs and small pectorals. The thrushes should be better fliers, using their legs less. The troupials make much use of their legs, as do also some finches.

Among all these birds two groups are most striking: The timamous, with large flight muscles, large lower-extremity muscles, and the smallest hearts; and the hummingbirds, with the largest hearts, large flight muscles, and very small lower-extremity muscles.

Our data show that muscle weights are just as characteristic as is body weight, and this, coupled with the values of certain muscle groups, helps to identify the species. Beddard (1898) said, "the muscular system of birds is remarkably constant for the species." He was referring to the presence and arrangement of the individual muscles.

Although the size of a muscle is inherited through many generations and is usually related to the activity, this is not always so. In a comparison of domesticated and wild forms in the same families, we find that in the domesticated parakeet, *Melopsitticus undulatus,* the various values are similar to those of the wild forms, while in the domestic fowl, *Gallus gallus,* the pectoral muscles and wings are much smaller, but the leg muscles are equal to those in wild species of the family. Although the parakeet leads a rather inactive life, it is not far removed from its wild ancestor. On the other hand the domestic fowl has passed through countless generations of selective breeding.

In conclusion, our observations show that muscle weights are related to the activities of the bird. Since the heart is the driving force that circulates oxygen and nutrients and removes waste products, a small heart limits activity, while a large heart can maintain it much longer. In other words, heart size indicates staying power. The flight muscles tend to parallel the performance in the air, or at least the ability to perform. The area of the wings together with their aspect ratio gives further indication of their use. Finally, the relative weight of a muscle or group of muscles, and the wing areas together with their aspect ratios, appear to be just as characteristic of a species as is the body weight.

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TABLE 1.—*Data obtained in the present study of the locomotor mechanism of birds* (Species marked with an asterisk give typical values for each family as used in drawing the figures. Figures in parentheses indicate the number of individuals of the species.)

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
TINAMIDAE						
Tinamus major	1♀ 1175 4♂ 1168±61	(5)0.19±0.03	(3)40.73±2.39	(4)13.0±0.18	(4)0.89±0.06	(4)1.49±0.03
Nothocercus bonapartei	1♀ 1050 4♂ 844±18.1	(3)0.25±0.02	...	17.5, 18.2	(4)1.04±0.05	(4)1.46±0.03
**Crypturellus soui*	6♀ 245±4 8♂ 225±6	(12)0.25±0.01	(6)37.33±1.26	(8)13.90±0.74	(12)1.33±0.04	(12)1.62±0.03
PODICIPEDIDAE						
**Podiceps dominicus*	12♀ 116±3.42 12♂ 129±3.29	(19)1.05±0.04	(5)14.30±0.42	(8)15.85±0.48	(11)1.48±0.04	(11)2.51±0.06
Podilymbus podiceps	6♀ 321±19 5♂ 411±37	(7)1.00±0.05	9.45, 13.63	(3)18.5±0.70	(5)0.86±0.06	(5)2.91±0.12
PELECANIDAE						
**Pelecanus occidentalis*	47♀ 3174±48 56♂ 3702±52	6♀ 0.72±0.06 8♂ 0.89±0.05	2♀ 14.99, 15.94 6♂ 19.48±0.18	2♀ 4.48, 4.52 6♂ 5.66±0.26	(12)1.19±0.06	(12)3.89±0.08
PHALACROCORACIDAE						
Phalacrocorax auritus	32♀ 1540±38 33♂ 1808±39	(11)0.91±0.03	4♀ 17.00±0.80	(4)12.1±0.50	(11)0.97±0.05	(11)2.86±0.13
Phalacrocorax **olivaceus*	3♀ 1070±67 10♂ 1260±4	(7)0.91±0.03	(5)17.68±0.55	(6)10.73±0.46	(7)1.07±0.09	(6)2.68±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
TINAMIDAE							
Tinamus major	(4)32.33±1.37	(3)25.2±1.46	(7)7.91±0.23	(3)7.62±0.70	(4)0.07±0.01	(4)1.11±0.05	2.96
Nothocercus bonapartei	(4)21.85±0.83	...	...	...	(4)0.05±0.01	(4)1.24±0.06	3.14
**Crypturellus soui*	(12)29.49±0.68	(7)22.46±1.20	(7)7.55±1.36	(6)6.83±0.23	(12)0.09±0.02	(12)1.62±0.03	2.86
PODICIPEDIDAE							
**Podiceps dominicus*	(7)11.14±0.20	(5)9.86±0.19	(5)1.41±0.19	(5)2.91±0.23	...	(11)1.83±0.04	2.72
Podilymbus podiceps	(5)9.97±1.40	4.83, 5.24	0.68, 0.77	2.07, 3.44	0.02, 0.05	(5)1.13±0.08	2.48
PELECANIDAE							
**Pelecanus occidentalis*	6♀ 12.46±0.65 8♂ 14.07±0.29	2♀ 8.70, 9.86 6♂ 12.1±0.22	2♀ 1.49, 1.51 6♂ 1.99±0.04	2♀ 4.57, 4.80 6♂ 5.41±0.24	(14)0.09±0.01	(12)1.39±0.07	4.22
PHALACROCORACIDAE							
Phalacrocorax auritus	(11)12.16±0.34	4♀ 11.3±0.70	4♀ 1.04±0.03	4♀ 4.61±0.37	(11)0.11±0.01	(11)1.24±0.07	3.40
Phalacrocorax **olivaceus*	(7)12.72±0.17	(5)11.51±0.17	(5)1.07±0.06	(5)5.10±0.26	(7)0.15±0.01	(7)1.38±0.10	3.27

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.*^{2} *per gram*	Aspect ratio
ANHINGIDAE						
*_Anhinga anhinga_	14♀ 1227±32.1 12♂ 1244±44.6	(22)0.89±0.03	(5)21.99±0.30	(7)9.01±0.30	(13)1.31±0.04	(14)2.69±0.04
FREGATIDAE						
*_Fregata magnificens_	6♀ 1667±29.4 16♂ 1281±8.7	(2)0.81, 1.03	...	...	2.52, 3.06	3.67, 4.38
ARDEIDAE						
Ardea herodias wardi	15♀ 2204±87 17♂ 2576±72.5	(19).83±0.02	...	(2)9.3, 12.0	(7)2.06±0.13	2.63±0.05
Butorides virescens (Florida)	20♀ 212±3.6 14♂ 211±4.7	(10)0.83±0.04	...	...	2.85±0.09	(14)2.34±0.08
Butorides virescens (Panamá)	6♀ 175±9.29 2♂ 156, 157	(8)0.70±0.03	(3)20.52±0.90	(3)10.78±0.21	(6)3.25±0.18	(6)2.43±0.08
Florida caerulea (Florida)	3♀ 378±40 2♂ 375, 390	(5).83±0.05	...	...	(5)2.95±0.11	(5)2.6±0.04
Florida caerulea (Panamá)	3♀ 288±32.2 8♂ 341±12.5	(13).71±0.018	(4)22.28±0.34	(5)10.6±0.35	(10)3.42±0.07	(10)2.66±0.01
Bubulcus ibis	7♀ 341.5±11.6 2♂ 295, 351	(9).88±0.02	(9)23.54±0.47	(9)8.97±0.22	(8)3.05±0.27	(7)2.69±0.08

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.*^{2} *per gram*	Glide *cm.*^{2} *per gram*	Buoyancy index
ANHINGIDAE							
*_Anhinga anhinga_	(13)14.38±0.30	(5)14.10±2.7	(5)1.30±0.15	(6)6.07±0.38	(13).32±0.03	(13)1.79±0.06	3.7
FREGATIDAE							
*_Fregata magnificens_	(2)13.7, 17.4	...	...	...	2.38, 2.88	2.94, 3.59	5.48
ARDEIDAE							
Ardea herodias wardi	(8)13.94±0.72	(1)15.0	1.06	7.11	0.12±0.01	2.32±0.13	5.28
Butorides virescens (Florida)	(10)14.2±0.45	...	...	...	0.16±0.013	3.0±0.13	4.12
Butorides virescens (Panamá)	(6)13.53±0.61	(3)12.65±0.77	(3)1.21±0.19	(3)6.67±0.58	(6)0.19±0.019	(6)3.75±0.21	4.24
Florida caerulea (Florida)	(5)14.2±0.01	...	...	...	0.19±0.02	3.38±0.14	4.62
Florida caerulea (Panamá)	(11)15.12±0.22	(4)14.5±0.26	(4)1.24±0.10	(4)6.55±0.34	(10)0.22±0.02	(10)3.86±0.07	4.87
Bubulcus ibis	(9)16.42±0.37	14.85±0.37	1.59±0.08	(9)7.12±0.15	(7)0.18±0.02	(8)3.50±0.11	6.40

(continued)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
******Casmerodius albus*	9♀ 812±28.1 $P<0.05$ 12♂ 935±38.8	(16)0.77±0.023	(5)22.29±0.81	(7)10.4±0.14	(13)2.82±0.10	(13)2.60±0.04
Leucophoyx thula	5♀ 348±22.7 12♂ 380.7±18.4	(6)0.78±0.05	(5)21.53±0.51	(6)8.21±1.10	(6)3.41±0.15	(6)2.54±0.06
Hydranassa tricolor	5♀ 334±21.2 35♂ 415±7.66	(25).86±0.28	(3)22.81±0.440	11.3±1.73	(20)3.09±0.063	2.58±0.03
Agamia agami	1♀ 475 3♂ 535±9.35	(2)0.67, 0.72	(1)29.17	(1)11.9	(1)2.73	(1)2.38
Nycticorax nycticorax	2♀ 775,780 2♂ 725, 780	(4)0.73±0.02	. . .	12.15	2.42±0.08	2.49±0.02
Tigrisoma lineatum	6♀ 823±22 5♂ 897±12.44	(11).69±0.023	(4)25.81±0.93	(4)12.06±0.27	(7)2.09±0.04	(7)2.02±0.03
Heterocnus mexicanus	4♀ 1046±49.3 3♂ 1274±110	(7)0.57±0.02	(5)21.69±1.00	(5)11.3±0.30	(7)1.89±0.084	(7)2.12±0.04
Ixobrychus exilis	6♀ 83.69±3.78 14♂ 87.4±1.96	(4)0.815±0.03 $P<0.01$ (Fla.) (6)0.55±0.03 (Pan.)	(3)13.89±0.11	(3)12.16±0.17	(7)3.09±0.06	(8)2.18±0.05
COCHLEARIIDAE **Cochlearius cochlearius*	3♀ 530±18.7 4♂ 584±16.3	(6).77±0.021	(5)25.13±0.43	(6)10.69±0.24	(6)2.72±0.10	(6)2.10±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
**Casmerodius albus*	(13)13.56±0.31	(5)13.04±0.54	(6)1.17±0.04	(5)7.68±0.31	(13)0.15±0.01	(13)3.12±0.11	5.19
Leucophoyx thula	(5)14.40±0.55	(3)12.3±1.29	(5)1.26±0.07	(6)6.85±0.26	(6)0.16±0.04	(6)3.82±0.08	5.11
Hydranassa tricolor	(19)13.97±0.25	(3)13.8±0.6	(3)1.18±0.22	(3)7.77±0.49	(19)0.15±0.01	(19)3.44±0.07	4.77
Agamia agami	(1)20.03	(1)18.4	(1)1.63	(1)9.14	(1)0.17	(1)3.11	4.64
Nycticorax nycticorax	(4)14.3±0.29	. . .	. . .	. . .	0.16±0.02	2.69±0.09	4.71
Tigrisoma lineatum	(9)17.02±0.43 $P<0.05$	(4)15.40±0.96	(4)1.43±0.03	(4)8.99±0.19	(7)0.11±0.00	(7)2.32±0.06	4.38
Heterocnus mexicanus	(7)14.85±0.79	(5)12.41±0.58	(5)1.19±0.10	(5)8.08±0.37	(7)0.08±0.01	(7)2.06±0.04	4.43
Ixobrychus exilis	(2)9.55, 10.10 (Fla.) (6)9.34±0.22 (Pan.)	(3)8.39±0.04 (Pan.)	(3)1.39±0.22 (Pan.)	(3)4.11±0.21 (Pan.)	(7)0.37±0.12	(8)3.54±0.11	3.68
COCHLEARIIDAE **Cochlearius cochlearius*	(6)15.97±0.32	(5)14.53±0.19	(5)1.71±0.13	(5)8.80±0.21	(6)0.12±0.01	(6)3.02±0.08	4.84

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
Cochlearius cochlearius, immature	1♀ 520 2♂ 505,515	(3)0.59±0.4	(3)10.99±0.97	(3)9.6±0.28	. . .	. . .
CICONIIDAE						
**Mycteria americana*	1♀ 2050 9♂ 2702±250	(10)0.82±0.05	(3)27.29±0.28	(4)10.9±0.02	(6)1.54±0.07	(6)2.85±0.07
THRESKIORNITHIDAE						
**Eudocimus albus*	18♀ 718±15.65 12♂ 908±31.30	(19)1.02±0.03	(1)31.32	8.48	(13)1.65±0.02	(14)2.33±0.05
ANATIDAE						
Cairina moschata (domestic)	3♀ 2022±39.4 3♂ 2915±115	(6)0.79±0.05	3♀ 23.51±0.54 $P < 0.01$ 3♂ 20.85±0.47	3♀ 9.52±0.08 $P < 0.01$ 3♂ 10.85±0.12	(6)0.84±0.03	(6)2.16±0.01
Anas acuta	3♀ 568±19.8 1♂ 675	(4)1.23±0.05	(4)31.36±1.56	(4)5.69±0.13	(4)1.13±0.07	(4)3.37±0.07
Anas discors	3♀ 365±10.4 8♂ 333±9.3	(5)1.15±0.03	(4)29.24±0.41	(4)4.85±0.32	(4)1.16±0.04	(4)2.84±0.13
Mareca americana	1♀ 545	0.98	27.17	5.82	1.08	2.75
**Aythya affinis*	7♀ 577±35.3 11♂ 621±22.6	(15)0.90±0.03	(7)22.38±0.96	(8)6.67±0.37	(10)0.79±0.03	(10)3.10±0.10
Oxyura dominica	3♀ 368±23.6 4♂ 359±36	(7)1.12±0.06	. . .	(1)7.77	(5)0.97±0.08	2.47±0.14

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
Cochlearius cochlearius, immature	(3)5.55±0.30	(3)4.82±0.24	(3)0.73±0.09	(3)5.45±0.66	. . .	. . .	. . .
CICONIIDAE							
**Mycteria americana*	(6)18.4±0.41	(3)17.6±0.61	(3)1.30±0.09	(3)8.37±0.58	(6)0.10±0.00	(6)1.76±0.08	4.62
THRESKIORNITHIDAE							
**Eudocimus albus*	(13)20.16±0.43	19.40	2.24	9.68	(14)0.10±0.01	(13)1.96±0.05	3.85
ANATIDAE							
Cairina moschata (domestic)	3♀ 17.30±0.27 $P < 0.05$ 3♂ 14.95±0.58	3♀ 15.25±0.31 $P < 0.01$ 3♂ 13.09±0.44	3♀ 2.08±0.06 3♂ 1.86±0.14	3♀ 6.20±0.28 3♂ 6.23±0.31	(6)0.14±0.03	(6)1.09±0.02	3.36
Anas acuta	(4)24.26±0.22	(4)21.3±0.35	(4)2.94±0.29	(4)7.11±0.62	(4)0.07±0.01	(4)1.45±0.09	3.10
Anas discors	(4)22.41±0.30	(4)19.64±0.21	(4)2.77±0.09	(4)6.83±0.27	(4)0.11±0.03	(4)1.55±0.07	2.84
Mareca americana	20.77	18.38	2.39	6.40	0.12	1.45	2.55
**Aythya affinis*	(11)17.24±0.60	(7)14.7±0.64	(7)1.94±0.11	(7)5.70±0.34	(10)0.05±0.01	(10)1.07±0.04	2.62
Oxyura dominica	(5)19.7±0.47	. . .	. . .	. . .	0.18±0.01	1.33±0.11	2.63

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
CATHARTIDAE						
Coragyps atratus (Florida)	1♀ 1950 5♂ 2065±76	(8)0.89±0.03 $P<.05$	...	...	1.59±0.06	2.20±0.15
**Coragyps atratus* (Panamá)	3♀ 1865±82.7 4♂ 1775±127	(7)0.79±0.03	(5)25.02±1.24	(6)15.0±0.65	(7)1.54±0.10	(7)2.31±0.03
Cathartes aura (Florida)	5♀ 1589±118.35 15♂ 1426±10	(15)0.74±0.02	...	...	2.98±0.10	2.65±0.04
Cathartes aura (Panamá)	3♀ 1458±208 6♂ 1175±58.9 smaller than Fla. $P<0.01$	(9)0.66±0.01 smaller than Fla. $P<0.01$	(3)28.86±0.79	(3)9.90±0.68	(4)3.15±0.23	(4)2.63±0.06
ACCIPITRIDAE						
Elanoïdes forficatus	2♂ 445, 505	0.81, 0.81	(1)23.30	4.67, 5.14	2.72, 3.28	3.37, 3.48
Leptodon cayanensis	1♀ 540 2♂ 435, 445	(3)0.43±0.04	(1)31.45	(2)9.06, 10.11	(3)3.29±0.31	(3)2.01±0.09
Chondrohierax uncinatus	3♀ 296±22.2 4♂ 265±11.6	(7)0.56±0.01	(6)29.92±0.56	(7)7.54±0.10	(6)5.24±0.14	(7)1.94±0.02
Harpagus bidentatus	1♀ 206.0 1♂ 165.0	(1)0.49	...	...	3.44	2.01
Accipiter bicolor	♂ 235	1.28	...	10.3	3.17	2.01

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
CATHARTIDAE							
Coragyps atratus (Florida)	(8)16.0±0.44	...	...	...	0.15±0.01	1.99±0.11	4.50
**Coragyps atratus* (Panamá)	(6)16.39±0.43	(5)14.33±0.76	(4)1.31±0.19	(5)9.38±0.31	(7)0.18±0.01	(7)1.91±0.07	4.47
Cathartes aura (Florida)	(11)15.8±0.21 $P<0.01$	...	...	...	0.43±0.01	3.90±0.16	5.81
Cathartes aura (Panamá)	(4)17.45±0.51	(3)16.4±0.64	(3)1.26±0.03	(3)11.2±0.13	(4)0.53±0.04	(4)3.94±0.27	5.86
ACCIPITRIDAE							
Elanoïdes forficatus	14.0, 14.29	13.90	0.39	9.02	0.58, 0.66	3.66, 4.06	4.84
Leptodon cayanensis	(3)16.60±2.23	(1)14.56	(1)5.65	(1)11.24	(3)0.65±0.10	(3)4.14±0.39	4.79
Chondrohierax uncinatus	(7)18.30±0.29	(6)17.64±0.32	(6)0.68±0.05	(6)11.61±0.36	(7)1.11±0.08	(6)6.99±0.16	5.56
Harpagus bidentatus	(1)17.65	16.87	0.78	...	0.83	4.55	4.51
Accipiter bicolor	22.00	...	...	...	0.77	4.13	4.42

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.² per gram*	Aspect ratio
Accipiter cooperii	6♀ 535±19 1♂ 315	0.81	...	...	2.54	2.19
Accipiter striatus	1♀ 171.0	0.73	...	10.2	3.49	2.18
Heterospizias meridionalis	2♀ 800, 866 5♂ 776±33.5	(4)0.69±0.06	18.09, 25.09	(4)14.08±0.67	(4)2.97±0.25	(4)2.35±0.18
Buteo lineatus	14♀ 643±25.7 10♂ 475±25.6	(7)0.55±0.03	(1)22.71	(1)15.9	3♀ 2.46±0.14 5♂ 3.14±0.16 $P < 0.05$	(8)2.24±0.06
**Buteo platypterus*	4♀ 412±14 12♂ 359.6±8.7	(9)0.54±0.02	(5)21.39±0.78	(6)13.96±0.25	(7)2.70±0.10	(7)2.28±0.02
Buteo magnirostris	7♀ 272±11.68 9♂ 266±8.6	(13)0.56±0.02	(4)21.70±0.09	(7)13.8±0.26	(12)2.97±0.07	(2)2.01±0.03
Buteo nitidus	1♀ 420	0.40	...	...	2.59	2.21
Busarellus nigricollis	2♀ 895, 900 1♂ 725	(3)0.65±0.03	...	15.2	3.21±0.12	1.98±0.03
Buteogallus anthracinus	4♀ 1199±142 6♂ 793±95.8	(8)0.57±0.03	(3)22.21±0.56	(5)17.6±0.96	(8)2.60±0.20	(8)2.07±0.05
Hypomorphnus urubitinga	2♀ 625, 900	(2)0.40, 0.48	...	15.4	2.95, 3.08	1.99, 2.41
Spizastur melanoleucus	1♀ 525	0.42	26.41	10.5	(1)2.76	1.95

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Accipiter cooperii	13.3	...	...	...	0.54	3.32	4.50
Accipiter striatus	22.2	...	...	...	1.14	4.84	4.40
Heterospizias meridionalis	(2)13.99, 0.74	12.2, 15	0.38, 0.59	6.35, 9.50	(4)0.26±0.04	(4)3.45±0.22	5.29
Buteo lineatus	3♀ 13.60±0.88 5♂ 11.31±0.74	...	(1)0.47	(1)7.74	(8)0.56±0.05	3♀ 3.19±0.23 5♂ 4.00±0.22	4.76
**Buteo platypterus*	(7)13.76±0.57	(5)12.81±0.58	(5)0.42±0.05	(5)7.59±0.27	(7)0.59±0.07	(7)3.59±0.17	4.35
Buteo magnirostris	(12)12.79±0.27	(4)12.65±0.35	(4)0.45±0.04	(5)7.59±0.27	(12)0.62±0.03	(12)3.78±0.08	4.36
Buteo nitidus	12.28	...	...	...	0.62	3.38	
Busarellus nigricollis	(3)13.9±0.33	...	...	...	0.26±0.01	3.61±0.14	5.50
Buteogallus anthracinus	(8)13.52±0.44	(3)13.05±0.37	(3)0.52±0.03	(3)8.71±0.36	(8)3.8±0.04	(8)3.10±0.24	5.06
Hypomorphnus urubitinga	(2)12.5, 12.8	...	...	...	...	3.44, 3.51	5.19
Spizastur melanoleucus	15.61	15.05	0.56	10.8	0.58	3.64	4.72

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Spizaëtus ornatus	1♂ 1215	0.35	29.33	17.1	(1)1.75	1.74
Geranospiza caerulescens	1♀ 430 1♂ 325	(2)0.61, 0.69	18.86, 20.97	17.0, 18.6	(2)3.82, 3.25	2.02, 1.91
PANDIONIDAE						
**Pandion haliaetus*	3♀ 1837±235 2♂ 1530, 1500	(1)0.84	24.79	8.5	(1)2.16	3.00
FALCONIDAE						
Herpetotheres cachinnans	1♀ 800 1♂ 675	(2)0.71, 0.49	23.14, 22.14	14.05, 15.05	2.41, 1.53	2.17, 2.08
Micrastur ruficollis	6♀ 196±6.62 6♂ 161±2.44	(11)0.60±0.03	3♀ 21.43±0.46 3♂ 23.21±0.20	(8)18.59±0.49	(8)2.83±0.11	(8)1.72±0.04
Micrastur semitorquatus	1♀ 900	0.62	25.63	23.5	1.72	1.58
Milvago chimachima	1♀ 410 1♂ 325	0.65, 0.75	. . .	11.3, 12.0	2.85, 3.65	2.34, 2.41
**Caracara cheriway*	10♀ 953±20.0 $P < 0.01$ 14♂ 834±35.5	(12)1.11±0.04	(3)23.22±0.09	(4)12.9±0.54	(11)2.02±0.07	2.60±0.04
Falco peregrinus	2♀ 825, 825	(1)1.23	29.92	12.0	(1)1.69	3.06

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Spizaëtus ornatus	13.93	13.50	0.43	15.4	0.45	2.42	4.32
Geranospiza caerulescens	12.51, 11.27	12.1, 10.9	0.37, 0.41	7.59, 8.46	0.77, 1.18	5.51, 5.25	5.25
PANDIONIDAE							
**Pandion haliaetus*	14.69	14.0	0.69	10.10	0.18	2.49	5.05
FALCONIDAE							
Herpetotheres cachinnans	13.48, 14.79	13, 14	0.48, 0.79	8.66, 8.35	0.45, 0.43	3.05, 2.18	4.66
Micrastur ruficollis	6♀ 12.80±0.16 4♂ 14.56±0.17	4♀ 12.11±0.20 4♂ 13.7±0.77	5♀ 0.73±0.01 $P < 0.01$ 4♂ 0.85±0.01	(6)8.72±0.13	(8)0.78±0.08	(8)3.94±0.20	4.01
Micrastur semitorquatus	16.99	15.95	1.04	8.64	0.67	2.61	4.07
Milvago chimachima	14.1, 15.2	14.1, 15.2	. . .	. . .	0.62, 0.80	3.60, 4.60	4.79
**Caracara cheriway*	(11)15.4±0.09	(3)14.4±0.64	0.64±0.04	(3)8.21±0.57	0.35±0.02	2.53±0.07	4.42
Falco peregrinus	19.20	18.2	0.82	10.9	0.37	2.19	3.98

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Falco albigularis	1♂ 149.9	1.07	24.68	9.04	1.98	3.05
Falco sparverius	11♀ 112.5±3.43 4♂ 85.7±7.42	(15)1.01±0.03	(5)21.82±0.55	(8)8.54±0.22	(11)3.49±0.09	(11)2.63±0.04
CRACIDAE						
Ortalis garrula	1♀ 470 6♂ 541±25.5	(7)0.62±0.04	(5)23.20±0.53	(6)19.86±0.58	(7)1.63±0.07	(7)1.51±0.04
**Chamaepetes unicolor*	7♀ 1148±51.9 5♂ 1116±78.6	(10)0.48±0.02	(1)26.46	(2)15.7, 15.7	(5)1.36±0.11	(5)1.38±0.07
PHASIANIDAE						
Colinus virginianus floridanus	2♀ 150, 170 8♂ 150±5.28	(10)0.38±0.02	(4)34.31±0.60	(4)14.6±0.60	(4)1.19±0.03	(4)1.74±0.10
**Odontophorus guttatus*	4♀ 294±5.95 18♂ 314±5.10	(11)0.34±0.01	(5)30.02±0.97	(6)16.38±0.56	(9)1.26±0.03	(8)1.56±0.06
Coturnix coturnix japonica	3♀ 123.48±4.2	(3)1.00±0.08	(3)25.60±0.08	(3)12.16±0.85	(3)1.13±0.04	(3)2.15±0.07
Gallus gallus (White Leghorn)	10♀ 1705±48.3 $P<0.01$ 10♂ 2430±54.0	10♀ 0.36±0.01 $P<0.01$ 10♂ 0.50±0.01	(1)16.56	7♀ 12.5±0.39 $P<0.01$ 7♂ 17.1±0.89	(20)0.53±0.02	(20)1.31±0.02
(Buff Orpington)	2♀ 2846, 3126	(2)0.32, 0.38	...	(2)6.92, 7.23	(2)0.30, 0.32	1.48, 1.53

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Falco albigularis	16.96	16.35	0.61	7.72	0.35	2.58	3.25
Falco sparverius	(13)15.0±0.33	(7)14.82±0.39	(7)0.59±0.03	(7)6.92±0.17	1.05±0.06	(11)4.92±0.16	4.04
CRACIDAE							
Ortalis garrula	(7)15.05±0.39	(5)12.83±0.63	(5)2.28±0.13	(5)8.09±0.18	(7)0.74±0.03	(7)2.55±0.07	3.68
**Chamaepetes unicolor*	(5)16.6±0.41	14.7	3.30	8.46	(5)0.52±0.02	(5)2.05±0.18	3.66
PHASIANIDAE							
Colinus virginianus floridanus	(4)28.79±0.47	(4)21.6±0.55	(4)7.16±0.10	(4)5.53±0.32	(4)0.24±0.01	(4)1.70±0.04	2.62
**Odontophorus guttatus*	(8)24.06±0.50	(6)18.06±0.63	(6)5.89±0.29	(5)6.17±0.40	(8)0.13±0.01	(9)1.54±0.03	3.10
Coturnix coturnix japonica	(3)21.14±0.12	(3)15.49±0.32	(3)5.66±0.40	(3)4.46±0.14	(3)0.04±0.01	(3)1.49±0.06	2.38
Gallus gallus (White Leghorn)	(20)10.6±0.23	(1)8.78	3.50	4.28	(15)0.08±0.02	(17)0.85±0.02	2.60
(Buff Orpington)	(2)5.53, 5.85	...	...	...	0.73, 0.78	...	2.11

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
NUMIDIDAE **Numida meleagris*	7♀ 1299±41.64 3♂ 1299±25.23	(10)0.57±0.02	(10)24.97±0.28	(10)16.6±0.20	(10)0.90±0.02	(10)1.48±0.02
ARAMIDAE **Aramus guarauna*	3♀ 863±16.1 P<0.01 3♂ 1028±13.0	(6)0.71±0.04	(2)24.12, 21.39	16.2, 16.9	1.36, 1.74	2.20, 2.90
RALLIDAE *Aramides cajanea*	13♀ 385±20.0 5♂ 427±22.7	(11)0.59±0.02	(7)15.93±0.65	(6)23.16±1.14	(8)1.50±0.05	(8)1.67±0.04
**Lateralluṡ albigularis*	12♀ 44.99±1.83 13♂ 49.68±1.60	(20)0.61±0.02	(6)11.97±0.67	(7)17.41±0.60	(16)2.32±0.09	(16)1.65±0.04
Gallinula chloropus	10♀ 312±11.0 10♂ 356±22.0	(15)0.58±0.03	(3)16.31±0.85	(4)16.1±0.51	(11)1.26±0.06	(11)2.09±0.03
Porphyrula martinica	8♀ 215±6.34 P<0.01 20♂ 257±6.05	(23)0.63±0.02	(3)13.66±0.52	(5)15.7±0.76	(14)1.61±0.05	(14)2.29±0.04
Fulica americana	14♀ 460±14.2 11♂ 562±26.7	(11)0.65±0.04	(3)13.47±0.31	(3)11.4±0.88	(9)1.00±0.03	(9)2.32±0.10
HELIORNITHIDAE **Heliornis fulica*	3♀ 129.9±3.10 4♂ 139.8±2.4	(6)0.67±0.03	(4)17.64±0.56	(5)14.90±0.73	(5)1.83±0.05	(5)2.07±0.03

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
NUMIDIDAE **Numida meleagris*	(10)18.83±0.22	(10)14.31±0.14	(10)4.51±0.13	(10)6.14±0.13	(10)0.14±0.01	(10)1.19±0.05	3.13
ARAMIDAE **Aramus guarauna*	14.28, 14.78	13.0, 13.4	1.28, 1.38	7.11, 9.34	0.12, 0.18	2.03, 2.44	3.59
RALLIDAE *Aramides cajanea*	(8)9.75±0.33	(6)8.62±0.26	(6)1.34±0.13	(6)5.72±0.29	(7)0.06±0.01	(8)1.72±0.05	3.34
**Lateralluṡ albigularis*	(17)7.76±0.06	(6)7.01±0.31	(6)1.29±0.14	(6)3.29±0.33	(10)0.11±0.01	(16)2.81±0.11	2.90
Gallinula chloropus	(12)11.63±0.44	(3)10.2±0.45	(3)1.50±0.05	5.39, 5.43	(12)0.11±0.01	(11)1.58±0.06	2.96
Porphyrula martinica	(13)10.83±0.34	(3)8.93±0.21	(3)1.12±0.06	(3)3.61±0.35	(14)0.10±0.01	(12)2.02±0.07	3.15
Fulica americana	(9)9.32±0.40	(3)8.20±0.21	(3)1.24±0.14	(3)4.04±0.33	(6)0.04±0.01	(6)1.25±0.04	2.79
HELIORNITHIDAE **Heliornis fulica*	(5)12.36±0.32	(4)10.66±0.34	(4)1.86±0.08	(4)5.12±0.16	(5)0.51±0.06	(5)2.60±0.08	3.04

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Jacanidae						
**Jacana spinosa*	16♀ 112.0±2.7 20♂ 78.9±1.9	(23)0.77±0.02	5♀ 25.24±0.51 2♂ 17.68, 19.45	4♀ 12.1±0.54 2♂ 9.80, 10.45	(15)2.98±0.10	(14)1.99±0.03
Charadriidae						
**Charadrius vociferus*	4♀ 86.5±0.48 8♂ 80.96±3.78	(8)1.36±0.05	(1)29.30	7.88	(1)3.34	3.00
Scolopacidae						
Totanus flavipes	6♀ 91.16±4.34 6♂ 78.15±2.29	(9)1.29±0.04	(7)27.81±0.50	(9)4.64±0.06	(9)2.63±0.14	(8)3.09±0.02
Totanus melanoleucus	4♀ 221±19 5♂ 200±13	(2)1.21, 1.26	(1)30.61	(1)6.57	(1)2.34	(1)3.17
Tringa solitaria	2♀ 54.5, 66.0 3♂ 51.5±10	(3)1.08±0.09	...	(1)6.05	(1)4.16	(1)2.81
Actitis macularia	2♀ 38,45 1♂ 28.6	(3)1.04±0.06	...	...	(1)3.82	(1)2.51
Catoptrophorus semipalmatus	1♀ 250 3♂ 213±24	(1)1.10	(1)30.43	(1)8.91	(1)2.20	(1)2.73
Limnodromus griseus	5♀ 105±2 6♂ 98±2	(5)1.45±0.09	...	...	(1)2.13	(1)2.95
Capella gallinago	5♀ 114.7±0.5 3♂ 99±6	(7)1.22±0.05	(4)31.67±1.20	(5)9.30±0.25	(5)1.95±0.18	(4)2.63±0.12

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Jacanidae							
**Jacana spinosa*	9♀ 18.35±0.36 $P<0.05$ 6♂ 16.29±0.64	4♀ 16.21±0.18 2♂ 12.4, 13.3	4♀ 2.83±0.09 2♂ 1.82, 1.98	4♀ 6.35±0.38 2♂ 3.30, 4.33	(12)0.07±0.01	(15)3.33±0.08	3.64
Charadriidae							
**Charadrius vociferus*	(1)23.04	(1)21.5	(1)2.54	5.26	0.71	4.42	3.83
Scolopacidae							
Totanus flavipes	(7)23.19±0.33	(7)20.5±0.26	(9)2.59±0.14	(9)4.64±0.06	(9)0.46±0.02	(9)3.79±0.05	3.62
Totanus melanoleucus	(1)25.03	21.6	3.43	5.58	0.31	2.88	3.66
Tringa solitaria	(1)22.20	...	...	...	0.48	4.93	3.82
Actitis macularia	(1)19.8	...	...	...	0.48	4.85	3.44
Catoptrophorus semipalmatus	(1)23.91	21.1	2.81	6.52	0.18	2.73	3.62
Limnodromus griseus	(1)18.8	...	...	...	0.27	2.74	3.12
Capella gallinago	(5)27.86±0.83	(4)22.94±0.79	(4)4.55±0.34	(4)4.19±0.72	(5)0.22±0.02	(4)2.59±0.13	2.90

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Crocethia alba	4♀ 58.14±2.59 6♂ 53.16±0.87	(9)1.54±0.05	(7)26.13±0.28	(7)4.85±0.21	(9)2.89±0.07	(8)3.17±0.07
**Ereunetes mauri*	4♀ 28.33±2.20 9♂ 26.06±0.84	(8)1.26±0.08	(6)22.88±0.38	(6)4.50±0.14	(7)3.70±0.10	(7)2.94±0.07
Erolia melanotos	1♀ 48.9 1♂ 41.0	(2)1.13, 1.25	(2)28.66, 32.40	(2)5.86, 6.10	(2)3.52, 3.93	(2)2.77, 3.00
Erolia alpina	3♀ 57.36±2.32 7♂ 52.36±2.74	(6)1.48±0.04	(6)26.74±0.38	(6)4.75±0.12	(6)2.87±0.09	(6)3.23±0.05
RECURVIROSTRIDAE						
**Himantopus mexicanus*	7♀ 152±10 8♂ 173±5	(15)1.22±0.04	...	...	(4)2.87±0.28	(4)2.94±0.08
LARIDAE						
Larus delawarensis	4♂ 502±24.1	(3)0.85±0.09	(3)20.43±0.53	(3)5.28±0.17	(3)2.81±0.09	(3)3.75±0.09
Larus argentatus	11♀ 762±34.8 18♂ 907±17.1	(3)0.84±0.06	(2)19.47, 22.46	6.38, 8.20	1.78, 2.11	3.53, 3.88
Larus atricilla	10♀ 299±20.5 36♂ 295±5.5	(13)0.85±0.03	(5)19.81±0.61	(4)4.74±0.37	(10)3.44±0.10	(11)3.46±0.08
Larus pipixcan	2♂ 230, 289	(3)0.68±0.10	(3)17.54±0.70	(3)4.48±0.32	(3)3.33±0.29	(3)3.35±0.09
Sterna hirundo	9♀ 99±2.96 10♂ 115±6.17	(10)1.08±0.05	(3)20.38±0.35	(3)2.72±0.07	(3)3.69±0.25	(3)4.48±0.12

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Crocethia alba	(9)22.13±0.39	(7)20.0±0.31	(7)2.54±0.11	(6)3.58±0.08	(7)0.42±0.03	(9)3.71±0.10	3.36
**Ereunetes mauri*	(8)19.7±0.36	(6)17.7±0.32	(6)2.37±0.11	(6)2.85±0.10	(7)0.59±0.06	(7)4.76±0.18	3.83
Erolia melanotos	(2)23.8, 26.59	20.50, 22.95	3.32, 3.65	4.84, 5.81	0.57, 0.70	4.50, 4.98	3.65
Erolia alpina	(6)22.98±0.35	(6)20.0±0.28	(6)2.96±0.11	(6)3.75±0.05	(6)0.48±0.02	(6)3.75±0.12	3.31
RECURVIROSTRIDAE							
**Himantopus mexicanus*	(4)17.1±0.15	...	...	...	0.22±0.01	(4)3.38±0.28	4.00
LARIDAE							
Larus delawarensis	(3)14.32±0.16	(3)13.3±0.19	(3)1.02±0.05	(3)6.45±0.41	(3)0.51±0.01	(3)3.59±0.11	4.79
Larus argentatus	(2)12.96, 15.91	11.8, 14.8	1.11, 1.16	6.51, 6.55	0.29, 0.30	2.27, 2.68	4.55
Larus atricilla	(12)12.86±0.31	(5)12.6±0.54	(5)1.04±0.07	(5)6.15±0.18	(12)0.44±0.04	(9)4.18±0.14	4.78
Larus pipixcan	(3)12.24±0.29	(3)11.32±0.27	(3)0.91±0.07	(3)5.30±0.43	(3)0.49±0.08	(3)4.18±0.43	4.63
Sterna hirundo	(3)15.34±0.24	(3)14.0±0.25	(3)1.31±0.12	(3)5.04±0.11	(3)0.44±0.04	(3)4.50±0.32	4.32

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
Sterna forsteri	4♀ 117±3.3 3♂ 118±3	(3)1.08±0.14	...	...	3.8, 4.0	3.85, 4.08
**Thalasseus maximus*	11♀ 463±18.6 17♂ 475±6.47	(23)0.98±0.03	(9)20.12±0.44	(9)2.68±0.10	(18)2.06±0.05	(18)4.69±0.14
Thalasseus sandvicensis	1♀ 270 2♂ 330, 210	(4)0.84±0.03	(1)18.74	(1)2.28	(4)2.97±0.16	(4)3.72±0.66
RYNCHOPIDAE						
**Rynchops nigra*	5♀ 235±14.9 8♂ 351±18.5	(10)1.00±0.05	(10)20.75±0.35	(10)2.73±0.09	(10)3.34±0.22	(10)4.42±0.14
COLUMBIDAE						
Columba livia	1♀ 278 6♂ 307±10.63	(7)1.29±0.05	(6)30.90±0.82	(7)6.10±0.16	(7)1.85±0.04	(7)2.28±0.05
Columba albilinea	5♀ 312±9.5 12♂ 309±6.6	(17)1.17±0.03	(3)34.06±2.33	(5)5.54±0.36	(12)1.79±0.04	(12)1.98±0.06
Columba speciosa	6♀ 255±5.8 $P<0.05$ 13♂ 262±3.2	(7)1.25±0.40	(7)37.68±0.85	(8)5.01±0.13	(8)1.56±0.05	(8)1.95±0.03
Columba nigrirostris	2♂ 128, 160	(2)1.24, 1.58	...	(1)6.95	(2)2.19, 2.97	1.80, 1.82
Columba subvinacea	1♀ 150, 157.2 3♂ 180.7±8.43	(5)1.20±0.15	(3)36.45±1.02	(3)5.28±0.15	(4)2.29±0.08	(5)2.00±0.11

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supracoracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
Sterna forsteri	(2)14.3, 13.6	...	...	...	0.47, 0.53	(2)4.6, 4.8	4.37
**Thalasseus maximus*	(18)14.40±0.21	(9)13.5±0.35	(9)1.19±0.02	(9)5.57±0.13	(18)0.21±0.01	(18)2.51±0.06	3.95
Thalasseus sandvicensis	(4)12.6±0.76	(1)12.8	1.09	4.85	(4)0.38±0.02	(4)3.69±0.24	4.44
RYNCHOPIDAE							
**Rynchops nigra*	(10)14.29±0.27	(10)13.35±0.24	(10)1.04±0.04	(10)6.46±0.17	(10)0.33±0.02	(10)3.97±0.24	5.00
COLUMBIDAE							
Columba livia	(7)23.50±0.65	(7)20.3±0.54	(7)3.22±0.17	(6)7.18±0.26	(7)0.61±0.06	(7)2.72±0.09	3.52
Columba albilinea	(12)25.16±0.49	(3)21.30±1.62	(3)3.89±0.41	(3)8.87±0.47	(12)0.54±0.02	(12)2.54±0.04	3.49
Columba speciosa	(8)29.07±0.59	(8)25.0±0.57	(7)4.57±0.08	(7)8.38±0.06	(8)0.48±0.03	(8)2.27±0.08	3.16
Columba nigrirostris	(1)28.73	24.15, 36.2	(1)4.58	...	0.61, 1.16	3.07, 4.42	3.66
Columba subvinacea	(5)26.85±0.79	(4)23.1±0.58	4.33±0.11	(3)8.61±0.75	(4)0.85±0.07	(4)3.40±0.18	3.64

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Columbigallina passerina	3♀ 41.1±5.2 9♂ 44.0±1.3	(8)1.11±0.05 P < 0.05	...	...	2.87±0.15	1.59±0.28
Columbigallina minuta	3♀ 45.57±2.46 1♂ 33.8	(2)1.00, 1.00	(2)33.52, 34.42	5.42, 5.57	2.13, 2.99	1.62, 1.69
**Columbigallina talpacoti rufipennis*	14♀ 47.12±0.85 26♂ 46.74±1.01	(16)0.96±0.04	(5)34.08±0.45	(5)5.39±0.16	(15)2.86±0.05	(15)1.69±0.03
Claravis pretiosa	1♀ 59.56 11♂ 70.97±1.36	(10)1.27±0.04 P < 0.01	(5)38.97±1.01	(6)4.53±0.06	(10)2.69±0.05	(10)1.85±0.02
Claravis mondetoura	3♂ 82.93±1.76	(3)1.04±0.08	...	6.62	(3)2.28±0.06	1.74±0.08
Leptotila verreauxi	15♀ 154±3.67 19♂ 152±3.38	(23)0.93±0.02	(7)36.9±0.89	(7)5.31±0.22	(16)2.01±0.06	(16)1.63±0.03
Leptotila cassini	2♀ 131.1, 150 5♂ 157.7±8.3	(10)0.49±0.02	(4)42.35±0.27	(6)5.55±0.17	(6)2.24±0.09	(8)1.82±0.06
Leptotila rufinucha	3♀ 155±1.8 6♂ 170±0.25	(8)0.57±0.01	(5)43.9±0.69	(5)5.63±0.20	(6)1.77±0.05	(6)1.71±0.03
Geotrygon costaricensis	2♀ 225, 283 2♂ 310, 330	0.31, 0.31	37.96	(3)7.81±0.70	(4)1.42±0.16	(4)1.59±0.06
Geotrygon montana	4♀ 128±3 4♂ 141±6.7	(7)1.08±0.06	(7)34.37±1.04	(7)5.72±0.25	(8)2.00±0.09	(8)1.85±0.03
Geotrygon chiriquensis	8♀ 306±7.05 11♂ 309±6.33	(14)0.32±0.02	(5)38.04±0.52	(6)8.84±0.37	(10)1.30±0.03	(10)1.58±0.02

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Columbigallina passerina	(6)29.3±0.76	...	...	...	(6)0.68±0.04	4.07±0.16	3.17
Columbigallina minuta	27.7, 28.16	22.7, 22.7	5.00, 5.46	5.82, 6.26	0.71, 0.80	3.23, 4.31	3.04
**Columbigallina talpacoti rufipennis*	(14)28.09±0.44	(5)22.76±0.54	(5)5.63±0.27	(5)5.70±0.69	(15)0.72±0.02	(15)3.99±0.06	3.22
Claravis pretiosa	(10)30.92±0.42	(5)26.21±0.44	(5)5.40±0.16	(5)7.36±0.43	(10)0.74±0.05	(10)3.78±0.06	3.31
Claravis mondetoura	(3)30.2±0.92	...	...	...	(3)0.63±0.09	3.20±0.02	3.15
Leptotila verreauxi	(18)30.33±0.37 P < 0.01	(9)24.7±0.57	(8)5.99±0.25	(8)6.82±0.55	(15)0.66±0.03	(15)2.96±0.09	3.28
Leptotila cassini	(8)34.16±0.76	(4)27.99±1.25	(4)6.78±0.04	(4)7.58±0.26	(6)0.48±0.05	(5)2.97±0.08	3.47
Leptotila rufinucha	(6)36.65±0.19	(6)29.34±0.47	(6)7.31±0.16	(5)7.36±0.37	(5)0.44±0.02	(6)2.38±0.05	3.11
Geotrygon costaricensis	(4)30.59±1.23	24.35	6.42	7.19	(4)0.23±0.04	(4)1.81±0.20	3.06
Geotrygon montana	(8)26.38±0.60	(8)22.36±0.65	(8)4.65±0.21	(7)7.58±0.22	(8)0.40±0.04	(8)2.66±0.05	2.72

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
PSITTACIDAE						
**Pyrrhura hoffmanni*	17♀ 81.8±1.2 17♂ 82.8±3.0	(21)1.41±0.06	(3)27.36±0.16	(4)5.52±0.18	(6)3.17±0.05	(6)1.87±0.05
Brotogeris jugularis	9♀ 65.50±0.13 $P < 0.05$ 14♂ 61.00±1.17	(12)1.33±0.05	(4)28.51±0.13	(5)6.30±0.14	(9)2.54±0.07	(9)2.36±0.05
Bolborhynchus lineola	1♀ 53.2 1♂ 45.2	(2)1.58, 1.81	(1)28.92	(1)5.44	(2)2.34, 2.72	(2)2.22, 2.44
Pionopsitta haematotis	4♀ 146.1±6.5 4♂ 145.4±0.6	(7)1.51±0.04	(4)28.66±0.91	(5)6.70±0.14	(7)1.91±0.14	(7)2.22±0.05
Pionus senilis	7♀ 208.9±8.4 4♂ 217±5.0	(7)1.19±0.06	(2)31.28, 29.75	(4)7.24±0.64	(8)2.17±0.10	(8)2.17±0.06
Amazona autumnalis	8♀ 408±10.3 8♂ 424±9.1	(15)1.03±0.03	(5)26.94±1.06	(6)8.00±0.22	(11)1.66±0.07	(14)2.00±0.03
Melopsittacus undulatus	9♀ 33.1±0.19 7♂ 32.9±0.60	9♀ 1.36±0.04 7♂ 1.45±0.07	(16)26.39±1.08	(16)5.54±0.16	(16)2.52±0.11	(16)2.44±0.04
CUCULIDAE						
Coccyzus americanus	5♀ 57.60±0.35 2♂ 62, 63	(6)1.15±0.04	(2)19.95, 20.92	6.33, 6.66	(2)4.54, 4.76	2.14, 2.37
**Piaya cayana* (sea level)	5♀ 116±7.1 8♂ 106.8±2.7	(9)0.57±0.02 $P < 0.01$	(4)13.59±0.36 $P < 0.01$	(7)13.93±0.64	(10)3.26±0.15	(10)1.34±0.03

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
PSITTACIDAE							
**Pyrrhura hoffmanni*	(14)21.36±0.38	(3)18.7±0.25	(3)2.97±0.05	(3)5.69±0.11	(6)0.46±0.04	(6)4.01±0.11	3.71
Brotogeris jugularis	(9)21.82±0.50	(4)19.96±0.35	(4)3.12±0.09	(4)5.43±0.21	(9)0.40±0.02	(9)3.25±0.13	3.20
Bolborhynchus lineola	(2)23.81, 23.85	(2)20.05, 20.07	3.76, 3.78	(1)5.11	(2)0.52, 0.73	(2)3.07, 3.75	3.04
Pionopsitta haematotis	(7)22.10±0.57	(4)19.12±0.88	(4)2.97±0.19	(4)6.57±0.53	(7)0.31±0.02	(7)2.42±0.11	3.23
Pionus senilis	(6)20.82±0.95	(1)19.3, 20.0	(1)2.98, 3.36	(1)9.0, 6.39	(7)0.34±0.04	(8)2.76±0.16	3.49
Amazona autumnalis	(14)18.73±0.36	(4)17.27±0.93	(4)2.38±0.14	(4)7.56±0.31	(13)0.31±0.04	(12)2.20±0.06	3.51
Melopsitticus undulatus	(16)23.91±0.87	(16)20.0±0.70	(6)3.87±0.14	(16)4.98±0.16	(15)0.77±0.04	(16)4.04±0.12	2.84
CUCULIDAE							
Coccyzus americanus	13.57, 14.60	12.41, 13.78	0.82, 1.16	6.32, 6.38	1.87, 2.63	7.00, 7.65	4.22
**Piaya cayana* (sea level)	(9)8.81±0.31 $P < 0.01$	(4)7.56±0.26 $P < 0.01$	(4)0.63±0.05	(4)4.52±0.13 $P < 0.01$	(9)2.61±0.20	(10)6.37±0.32	3.93

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Piaya cayana Chiriquí)	9♀ 108.4±1.8 11♂ 107±1.6	(14)0.64±0.02	(4)17.77±0.67	(4)15.5±0.79	(6)3.43±0.10	(6)1.36±0.03
Piaya minuta	2♂ 36.62, 37.2	(2)0.72, 0.64	(1)18.98	10.3	(1)4.31	1.35
Crotophaga major	9♀ 140±3.25 P < 0.01 16♂ 157±3.16	(16)0.67±0.02	(7)19.59±0.89	(7)11.27±0.34	(16)3.65±0.08	(16)1.76±0.02
Crotophaga ani (sea level)	15♀ 87.7±0.83 P < 0.01 23♂ 104.37±1.99	(31)0.59±0.02 P < 0.01	(5)16.69±0.68 P < 0.01	(8)13.05±0.44	(11)3.38±0.14	(10)1.75±0.01
Crotophaga ani (Chiriquí)	6♀ 104.1±7.8 9♂ 117.1±7.4	(15)0.80±0.02	(9)17.91±0.35	(9)12.7±0.43	(14)2.89±0.07	(15)1.79±0.04
Crotophaga sulcirostris	5♀ 65.1±1.55 P < 0.05 9♂ 72.8±2.14	(9)0.75±0.03	(3)20.39±0.35	(4)13.00±0.57	(9)3.75±1.11	(9)1.67±0.03
Tapera naevia	4♀ 47.49±5.0 6♂ 55.1±1.00	(7)0.78±0.04	(4)20.65±0.12	(4)10.7±0.89	(5)3.78±0.08	(5)1.73±0.04
Dromococcyx phasianellus	♂ 85.63	0.94	...	6.7	4.84	1.67
TYTONIDAE **Tyto alba*	4♀ 516±10.3 P < 0.01 4♂ 439±15.9	(5)0.72±0.04	(3)19.23±0.72	(4)13.8±1.35	(5)3.17±0.06	(5)2.68±0.07

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Piaya cayana Chiriquí)	(5)10.31±0.20	(4)9.67±0.15	(4)0.78±0.05	(4)6.57±0.10	(6)2.95±0.26	(6)6.72±0.33	3.98
Piaya minuta	(1)11.99	11.0	0.99	6.99	2.54	7.81	3.77
Crotophaga major	(16)11.25±0.33	(7)11.29±0.35	(7)0.80±0.06	(7)7.50±0.52	(16)2.08±0.06	(16)5.99±0.13	4.40
Crotophaga ani (sea level)	(11)10.44±0.31 P < 0.01	(6)9.99±0.17	(6)0.86±0.04	(6)6.15±0.62	(11)1.68±0.13	(11)5.40±0.23	3.90
Crotophaga ani (Chiriquí)	(14)11.72±0.18	(9)10.78±0.19	(9)0.75±0.06	(9)6.36±0.19	(13)1.62±0.08	(13)4.94±0.20	3.72
Crotophaga sulcirostris	(9)12.8±0.19	(3)12.4±0.21	(3)0.92±0.04	(3)7.13±0.11	(9)1.56±0.15	(9)5.67±0.22	3.92
Tapera naevia	(5)12.63±0.58	(4)12.03±0.43	(4)1.02±0.07	(4)7.60±0.42	(5)1.91±0.11	(5)6.17±0.25	3.73
Dromococcyx phasianellus	22.3	...	...	...	1.88	6.94	4.20
TYTONIDAE **Tyto alba*	(5)10.63±0.92	(4)9.79±1.11	(4)0.62±0.05	(3)9.16±1.02	(5)0.33±0.02	(5)3.71±0.11	4.96

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
STRIGIDAE						
Otus choliba	3♀ 143±18.8	(5)0.52±0.02	(3)24.34±0.74	(3)10.64±1.35	(4)3.55±0.49	(4)1.88±0.08
**Pulsatrix perspicillata*	2♀ 900, 970 2♂ 710, 800	(4)0.31±0.03	(1)22.0	(2)12.9, 14.3	(4)2.52±0.26	(4)2.08±0.03
Speotyto cunicularia	5♀ 149±7.4 6♂ 146.7±9.7	(10)0.89±0.01	...	...	(3)3.51±0.34	(3)1.88±0.19
Ciccaba nigrolineata	1♀ 500 1♂ 417	(2)0.50, 0.40	(1)27.19	10.5, 11.42	2.75, 3.44	1.93, 1.96
Ciccaba virgata centralis	1♂ 230	0.46	21.82	9.86	4.05	1.94
Strix varia alleni	2♀ 850, 875 6♂ 718±35.1	(7)0.58±0.04	...	...	(4)2.49±0.2	1.83±0.10
Rhinoptynx clamator	4♀ 425±22.7 (young) 2♂ 305, 335	0.50, 0.44 0.39,0.42	(1)20.55 ...	16.2, 17.59 ...	2.75 ...	2.25 ...
NYCTIBIIDAE						
**Nyctibius griseus*	13♀ 185±4.6 8♂ 184±10	(19)0.60±0.02	(6)28.06±0.77	(8)2.46±0.04	(14)4.66±0.19	(13)2.47±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
STRIGIDAE							
Otus choliba	(3)14.27±0.53	(3)13.44±0.66	(3)0.85±0.14	(3)10.07±1.08	(4)0.36±0.10	(4)4.74±0.16	4.36
**Pulsatrix perspicillata*	(3)13.01±0.96	(1)11.3	(1)0.42	(1)10.3	(3)0.27±0.03	2.92±0.30	4.78
Speotyto cunicularia	(3)12.37±0.38	...	...	...	(3)0.59±0.04	(3)4.20±0.27	4.24
Ciccaba nigrolineata	17.3, 15.32	14.75	0.57	11.87	0.45, 0.49	3.48, 4.08	5.08
Ciccaba virgata centralis	12.45	11.8	0.65	9.37	0.54	4.93	5.11
Strix varia alleni	(4)12.8±0.64	...	...	...	0.28±0.05	3.07±0.26	4.72
Rhinoptynx clamator	12.8, 11.50	10.32	1.18	9.05	0.32	3.22	4.58
NYCTIBIIDAE							
**Nyctibius griseus*	(14)17.07±0.26	(6)15.91±0.53	(6)0.94±0.04	(6)11.11±0.35	(14)1.37±0.04	(14)6.25±0.17	5.19

(continued)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
CAPRIMULGIDAE						
Chordeiles acutipennis	1♀ 57.2 4♂ 52.40±0.20	(4)1.12±0.06	(4)29.41±0.71	(4)2.73±0.31	(3)5.7±0.52	(3)3.09±0.04
Chordeiles minor chapmani	5♀ 64±4.8 8♂ 60±1.53	(2)1.04, 1.38	...	...	4.96, 5.6	3.26, 3.40
**Nyctidromus albicollis*	15♀ 52.53±0.96 22♂ 53.58±1.11	(27)0.78±0.02	(9)25.60±0.82	(11)5.71±0.19	(19)5.42±0.16	(2)2.20±0.04
Caprimulgus carolinensis	(1)110	(1)0.95	...	...	5.13	2.56
TROCHILIDAE						
Glaucis hirsuta	7♀ 5.53±0.18 $P < 0.05$ 5♂ 6.86±0.20	(5)2.54±0.15	(3)32.16±1.73	(5)1.23±0.08	(6)4.43±0.51	(5)2.36±0.17
**Phaethornis guy*	7♀ 5.53±0.25 24♂ 5.99±0.04	7♀ 2.26±0.07 23♂ 2.51±0.06 $P < 0.01$	3♀ 27.52±0.30 5♂ 32.94±1.36 $P < 0.01$	(9)1.13±0.09	(20)4.15±0.09	(21)3.04±0.05
Phaethornis longuemareus	4♀ 2.71±0.03 7♂ 2.52±0.04	3♀ 2.29±0.09 7♂ 2.53±0.10	1♀ 27.11 4♂ 32.05±2.70	(5)1.17±0.16	(8)3.75±0.16	(8)3.11±0.11
Phaeochroa cuvierii	9♀ 8.35±0.25 16♂ 9.19±0.15	4♀ 1.65±0.11 7♂ 1.91±0.08	1♀ 27.09 3♂ 35.99±1.84	(6)2.33±0.14	(7)3.51±0.08	(7)2.95±0.10
Campylopterus hemileucurus	1♀ 9.05, 9.56 13♂ 11.76±0.21	5♀ 1.94±0.04 9♂ 2.08±0.06	1♀ 27.23 4♂ 36.02±0.97	(6)1.64±0.11	(11)3.68±0.10	(10)2.64±0.08

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supracoracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
CAPRIMULGIDAE							
Chordeiles acutipennis	(4)21.50±0.76	(4)19.58±0.78	(4)1.92±0.04	(4)7.91±0.30	(3)1.27±0.25	(3)7.60±0.66	4.83
Chordeiles minor chapmani	(2)19.4, 21.2	...	...	...	0.75, 0.85	6.5, 5.6	4.36
**Nyctidromus albicollis*	(19)17.23±0.25	(10)15.47±0.29	(10)1.80±0.07	(9)8.28±0.05	(20)1.79±0.05	(20)7.54±0.15	4.52
Caprimulgus carolinensis	19.90	...	...	...	1.25	6.24	4.96
TROCHILIDAE							
Glaucis hirsuta	(6)29.88±1.17	(5)19.4±1.09	(5)10.02±0.36	(3)2.88±0.20	(4)2.53±0.20	(6)7.14±0.34	1.31
**Phaethornis guy*	8♀ 27.63±0.09 10♂ 29.11±0.81	3♀ 16.88±0.46 10♂ 19.9±0.07	3♀ 8.27±0.35 10♂ 9.18±0.23	(3)♀ 2.36±0.33 (5) 2.64±0.12	(21)2.57±0.09	(21)7.14±0.19	1.92
Phaethornis longuemareus	3♀ 25.33±0.20 7♂ 30.00±1.57	2♀ 15.60, 15.88 4♂ 18.38±1.82	2♀ 9.31, 9.54 4♂ 10.40±1.24	1♀ 1.92 4♂ 3.27	(8)2.46±0.17	(8)6.84±0.09	2.26
Phaeochroa cuvierii	2♀ 24.08, 25.25 7♂ 33.12±0.88	2♀ 16.08, 16.22 4♂ 20.02±0.97	2♀ 8.00, 9.03 4♂ 12.22±0.51	1♀ 3.01 3♂ 3.67±0.08	(7)1.74±0.17	(7)5.88±0.21	2.72
Campylopterus hemileucurus	2♀ 23.66, 26.80 9♂ 32.28±0.67	1♀ 16.01 5♂ 19.82±0.71	1♀ 7.65 5♂ 12.11±0.35	1♀ 3,51 4♂ 3.85±0.46	(11)2.56±0.13	(11)6.64±0.20	2.83

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Florisuga mellivora	4♀ 7.08±0.19 2♂ 7.82, 7.83	3♀ 1.98±0.09 2♂ 2.33, 2.54	2♀ 25.33, 27.33 2♂ 31.81, 35.04	(4)1.02±0.02	(4)3.47±0.18	(4)3.26±0.13
Colibri thalassinus	1♀ 4.80 3♂ 5.56±0.37	1♀ 1.88 2♂ 2.40, 2.46	...	(1)1.38	(2)4.88, 4.90	(2)2.81, 2.96
Anthracothorax nigricollis	5♀ 6.99±0.22 7♂ 6.84±0.14	4♀ 1.99±0.01 $P<0.01$ 6♂ 2.75±0.10	1♀ 26.73 3♂ 33.52±1.06	(4)1.25±0.06	(7)3.61±0.13	(7)3.08±0.09
Klais guimeti	3♀ 2.55±0.11 1♂ 2.63	3♀ 2.10±0.04 1♂ 2.39	2♀ 24.89, 30.22 1♂ 27.86	(3)1.33±0.17	(4)5.16±0.11	(4)3.06±0.19
Chlorostilbon canivetii	13♀ 3.15±0.07 3♂ 3.08±0.06	12♀ 1.86±0.05 3♂ 2.24±0.08 $P<0.01$	2♀ 27.86, 29.24 2♂ 27.02, 30.33	(4)1.43±0.25	(5)3.99±0.26	(5)3.03±0.18
Thalurania furcata	2♀ 3.86, 4.47	(2)1.95, 2.33	(1)24.76	(1)1.19	(2)4.12, 4.25	3.01, 3.56
Damophila julie panamensis	8♀ 3.07±0.05 $P<0.01$ 26♂ 3.41±0.04	5♀ 1.88±0.10 11♂ 2.29±0.06 $P<0.01$	2♀ 25.02, 32.86 5♂ 29.52±0.71	(8)1.42±0.12	(9)3.71±0.13	(9)3.07±0.13
Lepidopyga coeruleogularis	3♀ 4.20±0.31	3♀ 1.98±0.20	...	2.13	(3)3.87±0.18	(3)2.91±0.14
Amazilia amabilis	8♀ 3.90±0.10 $P<0.01$ 12♂ 4.70±0.10	7♀ 2.03±0.08 5♂ 2.32±0.13	4♀ 27.99±0.79 3♂ 33.30±1.23 $P<0.01$	(7)1.40±0.12	(8)4.15±0.13	(8)3.13±0.13
Amazilia edward	18♀ 4.39±0.05 $P<0.01$ 20♂ 4.90±0.07	13♀ 2.21±0.05 9♂ 2.64±0.10 $P<0.01$	4♀ 28.34±0.45	(7)1.32±0.10	(17)3.97±0.11	(17)2.94±0.05

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Florisuga mellivora	2♀ 23.47, 24.79 2♂ 29.0, 32.10	2♀ 16.25, 16.30 2♂ 19.1, 21.2	2♀ 7.12, 8.54 2♂ 9.9, 10.9	2♀ 1.86, 2.44 2♂ 2.81, 2.94	(4)2.44±0.44	(4)6.57±0.54	2.59
Colibri thalassinus	(2)26.86, 28.74	...	...	...	(2)2.58, 2.73	(2)8.15, 8.19	1.37
Anthracothorax nigricollis	3♀ 24.60±1.99 $P<0.05$ 4♂ 30.51±0.70	2♀ 15.84, 15.92 3♂ 21.5±0.68	2♀ 7.40, 7.63 3♂ 8.56±0.15	1♀ 3.41 3♂ 3.46±0.43	(7)2.29±0.21	(7)6.68±0.30	2.65
Klais guimeti	3♀ 23.33±1.35 1♂ 25.20	3♀ 15.4±0.61 1♂ 16.6	3♀ 7.97±0.74 1♂ 8.6	2♀ 3.27, 4.64 1♂ 2.66	(4)2.44±0.19	(4)8.71±0.21	2.66
Chlorostilbon canivetii	3♀ 24.77±1.77 2♂ 23.86, 29.07	3♀ 15.89±1.23 2♂ 15.5, 19.1	3♀ 8.88±0.61 2♂ 8.36, 9.97	2♀ 2.02, 2.68 1♂ 3.16	(5)1.91±0.23	(5)6.93±0.39	2.37
Thalurania furcata	(2)21.82, 22.58	(2)15.2, 16.1	(2)6.62, 6.48	(1)2.18	(2)2.46, 1.81	(2)6.94, 6.34	2.58
Damophila julie panamensis	4♀ 26.18±2.09 5♂ 26.89±0.74	3♀ 16.19±0.42 4♂ 16.24±1.00	3♀ 10.30±0.51 5♂ 10.30±0.51	1♀ 2.16, 1.79 5♂ 2.63±0.05	(9)2.21±0.23	(9)6.84±0.21	2.32
Lepidopyga coeruleogularis	(3)24.08±1.43	...	...	...	(3)1.57±0.06	(3)6.05±0.26	2.50
Amazilia amabilis	4♀ 24.50±0.43 3♂ 30.43±0.45 $P<0.01$	4♀ 16.99±0.57 4♂ 20.3±0.43	4♀ 7.51±0.67 3♂ 10.11±0.67	4♀ 3.48±0.62 3♂ 3.19±0.97	(8)2.03±0.13	(8)6.97±0.22	2.63
Amazilia edward	8♀ 26.20±0.41 4♂ 32.54±1.48 $P<0.01$	5♀ 17.35±0.23 1♂ 24.5	5♀ 8.33±0.22 1♂ 9.39	...	(16)1.98±0.08	(17)6.58±0.14	2.58

(continued)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.*^{2} *per gram*	Aspect ratio
Amazilia tzacatl	24♀ 4.73±0.06 28♂ 5.29±0.07	14♀ 2.09±0.06 $P<0.05$ 19♂ 2.35±0.07	3♀ 28.98±1.59 4♂ 38.73±2.67	(8)1.66±0.10	(18)4.01±0.09	(18)3.10±0.08
Eupherusa eximia	5♀ 4.25±0.10 7♂ 4.49±0.12	4♀ 2.31±0.06 5♂ 2.43±0.12	5♀ 26.43±0.69	(4)1.51±0.10	(7)4.62±0.10	(7)3.00±0.07
Elvira chionura	10♀ 3.08±0.06 4♂ 3.24±0.14	10♀ 2.07±0.08 4♂ 2.58±0.12 $P<0.01$	3♀ 26.56±1.02	(4)1.49±0.15	(14)4.55±0.12	(14)3.08±0.09
Lampornis castaneoventris	15♀ 5.14±0.06 $P<0.01$ 21♂ 6.07±0.06	15♀ 2.08±0.06 $P<0.01$ 20♂ 2.33±0.05	3♀ 26.52±1.18 1♂ 37.84, 32.87	(7)2.48±0.23	(33)4.21±0.05	(32)3.04±0.05
Heliodoxa jacula	2♀ 7.39, 8.37 4♂ 9.14±0.22	2♀ 1.98, 2.09 4♂ 2.51±0.17	...	(1)2.37	(5)3.44±0.12	(5)3.39±0.15
Heliothrix barroti	5♀ 5.48±0.20 3♂ 5.46±0.25	4♀ 2.03±0.06 3♂ 2.20±0.11	2♀ 29.24, 30.26	(2)1.03, 1.05	(7)5.07±0.30	(6)3.07±0.10
Philodice bryantae	1♀ 3.31	(1)3.25	(1)29.42	2.06	3.11	3.00
Heliomaster longirostris	1♀ 6.01 2♂ 6.96, 7.20	1♀2.68 2♂ 2.11, 2.31	1♀ 36.82	(2)1.46, 1.52	(3)3.23±0.17	(3)3.08±0.19
Archilochus colubris	3♀ 3.36±0.21 3♂ 3.40±0.28	(4)2.30±0.15	...	...	(1)2.51	2.67
Selasphorus scintilla	15♀ 2.24±0.06 $P<0.01$ 12♂ 2.05±0.03	16♀ 2.36±0.07 8♂ 2.74±0.11 $P<0.01$	1♀ 29.18 5♂ 28.31±0.84	(7)1.18±0.09	(16)2.27±0.14	(16)3.08±0.08

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.*^{2} *per gram*	Glide *cm.*^{2} *per gram*	Buoyancy index
Amazilia tzacatl	6♀ 26.04±0.55 $P<0.01$ 10♂ 33.14±1.29	5♀ 17.32±0.92 5♂ 23.46±2.58	5♀ 8.05±0.28 5♂ 10.0±0.37	3♀ 2.93±0.64 4♂ 2.80±0.35	(18)2.11±0.10	(18)6.70±0.16	2.61
Eupherusa eximia	5♀ 21.26±0.96 2♂ 22.90, 25.98	4♀ 13.53±0.99 1♂ 18.1	4♀ 7.35±0.37 1♂ 7.88	(3)2.59±0.30	(7)2.46±0.30	(7)7.58±0.38	2.72
Elvira chionura	9♀ 23.42±0.62 3♂ 27.66±0.84	7♀ 16.25±0.69 1♂ 18.88	7♀ 7.20±0.40 1♂ 7.90	4♀ 2.22±0.21	(13)2.33±0.13	(14)7.39±0.21	2.60
Lampornis castaneoventris	11♀ 24.41±0.31 $P<0.01$ 14♂ 30.98±0.67	4♀ 16.63±0.57 3♂ 21.64±2.20	4♀ 7.69±0.39 3♂ 9.36±0.26	(5)2.62±0.23	(33)2.02±0.05	(33)6.84±0.09	2.69
Heliodoxa jacula	1♀ 26.04 4♂ 31.9±1.14	1♀ 19.8 1♂ 22.9	1♀ 6.24 1♂ 8.90	...	(5)2.23±0.23	(5)6.14±0.25	2.62
Heliothrix barroti	4♀ 26.50±0.50 3♂ 26.47±1.36	3♀ 18.2±0.60 2♂ 16.20, 19.04	3♀ 8.10±0.29 2♂ 7.41, 8.36	(2)2.79, 3.50	(7)2.95±0.24	(7)8.53±0.42	3.09
Philodice bryantae	27.67	18.00	9.67	1.75	1.66	5.68	2.15
Heliomaster longirostris	1♀ 34.46 2♂ 29.18, 35.4	1♀ 25.6 1♂ 25.6	1♀ 8.86 1♂ 9.80	1♀ 2.36	(3)1.71±0.10	(3)5.33±0.11	2.49
Archilochus colubris	(1)25.5	...	...	...	1.58	4.79	2.06
Selasphorus scintilla	6♀ 25.40±0.28 7♂ 29.50±1.44	2♀ 16.8, 19.24 6♂ 17.89±0.56	2♀ 9.23, 8.28 6♂ 9.36±0.41	1♀ 1.66 4♂ 1.84±0.42	(16)2.27±0.14	(16)7.08±0.23	1.87

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
TROGONIDAE						
Pharomachrus mocinno	8♀ 206±7.0 9♂ 205±4.5	(14)1.29±0.09	2♀ 31.60, 32.08 2♂ 32.64, 33.64	(5)3.41±0.48	(9)2.40±0.05	(10)1.90±0.03
Trogon massena	11♀ 139±5.19 15♂ 142±4.27	(18)1.24±0.06	6♀ 30.04±2.84	(9)3.21±0.12	(17)2.90±0.16	(17)1.99±0.04
Trogon melanurus	5♂ 118.8±0.25	(6)1.25±0.07	(3)29.65±0.09	(4)3.11±0.17	(6)3.11±0.17	(6)2.05±0.12
Trogon strigilatus	2♀ 63.7, 62.4 1♂ 93.71	(1)1.29	(1)34.26	(1)2.88	(1)3.17	(1)2.00
**Trogon collaris*	18♀ 65.42±0.96 29♂ 63.36±0.66	(40)1.05±0.02	(7)31.15±0.22	(9)2.81±0.10	(23)3.32±0.10	(22)1.92±0.03
Trogon aurantiiventris	1♀ 61.85	1.14	...	2.68	3.59	1.91
Trogon curucui	2♀ 48.3, 57.17 4♂ 51.92±1.96	(6)1.10±0.04	(4)31.16±1.09	(6)2.67±0.13	(6)3.51±0.15	(5)2.07±0.08
Trogon caligatus	5♀ 58.18±3.32 13♂ 56.08±1.63	(16)1.18±0.03	(8)30.54±1.00	(10)2.67±0.13	(13)3.51±0.07	(13)2.01±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
TROGONIDAE							
Pharomachrus mocinno	5♀ 21.76±0.08 P<0.01 6♂ 22.69±0.18	2♀ 19.2, 20.2 2♂ 20.5, 20.82	2♀ 17.8, 1.90 2♂ 1.88, 2.14	2♀ 10.1, 10.5 2♂ 9.86, 10.68	(9)1.50±0.22	(11)4.21±0.18	3.79
Trogon massena	(17)21.78±0.33	(9)19.57±0.35	(9)1.92±0.09	(6)10.72±0.70	(17)1.59±0.10	(17)4.64±0.20	3.80
Trogon melanurus	(6)20.13±0.43	(3)19.1±0.67	(3)1.65±0.04	(3)8.94±0.29	(6)1.37±0.06	(6)4.30±0.15	3.91
Trogon strigilatus	(1)24.82	(1)22.6	(1)2.22	(1)9.44	(1)2.26	(1)5.76	3.79
**Trogon collaris*	(28)23.37±0.21	(14)20.82±0.31	(14)2.40±0.06	(8)8.87±0.37	(21)1.80±0.07	(22)5.52±0.12	3.69
Trogon aurantiiventris	21.8	...	...	...	1.94	5.94	3.71
Trogon curucui	(6)22.27±0.38	(4)20.09±0.49	(4)2.12±0.17	(4)9.05±0.58	(6)1.99±0.13	(6)6.10±0.42	3.68
Trogon caligatus	(19)22.90±0.42	(9)19.54±0.58	(9)2.23±0.10	(8)8.78±0.29	(12)1.74±0.11	(13)5.71±0.14	3.68

(continued)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
ALCEDINIDAE						
Megaceryle torquata	5♀ 335±7.4 4♂ 317±5.9	(9)1.02±0.06	(4)26.27±1.02	(5)3.07±0.20	(7)1.97±0.06	(8)2.33±0.04
Megaceryle alcyon	13♀ 148±2.8 11♂ 147±3.4	(12)1.38±0.03	...	(1)2.48	(1)2.49	2.50
**Chloroceryle amazona*	6♀ 131.8±4.48 11♂ 120.9±2.4	(10)1.06±0.03	(5)25.90±1.02	(5)2.99±0.17	(8)2.59±0.06	(8)2.16±0.03
Chloroceryle americana	6♀ 39.81±2.03 14♂ 36.54±0.6	(12)1.23±0.04	(5)24.12±0.78	(6)2.84±0.11	(11)3.36±0.17	(11)2.19±0.06
Chloroceryle aenea	1♀ 15.1 4♂ 15.59±0.49	(5)1.35±0.06	(3)23.27±0.64	(3)2.66±0.32	(3)3.81±0.36	(3)1.94±0.07
MOMOTIDAE						
Momotus momota lessoni	5♀ 130.3±4.0 10♂ 135.0±4.2	(11)0.49±0.02	(5)31.02±0.73	(5)6.23±0.24	(11)2.94±0.07 $P<0.01$	(11)1.70±0.03
**Momotus momota conexus* (Chagres)	5♀ 102±1.5 11♂ 112±2.0	(10)0.39±0.01	(5)28.69±1.08	(6)6.44±0.30	(10)3.36±0.08	(10)1.74±0.02
BUCCONIDAE						
**Notharchus macrorhynchos*	5♀ 97.0±5.2 12♂ 95.4±2.0	(11)0.45±0.02	(6)28.56±0.66	(6)4.70±0.21	(3)2.68±0.22	(4)2.03±0.35
Malacoptila panamensis	4♀ 43.9±1.30 6♂ 44.1±0.55	(6)0.58±0.02	(4)27.90±0.59	(4)4.21±0.08	(6)3.28±0.04	(5)1.81±0.12

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
ALCEDINIDAE							
Megaceryle torquata	(9)15.41±0.57	(3)14.9±0.41	(4)1.25±0.05	(4)9.43±0.32	(7)0.30±0.01	(7)2.46±0.05	3.68
Megaceryle alcyon	(1)17.40	...	...	...	0.48	3.16	3.63
**Chloroceryle amazona*	(9)16.48±0.43	(5)15.78±0.49	(5)1.56±0.08	(5)8.56±0.72	(8)0.49±0.04	(8)3.38±0.10	3.60
Chloroceryle americana	(11)16.56±0.45	(5)15.42±0.63	(5)1.54±0.11	(5)7.16±0.29	(11)0.72±0.07	(11)4.80±0.33	3.35
Chloroceryle aenea	(4)16.98±0.19	(3)15.22±0.31	(3)1.85±0.10	(3)6.53±0.15	(3)0.69±0.09	(3)5.15±0.26	3.09
MOMOTIDAE							
Momotus momota lessoni	(11)20.48±0.32	(7)19.29±0.32	(7)1.63±0.09	(5)10.07±0.39	(10)1.03±0.03	(10)4.30±0.13	3.85
**Momotus momota conexus* (Chagres)	(9)19.05±0.55	(5)17.73±0.97	(5)1.67±0.07	(5)9.30±0.11	(10)1.19±0.06	(10)4.76±0.11	3.99
BUCCONIDAE							
**Notharchus macrorhynchos*	(10)18.72±0.49	(6)18.02±0.43	(6)1.38±0.07	(6)9.17±0.23	(4)0.45±0.11	(3)3.39±0.29	3.53
Malacoptila panamensis	(6)18.09±0.46	(6)16.9±0.33	(6)1.21±0.04	(4)9.48±0.16	(6)0.84±0.05	(6)4.58±0.11	3.40

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Nonnula frontalis	2♀ 14.5, 15.0 1♂ 15.66	(1)0.76	(1)24.03	3.91	5.11	1.63
CAPITONIDAE **Eubucco bourcierii*	8♀ 32.80±0.50 12♂ 34.00±0.60	(13)0.75±0.02	(6)19.54±0.70	(6)9.4±0.37	(13)3.03±0.14	(13)1.64±0.03
RAMPHASTIDAE **Aulacorhynchus prasinus*	16♀ 149±4.05 15♂ 160±3.49	(26)0.62±0.01	(4)22.19±1.01	(5)11.0±0.23	(15)1.88±0.05	(15)1.69±0.28
Pteroglossus torquatus (sea level)	8♀ 216±9.0 10♂ 236±7	(18)0.68±0.02 $P < 0.01$	(5)21.87±1.07	(6)9.93±0.39	(15)1.91±0.08	(14)1.71±0.02
Pteroglossus frantzii	16♀ 263±4 10♂ 266±5	(14)0.77±0.01	(6)23.29±0.36	(6)10.92±0.29	(11)1.76±0.03	(11)1.69±0.03
Ramphastos swainsonii	6♀ 563±20 2♂ 397, 432	(7)0.79±0.05	(6)23.55±0.77	(6)12.98±0.64	(7)1.80±0.05	(6)1.64±0.03
PICIDAE *Picumnus olivaceus*	5♀ 10.57±0.20 8♂ 10.63±0.18	(9)1.24±0.04	(6)22.36±0.37	(8)8.41±0.33	(9)5.24±0.15	(9)1.62±0.04
Colaptes auratus luteus (Ohio)	9♀ 136±2.32 16♂ 135±2.99	(4)1.19±0.10		6.2, 7.69	2.15, 2.91	1.78, 1.85

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Nonnula frontalis	16.75	15.6	1.15	7.28	1.34	7.09	3.56
CAPITONIDAE **Eubucco bourcierii*	(13)13.07±0.26	(7)11.8±0.50	(7)1.10±0.03	(6)6.52±0.36	(12)0.49±0.03	(13)3.90±0.18	3.04
RAMPHASTIDAE **Aulacorhynchus prasinus*	(16)14.39±0.29	(4)13.1±0.59	(4)1.25±0.09	(4)7.81±0.46	(16)0.38±0.02	(15)2.49±0.06	3.19
Pteroglossus torquatus (sea level)	(15)13.73±0.30 $P < 0.01$	(5)13.06±0.50	(5)1.14±0.05	(5)7.88±0.52	(15)0.42±0.02	(15)2.56±0.07	3.43
Pteroglossus frantzii	(11)14.75±0.16	(6)13.70±0.14	(6)1.16±0.06	(6)8.43±0.30	(11)0.46±0.03	(11)2.40±0.06	3.34
Ramphastos swainsonii	(7)14.19±0.48	(6)13.12±0.50	(6)1.27±0.06	(6)9.16±0.45	(7)0.42±0.04	(7)2.42±0.08	3.77
PICIDAE *Picumnus olivaceus*	(9)15.91±0.66	(6)14.3±0.55	(6)1.35±0.07	(6)6.75±0.58	(9)0.58±0.03	(9)6.37±0.13	3.39
Colaptes auratus luteus (Ohio)	25.72, 28.90	16.9, 18.7	1.09, 1.44	7.73, 8.76	0.53, 0.68	3.00, 3.99	3.67

(*continued*)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Colaptes auratus (Florida)	8♀ 102.8±3.41 5♂ 114±3.08	(10)1.14±0.03	(3)29.62±0.35	(3)7.47±0.15	(8)3.15±0.13	(8)1.87±0.03
Piculus rubiginosus	6♀ 72.42±2.14 7♂ 79.60±1.9	(10)1.32±0.04	(5)26.85±0.87	(6)7.83±0.18	(9)3.18±0.10	(8)1.86±0.04
Dryocopus lineatus	6♀ 175±5 8♂ 185±4	(11)1.06±0.03	(8)27.79±0.58	(8)8.37±0.17	(9)3.04±0.07	(7)1.84±0.02
Melanerpes formicivorus	11♀ 76.1±1.68 13♂ 78.6±1.7	(20)1.12±0.03	(5)24.97±1.30	(6)6.36±0.12	(16)3.70±0.13	(16)2.07±0.08
Melanerpes erythrocephalus	6♀ 65.8±3.98 1♂ 66	(5)1.17±0.11	(1)26.32	(1)6.04	(4)3.84±0.25	(4)1.98±0.06
Centurus carolinus	9♀ 56.24±2.22 22♂ 67.22±1.25	(20)1.18±0.03	(7)28.27±0.31	(8)6.29±0.24	(20)4.05±0.12	(20)1.86±0.02
Centurus rubricapillus	12♀ 49.0±1.11 $P<0.01$ 19♂ 55.9±0.97	(12)1.23±0.03,	(6)27.3±0.90	(7)6.02±0.15	(10)3.74±0.14	(10)1.89±0.04
Centurus pucherani	2♀ 49.87, 51.6 1♂ 58.37±1.82	(8)1.23±0.04	(8)25.85±0.54	(8)7.06±0.16	(8)3.58±0.14	(8)1.99±0.04
Centurus chrysauchen	5♀ 47.0±0.51 $P<0.01$ 4♂ 58.6±2.60	(11)1.24±0.02	24.25	5.45, 6.92	(8)4.08±0.17	(7)1.88±0.05
Sphyrapicus varius	7♀ 46.12±1.80 18♂ 47.2±0.93	(7)1.41±0.05	23.90, 34.22	5.18, 8.45	(4)4.74±0.25	(4)1.97±0.12

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Colaptes auratus (Florida)	(5)20.01±0.27	(3)19.22±0.02	(3)1.24±0.09	(3)9.16±0.43	(8)0.59±0.05	(8)4.12±0.18	4.25
Piculus rubiginosus	(10)18.51±0.38	(8)17.25±0.44	(8)1.31±0.06	(5)8.67±0.14	(10)0.46±0.03	(9)4.02±0.09	3.67
Dryocopus lineatus	(10)17.98±0.29	(8)16.41±0.28	(8)1.33±0.03	(8)9.55±0.36	(9)0.36±0.02	(9)3.71±0.08	4.22
Melanerpes formicivorus	(17)18.41±0.33	(6)17.03±0.29	(6)1.14±0.07	(5)8.77±0.44	(15)0.53±0.02	(16)4.68±0.13	3.92
Melanerpes erythrocephalus	(4)16.2±0.88	(1)16.9	0.99	8.43	(4)0.55±0.09	(4)4.72±0.33	3.80
Centurus carolinus	(16)17.80±0.55	(8)18.7±0.25	(7)0.98±0.06	(8)8.32±0.16	(19)0.63±0.04	(20)5.11±0.19	3.91
Centurus rubricapillus	(9)19.09±0.45	(7)18.04±0.51	(7)1.13±0.08	(6)8.21±0.29	(10)0.39±0.03	(10)4.50±0.19	3.76
Centurus pucherani	(8)17.90±0.52	(8)16.81±0.49	(8)1.09±0.05	(8)7.95±0.17	(8)0.40±0.04	(8)4.56±0.22	3.69
Centurus chrysauchen	(8)18.77±0.47	16.2	1.03	7.02	(7)0.45±0.03	(7)4.78±0.17	3.91
Sphyrapicus varius	(3)22.74±1.1	(3)21.34±1.02	(3)1.31±0.14	6.76, 10.70	(4)0.76±0.01	(4)6.01±0.27	4.02

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.² per gram*	Aspect ratio
Veniliornis fumigatus	4♀ 31.79±1.85 3♂ 30.28±0.81	(8)1.35±0.05	(2)25.36, 26.49	(4)6.79±0.19	(8)4.48±0.13	(7)1.60±0.05
Dendrocopos villosus	6♀ 42.30±3.16 3♂ 44.84±1.64	(7)1.22±0.06	(3)29.24±0.70	(4)7.71±0.47	(8)3.96±0.20	(8)1.81±0.03
**Dendrocopos pubescens*	22♀ 27.16±0.43 25♂ 26.22±0.38	(6)1.34±0.03	(9)25.08±0.54	(9)6.08±0.22	(9)5.25±0.16	(8)1.96±0.03
Dendrocopos borealis	5♀ 44.7±3.0 7♂ 42.9±2.5	(10)1.31±0.04	...	...	(2)4.18, 4.50	1.87, 1.91
Phloeoceastes guatemalensis	6♀ 233±10 11♂ 247±5	(10)0.91±0.03	(5)24.42±0.37	(6)11.51±0.62	(9)2.42±0.07	(9)1.74±0.06
Phloeoceastes melanoleucos	4♀ 225±7 2♂ 215, 248	(6)0.87±0.05	(6)23.83±0.56	(6)11.36±0.21	(6)2.61±0.10	(6)1.79±0.04
DENDROCOLAPTIDAE						
Dendrocincla fuliginosa	4♀ 41.73±1.94 1♂ 43.0	(3)1.09±0.09	(2)24.95, 27.40	(3)7.65±0.68	(3)4.81±0.39	(3)1.69±0.09
Dendrocincla homochroa	4♀ 36.8±0.32 6♂ 45.3±1.07	(6)1.53±0.06	(2)29.45, 31.86	(2)7.9, 7.45	(4)4.32±0.24	(3)1.67±0.12
**Sittasomus griseicapillus*	11♀ 12.89±0.22 P<0.01 21♂ 14.32±0.13	7♀ 1.10±0.04 P<0.01 13♂ 1.29±0.06	4♀ 23.82±0.94 6♂ 31.68±1.40	(11)6.57±0.33	(22)6.91±0.13	(20)1.72±0.03
Glyphorynchus spirurus	3♀ 12.53±0.92 7♂ 13.90±0.78	(9)1.45±0.11	2♀ 19.54, 21.11 6♂ 24.85±0.40	(8)7.56±0.21	(9)5.81±0.23	(8)1.78±0.05

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Veniliornis fumigatus	(8)17.42±0.52	(5)15.22±0.49	(5)1.38±0.05	7.89, 8.70	(8)0.65±0.03	(8)5.57±0.15	3.78
Dendrocopos villosus	(7)19.19±0.75	(4)18.37±0.49	(4)1.63±0.09	(4)8.56±0.44	(7)0.66±0.09	(8)4.96±0.21	3.80
**Dendrocopos pubescens*	(9)18.04±0.41	(9)16.69±0.36	(9)1.35±0.05	(9)7.00±0.59	(8)1.19±0.06	(9)7.03±0.20	3.97
Dendrocopos borealis	(2)15.6, 16.12	...	...	...	(2)0.79, 0.87	(2)5.50, 5.83	3.90
Phloeoceastes guatemalensis	(9)15.53±0.23	(5)14.8±0.20	(5)1.13±0.08	(5)8.49±0.36	(9)0.25±0.01	(9)2.92±0.11	3.90
Phloeoceastes melanoleucos	(6)15.32±0.41	(6)14.20±0.44	(6)1.15±0.08	(6)8.48±0.14	(6)0.27±0.02	(6)3.12±0.13	4.16
DENDROCOLAPTIDAE							
Dendrocincla fuliginosa	3♀ 20.25±3.0 1♂ 27.40	15.15, 17.34	1.54, 1.73	8.07, 8.52	(3)1.22±0.09	(3)6.36±0.46	4.09
Dendrocincla homochroa	(4)20.62±0.97	(3)19.23±1.1	(3)1.87±0.11	(3)8.68±0.34	(4)0.87±0.12	(4)5.65±0.25	3.83
**Sittasomus griseicapillus*	(8)16.90±0.38 (12)22.13±0.74	5♀ 15.54±0.51 9♂ 20.91±0.55	5♀ 1.71±0.07 9♂ 2.11±0.05	4♀ 6.52±0.59 6♂ 8.51±0.59	(20)2.06±0.08	(20)9.64±0.15	4.13
Glyphorynchus spirurus	2♀ 14.98, 16.80 7♂ 18.35±0.44	2♀ 13.7, 15.30 6♂ 16.35±0.36	2♀ 1.28, 1.50 6♂ 1.76±0.14	2♀ 4.56, 4.31 6♂ 6.73±0.15	(7)1.56±0.17	(8)7.96±0.38	3.74

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Dendrocolaptes certhia	2♂ 67.10, 69.07	(2)0.62, 0.66	(2)23.63, 26.21	8.71, 9.30	4.29	1.66, 1.70
Xiphorhynchus guttatus	10♀ 44.85±0.42 P<0.01 9♂ 48.16±0.99	(12)0.78±0.02	3♀ 24.17±0.33 ♂ 27.32	(5)8.19±0.33	(11)4.29±0.15	(11)1.68±0.02
Xiphorhynchus erythropygius	8♀ 45.57±0.56 7♂ 49.0±0.70	(11)1.00±0.04	3♀ 23.88±1.10 5♂ 31.17±2.53	(8)7.37±0.42	(9)4.46±0.11	(8)1.76±0.03
Lepidocolaptes affinis	20♀ 34.6±0.50 16♂ 35.36±0.58	(35)0.90±0.02	3♀ 25.99±1.08 3♂ 29.8±1.78	(7)8.41±0.40	(27)5.38±0.09	(30)1.73±0.02
Campylorhamphus pusillus	1♀ 45.33 1♂ 39.0	(2)0.78, 0.97	...	...	(2)3.33, 4.34	1.66, 1.62
FURNARIIDAE						
Synallaxis albescens	2♀ 13.24, 15.53 6♂ 13.50±0.21	(8)1.07±0.04	1♀ 16.30 4♂ 19.55±0.69	(6)11.08±0.50	(7)4.01±0.13	(5)1.53±0.01
Synallaxis brachyura	1♀ 16.89 5♂ 18.84±0.96	(7)1.00±0.07	(3)18.49±0.89	(4)12.77±0.77	(5)3.65±0.13	(4)1.54±0.04
Cranioleuca erythrops	6♀ 16.78±0.62 12♂ 17.04±0.26	(4) ♀ 1.05±0.02 P<0.01 7♂ 1.26±0.08	(8)19.77±0.69	(10)10.33±0.47	(17)5.01±0.09	(18)1.58±0.03
Margarornis rubiginosus	2♂ 16.1, 19.53	(2)0.97, 1.83	...	...	5.68	1.73
Premnoplex brunnescens	3♀ 15.68±0.50 5♂ 15.81±0.41	(8)1.00±0.03	20.64	(3)9.82±0.27	(6)4.56±0.13	(6)1.53±0.06

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Dendrocolaptes certhia	(2)16.30, 18.02	14.81, 16.3	1.49, 1.72	7.33, 8.19	0.97, 1.14	4.08, 5.61	4.19
Xiphorhynchus guttatus	6♀ 16.91±0.36 P<0.01 5♂ 21.18±1.01	3♀ 15.83±0.20 1♂ 17.0	3♀ 1.72±0.07 1♂ 1.81	3♀ 6.62±0.41 1♂ 8.51	(11)1.12±0.04	(11)5.73±0.06	3.92
Xiphorhynchus erythropygius	4♀ 17.13±0.74 5♂ 23.59±1.81	(9)18.95±1.47	4♀ 1.60±0.05 5♂ 1.89±0.05	3♀ 7.32±0.53 5♂ 9.58±0.59	(9)1.24±0.06	(9)6.39±0.28	3.88
Lepidocolaptes affinis	14♀ 17.33±0.28 P<0.01 13♂ 18.86±0.35	5♀ 17.0±0.65 4♂ 18.22±0.93	5♀ 1.58±0.05 4♂ 1.70±0.15	3♀ 7.82±0.57 3♂ 9.08±0.62	(26)1.58±0.06	(30)7.46±0.13	4.20
Campylorhamphus pusillus	16.63, 17.43	15.2, 16.0	1.43, 1.43	...	1.03, 1.46	4.77, 6.28	3.65
FURNARIIDAE							
Synallaxis albescens	2♀ 11.82, 14.40 5♂ 13.78±0.35	1♀ 10.4 5♂ 12.18±0.32	1♀ 1.42 6♂ 1.57±0.08	2♀ 4.48, 4.61 4♂ 5.83±0.24	(6)1.62±0.11	(5)6.51±0.20	2.98
Synallaxis brachyura	(6)12.98±0.54	(4)11.06±0.44	(4)1.54±0.08	(3)6.15±0.28	(5)1.43±0.08	(5)5.51±0.17	3.33
Cranioleuca erythrops	(18)13.75±0.30	(12)12.91±0.45	(12)1.20±0.03	(8)6.18±0.21	(18)1.61±0.08	(18)7.18±0.13	3.59
Margarornis rubiginosus	18.3	...	...	...	1.68	7.38	3.92
Premnoplex brunnescens	(6)14.14±0.29	(4)12.46±0.41	(4)1.52±0.11	5.74	(5)1.36±0.14	(6)6.22±0.19	3.37

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Pseudocolaptes lawrencii	3♀ 50.94±0.19 2♂ 52.55, 55.0	(5)1.16±0.22	...	12.7	(3)3.55±0.18	(3)1.73±0.06
Syndactyla subalaris	2♀ 33.41, 32.50 3♂ 34.60±0.37	(5)1.17±0.06	(2)27.12, 28.10	(3)10.48±0.21	(5)4.33±0.08	(6)1.59±0.05
**Anabacerthia striaticollis*	5♀ 20.57±0.44 11♂ 22.62±0.25	4♀ 1.19±0.04 $P<0.05$ 9♂ 1.49±0.11	(4)29.98±1.49	(8)7.99±0.19	(15)5.82±0.08	(15)1.66±0.02
Automolus ochrolaemus	1♀ 42.10 5♂ 40.05±1.00	(4)1.48±0.09	27.46	(4)8.83±0.19	(5)3.46±0.06	(5)1.53±0.03
Thripadectes rufobrunneus	2♀ 52.63, 64.8 2♂ 56.02, 51.5	(4)1.01±0.10	...	12.1	(4)3.02±0.13	(4)1.48±0.05
Xenops rutilans	5♀ 11.95±0.28 7♂ 12.40±0.19	(10)1.35±0.05	(1)20.57	5.95, 8.18	(11)6.11±0.11	(11)1.74±0.02
Sclerurus guatamalensis	1♀ 36.48 1♂ 37.65	(2)1.27, 1.32	(1)28.59	(1)9.98	(2)4.09, 4.50	1.57, 1.60
FORMICARIIDAE **Cymbilaimus lineatus*	2♀ 38.65, 40.53 6♂ 32.92±1.19	(6)0.55±0.02	(5)17.46±0.51	(5)10.98±0.55	(6)2.94±0.19	(6)1.45±0.05
Taraba major	5♀ 68.0±2.26 5♂ 67.15±0.74	(10)0.61±0.03	(5)17.26±0.50	(5)13.42±0.89	(5)2.60±0.10	(5)1.45±0.05
Thamnophilus doliatus	11♀ 28.10±0.31 13♂ 28.0±0.40	(12)0.70±0.03	(5)16.13±0.55	(7)10.8±0.45	(7)3.92±0.18	(7)1.48±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Pseudocolaptes lawrencii	(3)13.1±0.39	...	...	...	(3)1.07±0.07	(13)4.92±0.23	3.63
Syndactyla subalaris	(5)15.82±0.80	(5)15.11±0.91	(5)1.61±0.06	(2)7.63, 8.60	(5)1.36±0.10	(6)6.24±0.14	3.74
**Anabacerthia striaticollis*	4♀ 16.49±0.66 10♂ 20.36±0.82	3♀ 14.94±1.00 6♂ 19.49±1.08	3♀ 1.53±0.07 6♂ 1.75±0.07	(4)8.42±0.66	(14)1.47±0.04	(15)7.79±0.30	4.00
Automolus ochrolaemus	(6)18.60±0.72	(3)17.8±0.60	(3)1.68±0.24	7.71	(6)0.89±0.07	(5)4.73±0.08	3.44
Thripadectes rufobrunneus	(4)13.07±0.75	(2)12.52, 9.94	1.28, 1.36	...	(4)0.84±0.11	(4)4.29±0.13	3.40
Xenops rutilans	(10)16.13±0.51	(3)13.79±0.15	(3)0.88±0.24	6.28	(10)1.45±0.07	(11)8.08±0.18	3.73
Sclerurus guatamalensis	(2)21.38, 21.29	19.20, 19.25	2.04, 2.18	(1)7.30	0.72, 0.82	5.15, 5.82	3.78
FORMICARIIDAE **Cymbilaimus lineatus*	(6)11.59±0.39	(4)10.76±0.41	(4)1.19±0.12	(5)5.76±0.24	(6)0.79±0.11	(6)4.23±0.33	3.15
Taraba major	(6)11.12±0.27	(5)10.14±0.28	(5)1.12±0.05	(5)6.00±0.31	(5)0.53±0.06	(5)3.51±0.12	3.18
Thamnophilus doliatus	(7)11.50±0.19	(5)10.55±0.16	(5)1.15±0.07	(5)4.43±0.63	(7)0.76±0.05	(7)5.19±0.25	3.44

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Thamnophilus punctatus	2♀ 21.7, 24.95 4♂ 21.11±1.41	(8)0.79±0.03	(3)19.51±1.46	(6)8.63±0.34	(7)4.20±0.15	(8)1.45±0.04
Thamnistes anabatinus	2♀ 22.87, 23.58 2♂ 19.25, 19.67	(4)0.93±0.09	. . .	. . .	(4)4.35±0.26	(4)1.55±0.06
Dysithamnus mentalis	12♀ 14.55±0.28 18♂ 14.21±0.19	9♀ 1.10±0.05 9♂ 1.23±0.05	3♀ 19.37±0.81 5♂ 20.97±0.62	(10)8.77±0.36	(17)5.19±0.08	(16)1.51±0.02
Myrmotherula surinamensis	6♀ 9.60±0.11 4♂ 9.88±0.20	(7)0.99±0.03	(3)16.86±0.15	(4)8.69±0.61	(7)6.09±0.31	(7)1.48±0.02
Myrmotherula schisticolor	8♀ 9.57±0.22 8♂ 9.56±0.16	(11)1.26±0.05	(3)23.15±1.10	(6)8.07±0.29	(11)6.37±0.19	(11)1.50±0.04
Cercomacra tyrannina	8♀ 15.94±0.27 9♂ 16.58±0.36	(10)0.92±0.04	3♀ 14.80±1.34 5♂ 17.56±0.18	(7)11.12±0.30	(10)4.82±0.11	(11)1.42±0.03
Cercomacra nigricans	4♀ 15.6±0.20 7♂ 17.61±0.41	(10)0.84±0.05	(4)15.43±0.60	(4)10.13±0.47	(5)4.40±0.24	(4)1.36±0.12
Myrmeciza longipes	4♀ 28.23±0.72 5♂ 30.37±0.53	(7)0.63±0.03	3♀ 17.89±0.69 2♂ 18.86, 19.37	(6)12.70±0.44	(6)3.14±0.13	(6)1.42±0.06
Myrmeciza exsul	1♀ 28.80	(1)0.66	(1)19.60	14.01	2.64	1.25
Formicarius analis	4♀ 60.83±0.90 3♂ 61.92±1.63	(7)0.86±0.05	(6)30.68±0.98	(3)9.30±0.27	(6)2.92±0.12	(6)1.59±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Thamnophilus punctatus	(7)14.36±0.54	(3)12.3±0.82	(3)1.42±0.04	(3)5.79±0.66	(7)0.96±0.10	(7)6.99±0.57	3.40
Thamnistes anabatinus	(4)12.29±0.60	12.1	1.47	. . .	(4)0.89±0.05	(4)5.68±0.31	3.46
Dysithamnus mentalis	7♀ 13.50±0.33 10♂ 14.64±0.40	5♀ 13.9±0.90 5♂ 13.46±0.51	5♀ 1.32±0.14 7♂ 1.54±0.07	3♀ 5.68±0.68 5♂ 5.93±0.15	(17)0.73±0.05	(17)6.44±0.10	3.53
Myrmotherula surinamensis	(7)11.77±0.21	(3)10.31±0.48	(3)1.33±0.09	(3)5.25±0.19	(7)0.58±0.04	(7)7.19±0.35	3.62
Myrmotherula schisticolor	(11)15.72±0.56	(8)14.31±0.67	(8)1.51±0.07	(4)6.25±0.44	(11)0.99±0.05	(11)7.99±0.23	3.75
Cercomacra tyrannina	5♀ 11.33±0.63 5♂ 12.36±0.20	4♀ 9.85±0.71 5♂ 10.99±0.24	4♀ 1.22±0.04 5♂ 1.16±0.10	3♀ 4.25±0.68 5♂ 5.41±0.12	(10)1.15±0.04	(11)6.52±0.10	3.48
Cercomacra nigricans	(4)10.21±0.50	(4)9.20±0.55	(4)0.97±0.07	(4)5.22±0.46	(4)0.82±0.16	(5)6.23±0.16	3.23
Myrmeciza longipes	(6)12.72±0.27	(6)11.1±0.20	(6)1.59±0.03	(6)5.93±0.26	(6)0.70±0.07	(6)4.23±0.18	3.16
Myrmeciza exsul	13.14	11.68	1.46	6.46	0.31	3.54	2.85
Formicarius analis	(7)22.86±0.53	(7)20.14±0.48	(7)2.72±0.07	(3)7.37±0.28	(7)0.35±0.03	(7)3.50±0.16	3.39

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.^{2} per gram*	Aspect ratio
Gymnopithys bicolor	6♀ 29.58±1.03 5♂ 29.57±0.38	(10)1.01±0.05	(6)29.57±0.38	(8)13.22±0.56	(9)3.56±0.12	(8)1.46±0.04
Hylophylax naevioides	1♀ 16.5 1♂ 16.5	(2)0.72, 0.85	...	(2)10.42, 13.10	4.85, 5.36	1.54, 1.56
Pipridae						
Pipra mentalis	1♀ 16.11 6♂ 14.70±0.47	(7)1.03±0.05	1♀ 26.48 4♂ 29.50±1.01	1♀ 4.84 4♂ 5.99±0.14	(5)4.30±0.30	(4)1.66±0.02
Chiroxiphia lanceolata	4♀ 20.30±1.04	(4)1.11±0.07	(3)29.27±2.68	(4)6.49±0.30	(4)5.46±0.34	(4)1.61±0.05
Corapipo leucorrhea	3♀ 13.26±0.75 $P<0.01$ 10♂ 11.05±0.18	(13)1.51±0.06	22.84, 26.20	(4)5.24±0.58	(9)5.69±0.13	(9)1.59±0.03
**Manacus vitellinus*	16♀ 17.08±0.05 $P<0.01$ 17♂ 19.29±0.05	(22)1.08±0.04	4♀ 21.22±0.55 $P<0.01$ 4♂ 26.89±0.40	4♀ 8.42±0.37 4♂ 11.91±0.73	(13)2.91±0.09	(10)1.61±0.02
Schiffornis turdinus	2♂ 34.1, 36.1	(2)1.49, 1.52	(1)29.94	7.42	4.14	1.82
Cotingidae						
Cotinga ridgwayi	6♀ 61.04±2.2 16♂ 53.55±0.90	(16)1.19±0.03	(6)33.04±0.45	(9)6.36±0.20	(13)3.18±0.07	(14)1.94±0.02
Attila spadiceus	1♀ 37.7 7♂ 43.01±1.3	(10)1.40±0.08	(6)25.77±0.93	(8)7.80±0.18	(10)3.65±0.10	(9)1.68±0.02

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Gymnopithys bicolor	(10)13.69±0.68	(8)11.93±0.70	(8)1.38±0.16	(6)6.46±0.45	(8)0.58±0.03	(8)4.56±0.16	3.35
Hylophylax naevioides	(2)12.98, 13.70	...	...	...	(2)0.65, 0.73	(2)5.88, 6.42	3.62
Pipridae							
Pipra mentalis	1♀ 19.90 6♂ 19.88±1.26	1♀ 16.94 4♂ 18.79±0.80	1♀ 2.96 4♂ 4.72±0.11	1♀ 6.58 4♂ 8.00±0.17	(5)0.62±0.03	(5)5.42±0.34	3.26
Chiroxiphia lanceolata	(3)18.41±0.71	(3)16.98±0.36	(3)1.76±0.07	7.52±0.34	4)0.56±0.02	(4)6.48±0.38	3.85
Corapipo leucorrhea	(13)19.18±0.20	16.9, 18.2	1.69, 1.91	4.25, 6.1	(9)0.79±0.03	(9)7.01±0.14	3.58
**Manacus vitellinus*	5♀ 16.42±0.40 $P<0.01$ 8♂19.27±0.31	4♀ 13.88±0.52 4♂ 15.79±0.51	4♀ 2.58±0.09 4♂ 3.82±0.26	4♀ 4.76±0.54 4♂ 7.28±0.55	(13)0.45±0.03	(13)3.81±0.10	2.76
Schiffornis turdinus	(1)21.35	19.19	2.16	8.59	0.87	5.43	3.69
Cotingidae							
Cotinga ridgwayi	(15)25.20±0.26	(7)22.60±0.43	(7)2.51±0.12	(6)8.12±0.57	(15)0.69±0.03	(14)4.17±0.11	3.50
Attila spadiceus	(10)18.59±0.34	(9)16.66±0.29	(9)1.83±0.06	(6)7.20±0.51	(10)0.93±0.04	(10)4.96±0.19	3.76

(continued)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Rhytipterna holerythra	9♀ 36.25±0.61 9♂ 37.27±0.82	(15)1.41±0.06	4♀ 27.43±0.67 4♂ 30.23±1.32	(11)6.95±0.18	(16)5.21±0.08	(15)1.68±0.02
Lipaugus unirufus	1♀ 80.34	1.06	. . .	. . .	3.43	1.89
Pachyramphus versicolor	1♂ 14.86	1.68	. . .	7.00	4.82	1.65
Pachyramphus cinnamomeus	1♀ 21 2♂ 19.5, 20.2	(3)1.20±0.22	. . .	5.65, 7.43	5.19, 5.74	1.80, 1.84
Pachyramphus polychopterus	2♀ 20.52, 20.8 3♂ 18.79±0.54	(4)1.16±0.03	(2)22.44, 21.78	(3)8.18±0.94	(3)4.53±0.46	(3)1.73±0.06
**Tityra semifasciata*	10♀ 79.53±2.14 15♂ 79.17±1.12	(18)1.24±0.03	(7)25.98±0.48	(9)9.23±0.78	(16)3.02±0.06	(16)1.89±0.08
Erator inquisitor	1♀ 40.2 3♂ 42.0±3.0	(4)1.23±0.08	(3)25.05±1.25	(3)5.79±0.18	(4)4.49±0.20	(3)2.00±0.08
Querula purpurata	4♀ 100.1±2.98 4♂ 106.76±1.28	(8)1.05±0.04	(7)25.98±0.38	(7)5.00±0.13	(8)5.33±0.18	(8)1.66±0.03
TYRRANIDAE *Sayornis nigricans*	2♀ 20.46, 16.85 3♂ 20.05±0.76	(5)1.18±0.06	(1)32.93	4.27	(5)6.69±0.50	(5)1.79±0.05
Fluvicola pica	3♀ 10.8±0.27 P<0.01 4♂ 12.20±0.24	(3)1.26±0.07	(3)22.31±0.16	(3)7.35±0.36	(3)6.21±0.56	(3)1.64±0.13

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Rhytipterna holerythra	7♀ 19.41±0.21 7♂ 21.28±0.77	6♀ 17.82±0.46 4♂ 19.84±1.10	6♀ 1.71±0.10 4♂ 1.93±0.14	4♀ 8.11±0.45 4♂ 8.47±0.42	(16)1.55±0.05	(15)7.42±0.13	3.28
Lipaugus unirufus	21.14	19.1	2.04		1.08	1.89	3.86
Pachyramphus versicolor	16.00	. . .	. . .	. . .	1.06	6.39	3.47
Pachyramphus cinnamomeus	(3)16.56±2.01	. . .	. . .	. . .	1.24, 1.27	6.90, 7.52	3.87
Pachyramphus polychopterus	(3)16.85±0.84	(2)15.6, 14.25	(1)1.57, 1.73	(1)5.27, 5.85	(3)1.10±0.24	(3)6.17±0.78	3.31
**Tityra semifasciata*	(16)18.44±0.30	(7)17.35±0.36	(7)1.55±0.04	(7)7.56±0.25	(17)0.51±0.07	(17)3.79±0.24	3.60
Erator inquisitor	(4)17.52±0.51	(4)16.23±0.51	(4)1.55±0.02	(3)7.45±0.55	(4)0.76±0.06	(4)5.69±0.22	3.95
Querula purpurata	(7)17.06±0.26	(7)15.82±0.29	(7)1.25±0.04	(8)8.98±0.29	(7)0.97±0.06	(7)6.47±0.12	4.83
TYRRANIDAE *Sayornis nigricans*	(5)22.86±0.51	(3)20.5±1.0	(3)2.10±0.13	(1)8.92	(5)1.77±0.14	(5)8.96±0.49	4.19
Fluvicola pica	(3)16.00±0.21	(3)14.3±0.21	(3)1.70±0.17	(3)6.30±0.18	(3)1.11±0.11	(3)8.21±0.67	3.75

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.² per gram*	Aspect ratio
Muscivora tyrannus	5♀ 27.08±0.59 4♂ 28.88±0.90	(7)1.48±0.10	(3)33.88±2.75	(4)3.16±0.27	(7)5.42±0.20	(7)1.94±0.07
Tyrannus tyrannus	5♀ 38.8±0.16 5♂ 37.1±1.51	(5)1.28±0.07	...	...	(8)5.22±0.25	(8)2.05±0.04
Tyrannus melancholicus	7♀ 40.73±0.85 8♂ 38.98±1.33	(9)1.11±0.04	(6)32.72±0.68	(7)3.42±0.24	(9)4.79±0.21	(9)1.85±0.03
Legatus leucophaius	1♀ 25.64 3♂ 26.19±0.54	(4)1.71±0.17	(1)30.56	(3)4.29±0.46	(3)4.49±0.12	(3)1.95±0.09
**Myiodynastes maculatus*	11♀ 47.19±0.59 12♂ 45.1±0.08	(12)1.03±0.04	(6)33.66±1.19	(7)4.49±0.21	(11)4.43±0.10	(11)1.81±0.04
Myiodynastes hemichrysus	1♂ 43.4	(1)0.92	...	...	4.69	1.78
Megarynchus pitangua	2♀ 71.83, 78.2 4♂ 70.85±2.32	(5)1.23±0.14	(4)33.14±1.53	(5)3.86±0.01	(5)3.25±0.32	(5)1.70±0.03
Myiozetetes cayanensis	8♀ 25.33, 0.77 6♂ 28.7±1.33	(8)0.88±0.03	(3)27.25±1.09	(4)4.56±0.56	(4)4.94±0.36	(4)1.66±0.07
Myiozetetes similis	4♀ 29.7±4.0 4♂ 29.60±4.18	(7)0.89±0.05	(3)31.55±2.12	(4)3.97±0.34	(7)5.51±0.20	(6)1.77±0.03
Myiozetetes granadensis	5♀ 29.44±2.35 3♂ 27.6±1.69	(5)1.02±0.03	28.19, 39.83	(3)3.63±0.18	(5)5.11±0.26	(5)1.77±0.07
Myiarchus crinitus	2♀ 31.6, 32.2 3♂ 36.3±0.91	(6)1.10±0.04	...	...	(5)5.00±0.23	1.74±0.07

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Muscivora tyrannus	3♀ 23.8±1.77 3♂ 27.52±1.13	2♀ 20.1, 24.7 2♂ 23.6, 26.6	2♀ 1.97, 2.21 2♂ 2.29, 2.47	(3)8.12±0.49	(7)2.11±0.18	(7)8.03±0.10	4.06
Tyrannus tyrannus	(5)21.6±1.2	...	...	...	(8)1.15±0.11	7.06±0.30	4.71
Tyrannus melancholicus	(8)24.43±0.58	(7)22.27±0.68	(7)2.25±0.09	(6)8.83±0.27	(7)1.34±0.05	(8)6.79±0.19	4.04
Legatus leucophaius	(4)22.09±0.41	(2)20.8, 20.5	1.86, 2.21	(1)7.85	(3)1.07±0.14	(3)6.19±0.28	3.64
**Myiodynastes maculatus*	(11)24.65±0.59	(6)22.64±0.81	(6)2.26±0.09	(6)8.76±0.41	(11)1.20±0.07	(11)6.05±0.14	3.96
Myiodynastes hemichrysus	(1)23.53	21.39	2.14	...	1.15	8.09	4.04
Megarynchus pitangua	(5)24.04±1.10	(4)22.17±1.43	(4)2.23±0.21	(4)8.73±0.30	(5)0.87±0.06	(5)4.65±0.40	3.67
Myiozetetes cayanensis	(4)22.39±2.40	(3)20.15±3.36	(3)2.23±0.26	(3)7.87±1.69	(4)1.44±0.17	(4)8.08±0.47	3.84
Myiozetetes similis	(5)23.35±1.42	(5)21.65±1.02	(5)2.36±0.12	(3)7.46±0.42	(7)1.45±0.15	(7)7.51±0.17	4.27
Myiozetetes granadensis	(4)22.08±0.88	(3)19.9±1.13	(4)2.26±0.35	8.06, 9.25	(5)1.28±0.09	(5)7.63±0.49	3.96
Myiarchus crinitus	(5)19.94±1.23				(5)1.46±0.12	7.01±0.20	4.04

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Myiarchus ferox	6♀ 30.3±0.90 6♂ 32.1±0.98	(7)0.91±0.03	(4)29.52±1.61	(5)6.42±0.47	(5)5.35±0.19	(6)1.70±0.04
Myiarchus tuberculifer	11♀ 19.28±0.39 14♂ 20.44±0.38	(16)0.85±0.03	(4)29.54±1.63	(5)5.52±0.48	(15)5.86±0.11	(14)1.63±0.02
Nuttallornis borealis	1♂ 33.3	(1)1.26	24.98	3.94	4.47	1.74
Contopus virens	2♀ 13.35, 15.50 10♂ 14.03±0.31	(3)1.35±0.13	23.70, 27.94	3.02, 3.36	6.29, 7.61	1.73, 2.11
Contopus sordidulus	5♂ 12.6±0.5	(2)1.26, 1.35	...	(1)2.6	(2)7.15, 7.86	1.86, 1.91
Contopus lugubris	3♀ 21.01±0.76 20♂ 21.60±0.20	(24)1.16±0.03	(1)35.32, 32.93	(4)4.16±0.60	(14)5.56±0.13	(14)1.75±0.03
Empidonax flaviventris	7♀ 10.34±0.16 13♂ 11.72±0.28	(15)1.00±0.02	(3)24.83±0.34	(3)4.76±0.18	(13)6.33±0.13	(13)1.82±0.02
Empidonax flavescens	5♀ 11.97±0.38 6♂ 12.33±0.22	(15)1.01±0.02	(3)26.53±3.70	(7)4.76±0.15	(11)6.12±0.21	(11)1.70±0.03
Mitrephanes phaeocercus	8♀ 8.28±0.09 8♂ 8.91±0.13	6♀ 1.40±0.04 $P<0.01$ 8♂ 1.88±0.07	♀ 26.63 2♂ 27.90, 27.95	3.5, 3.68	(12)8.11±0.19	(12)1.75±0.02
Terenotriccus erythrurus	1♀ 6.45 1♂ 8.1	(2)1.05, 1.22	...	4.32	6.86, 7.16	1.71, 1.71
Myiobius sulphureipygius	4♀ 9.88±0.61 1♂ 10.0	(5)1.08±0.04	(3)24.36±0.47	(3)6.02±0.61	(4)6.56±0.25	(4)1.58±0.08

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Myiarchus ferox	(6)20.89±0.33	(4)18.97±1.05	(4)2.44±0.25	(4)8.12±0.44	(6)1.58±0.24	(6)7.40±0.46	4.10
Myiarchus tuberculifer	5♀ 19.3±0.28 $P<0.01$ 11♂ 22.11±0.50	(4)20.1±0.84	(4)2.13±0.16	(4)7.24±0.69	(15)1.87±0.07	(15)8.26±0.13	3.99
Nuttallornis borealis	20.49	18.57	1.92	4.49	1.00	5.89	3.80
Contopus virens	17.96, 23.70	16.48, 19.32	1.48, 2.12	5.74, 6.50	2.17, 2.25	9.36, 10.6	4.09
Contopus sordidulus	20.5, 22.08	(1)20.0	2.08	...	1.96, 2.03	9.92, 11.11	4.08
Contopus lugubris	(15)21.61±0.42	(2)26.20, 25.00	(2)2.47, 2.04	(1)8.28	(14)1.59±0.08	(14)7.49±0.17	3.94
Empidonax flaviventris	(13)18.74±0.25	(5)17.4±0.10	(5)1.93±0.09	(3)5.60±0.29	(12)1.66±0.09	(13)8.56±0.04	3.79
Empidonax flavescens	5♀ 17.90±0.54 $P<0.01$ 9♂ 24.05±0.89	♀ 16.2 4♂ 21.67±1.86	♀ 2.03 4♂ 2.35±0.31	(2)7.29, 7.47	(10)1.41±0.09	(11)8.11±0.23	3.73
Mitrephanes phaeocercus	5♀ 18.44±0.40 $P<0.01$ 6♂ 20.53±0.26	♀ 16.8, 14.2 ♂ 18.2, 19.5	♀ 1.12, 1.69 ♂ 1.83, 1.97	♀ 7.72 ♂ 6.62, 7.73	(11)2.18±0.09	(12)11.00±0.26	4.04
Terenotriccus erythrurus	(2)18.9, 20.4	...	...	...	1.53, 1.72	9.46, 8.90	3.67
Myiobius sulphureipygius	(4)18.29±0.50	(4)16.1±0.81	(4)2.15±0.17	(3)6.64±0.09	(4)2.08±0.29	(4)8.48±0.08	3.76

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
Myiobius atricaudus	1♂ 10.62	1.18	25.58	6.68	6.46	1.65
Myiophobus fasciatus	♂ 9.68	1.65	25.31	4.11	6.16	...
Onychorhynchus coronatus	3♀ 15.97±0.19 1♂ 19.83	(3)1.03±0.08	(2)25.14, 25.61	5.52, 5.59	6.93, 5.93	1.53, 1.70
Platyrinchus mystaceus	4♀ 9.65±0.18 2♂ 12.5, 12.3	(5)1.19±0.08	19.89, 19.42	(3)6.29±0.23	(6)6.04±0.16	(6)1.58±0.07
Cnipodectes subbrunneus	3♀ 21.94±0.05	(3)0.71±0.02	28.19	(3)3.79±0.09	(3)5.27±0.08	(3)1.63±0.07
Craspedoprion aequinoctialis	♂ 19.2 22.61	0.74	26.45	4.78	5.26	1.53
Tolmomyias sulphurescens	2♂ 11.63, 15.0	(1)0.89	...	4.30	6.10	1.52
Rhynchocyclus brevirostris	4♀ 24.83±1.03 7♂ 23.35±0.62	(10)0.83±0.04	4♂ 30.38±1.30	(7)4.44±0.37	(9)4.96±0.23	(11)1.56±0.03
Todirostrum cinereum	9♀ 6.34±0.16 14♂ 6.49±0.13	(13)1.08±0.03	(5)15.72±0.61	(4)8.72±0.49	(8)6.69±0.16	(8)1.64±0.02
Todirostrum sylvia	1♀ 7.70 2♂ 6.81, 8.05	(3)1.12±0.06	(2)16.96, 20.15	(3)7.21±0.46	5.72, 6.52	1.44, 1.51
Oncostoma olivaceum	2♀ 6.3, 7.08 1♂ 6.82	(3)0.98±0.03	...	5.11	(3)6.91±0.10	(3)1.66±0.01

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
Myiobius atricaudus	18.05	16.00	2.05	7.53	2.05	9.32	3.78
Myiophobus fasciatus	18.78	17.00	1.78	6.53	1.98	8.76	3.63
Onychorhynchus coronatus	18.15, 17.84	16.7, 16.33	1.45, 1.51	6.99, 7.77	2.18, 1.72	9.68, 8.34	4.16
Platyrinchus mystaceus	(5)14.43±0.18	(5)13.12±0.19	(5)1.35±0.02	4.93, 5.42	(5)0.68±0.09	(6)7.22±0.18	3.63
Cnipodectes subbrunneus	(3)21.02±0.61	18.7	2.23	7.26	(3)1.53±0.06	(3)7.23±0.19	3.84
Craspedoprion aequinoctialis	21.05	18.85	2.20	5.40	1.68	7.48	3.78
Tolmomyias sulphurescens	19.60	...	...	...	2.15	8.96	3.79
Rhynchocyclus brevirostris	4♀ 20.45±0.86 6♂ 24.37±1.78	(5)22.35±1.93	(5)2.45±0.22	(4)9.63±0.95	(10)1.23±0.07	(10)6.43±0.32	3.73
Todirostrum cinereum	(8)11.64±0.18	(5)10.1±0.50	(5)1.12±0.09	(5)4.46±0.21	(8)1.00±0.13	(8)8.39±0.35	3.52
Todirostrum sylvia	(3)13.45±0.57	(2)11.4, 12.29	1.12, 1.53	4.44, 6.33	0.91	7.14, 8.44	3.49
Oncostoma olivaceum	1♀ 12.93 2♂ 14.70, 14.84	...	...	...	(3)1.20±0.03	(3)8.53±0.07	3.60

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Lophotriccus pileatus	7♀ 6.93±0.15 9♂ 8.06±0.13	(12)1.04±0.04	(7)20.84±0.44	(7)4.68±0.21	(9)5.86±0.27	(10)1.64±0.04
Capsiempis flaveola	2♀ 6.80, 7.45 3♂ 7.85±0.62	(4)1.18±0.06	(4)23.36±0.94	(4)6.95±0.60	(5)6.14±0.07	(5)1.47±0.02
Serpophaga cinerea	3♀ 7.98±0.18 1♂ 8.31	(3)1.55±0.13	...	(1)5.95	(3)5.92±0.22	(3)1.64±0.05
Elaenia flavogaster	5♀ 24.7±0.11 13♂ 22.25±0.85	(7)1.37±0.10	1♀ 23.20 3♂ 29.89±0.57	(5)6.01±0.40	(5)4.87±0.33	(5)1.59±0.05
Elaenia frantzii	5♀ 19.81±1.02 6♂ 19.83±0.35	5♀ 1.07±0.05 4♂ 1.22±0.03	2♀ 27.03, 28.61 3♂ 33.20±0.26	(7)5.45±0.11	(8)5.56±0.19	(7)1.76±0.04
Elaenia chiriquensis	2♂218.2, 19.1	(2)1.48, 1.57	(2)33.30, 33.78	4.61, 5.27	5.49, 5.73	1.78, 1.94
Myiopagis viridicata	5♀ 12.75±0.33 7♂ 14.14±0.44	(8)1.04±0.04	(5)26.05±0.36	(6)5.97±0.28	(10)6.01±0.13	(10)1.67±0.03
Camptostoma obsoletum	2♀ 6.94, 7.00 2♂ 7.31, 8.12	(3)1.42±0.08	1♀ 24.52 2♂ 28.32, 29.42	(3)5.57±0.25	(3)6.84±0.44	(3)1.78±0.06
Tyranniscus vilissimus	5♀ 8.48±0.35 4♂ 9.29±0.33	(5)1.17±0.08	...	4.3	(5)6.27±0.31	(5)1.65±0.03
Tyranniscus elatus	1♀ 7.25 1♂ 7.34	(2)1.30, 1.32	(2)23.11, 24.06	4.92, 5.40	6.13, 6.62	1.69, 1.75
Acrochordopus zeledoni	1♂ 10.28	1.39	25.40	4.67	6.43	1.80

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Lophotriccus pileatus	(10)15.93±0.41	(8)13.8±0.28	(6)1.63±0.12	(7)5.23±0.36	(8)1.20±0.09	(10)7.62±0.33	3.39
Capsiempis flaveola	(4)16.78±1.02	(4)14.36±0.63	(4)1.75±0.09	(4)6.57±0.48	(5)1.36±0.18	(5)8.30±0.21	3.48
Serpophaga cinerea	19.49±0.44	(1)16.85	(1)2.21	...	(3)1.27±0.11	(3)7.78±0.11	3.49
Elaenia flavogaster	1♀ 17.27 6♂ 21.03±1.25	1♀ 15.7 4♂ 20.41±0.45	1♀ 1.57 4♂ 2.39±0.11	1♀ 6.03 3♂ 7.26±0.10	(5)1.71±0.11	(5)7.27±0.38	3.89
Elaenia frantzii	5♀ 20.30±0.38 4♂ 24.89±0.71	3♀ 18.26±0.41 3♂ 21.89±0.23	3♀ 2.20±0.19 3♂ 2.40±0.27	2♀ 7.34, 8.16 3♂ 8.88±0.18	(9)1.59±0.08	(10)7.59±0.23	3.88
Elaenia chiriquensis	25.62, 25.82	22.90, 23.30	2.52, 2.72	7.48, 8.16	1.52, 1.74	7.46, 8.27	3.88
Myiopagis viridicata	4♀ 18.80±0.61 3♂ 22.36±1.57	(6)16.85±0.35	(6)2.03±0.12	(5)6.92±0.15	(9)1.85±0.09	(9)8.38±0.19	3.78
Camptostoma obsoletum	1♀ 16.45 2♂ 21.67, 22.72	♀ 14.6 ♂ 18.71, 19.95	♀ 1.85 ♂ 2.77, 2.96	♀ 8.07 ♂ 6.65, 6.70	(3)1.07±0.11	(3)8.74±0.60	3.67
Tyranniscus vilissimus	3♀ 15.8±0.32 1♂ 21.91	1♀ 13.4 1♂ 19.6	1♀ 2.55 1♂ 2.31	...	(4)1.35±0.20	(5)8.33±0.44	3.61
Tyranniscus elatus	18.12, 18.43	16.4, 16.5	1.72, 1.93	4.99, 5.63	1.24, 1.77	9.11, 9.13	3.75
Acrochordopus zeledoni	19.23	17.11	2.12	6.17	1.65	8.90	3.74

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
Leptopogon superciliaris	3♀ 11.41±0.35 2♂ 13.15, 13.77	(15)1.08±0.06	(3)26.67±0.80	(3)4.55±0.04	(5)6.36±0.28	(4)1.58±0.04
Mionectes olivaceus	5♀ 13.65±0.76 6♂ 13.93±0.36	(9)1.41±0.05	♀ 23.22, 25.84 ♂ 29.84, 30.65	(7)4.97±0.35	(10)5.51±0.24	(9)1.66±0.03
Pipromorpha oleaginea	2♀ 9.6, 9.8 5♂ 11.93±0.27	(5)1.19±0.07	26.71, 37.02	(3)4.20±0.24	(4)6.00±0.36	(4)1.46±0.07
HIRUNDINIDAE						
Progne chalybea	6♀ 37.20±0.54 18♂ 39.66±0.65	(14)1.40±0.04	(5)24.05±1.28	(7)2.90±0.30	(14)3.89±0.09	(14)2.59±0.04
**Stelgidopteryx ruficollis*	6♀ 13.26±0.63 9♂ 14.51±0.54	(8)1.59±0.05	(4)25.55±0.31	(6)1.80±0.11	(9)7.49±0.24	(9)2.41±0.08
Pygochelidon cyanoleuca	7♀ 9.99±0.45 4♂ 10.49±0.37	(12)1.32±0.04	(4)19.70±0.27	(6)2.84±0.30	(7)7.89±0.30	(7)2.31±0.02
Iridoprocne albilinea	1♀ 13.53 3♂ 13.60±0.49	(4)1.61±0.17	(4)21.66±1.52	(3)2.53±0.12	(3)6.60±0.53	(3)2.46±0.06
CORVIDAE						
Corvus brachyrhynchos pascuus	6♀ 438±30.6 6♂ 457.6±35.8	(8)1.06±0.03	...	...	(3)2.89±0.13	1.83, 1.88
Cyanocorax affinis	2♀ 210,221 1♂ 204	(3)0.85±0.02	(1)22.40	(2)14.4, 16.34	(3)2.65±0.10	(3)1.56±0.06

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
Leptopogon superciliaris	(5)20.12±0.39	(5)17.93±0.36	(5)2.19±0.05	(3)7.36±0.45	(5)1.73±0.14	(5)8.77±0.40	3.87
Mionectes olivaceus	5♀ 18.50±0.98 5♂ 22.19±0.62	3♀ 17.45±0.59 4♂ 20.0±0.70	3♀ 2.08±0.10 4♂ 2.32±0.14	2♀ 4.68, 6.11 2♂ 7.12, 7.30	(9)1.14±0.08	(10)7.09±0.27	3.58
Pipromorpha oleaginea	(4)24.48±2.01	18.4, 25.8	2.37, 3.14	5.94, 8.08	(4)1.11±0.09	(4)8.00±0.51	3.71
HIRUNDINIDAE							
Progne chalybea	(15)17.69±0.31	(5)16.75±0.67	(5)1.39±0.05	(5)5.91±0.65	(13)0.76±0.03	(13)5.08±0.13	3.56
**Stelgidopteryx ruficollis*	(8)20.43±1.39	(4)17.74±2.31	(4)1.62±0.25	(4)6.19±0.93	(9)1.46±0.13	(9)9.55±0.33	4.30
Pygochelidon cyanoleuca	(7)14.70±0.34	(4)13.7±0.05	(4)1.25±0.11	(4)4.75±0.26	(7)1.55±0.10	(7)10.19±0.38	4.16
Iridoprocne albilinea	(4)16.99±1.03	(4)15.69±0.88	(4)1.30±0.27	(3)5.09±0.62	(4)1.00±0.25	(3)8.72±1.01	3.98
CORVIDAE							
Corvus brachyrhynchos pascuus	(3)14.2±0.33	...	...	...	(3)0.46±0.06	(3)3.63±0.23	4.70
Cyanocorax affinis	(3)12.45±0.64	(1)12.36	1.01	9.03	(3)0.83±0.01	(3)3.70±0.12	4.02

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Cyanolyca argentigula	1♀ 190 1♂ 210	0.90, 0.92	19.54	15.05	2.52, 2.58	1.40, 1.50
Aphelocoma coerulescens	12♀ 71.6±1.01 16♂ 75.79±1.24	(13)0.94±0.03	(2)19.55, 21.02	12.8, 14.5	(13)2.89±0.08	(13)1.54±0.02
**Cyanocitta cristata bromia*	8♀ 88.7±1.75 5♂ 92.3±1.24	(7)1.02±0.04	(4)23.67±0.42	(4)10.6±0.22	(4)3.33±0.05	(4)1.57±0.04
Cyanocitta cristata cristata	10♀ 70.71±1.30 $P<0.01$ 11♂ 77.38±1.31	(21)0.99±0.02	(9)25.48±0.37	(9)11.0±0.19	(21)3.46±0.07	(21)1.53±0.02
PARIDAE						
Parus carolinensis	24♀ 9.79±0.12 $P<0.01$ 18♂ 10.52±0.17	(5)1.49±0.06	(5)23.73±0.89	(5)7.18±0.21	(6)6.59±0.11	(6)1.62±0.03
**Parus bicolor*	17♀ 20.44±0.40 $P<0.01$ 20♂ 22.13±0.30	(11)1.35±0.05	(7)27.38±0.45	(7)7.35±0.21	(11)5.21±0.17	(11)1.60±0.02
SITTIDAE						
**Sitta carolinensis*	29♀ 20.7±0.23 22♂ 21.0±0.25	(16)1.29±0.03	(5)24.08	(5)8.37±0.16	(5)5.85±0.16	(5)1.95±0.02
Sitta pusilla	5♀ 9.14±0.21 5♂ 9.60±0.25	(10)1.22±0.07	...	...	(10)6.56±0.02	1.63±0.02
CERTHIIDAE						
**Certhia familiaris*	7♀ 8.21±0.24 14♂ 8.60±0.16	(9)1.48±0.04	(6)23.17±0.45	(7)5.95±0.17	(7)8.59±0.14	(7)1.65±0.02

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Cyanolyca argentigula	12.18, 12.85	11.2, 11.9	0.95, 0.98	7.34	0.69, 0.75	3.62, 3.63	3.86
Aphelocoma coerulescens	(11)11.78±0.11	(2)11.3, 12.9	1.03, 1.22	6.9, 7.22	(13)1.16±0.08	(13)4.38±0.16	3.44
**Cyanocitta cristata bromia*	(4)16.21±0.23	(4)15.0±0.24	(4)1.21±0.06	(4)7.68±0.05	(4)1.32±0.04	(4)5.10±0.02	3.87
Cyanocitta cristata cristata	(21)15.72±0.36	(9)16.0±0.23	(9)1.27±0.04	(9)8.21	(21)1.15±0.07	(21)5.16±0.12	3.86
PARIDAE							
Parus carolinensis	(5)18.07±0.46	(5)16.62±0.42	(5)1.45±0.11	(4)6.21±0.27	(5)2.22±0.22	(6)9.42±0.39	3.79
**Parus bicolor*	(11)18.25±0.69	(7)17.94±0.31	(7)1.71±0.13	(7)7.71±0.16	(9)1.43±0.10	(11)7.33±0.23	3.80
SITTIDAE							
**Sitta carolinensis*	(5)17.66±0.24	(5)16.37±0.24	(5)1.29±0.24	(5)6.41±0.02	(5)1.10±0.06	(5)7.65±0.18	4.02
Sitta pusilla	(10)14.5±0.43	...	...	...	0.81±0.03	8.31	3.72
CERTHIIDAE							
**Certhia familiaris*	(6)17.38±0.46	(6)16.16±0.50	(6)1.38±0.08	(6)5.62±0.10	(6)2.35±0.09	(7)11.80±0.16	4.22

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
TROGLODYTIDAE						
Thryothorus ludovicianus	4♀ 19.2±1.00 11♂ 21.6±0.56	(7)1.02±0.06	(1)20.27	(1)13.2	(6)3.28±0.13	(6)1.55±0.03
Thryothorus modestus	7♀ 17.90±0.50 6♂ 19.73±0.38 P<0.01	5♀ 0.85±0.04 P<0.01 7♂ 1.19±0.10	(3)15.65±0.35	(5)11.7±0.84	(11)3.77±0.11	(11)1.55±0.06
**Thryothorus leucotis*	6♀ 18.69±0.56 9♂ 20.03±0.41	(10)0.86±0.03	(5)17.69±0.69	(6)12.62±0.34	(7)4.17±0.20	(6)1.47±0.03
Thryothorus fasciato-ventris	3♀ 23.01±1.00	(3)0.77±0.03	(2)16.97, 18.13	(3)12.10±0.77	(3)3.67±0.02	(3)1.46±0.05
Thryothorus rutilus	2♀ 13.72, 13.62 4♂ 16.64±0.06	(5)0.99±0.04	18.03, 18.32	(4)11.0±0.43	(5)4.28±0.09	(4)1.53±0.05
Troglodytes musculus	7♀ 15.65±0.65 12♂ 14.76±0.21	(15)1.18±0.04	(7)20.24±0.67	(7)12.00±0.20	(14)3.84±0.10	(13)1.55±0.03
Troglodytes ochraceus	2♀ 9.35, 10.0 1♂ 10.0	(3)1.18±0.10	(1)16.85	(3)10.07±0.36	(3)4.54±0.37	(3)1.40±0.05
Henicorhina leucosticta	5♀ 16.48±0.14 6♂ 17.89±0.66	(8)1.03±0.06	(3)20.40±1.11	(4)12.7±0.47	(8)3.98±0.16	(7)1.48±0.04
Henicorhina leucophrys	6♀ 16.36±0.36 17♂ 18.1±0.25	(15)1.08±0.03	(6)16.43±0.39	(8)12.83±0.31	(14)4.06±0.08	(14)1.49±0.03
Leucolepis phaeocephalus	5♂ 27.08±0.60	(5)0.80±0.02	(3)26.98±2.27	(4)12.17±0.54	(4)3.54±0.06	(4)1.64±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
TROGLODYTIDAE							
Thryothorus ludovicianus	(6)13.5±0.61	(1)12.6	(1)1.41	(1)6.26	(5)0.75±0.09	(6)4.57±0.18	2.99
Thryothorus modestus	4♀ 10.8±0.37 7♂ 13.07±0.68 P<0.01	(4)9.13±0.32	(4)1.04±0.08	(3)5.30±0.29	(10)0.71±0.04	(11)4.96±0.14	3.12
**Thryothorus leucotis*	(7)11.51±0.40	(5)10.70±0.48	(4)1.30±0.15	(5)5.80±0.15	(7)0.70±0.04	(7)5.42±0.12	3.39
Thryothorus fasciato-ventris	(3)12.12±0.43	10.85, 10.30	1.20, 1.25	5.42, 6.08	(3)0.56±0.07	(3)4.75±0.22	3.19
Thryothorus rutilus	(5)12.38±0.14	(3)11.3±0.07	(3)1.27±0.06	5.55, 5.83	(4)1.18±0.07	(5)5.82±0.27	3.27
Troglodytes musculus	(15)14.06±0.25	(9)12.52±0.31	(9)1.48±0.07	(7)6.13±0.26	(13)0.72±0.03	(14)5.09±0.14	3.02
Troglodytes ochraceus	(3)11.87±0.46	(1)10.60	1.11	5.14	(3)0.63±0.04	(3)5.71±0.40	3.25
Henicorhina leucosticta	(8)12.88±0.69	(5)11.42±0.70	(4)1.45±0.05	(3)5.61±0.21	(8)0.46±0.07	(8)4.89±0.28	3.21
Henicorhina leucophrys	(14)11.31±0.21	(7)10.25±0.19	(7)1.04±0.03	(4)4.78±0.19	(13)0.41±0.03	(14)4.86±0.11	3.26
Leucolepis phaeocephalus	(5)19.02±1.20	(3)17.31±2.02	(3)2.09±0.30	(3)7.54±0.33	(4)0.27±0.03	(4)4.21±0.07	3.25

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
MIMIDAE						
Dumetella carolinensis	8♀ 38.8±1.56 10♂ 38.20±1.38	(5)1.09±0.05	(2)19.35, 19.89	8.24, 8.64	(2)3.53, 4.36	1.73, 1.76
**Mimus polyglottos*	15♀ 48.4±1.19 14♂ 53.4±1.46	(10)1.12±0.03	(7)23.15±0.72	(7)9.65±0.28	(11)4.11±0.12	(11)1.67±0.03
TURDIDAE						
Turdus assimilis	10♂ 67.50±1.90	(8)1.31±0.06	(3)31.06±0.44	(5)7.29±0.41	(8)3.56±0.12	(8)1.79±0.03
Turdus grayi	6♀ 76.66±2.27 10♂ 72.69±1.17	(11)1.04±0.05	4♂ 32.89±0.99	(4)7.25±0.22	(8)3.29±0.16	(8)1.77±0.03
Turdus plebejus	5♀ 91.93±2.35 $P < 0.01$ 16♂ 81.12±2.39	(21)1.22±0.05	(3)36.53±0.99	(4)7.56±0.35	(16)3.38±0.09	(16)1.85±0.03
Myadestes melanops	3♀ 32.07±2.42 6♂ 32.08±0.63	(8)1.03±0.01	(1)25.06	4.75, 4.94	(8)4.17±0.10	(8)1.73±0.03
**Hylocichla ustulata*	2♀ 39.73, 30.19 7♂ 30.61±0.96	(6)1.14±0.06	(4)27.30±0.57	(6)5.60±1.94	(6)4.12±0.21	(6)1.87±0.07
Catharus frantzii	1♂ 31.4	(1)1.38	(1)24.07	11.78	4.20	1.48
Catharus griseiceps	5♀ 30.87±0.57 1♂ 28.53	(5)0.82±0.04	(1)20.17	(1)9.47	(3)3.27±0.30	(3)1.53±0.01

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
MIMIDAE							
Dumetella carolinensis	13.75, 14.31	12.62, 13.02	1.13, 1.31	5.56, 5.60	1.90, 2.31	5.79, 7.18	3.67
**Mimus polyglottos*	(11)15.99±0.48	(7)14.8±0.66	(7)1.41±0.05	(7)6.94±0.05	(11)1.67±0.14	(11)6.33±0.24	3.75
TURDIDAE							
Turdus assimilis	(8)22.50±0.75	(3)20.75±0.35	(3)2.06±0.06	(3)8.25±0.05	(8)0.95±0.07	(8)4.83±0.18	3.81
Turdus grayi	2♀ 18.7, 19.8 6♂ 23.36±0.51	4♂ 21.29±0.60	4♂ 2.32±0.23	(4)9.28±0.24	(8)0.81±0.08	(8)4.48±0.05	3.79
Turdus plebejus	(16)21.98±0.70	(3)23.9±0.50	(3)2.25±0.06	(3)10.01±0.11	(15)0.84±0.04	(16)4.52±0.15	3.85
Myadestes melanops	(7)18.65±0.53	(3)17.3±0.46	(3)1.74±0.10	6.72	(8)1.30±0.09	(8)5.55±0.40	3.62
**Hylocichla ustulata*	(5)19.58±0.61	4♂ 18.57±0.36 1♀ 13.20	4♂ 1.73±0.04 ♀ 1.40	4♂ 7.03±0.27 ♀ 4.98	(6)1.24±0.05	(6)5.95±0.23	3.61
Catharus frantzii	16.88	15.29	1.59	7.19	1.15	5.65	3.64
Catharus griseiceps	(4)14.23±0.56	(3)12.87±0.58	(3)1.54±0.22	6.40	(3)0.76±0.10	(3)4.47±0.27	3.20

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *$cm.^2$ per gram*	Aspect ratio
Sialia sialis	15♀ 32.6±0.78 18♂ 30.8±0.48	(7)1.17±0.06	...	...	(9)4.41±0.23	1.95±0.07
Sylviidae *Polioptila plumbea	2♀ 6.07, 6.56 2♂ 6.80, 5.90	(4)1.19±0.15	(3)19.66±0.12	(4)6.55±0.52	(4)7.14±0.18	(4)1.64±0.04
Ramphocaenus rufiventris	2♂ 9.37, 10.08	(1)1.58, 1.10	(1)16.77	(1)9.72	(2)5.76, 4.15	1.38, 1.44
Motacillidae *Anthus parvus	5♀ 12.35±0.47 9♂ 12.67±0.18	(14)1.57±0.03	(3)27.99±0.89	(3)5.99±0.44	(14)5.62±0.09	(14)1.77±0.02
Bombycillidae *Bombycilla cedrorum	13♀ 33.9±0.68 28♂ 31.9±0.74	(18)1.54±0.03	(4)28.81±1.34	(4)3.98±0.43	(3)3.40±0.24	(3)2.13±0.08
Ptilogonatidae *Ptilogonys caudatus	1♀ 33.5 4♂ 39.1±0.96	(5)1.33±0.04	...	4.93	(2)4.43, 4.13	1.63, 1.65
Laniidae *Lanius ludovicianus	9♀ 48.1±0.05 11♂ 47.4±0.03	(12)1.19±0.003	...	...	(6)3.36±0.03	1.77±0.01

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *$cm.^2$ per gram*	Glide *$cm.^2$ per gram*	Buoyancy index
Sialia sialis	(7)16.8±0.63	...	...	...	(9)0.67±0.02	5.54±0.27	3.73
Sylviidae *Polioptila plumbea	(4)13.95±0.68	(3)12.87±0.76	(3)1.03±0.01	(3)5.76±0.54	(4)1.60±0.20	(4)9.42±0.44	3.53
Ramphocaenus rufiventris	10.95	(2)9.93, 11.6	(2)0.94, 1.02	(1)5.62	1.07, 0.75	7.36, 5.40	3.25
Motacillidae *Anthus parvus	(14)21.54±0.20	(3)19.9±0.57	(3)1.27±0.38	(3)6.85±0.47	(13)0.83±0.05	(14)7.05±0.10	3.66
Bombycillidae *Bombycilla cedrorum	(4)22.64±1.29	(4)20.8±1.19	(4)1.84±0.13	(4)6.17±0.15	(3)0.75±0.07	(3)4.57±0.32	3.29
Ptilogonatidae *Ptilogonys caudatus	(2)19.3, 18.5	...	...	...	1.81, 1.07	5.86, 6.41	3.80
Laniidae *Lanius ludovicianus	(6)14.4±0.11	...	...	...	0.88±0.006	4.84±0.03	3.50

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
STURNIDAE						
**Sturnus vulgaris*	6♀ 76.5±2.72 5♂ 89.0±6.25	(8)1.29±0.05	(3)27.55±1.05	(5)7.76±0.24	(5)2.30±0.19	(5)2.19±0.07
CYCLARHIDAE						
**Cyclarhis gujanensis*	5♀ 31.89±0.91 4♂ 30.22±0.78	(6)0.97±0.06	(3)20.42±0.75	(3)9.99±0.34	(4)3.45±0.23	(3)1.62±0.01
VIREONIDAE						
Vireo carmioli	1♀ 13.4 3♂ 12.99±0.36	(4)1.02±0.03	. . .	7.1	6.40	1.71
**Vireo flavifrons*	4♀ 18.85±0.45 5♂ 16.9±0.23	(5)1.13±0.06	(4)22.65±0.42	(4)6.55±0.14	(5)4.49±0.33	(5)1.97±0.04
Vireo olivaceus	19♀ 16.45±0.42 21♂ 17.7±0.28	(18)1.43±0.04	(3)24.44±0.80	(3)5.89±0.38	(3)5.65±0.25	(3)1.89±0.04
Vireo philadelphicus	5♀ 11.6±0.25 8♂ 10.9±0.21	(9)1.32±0.04	25.50	(3)6.61±0.64	(10)6.23±0.12	(10)1.79±0.03
Vireo leucophrys	3♀ 9.33±0.83 3♂ 9.39±0.08	(2)1.16, 1.22	. . .	(2)6.53, 6.70	(2)6.16, 4.96	1.76, 1.58
Hylophilus aurantiifrons	3♀ 9.33±0.81 3♂ 9.40±0.08	(7)1.06±0.05	(4)20.94±0.87	(6)7.63±0.10	(7)5.99±0.13	(7)1.61±0.27
Hylophilus viridiflavus	1♀ 12.3 5♂ 12.05±0.71	1♀ 1.06 4♂ 1.35±0.10	(3)20.29±0.43	(4)8.61±0.14	(5)5.55±0.37	(4)1.48±0.05

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
STURNIDAE							
**Sturnus vulgaris*	(5)20.12±0.46	(5)18.3±0.42	(5)1.80±0.08	(3)7.06±0.43	(5)0.37±0.06	(5)3.02±0.22	3.17
CYCLARHIDAE							
**Cyclarhis gujanensis*	(5)14.25±0.39	(5)13.11±0.39	(5)1.14±0.04	(3)6.24±0.03	(4)0.68±0.03	(4)4.85±0.10	3.41
VIREONIDAE							
Vireo carmioli	13.90	. . .	. . .	. . .	0.88	7.76	3.88
**Vireo flavifrons*	(5)17.60±0.58	(4)15.6±0.29	(4)1.50±0.15	(4)5.50±0.12	(5)0.96±0.14	(5)5.94±0.37	3.44
Vireo olivaceus	(3)18.55±1.36	(3)16.94±1.32	(3)1.59±0.07	(3)5.91±0.45	(3)1.08±0.15	(3)7.35±0.32	3.88
Vireo philadelphicus	8♀ 17.41±0.57 $P < 0.01$ 3♂ 13.90±0.14	♀ 12.7 ♂ 17.2	(1) ♀ 1.41 (1) ♂ 1.8	6.42	(12)1.19±0.05	(11)8.14±0.17	3.74
Vireo leucophrys	(2)14.15, 15.3	(1)12.84	1.31	6.61	1.53, 1.29	8.19, 6.85	3.41
Hylophilus aurantiifrons	(7)13.13±0.54	(4)12.65±0.55	(4)1.36±0.04	(4)6.93±0.54	(5)1.30±0.07	(7)7.78±0.24	3.57
Hylophilus viridiflavus	(5)13.92±0.59	(3)12.63±0.32	(3)1.31±0.17	(3)6.36±0.30	(3)1.14±0.10	(4)7.37±0.47	3.56

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Hylophilus decurtatus	3♀ 9.43±0.49 4♂ 9.94±0.31	(4)1.12±0.05	(5)20.72±1.25	(5)8.32±0.10	(5)5.90±0.25	(5)1.48±0.02
Hylophilus ochraceiceps	1♀ 16.78	1.34	...	...	3.73	1.42
COEREBIDAE						
**Chlorophanes spiza*	4♀ 18.71±0.89 4♂ 17.78±0.50	(5)1.28±0.06	(3)26.47±1.51	(5)8.07±0.48	(6)4.31±0.13	(6)1.68±0.04
Cyanerpes cyaneus	10♀ 13.20±0.29 15♂ 12.49±0.22	(17)1.44±0.03	(8)28.35±0.87	(10)5.98±0.21	(19)4.72±0.07	(19)1.82±0.02
Cyanerpes lucidus	2♀ 11.68, 11.76 4♂ 11.31±0.43	(6)1.32±0.05	(5)22.47±0.33	(6)7.01±0.31	(4)4.52±0.18	(3)1.76±0.01
Dacnis venusta	6♀ 16.04±0.41 37♂ 16.12±0.19	(37)1.35±0.02	(5)31.60±2.02	(8)6.26±0.44	(38)4.67±0.05	(39)1.83±0.02
PARULIDAE						
Mniotilta varia	18♀ 10.6±0.14 19♂ 10.3±0.14	(18)1.13±0.04	(5)23.04±0.80	(6)7.12±0.21	(9)7.09±0.29	(9)1.83±0.04
Protonatria citrea	4♀ 13.16±0.43 5♂ 14.09±0.30	(7)0.99±0.05	(4)22.13±0.82	(6)6.29±0.29	(8)5.73±0.16	(8)1.89±0.03
Helmitheros vermivorus	1♀ 12.90 2♂ 13.60, 13.47	(2)1.00, 1.03	...	8.70	5.86	1.78

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Hylophilus decurtatus	(4)13.92±0.62	(4)12.75±0.53	(5)1.21±0.10	(5)6.14±0.52	(5)0.99±0.08	(5)7.59±0.22	3.42
Hylophilus ochraceiceps	13.6	...	...	...	0.54	4.66	3.09
COEREBIDAE							
**Chlorophanes spiza*	(6)18.75±0.58	(3)16.58±0.60	(4)1.78±0.09	(3)7.05±0.70	(6)0.84±0.06	(6)5.63±0.16	3.36
Cyanerpes cyaneus	(11)20.62±0.65	(10)18.90±0.69	(10)1.85±0.16	(8)7.09±0.42	(19)0.87±0.03	(19)6.09±0.09	3.32
Cyanerpes lucidus	(6)17.49±0.46	(6)15.54±0.31	(6)1.78±0.17	(5)5.29±0.13	(4)0.53±0.06	(4)5.61±0.22	3.37
Dacnis venusta	(38)22.09±0.42	4♂ 22.3±0.13	3♂ 2.07±0.12	(5)8.39±0.54	(38)0.94±0.03	(39)6.11±0.06	3.39
PARULIDAE							
Mniotilta varia	(9)17.7±0.37	(5)15.8±0.52	(5)1.54±0.03	(5)5.71±0.29	(9)1.72±0.14	(9)9.52±0.41	3.91
Protonatria citrea	(8)16.44±0.34	(4)15.1±0.29	(4)1.52±0.14	(4)5.48±0.52	(8)1.12±0.08	(8)7.48±0.25	3.72
Helmitheros vermivorus	(1)20.68	18.9	1.78	...	1.11	7.65	3.73

(*continued*)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Vermivora chrysoptera	1♀ 8.4 3♂ 8.92±0.30	(4)1.30±0.18	(2)24.41, 26.18	(3)7.00±0.32	(5)6.95±0.10	(6)1.74±0.02
Vermivora pinus	(1)8.92	1.05	...	...	7.12	1.79
Vermivora peregrina	7♀ 9.42±0.38 17♂ 9.40±0.06	(24)1.26±0.03	(3)21.88±0.77	(5)6.56±0.33	(23)6.86±1.20	(21)1.85±0.02
Vermivora gutturalis	4♀ 9.2±0.24 3♂ 9.9±0.28	(9)1.22±0.07	...	7.55	(6)6.85±0.20	(6)1.70±0.03
Parula pitiayumi	6♀ 6.61±0.15 $P<0.01$ 10♂ 7.22±0.12	(16)1.34±0.04	(5)20.17±0.80	(6)7.05±0.32	(12)6.90±0.12	(15)1.69±0.03
Dendroica petechia	16♀ 9.6±0.40 17♂ 10.25±0.30	(8)1.40±0.11	(1)20.91	(2)6.18, 6.97	6.25	1.85
Dendroica virens	22♀ 8.64±0.12 26♂ 9.29±0.11	(15)1.26±0.04	(4)22.49±0.57	(6)6.35±0.37	(12)7.21±0.15	(9)1.84±0.02
Dendroica fusca	18♀ 9.5±0.14 12♂ 10.0±0.58	(18)1.14±0.03	(1)20.84	(2)5.3, 7.02	(9)6.51±0.41	1.98±0.02
Dendroica pensylvanica	17♀ 9.41±0.18 25♂ 9.49±0.14	(20)1.13±0.03	(3)20.21±0.94	(4)7.00±0.26	(10)7.03±0.23	(10)1.85±0.02
Dendroica pinus	3♀ 12.5±0.97 3♂ 12.0±0	(5)1.16±0.06	...	...	(5)5.93±0.38	1.76±0.06
Dendroica discolor	6♀ 11.5±0.43 3♂ 11.8±0.21	(11)1.17±0.04	...	...	(11)6.60±0.13	1.75±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Vermivora chrysoptera	(6)15.69±0.58	(3)15.35±1.31	(3)1.91±0.26	(1)6.56	(6)1.84±0.11	(5)9.46±0.25	4.05
Vermivora pinus	17.05	...	...	...	1.68	9.36	3.86
Vermivora peregrina	(16)17.05±0.25	(3)15.05±0.33	(3)1.63±0.15	(3)5.19±0.45	(23)1.42±0.05	(21)8.92±0.13	3.79
Vermivora gutturalis	(6)14.8±1.0	...	...	...	1.16±0.02	8.18±0.31	3.83
Parula pitiayumi	(16)14.99±0.31	(8)13.21±0.33	(8)1.37±0.09	(5)5.32±0.30	(12)1.44±0.07	(15)9.15±0.15	3.62
Dendroica petechia	(2)14.73, 15.0	(1)13.39	(1)1.34	(1)6.18	0.94	8.13	3.68
Dendroica virens	(11)16.35±0.35	(6)14.90±0.36	(5)1.45±0.02	(5)6.26±0.33	(8)1.68±0.06	(12)9.86±0.19	3.90
Dendroica fusca	(10)15.7±0.20	(1)14.40	(1)1.42	5.02	(9)1.77±0.01	8.69±0.51	3.74
Dendroica pensylvanica	(10)15.21±0.44	(3)13.61±0.71	(3)1.51±0.17	(3)5.09±0.16	(9)1.92±0.13	(10)9.73±0.30	3.66
Dendroica pinus	(5)14.9±0.81	...	...	...	1.23±0.12	8.02±0.09	3.71
Dendroica							

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
**Seiurus aurocapillus*	9♀ 18.86±0.49 12♂ 19.38±0.50	(15)1.17±0.03	(5)25.43±0.83	(5)6.10±0.12	(5)5.08±0.18	(5)1.84±0.48
Seiurus noveboracensis	6♀ 18.8±1.12 7♂ 16.4±0.98	(5)1.03±0.07	(3)25.84±1.21	(4)6.89±0.34	(5)6.86±0.17	(5)1.79±0.05
Seiurus motacilla	2♀ 18.1, 20.02	(2)1.20, 1.27	(1)29.59	(2)6.63, 6.40	(2)5.05, 5.13	1.83
Oporornis formosus	2♀ 13.92, 14.61 4♂ 14.48±0.89	(6)1.14±0.07	(4)23.35±0.23	(4)9.07±0.77	(6)5.05±0.19	(4)1.89±0.05
Oporornis philadelphia	4♀ 11.20±0.47 8♂ 11.69±0.17	(9)0.98±0.02	(4)20.51±0.86	(5)8.82±0.44	(5)5.58±0.08	(5)1.72±0.04
Geothlypis chiriquensis	1♀ 13.77 1♂ 14.70	(1)1.31	...	11.20	4.68	1.56
Icteria virens	3♀ 30.03±1.02 6♂ 24.73±0.42	(5)0.96±0.08	20.07	8.16	4.16	1.72
Wilsonia pusilla	12♀ 7.10±0.16 18♂ 7.47±0.06	(26)1.18±0.04	(5)20.21±0.75	(6)7.47±0.45	(18)7.38±0.09	(18)1.68±0.02
Setophaga ruticilla	11♀ 8.13±0.18 9♂ 7.9±0.21	(13)1.20±0.03	(3)22.14±1.29	(3)6.68±0.64	(4)7.93±0.34	(4)1.64±0.03
Myioborus miniatus	10♀ 9.41±0.43 27♂ 9.51±0.08	(32)1.39±0.03	(6)24.78±0.11	(8)7.10±0.45	(26)7.88±0.17	(25)1.54±0.05

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
**Seiurus aurocapillus*	(5)19.26±0.73	(5)17.33±0.72	(5)1.94±0.12	(5)6.16±0.20	(4)1.38±0.21	(5)7.01±0.18	3.70
Seiurus noveboracensis	(5)18.93±0.39	(3)17.48±0.93	(3)1.93±0.03	(3)6.43±0.32	(4)1.35±0.12	(5)7.83±0.31	4.16
Seiurus motacilla	(2)21.52, 23.00	19.2	2.32	8.07	(2)1.17, 1.12	6.74, 6.77	3.68
Oporornis formosus	(4)17.59±0.26	(4)15.80±0.34	(3)1.72±0.07	(4)5.77±0.13	(6)1.23±0.06	(6)6.90±0.27	3.50
Oporornis philadelphia	(5)15.68±0.60	(4)13.75±0.57	(4)1.66±0.14	(4)5.11±0.45	(4)1.13±0.03	(5)7.48±0.13	3.60
Geothlypis chiriquensis	12.30	...	...	...	1.90	6.56	3.39
Icteria virens	14.59	13.1	1.49	5.48	1.29	5.96	3.50
Wilsonia pusilla	(20)14.20±0.21	(5)13.19±0.49	(5)1.41±0.08	(6)5.55±0.21	(17)2.04±0.07	(18)10.11±0.12	3.80
Setophaga ruticilla	(4)16.26±0.52	(3)15.2±0.35	(3)1.48±0.04	(3)5.49±0.59	(4)2.65±0.45	(4)11.82±0.62	3.97
Myioborus miniatus	(29)15.78±0.38	(6)15.88±0.30	(6)1.63±0.10	(6)7.39±0.70	(26)2.45±0.09	(26)11.12±0.22	4.10

(*continued*)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Myioborus torquatus	3♀ 10.28±0.14 2♂ 10.12, 11.12	(5)1.18±0.06	(4)21.10±1.40	(4)7.84±0.31	(5)7.49±0.26	(4)1.55±0.06
Basileuterus culicivorus	7♀ 11.14±0.52 8♂ 12.14±0.63	(16)1.37±0.07	(4)20.78±1.22	(5)8.10±0.28	(15)5.84±0.09	(15)1.57±0.03
Basileuterus melanogenys	4♀ 11.78±0.12 5♂ 11.78±0.60	(5)1.07±0.05	(1)15.42	10.2, 10.38	(7)5.98±0.25	(6)1.54±0.02
Phaeothlypis fulvicauda	2♀ 14.32, 15.50 2♂ 14.15, 16.48	(5)1.12±0.04	(3)23.20±0.74	(3)9.73±0.61	(5)4.87±0.19	(4)1.55±0.05
PLOCEIDAE						
Passer domesticus	27♀ 26.15±0.56 28♂ 27.78±0.49	(22)1.39±0.03	(15)25.37±0.32	(19)6.47±0.14	(19)3.10±0.05	(20)1.88±0.08
ICTERIDAE						
Zarhynchus wagleri	7♀ 112.7±2.30 9♂ 214.0±0.41	(13)1.10±0.03	(6)24.92±0.59	(7)9.36±0.38	(12)2.93±0.13	(12)1.99±0.04
Psarocolius decumanus	1♀ 170 4♂ 314±0.88	(4)0.91±0.06	(5)23.54±0.38	(5)12.44±0.67	(5)2.44±0.14	(5)2.03±0.04
Cacicus vitellinus	10♀ 68.35±0.99 11♂ 113.1±2.49	(12)1.05±0.02	(5)21.66±0.18	(6)9.11±0.57	(9)3.57±0.11	(10)1.93±0.06
Cacicus microrhynchus	2♀ 52.7, 57.40 2♂ 56.5, 69.00	(4)1.08±0.03	(3)23.49±1.95	(3)9.91±1.37	(4)3.89±0.15	(4)1.74±0.10

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Myioborus torquatus	(5)14.75±0.73	(4)13.40±1.03	(4)1.25±0.04	(4)6.43±0.37	(4)1.96±0.15	(5)10.04±0.32	4.03
Basileuterus culicivorus	(14)14.59±0.54	(4)12.56±0.49	(4)1.29±0.11	(3)5.30±0.78	(15)1.66±0.06	(15)8.07±0.12	3.64
Basileuterus melanogenys	(4)12.7±0.60	9.45	(2)1.10, 1.38	4.87	(6)1.47±0.10	(7)8.09±0.28	3.81
Phaeothlypis fulvicauda	(4)16.29±0.42	(4)14.56±0.48	(5)1.75±0.07	(3)6.83±0.30	(5)1.22±0.10	(5)7.08±0.28	3.43
PLOCEIDAE							
Passer domesticus	(20)18.83±0.26	(20)17.1±0.24	(20)1.71±0.05	(15)6.29±0.12	(19)0.74±0.03	(19)4.45±0.08	3.05
ICTERIDAE							
Zarhynchus wagleri	(12)17.22±0.38	(6)15.69±0.30	(6)1.33±0.05	(6)7.90±0.32	(12)0.63±0.04	(12)3.75±0.16	3.77
Psarocolius decumanus	(5)15.28±0.16	(5)14.03±0.16	(5)1.25±0.04	(5)8.25±0.23	(3)0.85±0.12	(5)3.44±0.21	4.04
Cacicus vitellinus	(10)16.71±0.42	(5)14.2±0.10	(5)1.25±0.07	(5)6.18±0.49	(8)0.78±0.05	(8)4.65±0.19	4.41
Cacicus microrhynchus	(4)15.64±0.96	(4)14.80±1.00	(4)1.34±0.05	(3)6.92±0.68	(4)0.67±0.01	(4)5.00±0.23	3.83

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	cm.^{2} *per gram*	Aspect ratio
Amblycercus holosericeus	4♀ 56.4±0.73 13♂ 71.0±1.21	(9)0.91±0.02	(5)19.20±0.78	(3)15.23±0.67	(4)2.50±0.12	(4)1.31±0.07
Psomocolax oryzivorus	2♀ 132.60, 149.44 2♂ 175.30, 200	(4)1.18±0.03	(4)26.84±0.20	(4)9.32±0.24	(3)2.48±0.07	(4)1.96±0.04
Cassidix mexicanus	8♀ 100.5±3.00 20♂ 191.0±6.04	(22)0.98±0.02	1♀ 27.04 3♂ 23.61±1.05	2♀ 10.0, 11.0 3♂ 12.6±0.46	4♀ 2.91±0.14 P<0.05 5♂ 2.37±0.10	(9)1.83±0.03
Icterus spurius	1♀ 32.42 6♂ 24.06±1.22	(4)0.94±0.05	(5)21.89±0.97	(5)7.46±0.34	(5)4.01±0.40	(5)1.85±0.05
Icterus mesomelas	4♀ 50.75±1.50 5♂ 56.21±2.98	(7)0.91±0.06	(4)21.38±1.09	(4)12.16±0.13	(4)3.32±0.15	(4)1.59±0.06
Icterus galbula	4♀ 33.46±0.98 10♂ 33.82±0.48	(12)1.27±0.06	(2)25.48, 27.47	(3)8.12±0.11	(7)4.16±0.12	(7)1.84±0.34
Agelaius phoeniceus	4♀ 34.0±2.71 9♂ 50.7±0.79	(7)1.08±0.04	2♂ 26.89, 26.91	8.86, 8.94	(8)3.87±0.17	(6)1.61±0.04
Leistes militaris	4♀ 35.48±0.27 9♂ 46.16±0.83	(12)0.91±0.02	(3)28.00±0.54	(4)13.5±0.03	(12)3.86±0.10	(12)1.78±0.02
Sturnella magna (Panamá)	6♀ 72.61±2.95 8♂ 98.22±1.95	(13)0.85±0.02 P<0.01	(3)26.39±1.15	(4)14.91±0.17	(13)2.22±0.08	(13)1.83±0.08
Sturnella magna (Florida)	3♀ 73.0±5.26 8♂ 97.8±2.5	(11)1.08±0.02	...	...	(10)2.16±0.04	(10)1.68±0.03
THRAUPIDAE						
Chlorophonia callophrys	2♀ 25.2, 28.1 4♂ 25.4±1.02	(7)1.27±0.06	...	(3)7.15±0.09	(7)3.73±0.13	1.78±0.05

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail cm.^{2} *per gram*	Glide cm.^{2} *per gram*	Buoyancy index
Amblycercus holosericeus	(6)12.71±0.63	(5)11.86±0.51	(5)1.09±0.08	(3)6.52±0.42	(4)0.83±0.10	(4)3.82±0.26	3.87
Psomocolax oryzivorus	(4)18.44±0.05	(4)16.84±0.03	(4)1.60±0.03	(4)8.41±0.16	(4)0.71±0.04	(3)3.49±0.08	3.65
Cassidix mexicanus	4♀ 14.09±1.15 5♂ 15.66±0.59	1♀ 15.25 3♂ 14.8±0.66	1♀ 1.41 3♂ 1.50±0.08	2♀ 6.68, 7.37 3♂ 7.27±0.52	(9)0.79±0.09	4♀ 3.99±0.24 5♂ 3.68±0.18	3.67♀ 3.63♂
Icterus spurius	(5)15.76±0.87	(5)14.48±0.81	(5)1.28±0.14	(5)6.12±0.19	(4)0.69±0.12	(5)5.13±0.49	3.45
Icterus mesomelas	(4)14.47±0.69	(4)13.08±0.66	(4)1.38±0.10	(4)6.91±0.43	(3)1.36±0.13	(4)4.87±0.10	3.50
Icterus galbula	(7)17.95±0.37	(2)16.20, 17.40	1.96, 1.73	7.32, 8.34	(6)0.95±0.03	(7)5.59±0.11	3.65
Agelaius phoeniceus	2♀ 13.6, 15.2 6♂ 19.4±0.80	2♂ 18.0, 18.0	2♂ 1.39, 1.67	2♂ 7.22, 7.52	(7)0.85±0.19	(8)5.35±0.30	3.72
Leistes militaris	(3)20.44±0.34	(3)18.8±0.36	(3)1.83±0.09	(3)7.37±0.14	(12)0.59±0.02	(12)4.79±0.10	3.67
Sturnella magna (Panamá)	(14)19.56±0.36	(4)18.03±0.89	(4)1.82±0.10	(3)6.38±0.32	(11)0.33±0.02	(12)2.76±0.10	3.13
Sturnella magna (Florida)	(11)18.5±0.31	...	...	...	(7)0.33±0.02	2.88±0.05	3.13
THRAUPIDAE							
Chlorophonia callophrys	(6)18.3±0.54	...	...	...	(4)0.60±0.07	4.76±0.16	3.31

(*continued*)

TABLE 1.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Tanagra elegantissima	2♀ 12.7, 16.0 2♂ 17.70, 14.39	(5)1.43±0.06	(1)26.74	(3)5.61±0.42	(4)4.33±0.34	1.86±0.02
Tanagra fulvicrissa	2♀ 13.21, 19.93	1.10, 1.11	. . .	6.1	3.95, 4.76	1.69, 1.74
Tanagra minuta	1♀ 10.93 1♂ 11.28	(2)1.25, 1.38	. . .	(1)4.66	(2)4.27, 4.4	1.80, 1.92
Tanagra luteicapilla	2♀ 10.92, 14.98 1♂ 11.75	(3)1.33±0.07	(3)23.90±0.39	(3)5.19±0.31	(3)3.99±0.42	(3)1.81±0.13
Tanagra lauta	2♀ 10.53, 11.00	(2)1.29, 1.45	. . .	5.27	(2)4.11, 4.29	1.86, 2.03
Tanagra imitans	4♂ 13.28±0.24	(5)1.25±0.03	21.83	(3)6.09±0.33	(6)4.90±0.23	(5)1.69±0.03
Tangara icterocephala	17♀ 22.5±0.37 24♂ 21.49±0.24	(26)1.09±0.03	(3)28.92±0.61	(4)6.42±0.23	8♀ 4.09±0.03 9♂ 4.70±0.01 $P<0.01$	(16)1.78±0.02
Tangara inornata	1♀ 19.36 1♂ 19.97	(2)1.07, 1.21	(2)23.72, 25.97	6.82, 6.92	4.66, 4.76	1.76, 1.82
Tangara larvata	6♀ 19.79±0.20 10♂ 17.84±0.36	(11)1.16±0.04	2♀ 25.51, 28.67 4♂ 29.87±0.63	(6)6.07±0.39	(6)4.67±0.18	(7)1.73±0.05
Tangara gyrola	11♀ 22.12±0.42 8♂ 21.49±0.35	(15)0.98±0.03	(7)28.86±1.21	(8)7.49±0.30	7♀ 4.10±0.13 $P<0.05$ 5♂ 4.79±0.21	(12)1.68±0.03
Tangara guttata	6♀ 21.28±0.51 6♂ 19.58±0.12	(10)0.96±0.02	(5)25.75±1.39	(6)9.34±0.48	6♀ 3.45±0.10 $P<0.01$ 6♂ 4.27±0.11	(12)1.67±0.02

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Tanagra elegantissima	(5)19.91±0.85	(1)19.19	(1)1.85	(1)6.70	1.81±0.07	5.56±0.46	3.27
Tanagra fulvicrissa	(2)18.2, 18.11	16.5	1.61	. . .	0.36, 0.61	4.66, 5.86	2.82
Tanagra minuta	(1)17.00	. . .	. . .	. . .	0.48, 0.55	5.22, 5.48	3.10
Tanagra luteicapilla	(3)18.15±0.12	(3)16.63±0.08	(3)1.51±0.05	(3)5.75±0.35	(3)0.69±0.13	(3)5.21±0.55	2.98
Tanagra lauta	(2)15.2, 16.9	. . .	. . .	. . .	0.43, 0.58	5.15, 5.36	3.05
Tanagra imitans	(5)17.63±0.53	(3)17.26±1.66	(3)1.66±0.12	5.4	(6)0.73±0.06	(6)6.21±0.30	3.44
Tangara icterocephala	8♀ 19.7±0.39 $P<0.05$ 9♂ 20.9±0.22	(3)19.80±0.61	(3)1.85±0.09	(3)6.94±0.21	(17)0.84±0.04	(17)5.74±0.12	3.53
Tangara inornata	18.83, 19.65	16.2, 18.15	1.50, 1.63	5.89, 6.32	1.05, 1.14	6.46, 6.71	3.58
Tangara larvata	3♀ 20.15±0.94 6♂ 22.87±0.87	3♀ 17.84±1.18 4♂ 20.50±0.83	(7)1.34±0.21	(5)7.18±0.29	(5)1.01±0.07	(8)6.10±0.17	3.52
Tangara gyrola	(15)20.79±0.49	(8)17.14±0.92	(8)1.98±0.08	(7)7.80±0.48	(12)0.85±0.06	(15)5.72±0.17	3.53
Tangara guttata	(12)17.78±0.40	(5)17.19±0.56	(5)1.58±0.05	(5)7.18±0.73	(12)0.79±0.04	(12)5.15±0.20	3.23

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.^{2} per gram*	Aspect ratio
Thraupis virens	14♀ 32.90±0.53 19♂ 31.95±0.53	(23)1.33±0.03	4♂ 31.32±0.85	(7)6.90±0.20	(20)4.08±0.08	(20)1.76±0.02
Thraupis palmarum	1♀ 37.81 7♂ 39.17±1.46	(5)1.31±0.10	(3)29.04±1.45	...	(4)3.90±0.25	(4)1.61±0.13
Ramphocelus dimidiatus	2♀ 30.1, 30.6 10♂ 30.14±0.64	(6)0.83±0.07	(3)22.23±2.97	(4)7.41±0.29	(4)4.02±0.07	(4)1.64±0.04
Ramphocelus passerinii	5♀ 30.66±1.14 9♂ 33.56±0.75	(10)0.98±0.04	(3)25.95±0.57	(4)8.41±0.62	(9)3.38±0.11	(9)1.55±0.01
Ramphocelus iceteronotus	3♀ 33.98±0.18 1♂ 37.67	(2)0.70, 0.87	22.56, 25.62	8.18, 8.76	3.85, 3.89	1.68, 1.57
Piranga rubra	6♀ 28.81±0.59 11♂ 30.43±1.05	(12)1.15±0.05	(5)26.50±0.51	(6)5.63±0.22	(13)4.46±0.10	(13)1.89±0.02
Piranga olivacea	2♂ 30.68 32.10	1.11, 1.22	(1)27.57	5.67	(1)5.22	2.00
Piranga leucoptera	6♀ 16.27±0.19 13♂ 17.03±0.26	(17)1.07±0.03	4♀ 23.74±1.18 4♂ 26.05±0.62	(7)6.03±0.16	(20)5.34±0.08	(17)1.61±0.02
Piranga ludoviciana	1♂ 31.2	0.93			4.31	1.18
Piranga bidentata	1♀ 34.52 7♂ 36.47±0.56	(8)1.02±0.04	(2)26.26, 27.97	6.2, 6.5	(6)4.13±0.12	(8)1.70±0.04
Habia rubica	4♀ 37.12±0.98 7♂ 35.01±0.71	4♀ 1.05±0.04 P<0.01 7♂ 1.46±0.12	♀ 23.51, 24.81 3♂ 27.57±3.57	(5)8.81±0.15	(12)4.01±0.12	(12)1.54±0.03

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Thraupis virens	10♀ 19.67±0.34 P<0.01 10♂ 22.13±0.47	3♀ 18.60±0.60 4♂ 20.35±1.30	3♀ 1.65±0.24 4♂ 2.02±0.10	3♀ 8.05±0.22 4♂ 7.61±0.85	(20)0.88±0.04	(20)5.49±0.03	3.61
Thraupis palmarum	(4)20.83±1.06	(3)19.25±0.70	(3)1.72±0.02	(3)8.06±0.44	(4)0.90±0.11	(4)4.71±0.71	3.64
Ramphocelus dimidiatus	(5)15.90±0.81	(4)14.88±0.97	(4)1.59±0.21	(4)5.68±1.11	(3)1.34±0.01	(4)6.00±0.20	3.54
Ramphocelus passerinii	(9)18.26±0.65	(3)17.03±0.47	(3)1.91±0.12	(3)7.00±0.12	(9)1.12±0.04	(9)4.94±0.13	3.27
Ramphocelus iceteronotus	15.96, 17.42	14.27, 16.15	1.27, 1.69	6.60, 8.20	0.74, 1.24	5.04, 5.58	3.56
Piranga rubra	(7)19.05±0.22	(5)17.58±0.17	(5)1.74±0.07	(5)7.39±0.22	(11)1.14±0.04	(12)5.96±0.02	3.70
Piranga olivacea	20.09	18.25	1.84	7.50	1.14	4.46	4.06
Piranga leucoptera	6♀ 16.89±0.44 P<0.01 14♂ 18.71±0.30	3♀ 15.80±0.80 5♂ 16.83±0.57	3♀ 1.52±0.06 5♂ 1.60±0.12	3♀ 6.72±0.22 4♂ 7.44±0.23	(18)1.30±0.03	(15)7.05±0.10	3.73
Piranga ludoviciana	20.57	19.03	1.54		1.16	5.95	3.68
Piranga bidentata	(8)19.60±0.39	(3)17.05±0.75	(3)1.80±0.09	(4)6.60±0.02	(7)1.33±0.06	(8)5.82±0.15	3.69
Habia rubica	6♀ 16.81±0.62 7♂ 20.79±1.15	3♀ 16.36±1.62 5♂ 19.6±1.65	3♀ 1.61±0.16 5♂ 1.89±0.13	2♀ 6.89, 8.38 3♂ 7.33±0.86	(12)1.09±0.04	(12)5.64±0.20	3.64

(continued)

TABLE I.—*continued*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Habia fuscicauda	7♀ 38.05±0.82 11♂ 40.75±1.24	8♀ 0.74±0.04 $P<0.01$ 12♂ 0.84±0.03	3♀ 19.90±2.28 3♂ 26.00±2.08	(7)8.66±0.26	(13)4.65±0.14	(13)1.56±0.03
Tachyphonus rufus	5♀ 35.24±0.96 3♂ 35.53±1.31	(4)0.83±0.10	(3)25.56±2.04	(3)9.87±0.46	(3)3.93±0.07	(3)1.55±0.12
Tachyphonus luctuosus	3♀ 14.56±0.77 6♂ 15.55±0.91	(9)0.99±0.05	(4)21.02±1.38	(5)5.98±0.47	(7)5.36±0.19	(7)1.64±0.02
Eucometis penicillata	1♂ 30.86	(1)0.97	. . .	(1)7.25	4.78	1.67
Rhodinocichla rosea	3♀ 47.69±1.25 7♂ 50.09±0.42	(7)0.63±0.02	(4)25.09±0.94	(6)11.36±0.49	(6)2.96±0.10	(6)1.47±0.04
Chlorospingus ophthalmicus	4♀ 18.54±0.64 8♂ 21.14±0.36	(12)0.96±0.04	(4)19.32±0.75	(5)8.90±0.24	(11)4.07±0.09	(11)1.62±0.03
Chlorospingus pileatus	3♀ 17.9±0.43 3♂ 19.5±1.9	(5)1.07±0.06	. . .	7.95	(5)4.63±0.20	1.58±0.03
FRINGILLIDAE						
Saltator atriceps	2♂ 92.5, 96.74	0.82, 0.98	25.86, 25.97	7.90, 8.91	2.90, 2.99	1.50, 1.57
Saltator maximus	13♀ 49.07±0.82 17♂ 46.20±0.42	8♀ 1.23±0.05 $P<0.01$ 11♂ 1.57±0.07	4♀ 24.22±0.74 6♂ 28.65±0.74	(11)8.18±0.25	6♀ 3.57±0.08 $P<0.01$ 12♂ 4.04±0.05	(18)1.65±0.02
Saltator albicollis	8♀ 41.4±1.08 4♂ 40.64±1.79	(11)0.79±0.03	(5)22.17±0.52	(6)7.47±0.37	(8)3.67±0.14	(8)1.56±0.04

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Habia fuscicauda	7♀ 14.66±0.53 $P<0.01$ 9♂ 18.22±0.65	3♀ 13.03±1.37 3♂ 16.64±0.99	3♀ 1.29±0.10 3♂ 1.66±0.21	3♀ 5.58±1.37 3♂ 7.69±0.98	(12)1.41±0.04	(13)6.71±0.20	3.98
Tachyphonus rufus	(3)17.35±1.36	(3)15.62±1.25	(3)1.73±0.11	(3)8.21±0.74	(3)1.26±0.21	(3)5.28±0.32	3.57
Tachyphonus luctuosus	(9)16.11±0.44	(4)14.20±0.84	(4)1.33±0.05	(3)6.17±1.04	(7)1.49±0.10	(7)7.09±0.28	3.62
Eucometis penicillata	20.5	. . .	. . .	. . .	1.33	6.50	3.88
Rhodinocichla rosea	(4)17.17±0.49	(4)15.55±0.52	(4)1.87±0.10	(4)7.67±0.58	(4)1.27±0.05	(5)4.59±0.17	3.33
Chlorospingus ophthalmicus	(11)15.66±2.03	(5)12.42±0.43	(5)1.27±0.06	(4)5.39±0.23	(10)1.01±0.04	(11)5.55±0.13	3.32
Chlorospingus pileatus	(5)12.6±0.69	. . .	. . .	. . .	1.01±0.08	6.04±0.26	3.52
FRINGILLIDAE							
Saltator atriceps	18.03, 18.25	16.56, 16.70	1.47, 1.55	7.72, 7.83	0.74, 0.92	4.06, 4.24	3.66
Saltator maximus	7♀ 16.93±0.28 $P<0.01$ 11♂ 19.83±0.30	4♀ 15.05±0.36 7♂ 18.52±0.34	4♀ 1.61±0.07 7♂ 1.67±0.06	4♀ 7.56±0.34 6♂ 8.47±0.44	(20)1.23±0.04	6♀ 5.24±0.14 $P<0.01$ 12♂ 5.72±0.08	3.71
Saltator albicollis	(8)15.64±0.21	(5)14.54±0.26	(5)1.52±0.04	(5)6.11±0.48	(8)1.13±0.07	(8)5.22±0.11	3.57

	Body weight *grams*	Heart *% body weight*	extremities *% body weight*	extremities *% body weight*	*cm.² per gram*	Aspect ratio
Richmondena cardinalis floridana	3♀ 37.0±3.17 12♂ 38.0±0.50	(15)0.94±0.03	(4)29.51±1.16	(4)6.68±0.32	(9)3.80±0.11	(9)1.51±0.03
Richmondena cardinalis cardinalis	13♀ 43.2±0.66 19♂ 44.2±0.80	(12)1.21±0.09	(6)25.52±0.59	(6)6.66±0.29	(5)3.48±0.09	(6)1.59±0.03
Pheucticus tibialis	5♀ 61.1±0.85 7♂ 63.1±0.91	(7)1.03±0.04	26.21, 28.04	(3)7.15±0.21	(4)3.42±0.11	(5)1.79±0.01
Pheucticus ludovicianus	10♀ 44.91±0.49 14♂ 44.46±0.75	(19)1.10±0.02	4♀ 25.89±0.60 1♂ 30.50	(6)6.62±0.24	(18)3.55±0.04	(17)1.88±0.07
Cyanocompsa cyanoides	1♀ 32.06 3♂ 32.7±0.7	(2)0.95, 0.97	(1)28.52	(2)6.71, 6.87	(2)3.25, 4.34	(2)1.51, 2.00
Passerina cyanea	1♀ 14.0 8♂ 15.35±0.45	(7)1.38±0.07	27.84, 27.25	(3)5.43±0.20	(4)6.17±0.71	(3)1.78±0.06
Tiaris olivacea	8♀ 9.19±0.34 13♂ 8.81±0.16	(15)1.15±0.03	3♀ 20.58±1.74 5♂ 24.51±0.60	(9)7.65±0.43	(12)5.47±0.13	(10)1.61±0.01
Sporophila aurita	1♀ 10.19 11♂ 10.60±0.14	(8)1.19±0.06	(4)22.02±0.97	(5)5.63±0.41	(6)5.23±0.37	(6)1.58±0.06
Oryzoborus funereus	4♀ 12.42±0.95 7♂ 11.30±0.43	4♀ 1.04±0.05 4♂ 1.22±0.05	(7)22.67±0.46	(8)6.70±0.29	(5)5.59±0.02	(6)1.60±0.05
Volatinia jacarina	5♂ 9.01±0.26	(6)1.08±0.03	22.02	(3)7.86±0.57	(6)5.44±0.13	(6)1.52±0.02
Spinus xanthogaster	1♂ 13.12	1.59	27.70	5.18	4.99	2.00

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Richmondena cardinalis floridana	(10)18.46±0.89	(4)19.2±0.75	(4)2.01±0.10	(4)8.26±0.40	(9)1.54±0.22	(9)5.80±0.19	3.54
Richmondena cardinalis cardinalis	(6)18.32±0.41	(6)16.58±0.36	(6)1.74±0.11	(6)7.19±0.28	(5)1.35±0.23	(6)5.17±0.31	3.50
Pheucticus tibialis	(5)18.47±0.43	17.05, 18.6	1.62, 1.76	7.54, 7.68	(4)0.82±0.10	(4)4.59±0.08	3.68
Pheucticus ludovicianus	4♀ 18.26±0.25 10♂ 19.39±0.43	4♀ 16.68±0.25 1♂ 19.71	4♀ 1.61±0.04 1♂ 1.94	4♀ 7.61±0.36 1♂ 8.85	(17)0.95±0.07	(17)4.87±0.08	3.56
Cyanocompsa cyanoides	(2)17.12, 20.95	15.22, 19.00	1.90, 1.95	(1)7.57	(2)0.64, 1.24	(2)4.36, 6.10	...
Passerina cyanea	(3)20.96±0.03	19.2, 18.9	1.74, 2.03	6.9, 6.32	(3)1.77±0.18	(4)8.55±0.87	3.72
Tiaris olivacea	5♀ 15.95±0.66 7♂ 17.29±0.47	3♀ 13.88±0.52 5♂ 15.56±0.71	3♀ 1.42±0.16 5♂ 1.85±0.13	3♀ 5.28±1.22 5♂ 7.10±0.46	(12)1.34±0.07	(12)7.43±0.17	3.37
Sporophila aurita	(6)16.87±0.52	(5)15.17±0.60	(5)1.65±0.10	(4)5.41±0.46	(5)1.12±0.08	(6)7.10±0.27	3.39
Oryzoborus funereus	(8)16.37±0.48	(7)14.49±0.51	(7)1.78±0.07	(7)6.40±0.08	(6)1.45±0.06	(6)7.67±0.15	3.54
Volatinia jacarina	(6)15.10±0.42	14.4	1.83	5.79	(6)1.31±0.07	(6)7.44±0.21	3.36
Spinus xanthogaster	21.30	19.42	1.88	6.40	0.92	6.40	3.42

(*continued*)

TABLE 1.—*concluded*

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.² per gram*	Aspect ratio
Spinus tristis	7♀ 12.8±0.5 9♂ 13.1±0.4	(3)1.70±0.06	(2)25.96, 28.33	3.77, 4.82	5.41, 5.79	1.96, 1.96
Pezopetes capitalis	1♀ 55.94 1♂ 55.83	(2)0.59, 0.62	...	16.80	(2)2.40, 2.74	1.41, 1.45
Pselliophorus tibialis	5♀ 30.1±0.60 7♂ 32.1±0.70	(11)0.81±0.04	(3)21.04±2.36	(4)11.69±0.65	(8)4.39±0.18	(7)1.48±0.03
Atlapetes brunnei-nucha	5♀ 38.88±1.50 3♂ 40.76±0.48	(5)0.82±0.06	...	11.6, 14.0	(5)2.98±0.10	(5)1.42±0.03
Atlapetes assimilis	1♀ 39.03 2♂ 38.9, 43.8	(3)0.84±0.01	(2)20.05, 23.21	12.08, 13.12	(3)3.09±0.11	(3)1.46±0.06
Atlapetes torquatus	3♀ 44.14±1.62 3♂ 43.58±3.38	(4)0.82±0.06	22.24, 22.42	(4)11.2±0.59	(5)3.06±0.20	(4)1.45±0.04
Atlapetes gutturalis	3♀ 36.84±1.24 8♂ 36.15±0.52	(11)0.88±0.04	17.82, 19.43	(4)13.11±0.55	(9)3.14±0.05	(9)1.50±0.03
Arremonops conirostris	10♀ 37.23±0.69 $P < 0.01$ 7♂ 42.26±0.84	(10)0.85±0.04	(6)19.61±0.80	(6)12.97±0.63	(6)2.97±0.15	(6)1.51±0.07
Pipilo erythrophthalmus alleni	15♀ 38.0±0.90 26♂ 39.0±0.55	12♀ 0.83±0.03 $P < 0.05$ 23♂ 0.94±0.04	4♀ 19.83±0.69 6♂ 22.72±0.75	(10)13.2±0.17	10♀ 2.68±0.11 13♂ 3.10±0.07 $P < 0.01$	(23)1.53±0.02
Pipilo erythrophthalmus erythrophthalmus	3♀ 38.96±1.06 19♂ 42.17±0.48	(5)1.07±0.04	(4)24.58±0.66	(4)11.5±0.29	(4)2.86±0.14	(4)1.55±0.02

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.² per gram*	Glide *cm.² per gram*	Buoyancy index
Spinus tristis	19.78, 21.95	18.08, 20.5	1.45, 1.70	6.18, 6.38	0.99, 1.41	6.98, 8.02	3.63
Pezopetes capitalis	10.9, 13.4	...	...	...	0.73, 0.98	3.74, 3.83	3.13
Pselliophorus tibialis	(10)13.15±0.66	(3)12.59±1.83	(3)1.35±0.15	(3)7.09±0.42	(10)1.42±0.09	(10)6.06±0.20	3.72
Atlapetes brunnei-nucha	(5)14.57±0.47	12.95	1.70	...	(5)1.11±0.07	(5)4.40±0.11	3.19
Atlapetes assimilis	(3)15.16±1.01	(3)13.37±0.64	(3)1.79±0.03	(2)6.53, 7.13	(3)0.92±0.06	(3)4.45±0.09	3.28
Atlapetes torquatus	(4)15.26±0.69	14.05, 14.90	1.56, 1.92	5.78, 6.45	(5)0.82±0.08	(5)4.27±0.24	3.29
Atlapetes gutturalis	(10)13.23±0.28	(3)11.9±0.53	(3)1.39±0.01	5.44, 5.84	(8)1.27±0.08	(9)4.63±0.19	3.22
Arremonops conirostris	(7)14.49±0.37	(6)12.61±0.32	(6)1.68±0.03	(6)5.33±1.40	(6)0.60±0.09	(6)4.10±0.14	3.18
Pipilo erythrophthalmus alleni	(24)14.0±0.46	...	...	(10)6.18±0.15	10♀ 1.23±0.14 13♂ 1.45±0.10	10♀ 4.42±0.24 13♂ 5.17±0.12 $P < 0.01$	3.09
Pipilo erythrophthalmus erythrophthalmus	(4)18.04±0.59	(4)16.2±0.49	(3)1.63±0.20	(4)6.54±0.19	(4)1.05±0.06	(4)4.65±0.13	3.14

	Body weight *grams*	Heart *% body weight*	Upper extremities *% body weight*	Lower extremities *% body weight*	Wings *cm.^{2} per gram*	Aspect ratio
Spizella pusilla	3♀ 13.1±0.52 12♂ 13.2±0.27	(11)1.28±0.03	(3)26.21±0.27	(3)5.50±0.40	(4)5.77±0.22	(3)1.68±0.04
Zonotrichia capensis	11♀ 19.96±0.49 15♂ 20.96±0.23	(21)0.86±0.03	(4)19.44±0.55	(5)11.32±0.54	(16)3.74±0.06	(16)1.63±0.02
Melospiza melodia	10♀ 20.32±0.34 23♂ 22.1±0.42	(8)1.15±0.06	(3)25.99±2.35	(3)9.68±0.56	(3)3.73±0.21	(3)1.59±0.03

	Upper extremities						
	Pectoral and sup. *% body weight*	Pectoralis *% body weight*	Supra-coracoideus *% body weight*	"Rest" *% body weight*	Tail *cm.^{2} per gram*	Glide *cm.^{2} per gram*	Buoyancy index
Spizella pusilla	(3)20.20±2.05	(3)18.27±1.88	(3)1.94±0.25	(3)6.00±0.33	(4)1.52±0.17	(4)8.22±0.36	3.52
Zonotrichia capensis	(16)14.88±0.42	(5)12.84±0.64	(5)1.55±0.09	(4)5.55±0.08	(16)0.83±0.03	(16)5.08±0.12	3.21
Melospiza melodia	(3)16.82±1.94	(3)15.1±1.73	(3)1.69±0.22	(3)5.84±1.03	1.08, 1.10	(3)5.72±0.31	3.20

TABLE 2.—*Seasonal variation of proportional weight of the heart*

Species	No.	January February Percent of body weight	No.	June Percent of body weight	Significance of difference
Anhinga anhinga ...	(8)	1.01±0.03	(7)	0.79±0.038	$P<0.01$
Ardea herodias	(5)	0.90±0.04	(5)	0.76±0.04	$P<0.05$
Eudocimus albus ...	(13)	1.12±0.03	(13)	0.97±0.03	$P<0.01$
Buteo lineatus	(7)	0.73±0.05	(7)	0.55±0.03	$P<0.01$
Aphelocoma coerulescens	(6)	1.07±0.03	(11)	0.92±0.03	$P<0.01$

TABLE 3.—*Muscles of the upper extremities* (percent of body weight)

Species	Total	Pectoralis	Supra-cora-coideus	Shoulder	Brachium	Forearm
Tinamus major	43.74	26.9	8.17	3.44	2.43	2.80
Pelecanus occidentalis ..	18.96	11.30	1.85	2.24	2.30	1.26
Phalacrocorax olivaceus.	18.49	11.90	1.24	1.91	2.54	1.15
Anhinga anhinga	20.11	12.95	1.28	1.04	2.46	1.57
Ardea herodias	23.17	15.00	1.06	1.47	3.40	2.24
Heterocnus mexicanus ..	23.10	13.40	1.38	3.06	3.12	2.14
Ixobrychus exilis	14.06	8.32	1.57	1.25	1.77	1.15
Mycteria americana	27.25	18.35	1.44	2.77	2.23	2.45
Eudocimus albus	31.32	19.40	2.24	2.80	4.60	2.48
Aythya affinis	22.19	14.60	2.02	2.45	2.16	1.12
Coragyps atratus	26.11	15.10	0.81	2.49	4.65	2.48
Chondrohierax uncinatus	29.49	17.10	0.49	3.30	4.77	3.82
Caracara cheriway	22.53	14.30	0.62	1.60	3.81	2.19
Ortalis garrula	22.86	12.20	2.19	3.34	2.81	2.35
Coturnix coturnix japonica	25.17	15.36	5.58	1.90	1.59	0.74
Colinus virginianus	35.65	22.40	7.06	3.42	1.72	1.05
Odontophorus guttatus..	27.31	16.25	5.74	2.05	1.80	1.47
Gallus gallus .... (White Leghorn)	16.56	8.78	3.50	1.61	1.44	1.23
Laterallus albigularis ..	11.21	6.91	0.75	1.66	1.35	0.58
Squatarola squatarola ..	26.87	19.60	2.35	1.64	2.11	1.16
Ereunetes mauri	21.76	16.60	2.35	1.13	0.84	0.84
Sterna hirundo	20.02	14.00	1.13	1.57	1.71	1.61
Thalasseus sandvicensis.	18.74	12.80	1.09	1.37	1.88	1.57
Rynchops nigra	20.02	13.10	1.13	2.93	1.94	1.96
Columba livia	31.79	20.50	3.57	1.26	3.27	3.24
Columba speciosa	40.20	26.45	4.78	3.15	3.07	2.74
Crotophaga sulcirostris..	20.70	12.50	0.97	1.60	3.15	2.45
Otus choliba	23.35	14.00	1.04	1.87	4.24	2.20
Megaceryle torquata	25.31	14.50	1.26	3,25	4,24	2.06
Chloroceryle aenea	22.24	14.75	2.00	1.60	2.83	1.06
Colaptes auratus	30.16	19.20	1.10	2.90	4.53	2.34
Melanerpes erythrocephalus	26.32	16.90	0.99	2.59	3.78	2.06
Synallaxis albescens	18.07	11.00	1.34	2.14	3.04	0.50
Muscivora tyrannus	33.45	23.60	2.29	2.76	3.29	1.51
Iridoprocne bicolor	23.46	16.20	1.04	2.49	2.45	1.29
Aphelocoma coerulescens	21.02	12.90	1.22	2.24	2.84	1.82
Mimus polyglottos	19.89	11.70	1.35	2.19	3.11	1.53
Mniotilta varia	29.35	16.80	1.55	4.46	6.61	
Parula americana	21.53	14.30	1.39	2.19	2.36	1.29
Agelaius phoeniceus ...	26.89	18.00	1.67	2.54	2.80	1.87
Richmondena cardinalis .	32.04	21.00	2.08	2.85	4.14	1.97
Spizella passerina	26.61	18.30	1.63	2.06	2.97	1.62

TABLE 4.—*Muscles of the lower extremities* (percent of body weight)

Species	Total	Thigh	Leg
Tinamus major	13.14	7.36	5.78
Pelecanus occidentalis	5.71	3.37	2.42
Phalacrocorax olivaceus	11.30	3.95	5.93
Anhinga anhinga	8.72	4.36	4.36
Ardea herodias	12.00	5.79	6.28
Heterocnus mexicanus	12.20	6.31	5.88
Ixobrychus exilis	12.21	6.13	6.08
Mycteria americana	10.30	4.70	5.63
Eudocimus albus	8.48	4.65	2.72
Aythya affinis	5.20	2.78	2.42
Coragyps atratus	14.40	7.75	6.62
Chondrohierax uncinatus	7.50	4.36	3.14
Caracara cheriway	13.60	6.68	6.90
Ortalis garrula	20.10	10.60	9.40
Coturnix coturnix japonica	10.78	6.38	4.40
Colinus virginianus	13.20	7.43	5.77
Odontophorus guttatus	14.10	8.22	5.90
Gallus gallus (White Leghorn)	15.38	7.02	5.36
Laterallus albigularis	18.15	10.30	7.82
Squatarola squatarola	5.35	2.81	2.61
Ereunetes mauri	4.76	2.79	1.98
Sterna hirundo	2.63	1.52	1.11
Thalasseus sandvicensis	2.28	1.36	0.91
Rynchops nigra	2.46	1.41	1.04
Columba livia	6.38	3.39	2.55
Columba speciosa	4.78	2.73	1.97
Crotophaga sulcirostris	12.35	7.44	4.92
Otus choliba	8.83	3.34	5.49
Megaceryle torquata	2.95	2.10	0.86
Chloroceryle aenea	2.50	1.59	0.91
Colaptes auratus	7.25	4.60	2.66
Melanerpes erythrocephalus	6.04	3.11	2.93
Synallaxis albescens	10.20	5.01	5.15
Muscivora tyrannus	2.73	1.47	1.26
Iridoprocne bicolor	2.68	...	...
Aphelocoma coerulescens	14.50	6.87	7.57
Mimus polyglottos	10.80	5.29	5.50
Mniotilta varia	6.58	...	...
Parula americana	6.95	2.97	3.48
Agelaius phoeniceus	8.86	4.00	4.86
Richmondena cardinalis	7.14	3.67	3.47
Spizella passerina	6.14	3.15	2.99

TABLE 5.—*Comparative values of typical species*

Species	Body weight *grams*	Pectoralis plus supracoracoideus *% body weight*	Wings			Glide *cm² per gram of body*	Leg muscles *% body weight*	Heart *% body weight*
			cm.² per gram of body	Buoyancy index	Aspect ratio			
Campylopterus hemileucurus	11.85	31.75	3.67	2.91	2.63	6.71	1.17	2.10
Claravis pretiosa	72.20	30.20	2.58	3.28	1.82	3.71	4.65	1.31
Tinamus major	1140.0	30.00	0.95	3.31	1.44	1.16	12.80	0.20
Cotinga ridgwayi	55.00	25.30	3.22	3.50	1.92	4.18	6.00	1.17
Odontophorus guttatus	290.0	24.70	1.22	2.84	1.45	1.50	16.9	0.33
Trogon collaris	65.00	23.50	3.32	3.66	1.95	5.35	1.62	1.05
Stelgidopteryx ruficollis	14.50	21.40	7.54	4.30	2.40	9.69	1.60	1.61
Pyrrhura hoffmanni	84.00	21.30	2.85	3.53	2.18	3.87	5.60	1.43
Myiarchus tuberculifer	20.00	20.50	5.87	4.00	1.70	8.29	5.30	0.86
Melanerpes rubricapillus	52.00	18.8	4.12	3.92	1.92	4.77	5.70	1.22
Aythya affinis	575.00	18.20	0.81	2.60	2.84	1.06	7.00	0.89
Chloroceryle americana	35.50	16.80	3.31	3.31	2.24	4.43	2.92	1.24
Zonotrichia capensis	20.50	15.00	3.76	3.21	1.64	5.11	12.70	0.88
Butorides virescens	165.0	13.20	3.26	4.23	2.39	3.66	9.70	0.70
Podiceps dominicus	120.0	10.90	1.60	2.81	2.56	1.87	16.40	1.06
Aramides cajanea	385.0	9.10	1.65	3.48	1.62	1.87	24.40	0.54
Crotophaga sulcirostris	69.00	8.60	3.78	3.94	1.72	5.41	12.1	0.70

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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SIXTEEN-DAY WEATHER FORECASTS FROM SATELLITE OBSERVATIONS

By
C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4462)

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SIXTEEN-DAY WEATHER FORECASTS FROM SATELLITE OBSERVATIONS

By C. G. ABBOT
Research Associate, Smithsonian Institution

Measures of the solar constant of radiation are possible from satellites. Coursing above the obstructing atmosphere, a suitable pyrheliometer could measure the intensity of solar radiation directly, without spectrum observations. Many measurements could be made daily and no days omitted. Though they might not be individually as precise as those of the Smithsonian observers in the years 1924 to 1952, the mean value of a day from satellite measurements would be more precise than they were. It could readily be reduced at the ground from radio-transmission reports.

Twenty-five years ago I showed that upward and downward trends in solar radiation were followed, for at least 16 days, by trends in terrestrial temperature which were opposite, like the right and left hands.[1] Using identical dates of starting of solar trends, I found that Washington, St. Louis, Helena, Potsdam in Germany, and Ebro in Spain all presented opposite trends of temperature for rising and falling solar changes. Large solar changes produced large temperature variations and vice versa. Thus one perfect set of solar-constant measurements would suffice for 16-day temperature predictions worldwide. Dr. R. A. Millikan, supported by Dr. I. Bowman, Dr. K. T. Compton, and the then Chief of the U. S. Weather Bureau, prepared a recommendation whose text is printed in Smithsonian Publication 3397. It suggested that an appropriation of $300,000 be made to enable the Smithsonian Institution to set up several solar-constant stations at the best sites. These would be additional to the three stations then operative. It was hoped thus to get from their mean results high-grade solar-constant values daily.

This recommendation was approved by President Roosevelt and the Director of the Bureau of Budget. The appropriation passed the

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[1] Smithsonian Misc. Coll., vol. 95, No. 12, Publ. 3392, and vol. 95, No. 15, Publ. 3397, 1936.

Senate but was defeated in the House. It was never revived and would now be futile. The multiplication of airplanes and rockets now befoul the atmosphere, and the world turmoil which prevails would endanger observers. The conditions would now negative such a project. Besides, it could not produce without fail daily values as good as those now possible from satellites.

The two papers referred to, and another of somewhat later date to which I shall refer, are long out of print. They may be consulted in some 1,500 libraries, the world over, to which the Smithsonian Institution freely sends its publications.

To bring the matter to the attention of the present generation, my assistant, Mrs. Lena Hill, and I have collected all the solar-constant observations made at Montezuma, Chile, 1924 to 1955, and have repeated the study of solar-produced trends associated with them on the temperatures at Washington. We used about twice as many data as were formerly available. The present results are smoother than but not markedly different from those given in Publications 3392 and 3397.

These results are not to be used now for forecasting, but only to illustrate what may be done from satellite observations. I therefore omit details that would demonstrate what accuracy they may have for temperature forecasting. I merely show by graphs and tables what were the end results and how they compare with those of 25 years ago.

Before presenting this evidence, I refer to another paper.[2] Here it is shown that there is in the weather of Washington and New York a regular period of about $6\frac{2}{3}$ days. I now evaluate it as 6.6476 days. This is exactly $\frac{1}{1250}$ of 273 months, the master period on which I based my forecasts of precipitation to 1967.[3]

As shown in Publication 3892, this is a strong period in Washington and New York weather. Its effect on temperature sometimes overpowers the effects of upward and downward trends in solar variation. We did not know of its permanently continuous regular pulses when Publications 3392 and 3397 were published. Hence those results were somewhat confused by it.

Antecedent to our present determination of the regular trend effects on the temperature at Washington, Mrs. Hill and I redetermined the phases and the amplitudes of the period of 6.6476 days. Then we removed its effects from all the solar-constant measurements, 1924

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[2] Smithsonian Misc. Coll., vol. 107, No. 4, Publ. 3892, 1947.

[3] Smithsonian Misc. Coll., vol. 139, No. 9, Publ. 4390, 1960.

to 1955. This left the solar trends and their effects unaffected by this extraneous variable. This is the main reason why our present results on trends of temperature at Washington are smoother than those of 25 years ago. The 6.6476-day period would necessarily have to be taken account of, along with the solar trend effect, in any 16-day forecasts which I hope may be made from satellite observations.

Table 1 gives in eight groups, of 180 repetitions each, the average amplitudes of these groups, and finally the general mean of 1,440 repetitions of the 6.6476-day period. It will be clear from the graphical expression of these data in figure 1 that, though the phases of the period hardly ever differ more than a day from their mean predicted positions, their amplitudes are widely differing. Moreover, as pointed out in my paper (Publication 3990 of 1949) and clearly shown in figure 1, a period of $\frac{6.6476}{2}$ days also exists. These factors would have to be allowed for in any 16-day forecasts from satellite observations.

TABLE 1.—*Groups of 180—repetitions of the 6.6476-day solar period and mean of 1,440 of them*

Places:	1	2	3	4	5	6
1924-1927	466	462	465	474	472	454
1927-1930	450	444	438	461	456	442
1931-1934	461	474	456	470	459	463
1934-1937	485	470	459	475	475	467
1938-1941	467	466	457	474	481	465
1941-1944	465	457	461	466	462	461
1945-1948	481	486	479	482	485	478
1948-1951	504	493	489	510	501	482
Mean	472.4	469.0	464.2	476.5	473.9	463.9

Mrs. Hill and I have eliminated the effect of these two regular periodic solar variations. Our results on 16-day weather control by solar trends are shown graphically in figure 2 and numerically in table 2.

With figure 1 I have also given an example of the large, and I may even say almost *controlling,* effect of the period of 6.6476 days and 3.3238 days on the temperatures of Washington and New York.

TABLE 2.—*Washington temperature departures, 1924-1955*

Rising solar trends

Days from sun change	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
—5.......	—0.2	—2.6	—1.6	+0.9	—1.0	+0.4	+1.1	+0.2	+0.8	—2.4	—3.0	—0.6
—4.......	—0.1	—3.1	—0.7	—0.3	—2.5	—0.2	+1.6	—1.0	+1.2	—0.3	—3.0	—1.5
—3.......	+0.3	+0.4	—2.1	—0.7	—1.3	—1.2	+1.9	—0.1	0	+0.7	0	—2.1
—2.......	—2.2	+2.0	—2.9	—1.4	+1.4	—2.1	+2.1	+0.3	+0.3	+0.1	+1.3	—1.9
—1.......	—3.6	+3.6	—1.8	+1.9	+5.0	—2.1	+2.8	—0.1	+0.3	—1.1	0	—1.2
0.......	—1.1	+7.7	—1.9	+2.1	+3.2	—4.1	+2.6	—0.3	—1.7	—0.5	—0.9	—1.1
1.......	—2.2	+5.2	—3.2	—0.1	+2.3	—3.5	+0.6	—0.9	—1.4	—2.8	—2.3	—2.8
2.......	+2.5	+0.3	—1.3	—1.3	—1.6	—2.2	+0.7	—0.9	—0.8	—3.5	—2.8	+0.2
3.......	+2.0	—3.5	—2.7	—4.6	—3.3	—3.0	+0.5	—0.8	+0.3	—3.0	—2.7	+1.7
4.......	+2.3	—1.3	—5.8	—5.4	—3.5	—1.1	—0.5	—1.0	+2.5	—2.3	—5.6	—1.6
5.......	—0.8	+1.2	—6.2	—5.9	—1.8	—0.5	—1.4	—0.7	+2.5	—1.8	—6.7	—7.9
6.......	—1.3	+3.8	—9.1	—6.4	—1.5	+0.3	—2.7	+0.2	+3.0	—0.8	—6.0	—9.7
7.......	+2.5	+2.7	—6.9	—0.8	+0.2	+3.2	—2.6	+3.0	+5.2	+2.5	—1.3	—7.0
8.......	+6.9	+1.6	—4.2	+0.6	+1.0	+3.2	—1.7	+3.6	+1.5	+5.0	+1.8	—2.6
9.......	+10.3	—0.9	—3.7	—1.9	—1.5	+1.8	—0.5	+3.6	—2.6	+4.6	+2.8	—0.7
10.......	+5.5	—2.0	—4.1	—2.4	—3.9	—0.2	+0.7	+1.4	—3.5	+4.8	+2.0	+0.2
11.......	+5.2	—1.3	—2.6	—0.4	—3.8	—1.5	+1.8	0	—3.3	+0.9	+0.5	+0.4
12.......	—0.6	—0.9	—1.2	+2.8	—1.6	—2.5	+3.0	+0.4	—1.3	—2.8	0	+0.9
13.......	—0.4	—1.3	+1.7	+2.7	—0.1	—2.8	+1.2	—1.6	—1.2	—3.1	—3.2	+0.5
14.......	—0.2	—3.0	+3.3	+2.4	+0.7	—2.1	+0.1	—1.7	+0.7	—2.2	—3.1	—0.2
15.......	—0.2	—3.2	+4.6	+1.7	+1.4	—1.3	+0.3	—0.9	+1.3	—0.3	—1.2	+1.1
16.......	+1.2	—0.3	—2.4	+0.3	—1.1	—0.9	+0.8	—0.3	+0.4	+0.6	+0.4	+3.3

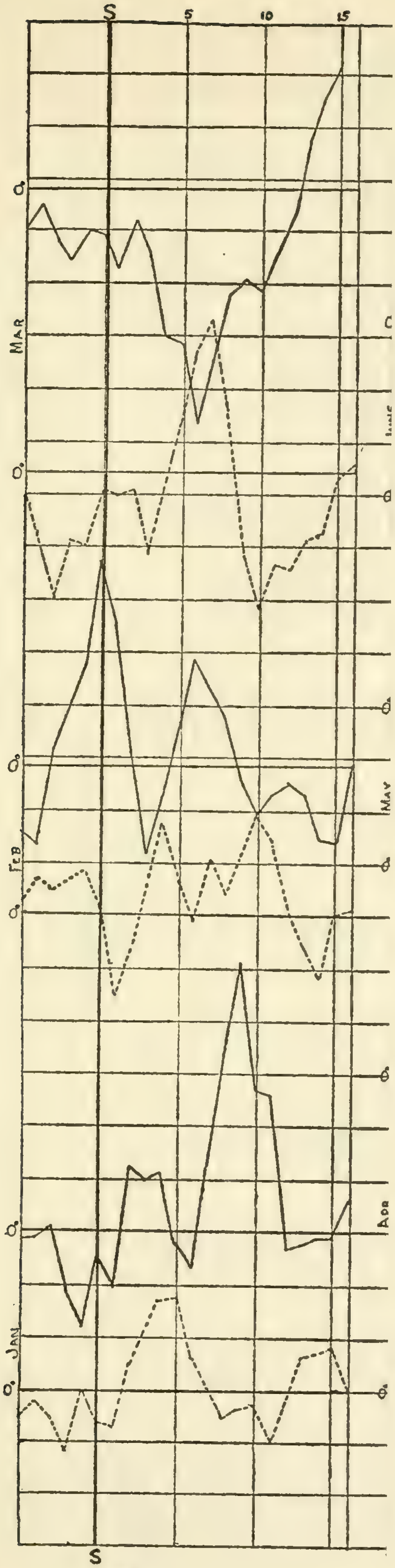

Fig. ~~1~~ 2.—Washington temperat
16 days. Full curves, solar radiat

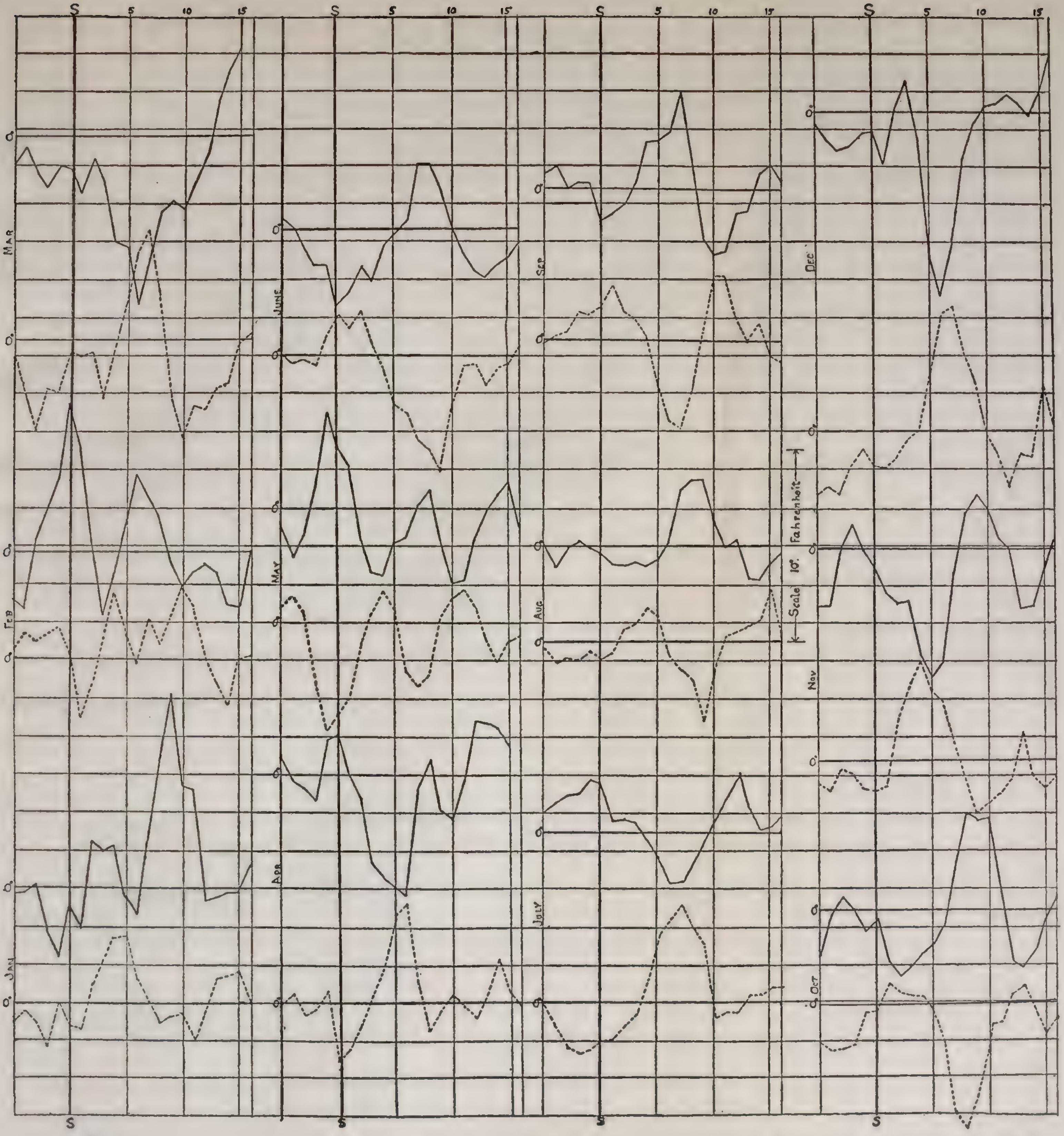

FIG. ~~1~~ 2.—Washington temperature controlled 16 days by sun's variation. The sun changes at *S*. Washington temperature, —5 to 16 days. Full curves, solar radiation rises; dotted curves, falls. Zero departures at *O*.

Falling solar trends

Days from sun change	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
—5.......	—1.0	+0.7	—0.6	—0.1	+0.9	+0.1	+0.2	—0.4	—0.2	—2.0	—1.3	—3.4
—4.......	—0.4	+1.5	—2.6	+0.5	+1.5	—0.3	—1.2	—1.1	+0.1	—2.4	—1.7	—2.9
—3.......	—1.0	+1.1	—4.7	—0.6	+0.5	—0.1	—2.4	—0.8	+0.3	—2.3	—0.5	—3.3
—2.......	—2.3	+1.5	—2.6	—0.3	—3.3	—0.4	—2.7	—0.9	+1.4	—2.1	—0.8	—1.8
—1.......	0	+1.8	—2.8	+0.6	—5.6	+1.2	—2.5	—0.5	+1.3	—0.4	—1.6	—0.9
0.......	—1.2	+0.4	—0.7	—3.1	—4.7	+2.3	—2.0	—0.9	+1.7	—0.3	—1.7	—1.8
1.......	—1.4	—3.0	—0.9	—2.4	—4.0	+1.6	—1.9	—0.5	+2.8	+1.1	—1.5	—1.9
2.......	+1.0	—1.2	—0.7	—1.1	—1.1	+2.5	—1.2	+0.7	+1.5	+0.6	+2.1	—1.4
3.......	+2.3	+1.4	—3.1	+0.4	+0.5	+0.6	—0.6	+1.0	+1.0	+0.5	+3.9	—0.4
4.......	+3.4	+3.6	—0.1	+1.8	+1.6	—0.6	+1.2	+1.8	+0.1	+0.4	+5.0	+0.2
5.......	+3.5	+1.5	+1.9	+4.6	+0.7	—2.5	+3.6	+1.4	—2.3	—0.3	+3.5	+3.3
6.......	+1.3	—0.2	+4.7	+5.2	—2.6	—2.9	+4.4	—0.7	—4.3	—2.1	+2.9	+6.2
7.......	+0.1	+2.3	+5.8	+1.0	—3.3	—4.3	+5.1	—1.5	—4.7	—6.0	+0.7	+6.6
8.......	—1.0	+0.9	+2.3	—1.5	—2.7	—4.8	+3.9	—2.0	—2.7	—6.6	—3.3	+4.3
9.......	—0.8	+2.3	—3.1	—0.4	+0.3	—6.0	+3.1	—4.1	+0.5	—4.9	—3.1	+2.7
10.......	—0.6	+4.0	—5.0	+0.4	+1.3	—2.6	—0.8	—1.1	+3.3	—1.1	—2.4	—0.1
11.......	—2.0	+2.9	—3.5	—0.2	+1.7	—0.5	—0.5	+0.3	+3.3	—1.0	—1.9	—1.2
12.......	—0.5	+0.3	—3.7	—0.8	+0.8	—0.4	—0.5	+0.6	+1.2	+0.5	—1.2	—2.9
13.......	+1.2	—1.1	—2.7	+0.2	—0.7	—1.5	+0.4	+0.9	—0.2	+0.9	+1.3	—1.2
14.......	+1.4	—2.3	—2.3	+2.2	—2.1	—0.6	+0.4	+1.1	+0.8	—0.4	—1.0	—1.3
15.......	+1.6	+0.1	—0.2	+0.5	—1.1	—0.3	+0.8	+2.7	—0.9	—1.6	—1.7	+2.4
16.......	—0.1	+0.3	+0.3	—0.3	—0.7	+0.6	+0.8	—0.7	—1.3	—0.8	—1.1	+0.2

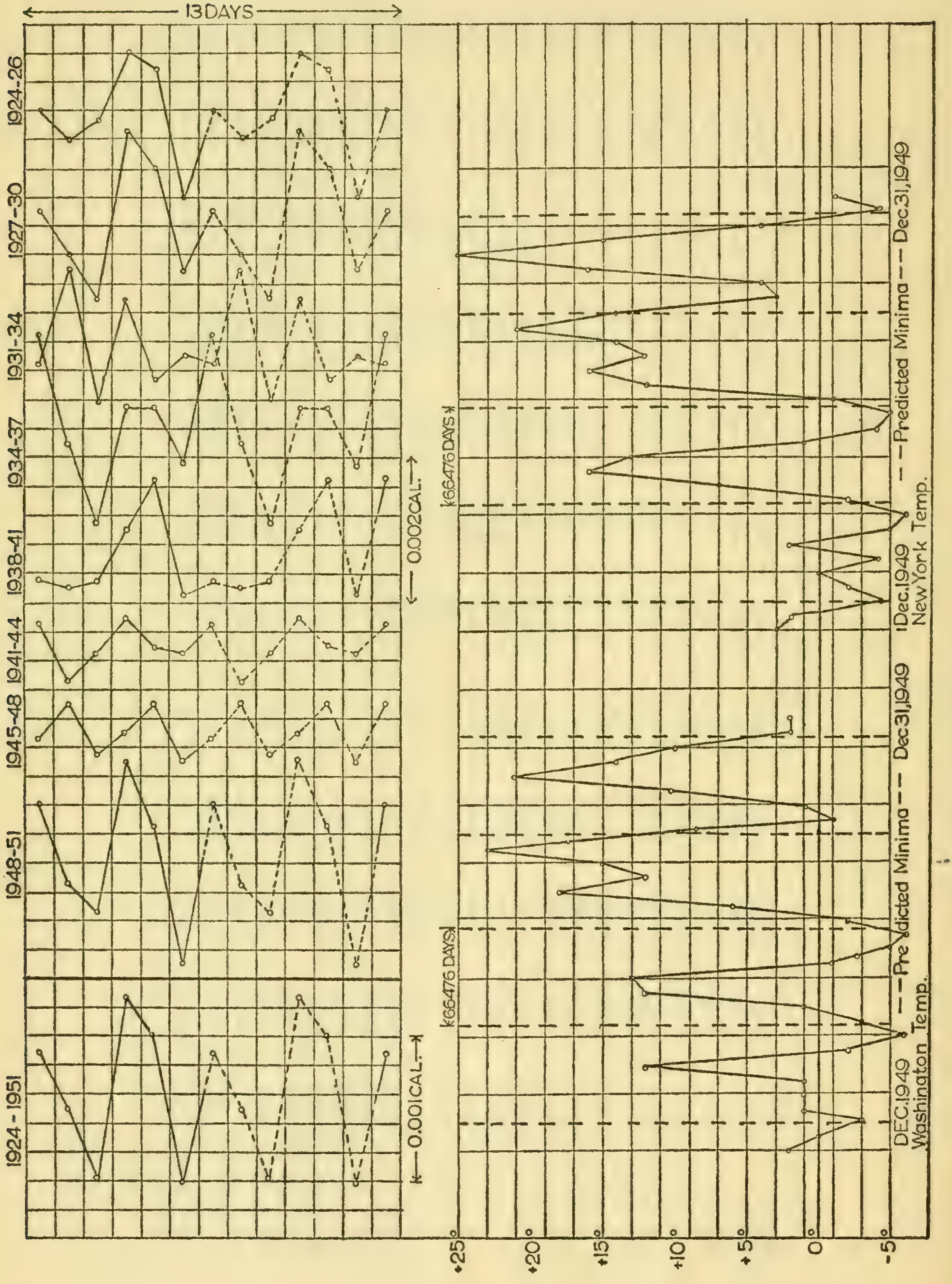

FIG. 2.—The 6.6476-day period in the sun and the earth.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 143, NO. 3

SUPPLEMENT TO THE ANNOTATED, SUBJECT-HEADING BIBLIOGRAPHY OF TERMITES 1955 TO 1960

By
THOMAS E. SNYDER
Honorary Research Associate
Smithsonian Institution

(Publication 4463)

CITY OF WASHINGTON
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1955 TO 1960

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INTRODUCTION

On September 25, 1956, an "Annotated, Subject-Heading Bibliography of Termites 1350 B.C. to A.D. 1954," by Thomas E. Snyder, was published as volume 130 of the Smithsonian Miscellaneous Collections. A few 1955 papers were included. The present supplement covers publications from 1955 through 1960; some 1961, as well as some earlier, overlooked papers, are included. A total of 1,150 references are listed under authors and titles, and 2,597 references are listed under subject headings, the greater number being due to cross references to publications covering more than one subject. New subject headings are Radiation and Toxicology.

ACKNOWLEDGMENTS

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Editors of the Smithsonian Institution have been very helpful in the preparation of the manuscript and index.

Mrs. Lucile W. Yates, cataloger of the Entomology Research Division, Agricultural Research Service, U.S. Department of Agriculture, has supplied many references. Miss Emily Bennett, librarian of the Division of Insects Library, U.S. National Museum, Smithsonian Institution, has been especially helpful in checking references and obtaining obscure publications, often difficult to locate. I am grateful to my wife for typing additional references.

Dr. E. W. Ligon, of the Pesticide Regulation Branch, Agricultural Research Service, U.S. Department of Agriculture, has kindly prepared some of the data under the heading "Toxicology."

Dr. Ivan Hrdý, of the Czechoslovak Academy of Science, Prague, was helpful in sending me publications and references.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 143, NO. 3

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NOTE.—In the "Index of American Economic Entomology," under the heading "Termites" and supplementary subject-headings, there are papers not referred to in this more or less selective bibliography; some are of minor importance, others repetitions.

SUBJECT HEADINGS

(For complete citations see List of Authors and Titles beginning on page 72.)

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termes brevis. Nature integument and natural environment factors.)

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1959a, pp. 231-242. (Central Java, new colonies start in dead branches in crowns teak trees, termites gnaw hole through rotten wood, winged *Neotermes tectonae* attracted to rotten wood, yellow clayey excrement on outside wood betray presence.)

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1960a, pp. 23-27. (India, Dehra Dun, biology *Capritermes dunensis, Eremotermes dehraduni, Microcerotermes beesoni, Microtermes anandi, M. unicolor, Neotermes megaoculatus, N. microculatus, Nasutitermes thanensis.*)

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1956, pp. 145-158. (The replacement sexuals in the higher termites, can have three origins—winged imagines, nymphs, and workers (neoteinics). In Termitidae only do imagines become sexually mature in nest, lay eggs in queenless colonies *Anoplotermes*. Formation substitute sexuals from nymphs widespread, preceded by molting. Only with the most primitive types Termitidae possible for workers to be sexualized, as in *Termes hospes*. Formation apterous reproductives takes place during two successive molts, live short time, must be constantly replaced, same in *Microcerotermes amboinensis*. In most highly developed forms sexual maturation only possible for imagines. Development supplementary reproductives influenced by neither diet nor ectohormones.)

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1957a, pp. 91-95. (Adipose tissue, not chitin fluorescent.)

1957b, pp. 238-240. (End-slotted moisture gradient test tubes set in battery jars, moisture 97½% optimum (*Reticulitermes hesperus*), prefer black-dyed wood.)

Pesson, P., 1959, pp. 41, 55, 78-79, 99, 104, 109, 132, 137-138, 152, 167. (General, polymorphism; nests 30 ft. high; habitats temperature never falls below 15° C., regulate temperature nests, go below ground to escape cold or heat; mate for life; nests in Africa 80 to 100 years old, longest-lived insect; queens *Bellicositermes* lay 36,000 eggs per day; neoteny; trophallaxis; social regulation—inhibition castes; cultivation fungi by higher termites for food for young; preferential nutrition controls production various castes; retrograde molts; temporary orientation, appreciation of duration of time?)

Pickens, A. L., 1956, pp. 233-238. (Links and gaps in the common castes of termites.)

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1959, p. 511-523. (India, *Coptotermes heimi*, swarms from early Mar. to early Aug. at and after dusk; nests in dead wood; individuals do not live more than 1 year; soldiers constitute 33% of a soldier-worker colony.)

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Sands, W. A., 1956, pp. 531-536. (Factors affecting the survival of *Odontotermes badius*, fungus *Termitomyces microcarpus* may not support life for prolonged periods, source of vitamins or similar essential substances, symbiosis necessary for survival.)

Schmidt, H., et al., 1955b, pp. 1-309. (Systematics, nests, biology, economic importance, control.)

Schmidt, H., 1956, pp. 129-130. (Laboratory studies of supplementary reproductives of *Reticulitermes*, the nymphs collect in herds of 80 to 100 and are guarded by a group of workers in a narrow chamber. They are kept isolated from other nymphs. Every 1 or 2 days they change their position. Further development always takes place in the form of herds. Workers feed the nymphs stomodeal food.)

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York State, *Reticulitermes flavipes* and *virginicus*.)

Sims, L., 1957, pp. 312, 322-323. (U.S.)

Skaife, S. H., 1955, pp. 1-134. (*Amitermes atlanticus* in South Africa, 12 workers first year.)

1957, pp. 373-390. (*Kalotermes durbanensis*, biology, distribution, damage, experimentation, rearing, food, protozoa.)

Snyder, T. E., 1957c, pp. 38-39. (Colony formation by supplementary reproductives of eastern *Reticulitermes*.)

1960a, pp. 284-288. (General biology, world species.)

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Stuart, A. M., 1961, p. 419. (Trail laying by various termites in laboratory tests, gland secretion produces trails.)

Szent-Ivany, J. J. H., 1959, p. 423. (Papua and New Guinea, *Coptotermes hyaloapex*.)

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Weesner, F. M., 1956, pp. 36-38. (Colony formation by *Reticulitermes hesperus*, U.S.)

1960, pp. 153-170. (World, termites more diverse than supposed. Variations great. Culture methods must be developed for Termitidae.)

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Williams, R. M. C., 1959a, pp. 291-304. (Africa, Uganda, *Cubitermes ugandensis* development incipient colonies, feed on soil, exuviae, dead and living brood, copulate third day after colony foundation in laboratory, parthenogenesis rare, males more active in care young. Egg laying began 5th day after foundation. One egg in 1½ days for 2 to 3 weeks, later, one every 5½ days, 7 workers on average, no soldier. *Dorylus* (*A.*) *kohli* predator.)

Zim, H. S., and Cottam, C., 1956, pp. 30-31. (U.S.)

BUILDING CODES

Clement, M. L., 1959, pp. 1-15. (U.S., southern standard building code, of Southern Building Code Congress, termite-proofing provisions, shields, resistant woods.)

1960, sections 101-2612. (U.S., sect. 1701.7, foundation sills, where clearance is less than 18 in., heartwood of durable species or pressure-treated wood using an approved preservative, sills separated from unit masonry by corrosive resistant metal shield. In appendix 3, Termite control, 1, Metal shields, 2, Foundation timbers treated with approved preservative.)

CASTE DETERMINATION

Brian, M. V., 1957, pp. 107-120. (Caste determination in social insects.)

Buchli, H., 1958, pp. 263-429. (France, *Reticulitermes lucifugus* and *santonensis*, nutrition and ectohormones influence caste determination. Larvae of first 2 stages undifferentiated, crowding and nutrition influence differentiation, workers differentiate in stage 3, and continue to molt and grow up to stage 9, live at 25° C. from 18 months to 5 to 6 years. Workers may be sexualized during stages 5 and 6, effected by an insertion of an intermediate stage of "pseudonymph." Soldiers transform from workers at all stages but principally at stages 5 and 6. Pseudoworkers may transform beyond stage 5 to neoteinic reproductives or soldiers. Swarming not indispensable for copulation and egg laying.)

Jucci, C., 1956, pp. 283-284. (Italy, endocrine gland important in differentiation of castes.)

Kaiser, P., 1955, pp. 303-304. (The organs of internal secretion in determination of caste.)

1956, pp. 651-653. (Hormone organs contribute to caste development.)

1956a, pp. 129-178. (The hormone organs in connection with the origin of castes.)

Karlson, P., and Butenhand, A., 1959, pp. 49-51. (Ectohormones of termites produced by reproductives influence colony members, refers to Grassi and Sandias, Grassé, et al., Light and Lüschner.)

Lüscher, M., 1958b, pp. 144-150. (Effect of corpora allata on the origin of substitute reproductives.)

1960, pp. 549-563. (Europe, *Kalotermes flavicollis,* caste determination is controlled by hormones, after each pseudoergate molt corpora allata secrete juvenile hormone bringing individual into reactive state of competence for differentiation. The relative duration and intensity of secretion of the different endocrine glands bring about differentiation.)

Lüscher, M., and Springhetti, A., 1960, pp. 190-212. (Europe, *Kalotermes flavicollis,* role of corpora allata, seems to produce two different kinds of hormones, the juvenile hormone probably increases the competence for supplementary reproductive differentiation. The gonadotropic hormone initiates presoldier differentiation.)

Pickens, A. L., 1956, pp. 233-238. (Links and gaps in the common castes of termites.)

Skaife, S. H., 1954, pp. 345-353. (Caste differentiation *Amitermes atlanticus* due to extrinsic causes.)

CHEMICAL ANALYSIS

Asenjo, C. F., Amoros-Marín, L., Torres, W., and Del Campillo, A., 1958, pp. 185-195. (Puerto Rico, analysis West Indian mahogany (*Swietenia mahogani*) isolated waxy-white substance strongly repellent to termites. P_2 fraction varied in effectiveness.)

Boyer, P., 1956, pp. 801-803. (Africa, study of soil, distribution and amounts of basic substances, in the mound material of *Bellicositermes natalensis.*)

1958, pp. 479-482. (Africa, influenced by the reuse by the termite and the erosion of it of the soil evolution of the cement of the mound of *Bellicositermes rex.*)

1958a, pp. 488-490. (Africa, the material composing the giant mound of *Bellicositermes rex,* clay is the base of the cement.)

Hesse, P. R., 1955, pp. 449-461. Soil of termite mounds are not altered chemically.)

Maldague, M., 1959, pp. 343-359. (Belgian Congo, Macrotermitinae take soils from depth, texture finer in mounds than in adjacent soils; no difference for *Amitermes* mounds; mounds *Cubitermes* and *Nasutitermes* have greater rate fine elements than surrounding soils which contain important amount of iron oxide concretions. Mounds Macrotermitinae poorer in organic matter than adjacent land, but contrary occurs in mounds *Cubitermes, Nasutitermes,* and *Amitermes.*)

Manzanilla, E. B., and Ynalvez, L. A., 1958, p. 36. (Essential amino acid content of some tropical termites, Philippines, arginine, histidine, lysine, and phenylalanine in three species tropical termites.)

CONTROL

Agarwala, S. B. D., 1955, pp. 533-537. (Aldrin and dieldrin most effective in control of *Microtermes obesi* attacking sugarcane, chiefly in India.)

Agarwala, S. B. D., and Haque, M. W., 1955, pp. 347-348. (Effects of BHC treatments of soils in protection against *Odontotermes assmuthi* and growth of sugarcane.)

Agarwala, S. B. D., and Sharma, C., 1954, pp. 78-79. (Aldrin and dieldrin outstanding in control *Microtermes obesi* on maize in Bihar.)

Anonymous, 1955, pp. 44, 46-48, 50. (Proper care and maintenance of termite equipment pays off.)

1956c, pp. 42-56. (Standard termite control methods for U.S. Dept. Defense.)

1956f, p. 186. (Best advice on control.)

1956g, pp. 18, 20, 22. (BRAB report criticized.)

1957a, pp. 66, 68. (Questions and answers on control.)

1957b, p. 85. (*Cryptotermes,* the drywood termite.)

1957d, pp. 6-8, 23, 25. (Vapor barriers, asphalt paper, penetrated.)

1957p, pp. 16, 18, 20, 30. (Clays kill drywood termites, cinders or sand soil barriers; dieldrin has some vapor toxicity; EDB fumigation slabs.)

1958c, pp. 34, 36, 38, 40. (PCO equipment directory.)

1958i, pp. 1-7. (Soil treatment.)

1958k, p. 22. (California, Dr. I. B. Tarshis, U.C.L.A., stated SG 67, a treated silica aerogel (Davison Chem. Co., Baltimore, Md.), nontoxic sorptive dust, effective preventive for drywood termite, use 1 lb. to 1,000 sq. ft. of attic area.)

1958l, pp. 113-119. (Termite protection, pp. 113-118, only mandatory in region of heavy attack; concrete foundations, reinforced concrete caps, metal shields, soil treatment, treated lumber; in areas where drywood or dampwood hazard, additional precautions required. Decay, p. 119, treated lumber, resistant woods.)

1958n, pp. 2-10. (Australia, termite-proofing, control.)

1959, pp. 17-19. (U.S. Dept. Agric. methods soil treatment.)

1959a, p. 17. (U.S., cooperation with builder, view building plans, bid early, advertise.)

1959b, pp. 19-20, 22-23. (U.S., Savannah, Ga. Navy project, timing pretreatment of construction, performance bond, work with field superintendent.)

1959d, pp. 1-4. (U.S., National Better Business Bureau warns against termite quackery and recommends National Pest Control Association's advice on how to purchase wisely.)

1959j, pp. 30, 32, 34. (Abbot Exterminating, pretreatment 837-unit Fort Campbell, Ky., housing project soil poisoning, wood preservation, 1958-1961.)

1960g, p. 5. (U.S., statistics by R. E. Heal, Exec. Secy., National Pest Control Assoc., on pest control industry; 15,000 to 20,000 service personnel in industry, 225-million-dollar annual business; 40% or 90 million dollars derived from pre- and post-construction termite work alone.)

1960k, pp. 56, 58. (U.S., no Approved Reference Procedure for pretreatment recommended as yet by National Pest Control Assoc., common procedures used outlined, use dyes, etc.)

1960l, p. 182. (U.S., 3 types termites, call on licensed pest control operator.)

1960n, pp. 28, 34, 36, 46, 48, 50, termites; pp. 50, 51, 56, fumigation; pp. 51, 54-56, safety. (U.S., equipment directory for control.)

1960o, pp. 62, 64-69. (U.S., how to choose efficient equipment and methods for drilling masonry, hardness, abrasiveness, moisture factors affecting drilling, also types bits, sharpening, application-pressure, speed, use of rigs.)

1960p, p. 70. (U.S., termite publicity program, series news stories sent to newspapers in various States, damage, issuance of statements by local authority, cartoon.)

1960t, p. 5. (U.S., National Pest Control Assoc. offers insured termite control service warranty on both corrective and pretreat work to qualified members.)

1960u, p. 46. (U.S., National Pest Control Assoc. board approves insured termite control service warranty program. Corrective work and preconstruction termite prevention treatment, qualified members participate for insurance by depositing $35 covering 10 warranty jobs; Lexington Insurance Co., Wilmington, Del.; members responsible for retreatment for first $100, repairs in excess of $100 filed with NPCA. Damage occurring within 1 year after service will be made at expense of TO and/or NPCA not to exceed $5,000.)

1960v, pp. 56-57. (U.S., how to sell soil poisoning pretreatment of buildings to various groups interested in building.)

1960w, pp. 28-30, 32-34. (U.S., termites pp. 28-30, heptachlor, and sodium arsenite added, in National Pest Control Assoc. supplement to ARP (approved reference procedures for termite control), to list chemicals accepted by FHA, rates application, inspections, etc.)

1960y, pp. 42-43. (U.S., free inspections on way out, term "clearance" not to be used, termite report safer legally.)

1960z, pp. 1-5. (Philippines, U.S. methods.)

1960a^1, pp. 34, 36. (U.S., should concrete block foundations be treated at grade level or near footings? Experiments under way; above grade level most effective?)

1960b^1, pp. 1-15. (U.S., design of wood structures for permanence, National Lumber Manufacturers Assoc. recommends: sanitation, sound foundation, drainage, ventilation, proper clearance, durable or treated wood, metal shields, periodic inspection for termite prevention, detailed diagrams.)

Ayoub, M. A., 1959, pp. 429-432. (Saudi Arabia, *Microcerotermes diversus* attacking live plants.)

Beal, J. A., 1958, pp. 20, 22. (Soil poisoning dosages, poisoned vapor barriers, insulating materials tested.)

Beechem, H. A., 1955, pp. 36, 50. (Methyl bromide poisoning, gas in applicator near lethal concentration.)

Beesley, J., 1957, pp. 4-6, pp. 1-3, 3-4. (Australia, eradicating termites from buildings.)

Bender, A. H., 1959, p. 68. (U.S., clean-up equipment—brushes, rags, trash cans, vacuum cleaner and drill combination.)

Boettger, C. R., 1957, pp. 105-121. (Protection of construction timber.)

Bowser, C. A., 1955, pp. 9-10, 12. (Federal Housing requirements.)

Brehm, W. L., et al., 1955, pp. 44, 46-48, 50. (Equipment care and maintenance.)

Brickey, P. M., 1957, pp. 33, 36. (Prices must be adjusted.)

Briegleb, P. H., 1954, pp. 73-76. (Resistant wire, soil poisons.)

Brinkman, G., 1956, pp. 199-202.

Buswell, W. S., Jr., 1955, p. 44. (In roof.)

Butts, W. L., 1959, p. 32. (Chemical dispersion in concrete blocks.)

Capinpin, R. I., 1955, pp. 170-172. (Philippines, termite-proofing foundations.)

Casimir, M., 1957, pp. 67-68. (Australia, detection and control.)

Ceylon Coconut Research Institute, 1958, pp. 1-2. (Ceylon, paradichlorobenzene in planting holes.)

Chaaraoui, A. M., and Chahouan, A. A. M., 1955, pp. 286-297. (Egypt.)

Chatterji, S., Sarup, P., and Chopra, S. C., 1958, pp. 399-405. (India, dieldrin, DDT, and BHC mixture (50:50) superior to DDT and toxaphene mixture (50:50), 5, 10, 15, and 20 lb. to acre applied to soil once before planting.)

1960, p. 108. (India, control termites attacking wheat by insecticides.)

Clements, W. B., 1955, p. 32. (U.S., Florida.)

Coaton, W. G. H., 1958, pp. 1-112. (South Africa, hodotermitid harvester termites, poison baits—sodium fluosilicate grassveld reclamation, arresting soil erosion.)

Das, G. M., 1959, pp. 493-498 (p. 8, reprint). (NE. India, *Microcerotermes* sp. live wood eater, dieldrin as soil poison, use leads to injury by other insects.)

Davis, J. J., 1955, pp. 1-3. (Prevention and control, U.S.)

Davletshina, A. G., and Bogolyubova, A. S., 1960a. (U.S.S.R., *Anacanthotermes turkestanicus,* results of experiments on control in Golodnaya Steppe.)

Dickinson, L. E., 1961, pp. 40-43. (General: Taiwan, damage to underground cable, control coat with pentachlorophenol. Australia, use of vaseline-based serving containing arsenic applied to outside lead sheathing, also attack on plastic sheathed cable. Panama, cables employing jute fillers attacked. Hawaii, termites eat through synthetic rubber, polyethylene or neoprene insulation, control blow pentachlorophenol or chlordane into ducts. Cuba, synthetic insulation type cable replaced. Congo, termite hills too close to lines must be removed.)

Diller, J. D., 1958, pp. 1-3. (U.S., in crawl-space houses, on basis cost and performance for 9 to 10 years, most desirable moisture-barrier ground cover two layers asphalt-saturated felt. Installed cost $24 for coverage 1,000 sq. ft. area. Where much physical wear, 45-lb. roll roofing, or heavier grade asphalt-saturated felt more durable.)

Dillon, R. M., (Ed.), 1956, pp. 1-60. (Protection against decay and termites in residential construction for FHA-concrete or masonry capped foundations, shields, treated wood, or soil poisons.)

1958, pp. 1-33. (Vapor-barriers not recommended; all structural lumber must be treated.)

Doering, K. W., 1958, pp. 46, 48, 50. (How termites affect approval of Veterans Administration home loans.)

Ebeling, W., 1959a, pp. 24-25, 46-47. (U.S., California, how to prevent termites from ruining your house, danger in doing control work yourself, licensed operators and trade associations have raised standards, structural alterations, insecticides, treated wood, poison dusts, wood preservation, fumigation, silica aerogel, for control drywood termites.)

Ebeling, W., and Pence, R. J., 1956, pp. 46, 50, 52, 54, 55, 56-57, 58, 62, 64. (U.C.L.A. entomologists evaluate research data on control *Kalotermes* and *Reticulitermes.*)

1958a, pp. 1-16. (Prevention and control western subterranean termite.)

Ebeling, W., Pence, R. J., and Wagner, R. E., 1958, pp. 50, 52. (Period for 50% paralysis: lindane outstanding; period for 50% mortality; pentachlorophenol, dilution affects results—subterranean termites. Drywood termites can be prevented from reinfesting buildings by dusting timbers with inert dusts which remove lipids of epicuticle causing rapid desiccation.)

Ebeling, W., and Wagner, R. E., 1959, pp. 40, 42, 44-46. (U.S., California, control drywood termites. Woodtreat-TC, to kill and aerogels to prevent attack.)

1959a, pp. 5-8. (Same as 1959.)

1959b, pp. 190-207. (U.S., California, drywood termites more susceptible to sorptive than to abrasive dusts, remove lipoid protective layer covering epicuticle caus-

ing rapid loss water after crawling on thin film dust. Lose 30% of body weight in water, then die. Silica aerogels particularly effective. Water soluble fluorides incorporated into the silica gels greatly increase effectiveness with increasing relative humidities. After wax is disrupted, fluorides can act as contact insecticides, ability to adhere to dusted surfaces increased.)

Emerson, A. E., 1958, *in* Weyer (Ed.), 1958, pp. 2798-2807. (Damage and control.)

Essig, E. O., 1958, pp. 112-119. (Western North America, *Zootermopsis, Reticulitermes.*)

Ferrero, F., 1959, pp. 30-31. (France, Banyuls, Eastern Pyrenees, *Calotermes flavicollis* attacking grapevines controlled by use dieldrin as dust (20% active material) or suspension with 1.5 l. dieldrin per 100 l. water, soil thoroughly treated especially around roots, and dust or spray applied under pressure. Wounds should be dusted.)

Feytaud, J., 1957, pp. 1-117. (France, control in buildings.)

Fonseca, J. P. C. da, 1952-1954, pp. 13-19. (Control *Syntermes* injurious to Eucalyptus seedlings with organic insecticides, Brazil.)

Forest Products Journal, 1957, pp. 23A-27A. (U.S., practical approach to prevention of decay and termites in building construction.)

Francia, F. C., 1957, pp. 29-30. (Philippines, control subterranean termites.)

1957a, pp. 15-17, 19. (Philippines, control drywood termites.)

Francia, F. C., and Valino, A. J., 1960, pp. 21-25, 31. (Philippines, importance various species, descriptive notes, habits, distribution, control.)

French Standards Association, 1957, pp. 1-12. (France, *Reticulitermes lucifugus* and *R. lucifugus* subsp. *santonensis,* detection, prevention, control.)

Garlick, G. G., 1956, pp. 485-488. (U.S., report of Building Research Advisory Board Committee on Protection Against Decay and Termites in Residential Construction.)

Gay, F. J., and Weatherly, A. H., 1959, pp. 26-28. (Australia, powerful contact toxic effect by adding small amount dieldrin to concrete during mixing, good permanence.)

Giraldi, G., 1955, pp. 487-498. (Italy, Venice, structural, soil poisons, wood preservation.)

Gösswald, K., 1958, pp. 129-151. (France, *Calotermes flavicollis* control by synthetic insecticide, Thiodan, carburetted hydrogen gas.)

Gouse, D., 1960, pp. 30, 64. (U.S., Muncie, Ind., pest control operator designs Ford tank truck for pumps, hose, tools, etc., for termite work.)

Graham, J. F., 1957, p. 64. (Africa, Kenya, destruction termite nests.)

Greaves, T., 1959, pp. 114-120. (Development even age stands in alpine areas will prevent attack by *Porotermes adamsoni; Coptotermes acinaciformis* controlled by blowing ¼ to ½ oz. white arsenic dust into nursery with portable dust gun. Silvicultural methods will assist in control *Coptotermes* but insecticides necessary in mixed age stands, Australia.)

Gunderson, H., 1957, pp. 1-8. (U.S., Iowa, detection and control.)

Gunn, J. W., 1952, p. 28. (Purdue University conference report.)

Harris, W. V., 1955a, pp. 12-13. (Australia, war on white ants.)

1955b, pp. 1-6 (Prevention damage to buildings, British Commonwealth.)

1959a, pp. 47-50. (World crops.)

1960a, pp. 73-76.

1960c, pp. 103-106. (Damage to timbers by different types termites of world, control by wood preservatives and barriers.)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands, concrete foundations, shields, wood preservation.)

Hartwig, E. K., 1955, pp. 361-366. (Destruction *Trinervitermes* nests, South Africa, by mechanical and chemical methods; winged appear in Apr. or June, according to rains; tobacco dust or dimethyl parathion powder, 20%, no harmful effect.)

1956, pp. 629-639. (Africa, *Trinervitermes,* population distribution as basis for control measures.)

Hatfield, I., 1958, pp. 36, 38, 40, 42, 44. (Most economical combined fungicide and wood insect control chemical—pentachlorophenol.)

Heisterburg, W., 1958, pp. 66-67. (Austria, criticism of Kurir's 1958 paper on termite danger in Austria.)

1959, pp. 142-143. (Austria, introduction and radical eradication possibility.)

Herfs, A., 1959, pp. 148-150. (India, dip sugarcane cuttings in aqueous emulsions DDT, 0.25% BHC, 1% chlordane, 1% aldrin, 0.25 to 5% dieldrin; dust furrows with 5% BHC or chlordane at a level of 20 lb. per acre effective. Dosages higher than 1 lb. BHC per acre injured growing shoots. Chlordane improves growth at 0.75 or 5 lb. per acre.)

Hickin, N., 1957, p. 23. (East Africa, *Cryptotermes brevis.*)

Hoag, R., 1959, pp. 3-5, 9. (California, Structural Pest Control Board rules.)

Holdsworth, H. P., 1959, pp. 1-6. (Ohio.)

Hrdý, I., and Hrdá, J., 1960, pp. 209-215. (Czechoslovakia, effect of DDT and gamma BHC, Lindane on *Kalotermes flavicollis* and *Reticulitermes lucifugus.*)

Hunt, F., 1958, pp. 1-3. (U.S., Florida homeowners termite guide.)

Isherwood, H. R., 1955, pp. 12, 14. (Equipment for subterranean termite control.)

Jacquiot, C., 1957, pp. 1-7. (France, resistant woods, products used for control.)

Jakobi, H., and Loyola E. Silva, J. de, 1959, pp. 113-117. (Portugal, control of parasites of termites by biochemistry, symbiosis, defaunation by an antibiotic—Acetarson, flagellates in *Eucryptotermes* in three days, no injury to termites.)

Jenkins, C. F. H., 1960, pp. 117-123. (West Australia, sanitation, ventilation, inspection, termite-proof construction, shields, soil poisons, wood preservation, resistant woods.)

Jones, G. D., 1958, pp. 1-2. (U.S., North Carolina.)

Jottrand, M., and Detilleux, E., 1959, pp. 111-129. (Belgian Congo, Elizabethville, leveling, tillage, and costs, mound nests.)

Kalyanaraman, V. M., Narayanaswamy, P. S., and David, A. L., 1960, pp. 166-171. (India, sugarcane, by insecticides.)

Kassab, A., Chaarawi, A. M., Hassan, M. I., and Shahwan, A. M., 1960, pp. 1-91. (Egypt, control *Anacanthotermes ochraceus, Psammotermes fuscofemoralis* and *assuanensis.*)

Katz, H., 1958, p. 49. (Treat soil, where old woody shrubs grow near foundation, with aqueous solution of toxicant to control subterranean termites.)

1959, p. 46. (Exposed threshold under door on side facing worst weather conditions accumulates water, can provide termites with moisture reservoir, no ground contact needed, use Woodtreat-TC on wood nearest wet threshold.)

Kirkpatrick, T. W., 1954, pp. 126-132. (British Commonwealth, developments in termite research.)

Koppenhafer, W. D., 1960, pp. 54-55. (U.S., Albany, N.Y., quotation sheet for estimating costs and justifying bids by Abalene Pest Control Service.)

Kowal, R. J., 1957, pp. 155-156. (The National Research Council's BRAB report on protection against decay and termites in residential construction.)

1957a, pp. 9, 10, 36. (Index to cooperating public agencies in termite control.)

1958, p. 401. (Southern U.S., research on control.)

Kurir, von A., 1958, pp. 8-15. (Austria, *Reticulitermes flavipes,* destruction all buildings in infested area and burning all wood in them, chemical treatment brick and mortar debris, fumigation soil.)

1958a, pp. 84-87. (Austria, *Reticulitermes flavipes* eradication with cobalt 60 or strontium 90, not in favor of Long-Term Control.)

1959, pp. 101-104. (Austria, radical control methods, radiation.)

Kyle, C. V., 1958, pp. 32, 34, 36, 38, 49. (U.S., removal and replacement floor tile.)

Latif, A., and Jilani, S. G., 1957, pp. 11-12. (Pakistan, control termites on chillies.)

Lee, P. G. M., 1959, pp. 34-35. (Malaya, structural and chemical barriers.)

1959a. pp. 63-64. (World, crops.)

Lefevre, F., 1956, pp. 47-50. (Control of termite damage, date palm station, Kan Kossa, Mauritius.)

Lemire, E. H., 1959, pp. 36, 38. (U.S., when to sell home building market preconstruction treatment.)

Lewis, R., 1958, pp. 33. (Chevrolet equipment truck with compartments and pump, Muncie, Ind.)

Long, E. J., 1955, pp. 14-16. (U.S., termite counterattack.)

Lyons, F. H., 1956, pp. 112-114, 203-206. (How to protect against termites in conventional construction.)

1956a, pp. 203-206. Idem. (Slab-type construction.)

Maher, P., 1955, pp. 18, 20, 44. (Pretreatment with 4% chlordane emulsion, slab homes.)

Mallis, A., 1960, pp. 219-324. (U.S., dampwood, drywood, subterranean termites.)

Manuel, M. W., 1958, pp. 36, 38, 40. (U.S., California, termite report must not misrepresent, inspection, legal liability.)

Martínez, J. B., 1956, pp. 102-117. (Spain.)

1957, pp. 147-161. (Canary Islands.)

Mason, N. P., 1958, p. 18. (Termite protection required by FHA in United States of building in danger zone; inspection once or twice a year; destroy tunnels, if reach wood, call an exterminator.)

1958a, pp. 19-20. (Minimum property standards for FHA in the U.S. for termite control, including both physical and chemical barriers.)

Mathur, R. N., 1960a, pp. 376-378. (India, control in houses, sanitation, ventilation, grading, drainage, sound foundations, proper clearance, periodic inspections, soil poisons, metal shields, resistant woods, wood preservatives, destruction nests by poisons.)

Mayer, P., 1955, pp. 18, 20, 44. (U.S., built-in termite proofing.)

Mesecher, R. B., 1957, pp. 20, 22, 45. (U.S., California, how to remove, repair, replace baseboards.)

Metcalf, R. L. (Ed.), 1957, pp. 147-192. (Use chemicals as pesticides, repellents: organic phosphorous insecticides.)

1958, pp. 1-426. (Application pesticides, residues, insect resistance.)

Moutia, L. A., 1955, pp. 48-51. (Mauritius, household.)

Newsam, A., and Rao, B. S., 1957, pp. 98. (*Coptotermes curvignathus* attacking rubber trees in Malaya controlled with aldrin, less costly than superior dieldrin, chlordane less persistent.)

1958, pp. 209-215. (Malaya, *Coptotermes curvignathus* controlled by treating soil about trunk with 0.4% BHC dust (2 oz. around collar); 5% DDT or 5% toxaphene failed; emulsions more effective than dusts. ½ gal. per planting hole, emulsions of chlordane, aldrin, dieldrin effective, dieldrin most persistent.)

New South Wales Dept. Agric., Entomological Branch, 1958, pp. 1-19. (Australia, N.S. Wales.)

Nirula, K. K., Anthony, J., and Menon, K. P. V., 1953, pp. 26-34. (Chlordane and parathion mixed with soil effective against *Termes obesus* attacking coconut seedlings, India.)

Orr, L. W., 1959, pp. 639-640. (U.S., soil poisons cannot be relied on alone, sanitation, drainage, ventilation, proper clearance, impervious foundations, treated wood; disturbance symbiosis with protozoa.)

Osmun, J. V., 1957a, pp. 592-593. (Response of *Reticulitermes flavipes* to certain insecticides.)

Osmun, J. V., and Pfendler, D. C., 1955, pp. 479-480. (Device for subslab injection of insecticides by pressure.)

Packard, H. R., 1955, pp. 25-26, 28. (Cooperation between termite operator and real estate agencies in California.)

Parcher, J. V., and Means, R. E., 1959, pp. 29-30, 32. (U.S., characteristics soil, cohesion, plasticity, strength, void ratio, loads on sand, clay, shrinking and swelling.)

1959a, pp. 57-58, 60. (U.S., chemical application, structural safeguards, penetration soil, soaking or low-pressure injection for coarse-grained soil, pressure injection for fine-grained soils; effect of building on water content of clay and dry soils.)

Parry, M. S., 1949, pp. 287-292. (Africa, Tanganyika, Eucalyptus plantations.)

Parsons, H. L., and Ehrlich, A., 1961, pp. 20, 23-24. (Use AM-9-American Cyanamid Co. water-soluble mixture of acrylamide and N,N-methylene-bisacrylamide to solidify soil. A 10% mixture by weight in water prepared and 2 catalysts added, resulting in a gel. Solution applied in rodding holes, 8 in. apart, parallel to wall. Mass of soil patricles held together. Dries out soil. Toxic, remove plants. May be applied with insecticide?, not determined.)

Pearson, E. O., and Maxwell-Darling, R. C., 1958, pp. 61-63. (Tropical Africa, damage to cotton by *Hodotermes* can be allowed for by closer spacing; subterranean termites can be controlled by use bait sawdust poisoned by paris green applied at time thinning; ground applications BHC effective.)

Pence, R. J., 1958, p. 56. (Chemically treated asphalt vapor barrier stops termites—1% chlorinated hydrocarbons added to asphalt.)

Pepper, J. O., and Gesell, S. G., 1959, pp. 1-8. (U.S., Pennsylvania, detection and control.)

Purushotham, A., Sebastian, V. O., and Grover, P. N., 1959, pp. 15-19. (India, protection timber logs from termites.)

Rangel, J., Gomes, J., and Souza, H. D., 1952-1955. (Control of *Nasutitermes brevioculatus* by disinfection of sugarcane cuttings with Rhodiatox, Rodiaclor, and other insecticides, Brazil.)

Redd, J. C., 1957, pp. 37-38, 46. (Special control specification needed for each structure.)

Reno, J., 1960, pp. 27-28. (Protection of houses with basements against termites.)

1960a, p. 77. (U.S., protection against termites for houses with slab floors.)

Roonwal, M. L., 1955a, pp. 22-23, 26, 30. (Fighting the white ant, India.)

1958a, pp. 77-100. (India, mounds, water suspensions chlorinated hydrocarbons, fumigation; sugarcane, soak setts, dust furrows BHC; other crops, chlorinated hydrocarbons—fruit trees, soil poisons, spraying trunks, paste on trunks, DDT, BHC; wood, resistant woods, shields, wood preservatives.)

Rui, D., 1956, pp. 1-2. (Italy, Venice, 4% malathion and 1% gamma benzene hexachloride in kerosene unsuccessful against *Reticulitermes lucifugus.*)

Russell, R. M., 1958, pp. 74, 76, 78, 80. (Relationships construction to infestations by subterranean termites, floating, supported, and monolithic slabs; costs resistant woods; vapor barriers, expansion joints.)

St. George, R. A., 1957, pp. 38, 40, 42, 44. (Subterranean termites attacking yews in Maryland controlled with chlordane emulsion.)

St. George, R. A., Johnston, H. R., and Kowal, R. J., 1960, pp. 1-30. (U.S., recommendations of Forest Service, following BRAB reports.)

Sands, W. A., 1960, pp. 106-108. (West Africa, control termites damaging living trees, dieldrin emulsion in planting holes; use polythene planting pots, use 2% dieldrin dust. Mechanical cultivation in plantations.)

Sastry, K. S. S., 1956, pp. 77-83. (India, Visvesvaraya Canal Tract, *Odontotermes obesus* injury to sugarcane.)

Schmidt, H., 1955a, pp. 222-224. (Methods of research on wood products.)

Schmitt, J. B., Libby, J. L., and Wilson, B. R., 1960, pp. 1-16. (U.S., chiefly *Reticulitermes flavipes.*)

Schmitz, G., 1956, pp. 1551-1596. (Belgian Congo.)

1957, pp. 229-230.

Scott, K. G., 1960, pp. 35, 36, 38. (U.S., Southern California, shields not necessary, usually 4 or 5 control methods necessary; all areas should be pretreated, not only critical areas, 5-year guarantee impractical.)

Sharma, D. K., 1959, pp. 18-19, 22. (India, termites must be tackled.)

Simeone, J. B., 1956, pp. 1-3. (U.S., New York State, prevention and control subterranean termites.)

Sims, L., 1957, pp. 312, 322-323. (U.S.)

Sinel'nikov, N. A., 1950, pp. 38-48, (U.S.S.R., the use of DDT in the control of termites.)

Singh, S. H., Sandhu, G. S., and Arora, K. S., 1958, pp. 331-332, 335-336. (India, Punjab sugarcane).

Singh, S. S., 1957, pp. 19-20. (India, prevention termites entry through cracks in floor, provide in certain areas layer clean dry sand of 9-inch thickness below floor.)

Singh, S. S., and Sharma, P. L., 1957, pp. 91-95. (India, aldrin 0.4 oz. 40% emulsion concentrate in 12 gal. water effective in destroying nests *Odontotermes gurdaspurensis.*)

Smith, C. F., 1954, pp. 16-17. (U.S., south, stop termite attack.)

1960, pp. 40-41. (U.S., North Carolina, 3-year-old inspection form for wood-destroying organisms developed through cooperation with the Veterans Administration still acceptable.)

Smith, D. N., 1945, pp. 1-12. (British Columbia, dampwood and subterranean.)

Smith, M. W., 1956a, pp. 36, 38, 40. (Subterranean termites.)

1957, pp. 34, 36, 38, 42. (Slab-type houses.)

Snyder, T. E., 1955f, pp. 50, 66. (Colonizing termites.)

1956, p. 36. (Venezuela, control by poison dust infestation from roof by subterranean termites.)

1956f, pp. 27-37. (World.)

1957b, p. 3. (Summary BRAB report, protection in residential construction.)

1960a, pp. 284-288. (Control, general.)

Soares, J., 1958, pp. 230-232. (Portugal.)

Spear, P. J., 1956, pp. 1-4. (Termite control in U.S. 35% of 100-million-dollar annual pest-control business; recommendations BRAB report; State legislation; 130 gradute entomologists in commercial work.)

1958, pp. 49-50. (Pest control in structures in the U.S. 100-million-dollar business annually, 35% termite control, 25% fumigation.)

Spector, W. S. (Ed.), 1956, p. 491. (Handbook.)

Srivastava, J. C., 1957, p. 743. (India, protection sugarcane.)

Strong, V. E., 1956, pp. 38, 40. (Cost routine inspection, California.)

Thakur, C., Prasad, A. R., and Singh, R. P., 1958, pp. 155-163. (0.5 lb. dieldrin per acre protects sugarcane against *Microtermes obesi, Odontotermes assmuthi,* and *Trinervitermes heimi,* India; no adverse effect on soil fertility.)

1961, pp. 127-131. (India, Pusa, in calcareous soil both aldrin and dieldrin effective as dust and emulsion in protecting sugarcane, dieldrin having longer residual effect.)

Thornhill, F., 1955, pp. 16, 18.

Toumanoff, C., and Toumanoff, T. C., 1959, pp. 216-218. (France, biological control by *Serratia marcescens, "Reticulitermes santonnensis."*)

Tu, T., 1953, pp. 277-287. (Formosa, insecticidal action of various chemicals and byproducts of camphor on *Coptotermes formosanus.*)

1956, pp. 12-18. (Formosa, control in buildings.)

Vance, A. M., 1956, pp. 10, 18, 24. (Southwestern U.S., lawns protected by 1¼ gal. 75% (8 lb. per gal.) chlordane emulsifiable concentrate, loosen soil before application, *Gnathamitermes.*)

Vanetti, F., 1959, pp. 437-443. (Brazil, *Cornitermes cumulans.*)

Vayssière, P., *in* Coste, 1955, p. 241. (World, biological control in coffee plantations.)

Vayssière, P., 1957, pp. 473-480. (Malaya.)

Wagner, R. E., and Ebeling, W., 1959, pp. 208-211. (U.S., California, insecticide diluents, silica gels, aerogels or precipitates, montmorillonite clays, attapulgite clays, diatomites, in decreasing order effectiveness as preventives. Lighter material superior to heavier, increase with distance from point of discharge.)

Ward, J. C., 1958, pp. 14-16. (U.S., use pesticides with care.)

Weidner, H., 1955g, *in* Schmidt, H. (ed.), 1955b, pp. 160-164. (Control of termites injurious to plants.)

Wilkinson, W., 1957a, pp. 493-494. (World.)

Willcocks, F. C., and Bahgat, S., 1937, p. 217. (Egypt, termites injure young cotton plants in Sudan, no records in Egypt.)

Wilson, H. B., 1959, pp. 35, 37, 39, 41, 43, 45, 47-49, 51, 53, 89-91, 93-95. (Australia.)

Wolcott, G. N., 1955, pp. 113-122. (Resistant woods, use chemicals.)

1955a, pp. 115-149. (Organic termite repellents tested against *Cryptotermes brevis.*)

Wolfenberger, D. O., 1959, pp. 1-51. (U.S., Florida, *Neotermes castaneus* damage to living avocado trees controlled by removing and burning old trees; in case young trees, ½ cup 5% chlordane dust, or aldrin, dieldrin, and heptachlor effective.)

Yeager, P., 1957, pp. 26, 28, 30, 43, 45. (Trend toward greater leniency in tax deductibility for termite loss, especially if damage has occurred within 1 year or so after inspection, cases cited.)

1958, pp. 70, 72, 98-99. (Enforcement restrictive covenant must not involve restraint of trade; trade secrets must not be disclosed.)

Žehelj, D., 1958, pp. 110-111. (Austria, struggle against termites.)

COURT RULINGS

Anonymous, 1957j, p. 46. (U.S., Michigan court held suppressing a material fact constitutes fraud.)

Yeager, P., 1957, pp. 26, 28, 30, 43, 45. (Trend toward greater leniency in tax deductibility for termite loss, especially if damage occurred within 1 year or so after inspection, cases cited.)

1958, pp. 70, 72, 98-99. (Enforcement restrictive covenant must not involve restraint of trade; trade secrets must not be disclosed.)

CYTOLOGY

Banerjee, B., 1957, pp. 288-289. (Haploid chromosome numbers in the testis of king *Odontotermes redemanni.*)

Denis, C., 1958a, pp. 240-247. (Cytology terminal nerves in course of ontogeny *Calotermes flavicollis.*)

Noirot, C., and Noirot-Timothée, C., 1960, 2779-2781. (General, *Anoplotermes* worker, *Microcerotermes,* structure posterior intestine.)

DAMAGE

Anonymous, 1949. (In 1849, C. Inge, probate court of Adams Co., Mississippi, had records destroyed by termites. Dr. T. W. Harris identified them, suggested paper be impregnated with alcohol solution of corrosive sublimate of mercury.)

1957, pp. 24, 25. (Estimates of incidence and damage by termites in States in 1956.)

1957d, pp. 6-8, 23, 25. (Florida, damage by termites and decay, asphalt impregnated building paper vapor barrier ineffective.)

1957l, p. 22. (Termites in inlaid floor, St. George's Hall, Kremlin, Moscow, 56° N.; former records, Ukraine, Odessa, 46° N.)

1958a, pp. 8-10. (Infestation Chicago homes, other northern localities listed.)

1958d, p. 48. (Rutgers University study estimates damage at 2 million dollars in New Jersey.)

1958n, pp. 2-10. (Australia, kinds damage.)

1959, pp. 17-19. (U.S., map showing regions heavy, medium, and light damage.)

1959f, p. 54. (U.S., damage allowable by Revenue Service if proven occurs between September and June of following year—not over several years.)

1959n, p. 16. (Italy, Venice, St. Mark's church damaged by "Lucifubis" (*Reticulitermes lucifugus*), United Press release Oct. 5, 1959, in New York Herald Tribune.)

1960, p. 25. (U.S., in California 25 to 60% of slab houses infested, 1 to 2 years old in one area inspected. In Louisiana, Alexandria and Lake Charles areas 25 to 30% infested in 5 years. In Jackson, Miss., 50 to 60% under 5 years old infested. In Texarkana, Tex., 90% slab houses in old forested area infested in first year; Texas in general 10 to 50% infested.)

1960j, p. 4. (U.S., Annapolis, Md., in 1957, 5-year-old Health Department building infested, termites crawled through cracks in concrete; also through lime mortar. In central Florida slab-on-ground homes 10 times more vulnerable, suspended floor next, crawl-space house with piers 3 ft. above ground least susceptible. 75 to 90% concrete-block homes infested within 3 to 5 years of completion. In Charleston, S.C., 600 brick veneer George Legere homes built in 1941 of untreated wood on concrete slab floors; 14 years later 240, or 40% of dwelling units, had to have wood replaced.)

1960q, pp. 23-24. (Honolulu, Hawaii, 3 million dollars spent in single year recently for repairs to buildings damaged by termites in city and county Honolulu; run from 20 to 50% permit values. Subterranean termites cause 75% total damage, drywood 25%; subterranean termites in almost every building in city; less infestations in outskirts.)

1960c,[1] pp. 20, 24. (Hawaii, damage by *Coptotermes formosanus* and a drywood termite severe, 3 million dollars (including decay) in 1956. Drywood termite responsible for one-quarter total termite damage.)

BAETA-NEVES, C. M. B., 1956a, pp. 156-158. (Lisbon, corks damaged.)

BECKER, G., 1957, pp. 403-410. (North Italy, Chioggia, first record in Europe cases of docks (pine) and piles (oak) infested with *Kalotermes flavicollis*.)

BOETTGER, C. R., 1957, pp. 105-121. (In Tropics, damage to commercial timber.)

BOURNIER, A., 1956, pp. 384-388. (France, damage by *Reticulitermes lucifugus*.)

BOWER, C. A., 1959, p. 15. (U.S., Oklahoma, increase of 25% of termite control jobs in 1957-1958 over 1956-1957; 6,843 in 1958, 5,121 in 1957; 118 new licenses issued in 1958.)

CARR, D. R., 1957, pp. 1-19. (New Zealand, decay and subterranean termites not as injurious as beetle borers and native drywood termite *Calotermes brounii*.)

COATON, W. G. H., 1958, pp. 1-112. (South Africa, hodotermitid harvester termites, damage to walls buildings, undermine, thatched roofs, linen, cotton, clothes, wallpaper, books, paper, matting.)

CORTESI, A., 1960, pp. 1, 4. (Italy, Rome, art treasures endangered by termites: books in National and Vatican libraries damaged, historic buildings, art treasures in large galleries, furniture in modern buildings in Rome and village of Oriago, devoured most of homes and trees that adorn streets. Historic Doge's Palace, Venice, invaded.)

DORSEY, C. K., 1958, pp. 1-10. (U.S., West Virginia.)

EBELING, W., 1959b, p. 4. (U.S., California, remarks before recent meeting American Society Testing Materials, San Francisco, Calif.: In California's San Fernando Valley, 20 to 25 million dollars worth of property every year in Southern California destroyed by termites, 350 firms engaged in eradication. One species increased activities during last several years. Approximately 18,000, or 75% of 24,000 representative buildings, inspected in 11 California counties, infested, 62% by subterranean termites, 25% by fungi, 5% by powder-post beetles. Both subterranean and drywood termites found in 49% of buildings in 4 regions. Concrete slabs provide no barrier, termites penetrate cracks 1/32 inch in width, ingest concrete and pass it through digestive tract, can widen minute cracks. In San Fernando Valley 46% slab houses infested within 5 years of construction, considerable proportion within 1 to 2 years.)

Emerson, A. E., 1958, *in* Weyer (Ed.), 1958, pp. 2798-2807. (Damage, the termite problem.)

Feytaud, J. C., 1955, pp. 32-38. (Increased hazard in France.)

Francia, F. C., 1957, pp. 27-30. (Philippines, damage by subterranean termites, *Coptotermes, Heterotermes, Macrotermes.*)

1957a, pp. 15-17, 19. (Philippines, damage by drywood termites.)

Francia, F. C., and Valino, A. J., 1960, pp. 21-25, 31. (Philippines, importance of various species.)

Giles, D. T., 1960, pp. 20, 22. (Del-Mar-Va peninsula, 75 to 95% houses infested by termites, many only 4 to 5 years old, older houses on Eastern Shore better constructed, less susceptible, crawl space; only 2% slab-on-ground type.)

Giraldi, G., 1955, pp. 487-498. (Italy, Venice, *Reticulitermes lucifugus.*)

Harris, W. V., 1955c, pp. 160-166. (Damage in Tropics.)

1955d, pp. 9-11. (Persistent termite.)

1956c, pp. 145-177. (Destruction of timber.)

1957c, pp. 20-32. (Malaya.)

1958, pp. 161-166. (East Africa, damage by drywood termites, *Cryptotermes.*)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands.)

Hatfield, I., 1958, pp. 50, 52-54, 56-58, 60. (U.S., damage by decay and subterranean termites, buildings.)

Henry, T. R., 1958, p. 45. (Panama, Canal Zone, eat lead, dissolve concrete, thrive on arsenic.)

Hepburn, C. A., 1959, pp. 14-16. (South Africa, properties.)

Herfs, A., 1959, pp. 178-181. (Europe, damage to paper and books by *Reticulitermes lucifugus.*)

Hickin, N., 1960, pp. 459-461. (France, *Kalotermes flavicollis, Reticulitermes lucifugus,* and *R. lucifugus,* var. *santonensis; flavicollis* injures vineyards, cuts life vine stock from 80 to 40 years; *santonensis* more injurious to buildings and trees than *lucifugus.*)

Kurir, von A., 1956, pp. 1-3, (Europe.)

1958, pp. 7-15. (Austria and Central Europe, *Reticulitermes flavipes* in 1955 at Hallein, near Salzburg, in a paper factory, introduced in 1950 or 1951 in wooden boxes from Hamburg, where first found in 1937. In beech flooring, spruce and larch doorposts, by 1957 spread to other buildings and railway sleepers.)

Kushwaha, K. S., 1960, pp. 39-40. (India, Udaipur (Rajasthan), type of damage by *Odontotermes* (*O.*) *obesus, O.* (*O.*) *obesus gurdaspurensis, O.* (*O.*) *bangalorensis, Microtermes anandi,* and *Trinervitermes biformis;* hosts.)

Luppova, A. N., 1955a, pp. 1-28. (S.S.R., Turkmenia, termites injuring buildings and their control.)

Mal'ko, B. D., 1934, pp. 34-35. (U.S.S.R., termites pest of wood.)

Martínez, J. B., 1957, pp. 147-161. (Canary Islands.)

Mathieu, H., 1957, pp. 87-91. (Hazard in France.)

1959, pp. 1-92. (Hazard in France.)

Mathur, R. N., 1960a, pp. 374-380. (India, most important termites damaging houses, *Coptotermes heimi, Heterotermes indicola, Odontotermes feae,* type of damage.)

Mercader, C., 1956, pp. 11, 37. (Destroyer, the termite.)

Meyer, M. T., 1960, p. 52. (U.S., Philadelphia, Pa., 100-year-old row house had window frame on second floor infested, no ground contact.)

Moneo-Trallero, M., 1959, pp. 21-22. (Spain.)

Moutia, L. A., 1955, pp. 48-51. (Mauritius, household.)

Novak, P., 1928. (Yugoslavia, Dalmatia, injurious insects.)

Roonwal, M. L., 1955, pp. 103-104. (*Heterotermes indicola* causing widespread damage in town Sri Hargobindpur in Punjab since 1940.)

1958, pp. 320-321. (India, damage to buildings.)

1959, pp. 511-523. (India, *Coptotermes heimi* one of the three most important termites that infest buildings in India.)

Rui, D., 1956, pp. 1-2. (Italy, Venice.)

Salmond, K. F., 1956, pp. 149-150. (Damage by Macrotermitinae in Nyasaland to stored groundnuts.)

Schmidt, H. (Ed.), 1955, pp. 193-207. (Commercial timber.)

1955a, pp. 222-224. (Wood products.)

1955b, pp. 1-309. (World.)

1956b, pp. 325-338. (Hamburg–Altona.)

1957, pp. 217-222. (*Reticulitermes,* Hamburg.)

Schultze-Dewitz, G., 1957, pp. 933-941. (*Populus* and *Pseudotsuga menziesii.*)

Silva, J. M. Barata da, 1952. (Portugal, Lisbon. *Leucotermes* (*Reticulitermes*) *lucifugus.*)

Simeone, J. B., 1956, pp. 1-3. (U.S., New York State, map danger zones.)

Sims, L., 1957, pp. 312, 322-323.

Skaife, S. H., 1957, pp. 373-390. (South Africa, Durban, *Kalotermes durbanensis.*)

Spencer, G. J., 1958, pp. 8-9. (British Columbia, damage to buildings by *Zootermopsis* and *Reticulitermes hesperus,* collapse of two houses due to *Reticulitermes* at Kamloops and Kelowna.)

Springhetti, A., 1957, pp. 1-13. (Italy, Padova, Venezia, Oriago, Mira.)

1957a, pp. 1-14. (Italy, Verona, Vicenza, Treviso, Ravigo.)

Tenisonas, A., 1955, pp. 13-15. (Europe.)

Tsvetkova, V. P., 1950, pp. 95-96. (Russia, construction.)

Tu, T., 1956, pp. 12-18. (Formosa.)

1956a, pp. 19-22. (Formosa, important documents.)

U.S. Dept. Agriculture, Plant Pest Control Div., Coop. Econ. Insect Rep., 1959a, p. 74. (Iran, *Amitermes vilis,* heavy damage to house timbers and railroad ties, Khuzistan Prov.; *Anacanthotermes vagans septentrionalis* does not cause extensive damage.)

Weidner, H., 1954, pp. 55-61. (*Reticulitermes,* Germany, Hamburg.)

Wilkinson, W., 1957a, pp. 493-494. (World.)

DAMAGE TO LIVING VEGETATION

Anonymous, 1955a, pp. 63-67. (Malaya, *Coptotermes curvignathus* damage to new plantings rubber.)

1958h, pp. 66. (Australia, Canberra, in hardwood forests presence of large colony *Coptotermes frenchi* results in increased temperature within infested tree, maximum increase in "nursery" region.)

1958o, p. 63. (Australia, Canberra, *Coptotermes acinaciformis* and *frenchi* most injurious to living trees. *Porotermes adamsoni* to trees in alpine forest in Victoria and New South Wales.)

1959s, p. 66. (Western Australia, in mallee country north of Murchison River, *Coptotermes brunneus* attacking living eucalyptus trees in forest, galleries extending over 90 ft. from mound. Near Pingrup, *Coptotermes acinaciformis* traced from mound to several gimlet gums (*Eucalyptus salubris*).)

Ayoub, M. A., 1959, pp. 429-432. (Saudi Arabia, *Microcerotermes diversus,* injury to live plants.)

Bhasin, G. D., Roonwal, M. L., and Singh, B., 1958, pp. 10, 17, 18, 63, 86, 95, 99, 102, 115, 124. (India, forest plants, p. 10, in split bamboos, *Termes feae;* p. 17, *Bassia latifolia, Odontotermes obesus,* under bark on dry stump; p. 18, *Bassia longifolia, Kalotermes* sp., possibly in green trees, *Coptotermes ceylonicus* damages living trees; p. 63, tea, *Glyptotermes dilatatus* nests in heartwood green bushes, infests through roots, *Neotermes greeni* same, *N. militaris* same; *Capritermes hutsoni* among roots, *Eurytermes ceylonicus* damages stems and roots, *Nasutitermes ceylonicus* damages bark living stems; *Odontotermes* (*O.*) *horni* same; *O.* (*O.*) *redemanni* damages living and dead bushes, *O.* (*O.*) *taprobanes* same; *O.* (*Hypotermes*) *obscuriceps* same; p. 86, *Cassia multijuga, Neotermes greeni,* borer in living trees; p. 95, *Casuarina equisetifolia, Glyptotermes dilatatus* nests in heartwood living trees, infests through snags, knots or wounds, *Neotermes greeni* same, *N. militaris* same; *Odontotermes brunneus* var. *wallonensis* injurious in plantations; p. 99, *Cedrela toona, Glyptotermes coordensis* in solid wood old logs; *G. dilatatus* nests in heartwood living trees, infests through snags, knots, wounds, *Kalotermes jepsoni* infests both dead and live wood, *Neotermes greeni* same; *N. militaris* same, *Heterotermes indicola* damages wood and wooden structures; p. 102, *Cedrus deodara, Archotermopsis wroughtoni* nests in fallen trees and moist, decaying stumps, *Microtermes mycophagus* damages wood or sleepers stacked on ground, *Odontotermes bangalorensis* same; p. 115, *Cistanche tubulosa, Amitermes belli* in roots; p. 124, *Citrus* sp., *Odontotermes obesus* attacks fallen wood.)

Bonaventura, G., 1956, pp. 465-467. (Italy, Naples, plane tree of "San Benedetto.")

Capco, S. R., 1956, pp. 9, 17, 32, 44, 51, 53, 55, 56, 64, 66. (Philippines, field crops, fruit trees, vegetables.)

Chatterji, S., Sarup, P., and Chopra, S. C., 1958, pp. 399-405. (India, dieldrin, DDT and BHC mixture (50:50) superior to DDT and toxaphene mixture (50:50), 5, 10, 15, and 20 lb. per acre applied to soil once before planting.)

Coaton, W. G. H., 1958, pp. 1-112. (South Africa, hodotermitid harvester termites, veld, standing crops, wheat, oats, rye, barley, groundnuts, beans, peas, lawns, flowerbeds, etc.)

1960, pp. 6-9. (South Africa, Rapid Karoo, destruction of grazing by harvester termites, *Hodotermes mossambicus.*)

Cohic, F., 1956, pp. 1-91. (New Caledonia, (1) alphabetical list plants, insect pests in various orders, pp. 1-32; (2) alphabetical list pest, order and family, plant hosts or prey, hosts of parasites.)

Das, G. M., 1958, pp. 553-560. (Northeast India, tea.)

1959, p. 8. (Northeast India, tea, *Microcerotermes,* live wood eater.)

Davis, S. H., 1954, pp. 35-43. (U.S., termite-proofing injuries to shade trees and shrubs.)

Dinther, J. B. M. van, 1960, p. 21. (Surinam, 3 families termites pests of cultivated plants.)

Dumbleton, L. J., 1954, pp. 1-202. (South Pacific Territories.)

Ebeling, W., 1959, pp. 155, 224, 263, 266, 267, 270-272, 274, 277. (Citrus pests—*Amitermes arizonensis, Coptotermes lacteus, niger, vastator, Gnathamitermes perplexus, Heterotermes aureus, Kalotermes minor, Macrotermes gilvus, Mastotermes darwiniensis, Nasutitermes costalis, Neotermes castaneus, Odontotermes* (*O.*) *formosanus, Paraneotermes simplicicornis, Reticulitermes flavipes, hesperus, lucifugus, virginicus, Zootermopsis angusticollis, Schedorhinotermes lamanianus, Tenuirostritermes incisus;* p. 317, avocado pests—*Reticulitermes hesperus, Kalotermes minor;* p. 325, grape pests.)

Eden, T., 1958, pp. 40, 130-131. (Pests of tea, low planting and heaping earth about stem leads to infestation; *Kalotermes* sp. rings collar.)

Essig, E. O., 1958, pp. 112-119. (Western U.S., apple tree, potato.)

Ferrero, F., 1959, pp. 30-31. (France, vine in Banyuls in eastern Pyrenees severely injured by *Calotermes flavicollis.*)

Fonseca, J. P. da, 1952-1954, pp. 13-19. (Brazil, *Syntermes* harmful to Eucalyptus seedlings.)

Garcia, M. L., 1958, pp. 25-27. (Philippines, *Neotermes malatensis* injuring avocado trees.)

Gay, F. J., 1957, pp. 86-91. (Australia, radiata pine timber in plantations by *Coptotermes.*)

Greaves, T., 1959, pp. 114-120. (Australia, *Porotermes adamsoni* most serious pest alpine forests in New South Wales, Tasmania, and Victoria. *Coptotermes acinaciformis* and *frenchi* serious pests trees in coastal forests and savannah woodland areas. Former can attack other living trees 120 ft. distant from infested living tree, mature colony population over 770,000; latter over 400,000. Temperature colonies in living trees (nursery area) higher (by over 20° C.) than ambient temperature. 170 species in 23 genera on Australian mainland.)

Guagliumi, P., 1958, p. 218. (Venezuela, sugarcane by *Heterotermes crinitus.*)

Gupta, B. D., 1955, pp. 1-80. (India, sugarcane.)

Harris, W. V., 1959, pp. 1-181. (British Honduras, forest trees, *Kalotermes tabogae, Cryptotermes brevis, Heterotermes convexinotatus, Coptotermes niger, Nasutitermes corniger, N. nigriceps.*)

1959b, p. 30. (British Honduras, *Coptotermes niger* causes serious damage to timber trees.)

Herfs, A., 1955a, *in* Schmidt, H. (Ed.), 1955b, pp. 131-159. (Plants.)

1959, pp. 148-150. (India, grains and field crops—sugarcane, peanuts injured. *Neotermes tectonae* kills living trees.)

Hetrick, L. A., 1961, pp. 53-54. (U.S., Florida, *Kalotermes approximatus* injures pear and cherry trees, causing breakage.)

Hickin, N., 1960, pp. 459-461. (France, *Kalotermes flavicollis, Reticulitermes lucifugus,* and *R. lucifugus,* var. *santonensis; flavicollis* injures vineyards, cuts life vine stock from 80 to 40 years; *santonensis* more injurious to buildings and trees than *lucifugus.*)

Huff, G. E., 1959, p. 61. (U.S., Indianapolis, Ind., subterranean termites damage refrigerated display case, moisture in bottom due to leak.)

Janjua, N. A., and Khan, M. H., 1955, pp. 69-70. (West Pakistan, *Termes obesus* and *Microtermes obesi* pests of wheat.)

Kalshoven, L. G. E., 1957, pp. 7-12. (Java, teak trees, rotten branches in crowns living trees more attractive to flying adults than branchwood from girdled trees, enter by biting hole in soft wood.)

1959, pp. 138-143. (Java, new teak plantations, 30% infested in 12-year-old compartment, not evident until 15 to 20 years old.)

Kapur, A. P., 1953, pp. 12-13. (India, *Odontotermes obesus,* nursery beds of palas, host for lac cultivation.)

Kay, D., 1960, p. 90. (Africa, Nigeria, *Neotermes aburiensis* damaging living tissue cacao trees.)

Latif, A., and Jilani, S. G., 1957, pp. 11-12. (Pakistan, injury to chillies.)

Le Pelley, R. H. (Compiler), 1959, pp. 62-66. (East Africa, injury to plants by many species termites, distribution, hosts, etc.)

Mamet, J. R., 1955, pp. 46, 47, 74, 79. (Mauritius, food plants.)

Marotta, A., 1954, pp. 337-338. (Italy, *Reticulitermes lucifugus* death of plants.)

Martelli, M., and Arru, G. M., 1957-1958, pp. 5-49. (Sardinia, *Calotermes flavicollis,* injury to cork oak, *Quercus suber.*)

Mathur, R. N., and Singh, B., 1960, pp. 1-45. (India and adjacent countries, termites injurious to forest plants, pp. 7, 10-11, 15-17, 29, 33, 36.)

1959, pp. 1-163. (India and adjacent countries, termites injurious to forest plants, pp. 13, 19, 26, 61, 68-70, 79-80, 84-85, 89, 92-94, 99, 103, 120, 123, 126, 141, 150, 153.)

1960a, pp. 1-91. (India and adjacent countries, termites as pest of forest plants.)

Milsum, J. N., 1959, pp. 425-428. (World, termites as pests of mango, *Mangifera indica.*)

Moutia, L. A., 1955, pp. 48-51. (Mauritius, orchards, food crops, vegetables, flower gardens.)

Nakajima, S., and Shimizu, K., 1959, pp. 261-266. (Formosan white ant injuring Japanese cedars.)

Neves, C. M. B., 1956, pp. 156-158. (Portugal, cork of bark and branches *Quercus suber* damaged by *Leucotermes lucifugus.*)

Nirula, K. K., and Menon, K. P. V., 1957, pp. 1-5. (India, *Odontotermes obesus* damage to coconut palms.)

Ossowski, L. L. J., and Wortmann, G. B., 1958-1959, p. 47. (Southern Africa, injury to wattle by *Hodotermes mossambicus, Macrotermes natalensis,* and *Microtermes* sp.)

Pearson, E. O., and Maxwell-Darling, R. C., 1958, pp. 61-63. (Tropical Africa, *Hodotermes mossambicus* pest of cotton seedlings. Mound-building termites affect soil fertility; subterranean termites attack cotton. *Microtermes* sp. serious in Tanganyika, attacks stem near collar, loss 10 to 30% of stand.)

Pierce, W. D., 1930, pp. 99-104. (Philippines, *Macrotermes gilvus* injury to seed sugarcane, in ground; *Coptotermes vastator* and *Microcerotermes los-banosensis* injury to young cane.)

Roonwal, M. L., 1958, pp. 320-321. (India, damage to plantations.)

Roonwal, M. L., and Bhasin, G. D., 1954, pp. 5-93. (India, forest plants.)

Roonwal, M. L., and Sen-Sarma, P. K., 1955, pp. 234-239. (India, *Neotermes gardneri* injury to living trees.)

Rui, D., 1956, pp. 1-2. (Italy, Venice.)

Sastry, K. S. S., 1956, pp. 77-83. (India, Visvesvaraya Canal Tract, *Odontotermes obesus* injury to sugarcane.)

Springhetti, A., 1957c, pp. 1-20. (Italy, Manduria (Puglia), infestation of vines.)

Srivastava, J. C., 1957, p. 743. (India, sugarcane.)

Szent-Ivany, J. J. H., 1956, pp. 82-87. (*Microcerotermes biroi* on *Cocos nucifera,* New Britain; *Nasutitermes novarum-hebridarum* on *Cocos nucifera,* Aroa Island; *Neotermes* sp. on *Theobroma cacao,* New Britain.)

1959, pp. 423-429. (Papua and New Guinea, p. 423, *Coptotermes hyaloapex,* hosts.)

Thakur, C., Prasad, A. R., and Singh, R. P., 1958, pp. 155-163. (India, *Microtermes obesi, Odontotermes assmuthi* and *Trinervitermes heimi* injury to sugarcane.)

U.S. Dept. Agric., Pest Control Div., 1959h, p. 922. (U.S., California, Vallejo, Solano County, *Reticulitermes hesperus* damage to roots and stems chrysanthemum plants, Sept. 25.)

1960, p. 1069. (Bolivia, Santa Cruz, *Heterotermes* sp., *Cornitermes* sp., *Nasutitermes globiceps* injuring sugarcane.)

Vance, A. M., 1956, pp. 10, 18, 24. (Southwestern U.S., injury to lawns.)

Vayssière, P., *in* Coste, 1955, p. 241. (World, injury to coffee plantations.)

Weidner, H., 1955c, *in* Schmidt, H. (Ed.), 1955b, pp. 160-164. (Plants.)

Wilkinson, W., 1957a, pp. 493-494. (World crops.)

Wolfenberger, D. O., 1958, pp. 36-38, figs. 26-27. (U.S., Florida, *Neotermes castaneus* (dampwood termite) usually causes infrequent minor loss to avocado trees, but may cause young trees to die and older trees to become unthrifty.)

Zondag, R., 1959, pp. 15-17. (New Zealand, *Calotermes brouni* attacking living *Pinus radiata,* unhygienic conditions provide sources infestations, stumps, prunings, dead trees.)

DETECTION

Anonymous, 1959, pp. 17-19. (U.S.)

Casimir, M., 1957, pp. 68-78. (Australia.)

Gunderson, H., 1957, pp. 1-8. (U.S., Iowa.)

Harris, W. V., 1958, pp. 161-166. (East Africa, drywood termites, *Cryptotermes*.)

Hobbs, K. R., 1961, pp. 14, 16, 18. (U.S., a key to help identify wood-destroying organisms. Subterranean termites: earth in galleries in wood; drywood termites: small conical pellets with longitudinal riflings; dampwood termites: larger pellets.)

Mason, N. P., 1958, p. 18. (U.S., by putty-colored tubes.)

New South Wales Dept. Agric., Entomological Branch, 1958, pp. 1-19. (Australia.)

Pepper, J. O., and Gesell, S. G., 1959, pp. 1-8. (U.S., Pennsylvania, detection and control.)

Simeone, J. B., 1956, pp. 1-3. (U.S., New York State, tubes, flight, damage.)

DIGESTION

Grassé, P. P., 1959a, pp. 385-389. (Africa, a new type of symbiosis, digestion by fungus-growing termites, through collaboration bacteria, illustrates strata of mastigated wood on which fungi grow, Macrotermitinae.)

Lasker, R., 1959, *in* Ray, 1959, pp. 348-355. (Reviews studies of symbiosis among termites by Oshima, 1919, Cleveland, 1924, 1925, 1928, Trager, 1932, and Hungate, 1946.)

Leopold, B., 1952, p. 784. (Digestion Douglas-fir wood by *Cryptotermes brevis* takes a few hours.)

McBee, R. H., 1959, *in* Ray (Ed.), 1959, pp. 342-347. (Termite cellulase, Cleveland found intestinal protozoa in species of Kalotermitidae, Rhinotermitidae, and Mastotermitidae, in Termitidae no protozoa except in 3 wood-feeding species. Most flagellates symbionts. Not all protozoa beneficial. *Trichonympha* most effective in wood digesting. A few cellulose-digesting bacteria and fungi in gut not significant. Protozoa cellulose fermenting, may be 16 to 36% of weight of termite.)

Pence, R. J., 1957, pp. 44, 58. (U.S., California, stucco and cement.)

Pochon, J., Barjac, H. de, and Roche, A., 1958, pp. 352-355. (Africa, digestion of cellulose by *Sphaerotermes sphaerothorax* through bacteria.)

Waterhouse, D. F., Hackman, R. H., and McKellar, J. W., 1961, pp. 96-112 (Australia, extracts whole termites (*Coptotermes lacteus*), break down undenatured chitin.)

DISTRIBUTION

Ahmad, M., 1955, pp. 25-27. (East Pakistan, *Microtermes pakistanicus*, n. sp.)
  1955a, pp. 202-264. (West Pakistan, new species of *Neotermes, Microcerotermes, Eremotermes, Amitermes, Angulitermes*.)
  1958, pp. 33-118. (Indomalayan.)
  1958a, pp. 119-198. (Indomalayan.)

Anonymous, 1957l, p. 22. (U.S.S.R., Moscow.)
  1957q, pp. 1-70. (Italy, Venice, *Reticulitermes lucifugus, Calotermes flavicollis*.)
  1958m, p. 42. (U.S., *Reticulitermes hageni* swarming in building, Trenton, N.J.)
  1958o, p. 63. (Australia, *Mastotermes darwiniensis* not present in Weipa area of Cape York Peninsula, results survey termite hazard.)
  1959, pp. 17-19. (U.S., map showing where termites most and least numerous.)

Araujo, R. L., 1958, pp. 185-217. (Biogeography termites State of São Paulo, Brazil, faunistic list 45 species, including 2 introduced species, only 3 species confined within its boundaries.)
  1958a, pp. 219-236. (Biogeography termites State of Minas Gerais, Brazil, faunistic list 31 species, only 2 species confined within its boundaries.)

Ayoub, M. A., 1959, pp. 429-432. (Saudi Arabia, *Microcerotermes diversus*.)

Banerjee, B., 1956b, pp. 204-206. (India, Calcutta.)

Bieberdorf, G. A., 1958, pp. 52-53. (U.S., Oklahoma.)

Calaby, J. H., 1956, pp. 89-92. (Western Australia.)
  1956a, pp. 93-96. (Western Australia.)
  1956b, pp. 111-124. (Western Australia, *Ahamitermes*.)

Calaby, J. H., and Gay, F. J., 1956, pp. 19-39. (Western Australia, *Coptotermes* *acinaciformis, raffrayi* subsp., *michaelseni, frenchi,* and *brunneus.*)

Chamberlin, R. V., 1944, p. 187. (New Hebrides, *Kalotermes* (*Neotermes*) *sanctaecrucis.*)

Chaudhry, G. U., 1955, pp. 40-43. (Pakistan, *Cryptotermes dudleyi, Odontotermes assamenensis, O. parvidens,* and *Eremotermes paradoxalis.*)

Chilson, L. M., 1960, p. 171. (Hawaii, Molokai, *Kalotermes immigrans,* Camp Halena, light trap, new record.)

Clagg, C. F., 1958, pp. 338-339. (Western Pacific Islands, *Prorhinotermes inopinatus,* Guam; *Coptotermes formosanus,* Guam, Midway, Kwajalein Naval Stat., Marshall Islands.)

Coaton, W. G. H., 1958, pp. 1-112. (South Africa, *Hodotermes mossambicus, Microhodotermes viator.*)

Cufodontis, G., 1955, pp. 501-519. (Africa, savannahs.)

Davletshina, A. G., and Bogolyubova, A. S., 1960. (U.S.S.R., termites in Golodnaya Steppe and how to control them.)

Emerson, A. E., 1958, *in* Weyer (Ed.), 1958, pp. 2798-2807.

Esaki, T., Bryan, E. H., Jr., and Gressitt, J. L., 1955, pp. 1-68. (Micronesia.)

Field, H., 1956, p. 488. (Baghdad, Iraq, *Microcerotermes diversus.*)

Fonseca, J. P. C. da, 1959, pp. 701-704. (Portuguese Guinea, lists species identified by Sjöstedt, Silvestri, and Harris, 16 species.)

Georghiou, G. P., 1957, p. 4. (Cyprus, *Reticulitermes lucifugus.*)

Ghidini, G. M., 1955, pp. 69-82. (Ethiopia, Sagan-Omo, *Bellicositermes jeanneli goliath* distinguishing characters, *Microtermes vadschaggae* var. *grasséi,* n.n. for var. *dubius* Grassé preoc., fig. *Termes* (*Cyclotermes*) *maledictus* and *Trinervitermes eldirensis.*)

Giraldi, G., 1955, pp. 487-498. (Italy, Venice, *Reticulitermes lucifugus.*)

Grassé, P., 1954, pp. 17-21. (France.)

Harris, W. V., 1954-1955a, p. 44. (Europe, *Reticulitermes flavipes* and *R. lucifugus* var. *santonensis.*)

1955, pp. 62-72.

1955a, pp. 12-13. (Australia.)

1955b, pp. 1-6. (British Commonwealth.)

1956a, pp. 926-937. (Africa, French Cameroons, *Microcerotermes progrediens, Pericapritermes amplignathus,* n. sp., *Odontotermes silvaticus,* n. sp.)

1957, *in* Gardner, J. C. M., 1957, p. 46. (East African forest termites.)

1957a, pp. 421-433. (Southwest Arabia, new species *Amitermes stephensoni, A. harleyi, Eremotermes sabaeus,* and *Trinervitermes arabiae.*)

1957b, pp. 25-30. (Solomon Islands, Rennell Island, 10 species in Solomon Islands.)

1957c, pp. 20-32. (Malaya.)

1958, pp. 161-166. (East Africa, *Cryptotermes dudleyi, domesticus,* and *brevis.*)

1958a, pp. 59-60. (Solomon Islands, *Schedorhinotermes browni,* n. sp.)

1958b, pp. 87-97. (Malaya.)

1959, pp. 181-185. (British Honduras, *Coptotermes niger, Heterotermes convexinotatus, Nasutitermes corniger, N. nigriceps, Kalotermes tabogae, Cryptotermes brevis.*)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands, 12 species listed.)

Hrdý, I., 1958, p. 12. (Czechoslovakia.)

Ikehara, S., 1957, pp. 44-61. (Ryukyu Islands.)

Ionescu, M. A., 1932, pp. 108-113. (Rumania.)

1936. (Rumania, frequence of *Reticulitermes lucifugus.*)

1936a, pp. 1-7. (Rumania, *Reticulitermes lucifugus.*)

1951, pp. 1-22. (Rumania.)

1959, p. 109. (Rumania, *Reticulitermes lucifugus, Kalotermes flavicollis,* map distribution in Balkans, *R. lucifugus* in Balkans has northern limit above Trieste, Belgrade, Bucharest to Kichinev and the Dniester River, *K. flavicollis* known along Adriatic coast near the Vardar River and above Turkey near eastern shore Black Sea.)

Kalshoven, L. G. E., 1960, pp. 34-40. (Java and Sumatra, occurrence of *Glyptotermes* and *Neotermes.*)

Karaman, Z., 1954, pp. 21-30. (Yugoslavia, *Kalotermes flavicollis* and *Reticulitermes lucifugus.*)

Kassab, A., Chaarawi, A. M., Hassan, M. I., and Shahwan, A. M., 1960, pp. 1-91. (Egypt, *Anacanthotermes ochraceus, Psammotermes fuscofemoralis* and *assuanensis.*)

Kempry, P., 1905. (Rumania, Neuropteroid fauna.)

Khalaf, K. T., 1959, pp. 18-19. (Iraq, *Microcerotermes diversus, Amitermes vilis, Anacanthotermes* sp.)

Khan, M. A., and Ahmad, M., 1954, p. 140. (Pakistan, Lahore, list termites.)

Krauss, N., 1957, p. 186. (Canton Island, *Coptotermes formosanus.*)

Kushwaha, K. S., 1960, pp. 39-40. (India, Udaipur (Rajasthan), *Odontotermes* (*O.*) *obesus; O.* (*O.*) *obesus gurdaspurensis; O.* (*O.*) *bangalorensis; Microtermes anandi; Trinervitermes biformis.*)

Le Pelley, R. H. (Compiler), 1959, pp. 62-66. (East Africa, list termite and hosts 111 species.)

Luppova, A. N., 1955, pp. 56-66. (U.S.S.R., Turkmenia, *Anacanthotermes ahngerianus.*)

1958, pp. 81-141. (S.S.R., Turkmenia, termites of.)

Martelli, M., and Arru, C. M., 1957-1958, p. 11. (Sardinia, *Calotermes flavicollis.*)

Martínez, J. B., 1956, pp. 102-117. (Spain, *Reticulitermes lucifugus, Calotermes flavicollis,* and *C. dispar.*)

Mathur, R. N., and Sen-Sarma, P. K., 1960a, pp. 23-27. (India, Dehra Dun, *Capritermes dunensis, Eremotermes dehraduni, Microcerotermes beesoni, Microtermes anandi, M. unicolor, Neotermes megaoculatus, N. microculatus, Nasutitermes thanensis.*)

Miller, D., 1956, pp. 477-478. (New Zealand.)

Moszkowski, L. I., 1955, pp. 15-41. (Madagascar, *Cryptotermes kirbi,* n. sp., and *C. havilandi,* introduced.)

Novak, G. B., 1890, pp. 119-128. (Yugoslavia, fauna of the Island of Lesina in Dalmatia.)

Paulian, R., 1957, p. 29. (Madagascar, Réunion Island, *Neotermes reunionensis, Procryptotermes* n. sp., and *Coptotermes havilandensis.*)

Petersen, E., 1910. (Rumania, additions to the knowledge of the Neuropterous fauna.)

Pierre, F., 1958, p. 149. (Africa, NW. Sahara, *Psammotermes hybostoma* in sand.)

Roemhild, G., 1960, pp. 1-7. (U.S., Montana.)

Roonwal, M. L., 1959, pp. 511-523. (India, *Coptotermes heimi,* India and Punjab, West Pakistan.)

1960, pp. 211-215. (India, Burma, Ceylon, Nepal, and East and West Pakistan have 170 species termites, probably 250 exist.)

Rui, D., 1956, pp. 1-2. (Italy, Venice, *Reticulitermes lucifugus.*)

Sands, W. A., 1959, pp. 127-156. (Ethiopian region, *Amitermes,* 13 species, 3 new.)

Sen-Sarma, P. K., and Mathur, R. N., 1957, p. 399. (India, *Cryptotermes dudleyi.*)

Silva, J. M. Barta da, 1952, (Portugal, *Leucotermes* (*Reticulitermes*) *lucifugus.*)

Simeone, J. B., 1956, pp. 1-3. (U.S., New York State.)

Sims, L., 1957, pp. 312, 322-323. (U.S.)

Skaife, S. H., 1957, pp. 373-390. (South Africa, *Kalotermes durbanensis.*)

Snyder, T. E., 1955g, pp. 28, 30. (Northward, U.S.)

1956d, pp. 189-202. (Puerto Rico.)

1957h, p. 70. (France and Italy.)

1957i, pp. 1-16. (U.S., Europe.)

1959a, p. 40. (U.S., *Reticulitermes hageni* to New Jersey; *R. virginicus* to Long Island, New York; *R. lucifugus* northward in France and Italy.)

Snyder, T. E., and Francia, F. C., 1961, in press. (Philippines.)

Spencer, G. J., 1958, pp. 8-9. (British Columbia, *Zootermopsis* on west coast Vancouver Island, around Victoria, at Nanaimo on mainland coast from international border to Prince Rupert, around Salmon Arm and Revelstoke, perhaps to Quesnal Lake. *Reticulitermes hesperus* in dry belt from Osoyoos up the Okanagan Valley to Kelowna, Kamloops, and from Lytton to Lillooet, on Vancouver Island on the eastern dry side from Victoria to Nanaimo and on some of the gulf islands.)

Stella, E., 1953-1954, *in* Zavattari (Ed.), 1953-1954, p. 229. (Italy, Pontine Island, Zannone.)

Suehiro, A., 1960, p. 291. (Midway Atoll, *Coptotermes formosanus* and *Cryptotermes brevis* (Keck, 1952, Proc. Hawaiian Ent. Soc., vol. 14, p. 351.)

Szent-Ivany, J. J. H., 1956, pp. 82-87. (*Microcerotermes biroi* on *Cocos nucifera* in New Britain and center distribution in Papua; *Nasutitermes novarum-hebridarum* on *Cocos nucifera* Aroa Island near Kieta, Bougainville district; *Neotermes* sp. on *Theobroma cacao,* New Britain, p. 83.)

1959, p. 423. (Papua, New Guinea, *Coptotermes hyaloapex.*)

Tu, T., 1955, pp. 30-39. (China.)

1955a, pp. 80-87. (Formosa.)

1956, pp. 12-18. (Formosa.)

U.S. Dept. Agric., Pest Control Div., 1957, p. 853. (U.S., Texas, *Reticulitermes hageni.*)

1958, p. 119. (U.S., *Reticulitermes flavipes* infesting buildings, St. Paul, Minn.)

1958a, p. 982. (U.S., *Reticulitermes flavipes,* St. Paul, Minn.; *R. hesperus* flying week of Nov. 23, Corvallis, Oreg.)

1959, p. 6, (U.S., Trenton, N.J., *Reticulitermes hageni.*)

1959a, p. 74. (Iran, *Amitermes vilis, Anacanthotermes vagans septentrionalis.*)

1959b, p. 239. (U.S., Oklahoma, Tulsa, *Reticulitermes hageni* swarming early Mar. in house; Ponca City, *R. tibialis* damage to house.)

1959c, p. 288. (U.S., Utah, infestation houses Pleasant Grove, Provo, Logan.)

1959d, p. 362. (U.S. infestation houses Monongalia County, W. Va., *Reticulitermes flavipes;* Twin Falls, Idaho, *R. hesperus;* Oregon, central and eastern, *R. hesperus.*)

1959e, p. 393. (U.S., Idaho, swarms in houses, *Reticulitermes hesperus,* Lewiston to Lapwai.)

1959f, p. 473. (*Cryptotermes dudleyi,* Neotropical, Indo-Malayan, Papuan, Australian, Ethiopian.)

1960, p. 1069. (Bolivia, Santa Cruz, *Heterotermes* sp., *Cornitermes* sp., *Nasutitermes globiceps.*)

1961, p. 326. (Superior, Douglas Co., Wis., *Reticulitermes flavipes* flying in building.)

1961a, p. 392. (*Rhynchotermes nasutissimus* intercepted from Peru.)

Usman, S., and Puttarudraiah, M., 1955, pp. 10-11. (India, Mysore State.)

Vayssière, P., *in* Coste, 1955, p. 241. (World.)

1957, pp. 473-480. (Malaya.)

Weidner, R. H., 1955c, pp. 157-164. (Southwest Europe.)

1955e, *in* Schmidt, H. (Ed.), 1955b, pp. 5-81. (World.)

1958, pp. 4-16. (Iraq.)

1959, pp. 28, 32-33. (Yugoslavia, Greece, Corfu.)

1960, pp. 30-39. (East Africa, 1 Rhinotermitidae, 6 Macrotermitidae, 3 Termitidae, Termitinae—all known species.)

1960a, pp. 43-70. (Afghanistan, Iran, Irak, map for *Anacanthotermes vagans, ahngerianus, baeckmannianus, murgabicus, septentrionalis, ubachi, macrocephalus, Heterotermes indicola, Amitermes vilis, Microcerotermes gabrielis* and *Angulitermes dehraensis.*)

Werner, F., 1920, pp. 189-234. (Yugoslavia, Dalmatia, studies of the fauna.)

Willcocks, E. C., and Bahgat, S., 1937, p. 217. (Egypt, termites in arid border between desert and arid land, *Anacanthotermes ochraceus* (Burm.) and *Psammotermes hybostoma* Desn.)

Williams, E. C., 1941, pp. 76, 92. (Panama rain forest.)

Zimmerman, E. C., 1957, p. 179. (Hawaii, corrections and additions.)

EMBRYOLOGY

Geigy, R., and Striebel, H., 1959, p. 474. (Europe, *Kalotermes flavicollis.*)

Obenberger, J., 1952, pp. 1-869.

Striebel, H., 1960, pp. 193-260. (Development of *Kalotermes flavicollis; Zootermopsis nevadensis* described.)

EVOLUTION

Barros-Machado, A., 1957, pp. 80-81. (Architecture and evolution of African *Apicotermes* nests.)

Desneux, J., 1956, pp. 1-12. (Africa, Congo, *Apicotermes lamani,* atypical subterranean nests.)

1956b, pp. 277-281. (Africa, Lower Congo, *Apicotermes.*)

Emerson, A. E., 1958a, *in* Roe and Simpson (Ed.), 1958, pp. 311-355. (Intraspecies group system prime unit, group unit of natural selection leading to adaptive evolution, behavior emphasized in group integration, social behavior in insects genetically determined, in man culturally.)

1959b, pp. 1416-1417. (Data substantiate many aspects theory recapitulation and evidence for long persistence of genetic elements.)

1960c, pp. 307-348. (Evolution of function directed toward ends can be demonstrated; modern biological analysis and synthesis give some understanding of the teleonomic processes.)

1960d, pp. 1-27. (Adaptive evolution progresses in improved individual, social, and ecological homeostasis. Phylogenetic persistence for millions of years of functionless characters explained on basis of homologies resulting from a degree of molecular identity in replicating genes.)

Grassé, P. P., and Noirot, C., 1957, pp. 974-979. (Equatorial Africa, giant termitaria.)

Lüscher, M., 1958c, pp. 48-65. (Evolution termite society.)

Schmidt, R. S., 1958, pp. 76-94. (Africa, *Apicotermes trägårdhi*, evolution of nest building, most primitive lack wall perforations, shagreen, internal arrangement cellular.)

EXPERIMENTATION

Alibert, J., 1959, pp. 1040-1042. France, study of trophallactic exchanges in *Calotermes flavicollis* with the aid of radioactive phosphorous.)

Briegleb, P. H., 1954, pp. 73-76. (Resistant wire insulation, soil poisons.)

Dick, W. E., 1957, pp. 1-150. (Tag underground insects with radioactive cobalt—cobalt-60—pick up with Geiger counter. Wood borers in wood treated by radiation dosage 1000 curies cobalt 60—Nucleonics, Dec. 1952.)

Ebeling, W., and Pence, R. J., 1957a, pp. 637-638. (Sodium pentachlorophenate and pentachlorophenol relax termites to lifelike appearance but turn them black.)

Gösswald, K., 1955, *in* Schmidt, H. (Ed.), 1955b, pp. 165-192. (*Calotermes flavicollis* as an experimental animal.)

1958, pp. 129-151. (Effect of Thiodan on *Kalotermes flavicollis*.)

Gösswald, K., and Kloft, W., 1959, pp. 268-278. (*Kalotermes flavicollis* 5th instar larvae and "Pseudoergates" good test animals, after molt larvae do not feed for 4 days; 30 larvae for 21-day test. Textile pulled into metal frame projector slide, termites gnaw through materials otherwise resistant, if covered with thin perforated film of termite-proof material.)

Grassé, P. P., 1956, *in* Autori, 1956, pp. 561-575. (Termite experiments, same instinct triggers building and feeding.)

Hrdý, I., Novák, V. J. A., and Škrobal, D., 1960, pp. 172-174. (Czechoslovakia, influence of the honeybee queen inhibitory substance on the development of supplementary reproductives in *Kalotermes flavicollis*.)

Klee, O., 1958, p. 20. (Germany, toxic effect of Thiodan on termites under different temperatures and humidities.)

Lüscher, M., 1958, pp. 69-70. (*Kalotermes flavicollis*, implantation corpora allata active in determination molting supplementary reproductives.)

Lüscher, M., and Karlson, P., 1958, pp. 341-345. (Classification of prothoracic gland hormone as a growth and differentiation hormone questionable.)

Pence, R. J., 1957a, pp. 91-95. (Fluorescent differentiation of internal organs and tissues, *Reticulitermes hesperus*, *Kalotermes minor*, and *Zootermopsis angusticollis* studied with ultraviolet radiation, adipose tissue, not chitin, fluoresced.)

Sebald, M., and Mellis, Y. de, 1958, pp. 357-360. (France, *Spherophorus*, n. sp., sulphite-reducing bacteria from intestine French termite injected in vein rabbit, toxic or allergenic, not infectious.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus*, nails inserted into mound nest to measure rate of growth, nest 2 ft. high 25 to 50 years old.)

1957, pp. 373, 390. (South Africa, *Kalotermes durbanensis*, effects temperature on protozoa, prefers newsprint.)

Springhetti, A., 1959, pp. 1-4. (Italy, mortality of *C. flavicollis* and *R. lucifugus* treated with diverse saline solutions.)

Springhetti, A., and Frizzi, G., 1957, pp. 395-396. (Italy, *Kalotermes flavicollis*, transplantation of endocrine organs.)

Verron, H., 1957, pp. 25-30. (France, *Calotermes flavicollis*, olfaction takes a part in reciprocal attraction between different individuals and density of grouping, no difference in responses between sexes.)

1958, pp. 309-314. (France, *Calotermes flavicollis*, olfaction attraction produced by last instar nymphs on larvae, nymphs with short wing pads, and neoteinics increases regularly with importance of crowding. Different types of individuals (soldiers excepted) do not react to last instar nymphs as well as they do to larvae. Soldiers exhibit a higher level of response toward nymphs, react in same way toward 10 nymphs or 20 larvae.)

Wybourn, J., 1958, pp. 171-172. (Reactions *Zootermopsis angusticollis* to variation in light and temperature.)

FLIGHT

Clagg, C. F., 1958, pp. 338-339. (*Coptotermes formosanus* flights Apr. 23, June 1957, Guam, Midway.

Clément, G., 1956, pp. 98-103. (*Anacanthotermes ochraceus,* Centres de Recherches, Béni-Abbès, Algeria, behavior workers, flights Jan. 31, May 10, humidity, temperature.

Coaton, W. G. H., 1958, pp. 1-112. (South Africa, *Hodotermes mossambicus* after rains Dec. to Feb., *Microhodotermes viator,* Aug. to Dec.)

Glick, P. A., 1960, p. 5. (U.S., Louisiana, Mississippi, Arkansas, at 200 ft. elevation *Reticulitermes virginicus* collected by airplane.)

Roonwal, M. L., 1958a, pp. 77-100. (India, *Neotermes bosei* flights from end Feb. to beginning July.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* after rains at the Cape, late Apr. or early May, 11 a.m. or 3 to 4 p.m., not all leave in first flight, 50 to 60 yd., small percentage survive predators.)

Spencer, G. J., 1957, p. 13. (British Columbia, *Zootermopsis angusticollis* Aug. 1, 1956, 150 to 200 ft., normally 300 to 500 ft. above ground, eaten by Bonaparte's gulls.)

Tang, C., and Li Shen, 1959, pp. 477-482. China, Hangchow, forecasting swarming *Reticulitermes flaviceps;* swarming usually mid-Mar. after spring rain, temperature and atmospheric pressure factors; sunny warm days, noon to 2 p.m. One swarm lasts 10 min. from small colony; in large, several swarms over successive favorable days.)

U.S. Dept. Agric., Plant Pest Control Div., 1959, p. 813. (*Reticulitermes flavipes* unseasonal swarm Providence, Rhode Island.)

Vishnoi, H. S., 1957, pp. 792-793. (India, Delhi, 7 species.)

Williams, R. M. C., 1959, pp. 203-218. (Africa, East Uganda, flight periods *Cubitermes ugandensis* and *C. testaceus,* wing shedding, calling attitude, tropisms, colony formation.)

FOLKLORE

Alphonse, E. S., 1957, p. 280. (Guaymi Indians, western Panama, victim bad dream put inside fence, heavy smoke caused by burning wood, termite nests, etc., to fumigate evil spirit.)

Gunther, J., 1953, pp. 291, 429, 680. (Africa, Bantu, dead buried in ant hills—the important individuals (p. 291); "One feature of the landscape, here (Jinja) as elsewhere in Uganda, is the procession of giant ant hills, which line the roads. They are jagged and craggy and often reach a height of 12 to 15 ft., towering like ugly sentinels; they are bright ocher red, and resemble mountain peaks in miniature. Oddly enough the *termites* or ants living in these fantastic structures contribute some form of chemical change to the earth, with the result that they make good as well as readily available material for road repair—earth harder and stickier than normal." (P. 429.) In Congo, on death a Bakutu is put into a termite hill, a simple procedure and quite sanitary. (P. 680.))

FOOD, TERMITES AS

Roonwal, M. L., 1958a, pp. 77-1000. (India, food of some tribes in Assam.)

FOSSIL

Buchsbaum, R., 1938, p. 332, fig. (Winged termite in amber.)

Emerson, A. E., 1958, *in* Weyer (Ed.), 1958, pp. 2798-2807. (In Age of Reptiles, evolved from roachlike ancestors. *Zootermopsis* and *Reticulitermes* confined to temperate regions, and fossils from Oligocene (Europe) and Miocene (Colorado) indicate these genera have been in temperate climates for at least 40 million years.)

Fenton, C. L., and Fenton, M. A., 1958, p. 247. (Winged termite in amber.)

Haupt, H., 1956, pp. 22-30. (Eocene, Termitina, 3 n. spp. in 3 n. gen., *Idomasto-*

termes mysticus, Eotermes multivenosus, Architermes simplex, Geiseltales.)

HURD, P. D., JR., and SMITH, R. F., 1957, pp. 6-7. (Mexican amber same age (Oligocene) as Baltic amber and shale from Florissant, Colo.)

HURD, P. D., JR., SMITH, R. F., and USINGER, R. L., 1958, p. 851. (Mexican amber, Chiapas, Mexico, Oligocene and Miocene, possibly some Eocene.)

MARTYNOVA, O., 1961, pp. 285-294. (General, fossil insects, including termites in references.)

PIERCE, W. D., 1958, pp. 13-24. (U.S., California, Miocene, *Cryptotermes ryshkoffi, Parastylotermes calico, Reticulitermes laurae, R. tibialis dubitans, Gnathamitermes magnoculus rousei,* n. sp.)

1959, pp. 72-78. (U.S., California, Miocene arthropods including termites among the insects, p. 76.)

RIEK, E. F., 1952, pp. 15-22. (Tertiary, Dinmore, Queensland, Australia, ?Eocene, *Blattotermes neoxenus,* Mastotermitidae, *M. wheeleri* (of Tennessee) to *Blattotermes,* n. gen.)

SANDERSON, M. W., and FARR, T. H., 1960, p. 1313. (Oligocene amber from Dominican Republic first reported by Christopher Columbus, 1494-1496. In 1959 near Pedro Garcia amber contained insects in several orders including Isoptera. Lists amber deposits of world.)

SNYDER, T. E., 1960, pp. 493-494. (Mexican amber, Oligocene, *Kalotermes nigritus* and *Heterotermes primaevus,* n. sp., winged.)

WEIDNER, H., 1955d, pp. 55-74. (Amber, in Geological States Institute, Hamburg, Germany.)

1956, pp. 363-364. (Amber, pellets, uncertain, only in Pleistocene?)

FUMIGATION

ANONYMOUS, 1957f, pp. 39, 41. (Ethylene dibromide and methyl bromide as soil fumigants.)

1957o, p. 37. (U.S., Oklahoma, *Kalotermes minor* introduced, 150 lb. methyl bromide and 2,000 lb. tarpaulins to fumigate house.)

1957p, pp. 16, 18, 20, 30. (Ethylene dibromide fumigation under slabs.

1958g, pp. 8, 10. (U.S., California, Structural Pest Act of California. Fumigation, 19 items of instruction, precautions, etc.)

1959k, p. 34. (U.S., Houston, Tex., large wooden drydock and pier infested by *Coptotermes crassus* fumigated with 20,000 lb. methyl bromide released into 3½ million cu. ft. of space tightly covered with plastic sheeting weighted on ends and dropped below water level, 24 to 48 hr. period for dock sections.)

1960i, pp. 60, 62. (U.S., Houston, Tex., successful fumigation with methyl bromide under tarps of large floating drydock infested by tropical *Coptotermes crassus* by Admiral Pest Control Co., of Bellflower, Calif.; fans were used for better circulation.)

1960n, pp. 50-51, 56. (U.S., equipment directory.)

BEECHEM, H. A., 1955, pp. 36, 50. (Methyl bromide left in applicator near lethal dosage for 20 min. in auto, operator recovered.)

BESS, H. A., and OTA, A. K., 1960, pp. 503-510. (Hawaii, *Cryptotermes brevis* infesting buildings, methyl bromide 2.5 lb. per 1,000 cu. ft. for 15 hr. effective within 23 of 24 buildings; mortality in exposed wooden block cages in 18 buildings varied from 10 to 100%. Sulfuryl fluoride at 2 lb. per 1,000 cu. ft. for 1.5 hr. killed all termites in blocks. Ethylene dibromide at 2 to 3 lb. per 1,000 cu. ft. for 24 hr. failed. Also gas failed in 2 out of 5 buildings. Sulfuryl fluoride in 8 buildings far superior to methyl bromide, also reduces exposure time. Methyl bromide far superior to ethylene dibromide.)

FORDE, E. L., 1958, pp. 18, 20. (Hawaii, *Cryptotermes brevis?,* methyl bromide under Fumiseal tents.)

GÖSSWALD, K., 1958, pp. 129-151. (Effect of carburetted hydrogen gas on *Calotermes flavicollis.*)

GRAY, H. E., 1960, pp. 43-46. (U.S., Vikane, sulfuryl fluoride, nonflammable, nonexplosive, noncorrosive, no objectionable odor or color, volatile, superior penetration, released from cylinders outside building; use fan for dispersion, 2 lb. per 1,000 cu. ft., at 55° F. and above, for 12 to 24 hr., aerate for 4 hr., fans for aeration, special detection devices. Fumigation for drywood termites as well as subterranean.)

HASSLER, K., 1960, pp. 36, 38, 40, 42. (U.S., ethylene dibromide greater penetrating power, dosage on 5 ft. centers 0.6 pt. per hole=3 gal. liquid per 1,000 sq. ft.; greater precautions required with lethal gases—do not wear gloves, keep skin dry, use halide lamp; 15% solution in petroleum solvent with flash point 350°, 3 pt. per hole.

Henderson, L. S., 1958, pp. 14, 16. (U.S., Div. Stored Product Insect Investigations in 1954 transferred to Marketing Research Div., Agricultural Marketing Service. Fumigation: measuring gas concentrations during fumigation and correction; use plastic film as tarpaulins.)

Hill, R. L., 1958, pp. 271-272. (Fumigation techniques, control *Cryptotermes dudleyi.*)

Kenaga, E. E., 1957, pp. 1-6. (Sulfuryl fluoride, no odor, nonflammable, 75.8 oz. per 1,000 cu. ft.)

Lance, W. D., 1958, pp. 9-10. (U.S., fumigation committee, Pest Control Operators California, proposed specifications, sealing, sampling gas (methyl bromide), injection hoses, circulation by fans, application, dosage, general provisions.)

1960, p. 6. (U.S., Houston, Tex., in fumigating floating drydock infested with *Coptotermes crassus,* termites will not eat water-soaked timber, usually stay above waterline, hence gas effective, penetrates wood.)

Monro, H. A. U., 1960, pp. 1-13. (General, modern fumigants for control of pests; the more important fumigants; treatments, residues, and tolerances; resistance; precautions.)

Padget, L. J., 1960, pp. 11-14. (U.S., Houston, Tex., program for eradication of *Coptotermes crassus,* a subterranean termite new to the U.S., at Todd Shipyards by fumigation with methyl bromide.)

Shaw, H. R., 1959, p. 13. (Panama, fumigation residence against drywood termites, use of tarpaulin.)

Stewart, D., 1957, pp. 7-11. (Sulfuryl fluoride, *Kalotermes minor,* California, not as toxic as methyl bromide to humans; only ⅓ lb. per 1,000 cu. ft. Vegetation killed, heavier than air; used above 45° F., forced circulation gas, no odor, nonflammable.)

Thornhill, F., 1955, pp. 16, 18. (Drywood termites.)

Young, T. R., 1955, pp. 45-46. (U.S., inexpensive heat-exchanger for methyl bromide drywood termite fumigation.)

FUNGI, ASSOCIATION WITH

Anonymous, 1960h, p. 65. (U.S., A. E. Lund (Koppers Co.) finds that a number of unidentified wood-destroying fungi may be antagonistic to subterranean termites, fungus *Lentinus lepideus* has definite influence.)

Bready, J. K., 1960, pp. 43-44. (U.S., studies 3 kinds microorganisms that interfere with termite diet. Methods for eliminating protozoa, fungi, and bacteria, the last-named with antibiotics.)

Lund, A. E., 1959a, pp. 320-321. (U.S., subterranean termites and fungi, mutualism or environmental association.)

1960, pp. 26-28. (U.S., presence of fungi or bacteria for prolonged existence of subterranean termites not resolved. (*Reticulitermes* spp. capable of initiating attack on sound yellow pine sapwood.)

1960a, pp. 40, 42, 44. (U.S., studies relationship termites and fungi. *Reticulitermes flavipes* and *virginicus* capable of attacking sound yellow pine. Nutritional needs. Degrees compatibility specific wood-destroying fungi with termites in order of decreasing compatibility to *R. flavipes:* 1, *Poria incrassata;* 2, *Lenzites trabea, Polyporus versicolor;* 3, *Poria monticola;* 4, *Lentinus lepideus;* last has definite antagonistic influence.)

FUNGUS CULTIVATION

Coaton, W. G. H., 1961, pp. 39-54. (Africa, Macrotermitinae, conidia of agaric *Termitomyces* fungi eaten by termites, symbiotic, fruiting bodies brought to surface.)

Grassé, P. P., and Noirot, C., 1957a, pp. 1845-1850. (Africa, Macrotermitinae.)

1958b, pp. 113-128. (Africa, Macrotermitinae, association with *Termitomyces,* construction of fungus garden.)

1958c, pp. 515-520. (Africa, Macrotermitinae, types nests.)

Hesse, P. R., 1957, pp. 104-108. (East Africa.)

Kalshoven, L. G. E., 1956a, pp. 455-461. (Java, *Macrotermes gilvus,* accumulations of finely cut vegetation in nests—wood particles, bark, leaves, grass, etc.)

Roonwal, M. L., 1958a, pp. 77-100. (India, agaric in mounds *Odontotermes obesus,* pH combs acidic.)

Sands, W. A., 1956a, pp. 531-536. (Africa, Kenya, Nairobi, *Odontotermes badius,* fungus comb maintains high humidity and heat, fungus only a parasite, not cultivated by the termites.)

GASEOUS ENVIRONMENT

Grassé, P. P., and Noirot, C., 1958a, pp. 1-28. (Behavior of termites with relation to atmosphere and air of nest and its renewal. Calotermitidae and Rhinotermitidae as well as humivorous African Termitidae (Apicotermitinae, Termitinae), except for *Anoplotermes,* do not need fresh air. Hodotermitidae, Macrotermitinae and Nasutitermitinae may go out to collect food, termitaria do not communicate directly with external air, no ventilation except by diffusion through walls. An undisturbed atmosphere necessary.)

Lüscher, M., 1955a, pp. 289-307. (Africa, Ivory Coast, Uganda, *Macrotermes natalensis,* mechanisms for a supply of oxygen for nests.)

1956a, pp. 273-276. (Africa, Ivory Coast, *Macrotermes natalensis,* air circulates in nest, heated in fungus combs in center, driven through channels downward through the wall, cooled air rises into nest again; in Uganda similar aeration system.)

Shimizu, K., 1959, pp. 267-271. (Formosa, expiration carbon dioxide.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* 15% CO_2 in nest.)

GENITALIA

Gelmetti-Bonomi, L., 1958, pp. 48-54. (*Calotermes flavicollis,* many anucleated spherules present in seminal vesicles resproductives, drops RNA (ribonucleic acid) trophic material for sperms.)

Noirot, C., 1958, pp. 557-559. (The appearance of heterologous gonoducts in the course of development of termites, cockroaches, and Orthoptera.)

Roonwal, M. L., 1955b, pp. 107-114. (External genitalia.)

In Tuxen (Ed.), 1956, pp. 34-38. (External.)

Snodgrass, R. E., 1957, p. 19. (Phallic organs greatly reduced.)

Weesner, F. M., 1955, pp. 323-345. (U.S., Arizona, *Tenuirostritermes tenuirostris,* internal, external, references to other publications on genitalia.)

GEOLOGIC AGENTS

Boyer, P., 1956, pp. 95-103. (Tropical Africa, action of termite structures on certain soils, *Bellicositermes natalensis, B. rex,* and *Thoracotermes brevinotus.*)

1956a, pp. 105-110. (Tropical Africa, *Bellicositermes natalensis,* the ingredients of the termitarium.)

De la Rüe, E. A., Bourlière, F., and Harroy, J. P., 1957, p. 151. (In Oubangui Chari, Africa, mounds of *Bellicositermes rex* 130 to 1,600 cu. yd. in volume, bring up clay from lateritic stratum, upward transport of clay. In savannas in Guinea, influence flora and fauna soils by mining. Their mass per unit surface area is equal to one-half entire microfauna, earthworms excepted.)

Robinson, J. B. D., 1958, pp. 58-65. (Africa, Kenya coffee fields, *Odontotermes badius* activities in soil decrease length effective mulch life, termite soil material has higher percent calcium plus magnesium and higher pH value than topsoil or subsoil.)

Shipman, R. F., 1958, pp. 23-24. (Africa, Rhodesia, anthills in sandy soils a valuable asset.)

HUMIDITY

Ernst, E., 1956, pp. 229-231. (In laboratory, reaction of termites to humidity, *Nasutitermes* 1 hr., *Kalotermes* and *Reticulitermes* 72 to 48 hr., *Zootermopsis* 3 to 6 hr.; receptors on antennae.)

1957, pp. 97-156. (Influence of humidity on duration of life and behavior of termites. *Kalotermes flavicollis* reacts in 3 days, *Reticulitermes lucifugus* in 2 days, *Zootermopsis nevadensis* in 5 to 6 hr., *Nasutitermes arborum* in 1 hr.)

Pence, R. J., 1957b, pp. 28-30. (*Reticulitermes hesperus* in laboratory, optimum moisture 97.5%.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus* seek humid atmosphere in artificial nest, shun dry part, where calcium chloride has absorbed water vapor.)

INTRODUCED

Anonymous, 1958j, p. 86. (U.S., Florida, *Nasutitermes nigriceps* (Hald.) winged in dead orchid pseudopods at Miami, Dade County.)

Dorward, K., 1956, p. 57. (U.S., Houston, Tex., *Coptotermes crassus* in dry dock, control by burning.)

Fullaway, D. T., and Krauss, N. L. H., 1945, pp. 21-23. (Hawaii, *Cryptotermes* present since 1904, *Coptotermes* since 1913.)

Harris, W. V., 1955e, pp. 366-367. (*Zootermopsis angusticollis* in Douglas fir from western Canada to England.)

1955f, pp. 36-37. (*Kalotermes jouteli* in lignum vitae lumber from Santo Domingo; *Zootermopsis angusticollis* in Douglas fir from North America to England.)

Heisterberg, W., 1959, pp. 142-143. (Austria, introduction and radical eradication possibility.)

Hickin, N., 1957, p. 23. (East Africa, *Cryptotermes brevis* from West Indies.)

1961, pp. 26-27. (England, colony of *Cryptotermes brevis* Walk., from Port-of-Spain, Trinidad; 5th known record of accidental importation; found in gramophone when household goods unpacked.)

Kurir, von A., 1958, pp. 1-15. (*Reticulitermes flavipes* introduced to Hallein (Salzburg) Austria—47.5° north latitude—in 1955, by way of Vienna, from Hamburg, Germany, in wooden boxes.)

1958a, pp. 84-87. (More data on above.)

Moszkowski, L. I., 1955, pp. 15-41. (*Cryptotermes kirbyi* n. sp., from Madagascar and *C. havilandi* from Africa and introduced into Madagascar, India, and South America.)

Schmidt, H., 1958, pp. 226-228. (Europe, experiences with introduced termites.)

Snyder, T. E., 1957, p. 30. (Danger of introduction of subterranean termites in ships.)

1957e, p. 92. (Danger of introduction of subterranean termites in ships.)

1959, p. 6. (U.S., Houston, Tex., *Coptotermes,* introduced, spread from drydock to waterfront structures, *Kalotermes nigritus* in logs from Guatemala, intercepted at San Francisco, Calif.)

U.S. Dept. Agric., Plant Pest Control Div., 1957, p. 651. (U.S., *Kalotermes minor* infesting building in Oklahoma.)

Wichmann, H. E., 1957, pp. 183-185. (Circumstances of importation of termites in families Kalotermitidae, Rhinotermitidae, and Termitidae, observations on *Zootermopsis angusticollis* and *Reticulitermes flavipes.*)

LEGISLATION

Anonymous, 1960r, p. 1. (U.S., California, Assembly Bill 1930, financial responsibility law holds operator in amount of $25,000 for personal or bodily injury and $25,000 for property damage, minimum cost under $100 per year; law does not limit liability to $25,000, suit can be brought for greater amounts.)

Bruer, H. L., 1960, pp. 66, 68, 70-72. (U.S., Tennessee, inadequate financing, personnel, operations stifle enforcement termite laws. PCO's required to pay for own regulation, trained personnel impossible to employ at salaries offered, minimum standards become maximum, routine inspections necessary. Violations due to ignorance, arrogance, fraudulent intent. Cost enforcement $25,000 per year at start, now higher.)

Concienne, E. A., 1959, pp. 40, 44. (U.S., Louisiana, either university degree in entomology or 4 years' experience working for state license holder. $2,000 surety bond posted, renewed yearly, report number jobs, pay $3 (reduced from $5) for each job, pays for inspection termite jobs.)

Du Chanois, F. R., 1960, pp. 37-39. (U.S., Florida, Structural Pest Control Act of 1959 strengthens Structural Pest Control Commission, liberalizes provisions of law favoring the industry; latter encouraged to become self-regulating; industry services based on applied entomology, indebted to entomology for its origin and present stature.)

1960a, p. 84. (U.S., Florida, commissions for structural pest control composed of nonindustry members more effective, wood treating should be licensed, large amount of preserved lumber in existing structures goes under guise of nonstructural pest control.)

Hoag, R., 1959, pp. 3-5, 9. (U.S., California, discussion new rules and regulations Structural Pest Control Board, and suggestions from industry for changes.)

Lewis, J. W., 1960, pp. 6-7. (U.S., New York, Buffalo, since 1944 law binding pest control operators flouted by nonlicensed workers without complying with the ordinance.)

Nelson, J. A., 1960a, pp. 6-7. (U.S., list States which license pest control operators: Alabama, Arkansas, California, Connecticut, Florida, Georgia, Kansas, Kentucky, Louisiana, Mississippi, North Carolina, Oklahoma, Tennessee—13 States in all. Cities in other States with such laws: District of Columbia; Cincinnati, Cleveland and Columbus, Ohio; New York City; Pasadena, Calif.; San Antonio, Houston, and La Porte, Tex.; 9 such cities, not a complete list.)

North Carolina Structural Pest Control Commission, 1960, pp. 5-6. (U.S., North Carolina, heptachlor approved as soil poison for termite control.)

Penn, L. A., 1960, p. 7. (U.S., Wisconsin, Milwaukee, exterminators who work with poisons and fumigants require license.)

Pest Control Operators California, 1953, pp. 1-11. (U.S., California, explanation terms accepted standards; inspection reports; good practice; recommendations.)

Plummer, J. M., 1960, p. 6. (U.S., Texas, Galveston and La Marque have city ordinance regulating pest control.)

Popham, W. L., 1960, pp. 4-7, *in* U.S. Dept. Agric., ARS Publ. 20-9, 1960. (U.S., functions Dept. Agric. and Dept. Health, Education, and Welfare in regulation pesticides.)

Robinson, M. C., 1960, p. 6. (U.S., Arizona, Maricopa County, requires license for pest control operators in Phoenix and other cities in county.)

Sheboygan, City of, 1957, p. 1. (U.S., to control spread of termites and provide protection of buildings, any structure, post, wooden article or building or part thereof infested with termites declared public nuisance; after inspection, public nuisances must be abated on advice provided by Building Inspection Dept. or the work done and costs charged against property as special tax, 146.14 (5) Wisconsin Statutes. No soil, fill, or building shall be moved without prior inspection—cost $1, violation forfeiture of $100 plus costs prosecution, or imprisonment for 30 days in county jail.)

Structural Pest Control Board California, 1953, pp. 1-26. (U.S., amendments on licenses, examinations, and fraud structural pest control act of California.)

Taylor, A. F., 1960, p. 7. (U.S., Texas, Pasadena, new ordinance passed for regulation pest control operators.)

MEDICINE, USES IN

Anonymous, 1957c, p. 5. (Panama, medicine is the supreme secret among the Guaymi Indians, according to Rev. Ephrain S. Alphonse, Wesleyan Methodist missionary. Certain sores, like those of yaws, are smoked. A hole is dug in the ground, the nest of a colony of wood termites is broken and put in, and a fire is set. This gives off a heavy smoke which rises for hours. An affected leg is held over this smoke for a whole day while the patient lies prostrate. The cure, Mr. Alphonse says, usually works so far as the sore is concerned.)

MORPHOLOGY

Banerjee, B., 1958, pp. 56-57. (India, *Odontotermes redemanni,* changes in cellular morphology oocytes, at different stages of development, in ovaries mature queen.)

Barth, R., 1955, pp. 257-263. (Brazil, *Syntermes dirus,* tergite glandular areas.)

Ernst, E., 1959, pp. 289-295. (Observations on the nasus in *Nasutitermes* soldiers.)

Gelmetti-Bonomi, L., 1958, pp. 48-54. (*Calotermes flavicollis,* many anucleated spherules present in seminal vesicles and reproductives as drops of RNA (ribonucleic acid) represent trophic material for sperms.)

Gupta, S. D., in press. (India, primitive termite *Anacanthotermes macrocephalus.*)

Jucci, C., 1959, pp. 16-28. (In the Mastotermitidae and Calotermitidae the tentorial gland occupies an extracephalic position as in the Blattidae, an ancestral condition. It probably originated in the thorax.)

Kushwaha, K. S., 1955, pp. 203-204. (India, *Odontotermes obesus,* external morphology soldier.)

1959, pp. 298-299. (India, *Odontotermes obesus,* external morphology worker and alate.)

1959a, pp. 415-417. (India, *Odontotermes obesus,* chaetotaxy soldier, worker, alate.)

McMahan, E. A., 1960, pp. 270-272. (Hawaii, external sex characteristics *Cryptotermes brevis* and *Kalotermes immigrans,* sterna and styles differentiate sexes.)

Morgan, F. D., 1959, pp. 155-195. (New Zealand, *Stolotermes ruficeps,* external morphology.)

Mosconi, P. B., 1958, pp. 77-90. (Study tentorial glands, "corpora allata," and neurosecretory cells *Mastotermes darwiniensis,* close affinity with Blattoidea. Glands composed of two parts, one in head, one in neck, structurally different. Neurosecretory cells with variable dimension in brain, in subesophageal and prothoracic ganglion.)

1958a, pp. 129-139. (*Zootermopsis angusticollis* in nymphal stage endocrine system studied. Neurosecretory cells in protocerebrum and in ganglia ventral chain. Corpora allata have round form and small or large cells, with uniform character. Tentorial (prothoracic) gland shows extracephalic part much greater than retrocerebral one. Cells very chromophilous, in intracellular spaces small black granules, perhaps a Gomori-positive material.)

Mukerji, D., and Banerjee, B., 1955, pp. 289-290. (India, *Odontotermes redemanni,* mouthparts.)

Noirot, C., and Kovoor, J., 1958, pp. 439-471. (Africa, Termitinae, study digestive tract 19 of 22 genera. From anatomical variations, two types tracts correspond to two lines evolution. Under *Thoracotermes* type: *Apilitermes, Crenetermes, Megagnathotermes, Orthotermes, Basidentitermes Fastigitermes, Probositermes, Cubitermes, Procubitermes, Noditermes, Tuberculitermes, Ophiotermes,* and *Euchilotermes;* the gizzard is simple, the enteric valve is complex, a blind diverticulum is present on second pouch of hindgut. Among *Termes* and allied *Pericapritermes, Capritermes,* and *Promirotermes,* the internal wall gizzard is covered with longitudinal folds, as in lower termites, simpler enteric valve, second pouch hindgut without blind diverticulum. *Ceratotermes* classification difficult.)

Obenberger, J., 1952, pp. 1-869. (Anatomy and morphology.)

Richard, G., 1956, pp. 487-489. (France, *Calotermes flavicollis,* nerves and tracheae.)

Roonwal, M. L., and Chhotani, O. B., 1960, pp. 125-132. (Tibial spur formula for *Coptotermes* 3:2:2 based on study 32 world species.)

Schmidt, H., 1956a, pp. 115-125. (Nourishment organs and biology.)

1959, pp. 79-86. (Nourishment organs and biology of nutrition, grinding, and predigestion. Importance of proventriculus in *Macrotermes natalensis* different. Basically gizzard consists of 12 chewing plates, thickened chitinized projections of the inner cuticular layer of the foregut, different in each species and provided with teeth and ridges. Gizzard activated by muscles. Opposed chewing plates have grinding effect and break up solid food (wood) into food (mechanical predigestion). Padlike lobes ("wing folds") reaching from the chewing plates into the cardiac valve press back the chewed food into the crop. Important proventriculus "social feeding organ," food ground and fed growing larvae as a brei rich in carbohydrates.)

Springhetti, A., 1957b, pp. 333-349. (Italy, *Kalotermes flavicollis,* tentorial glands (ventral, prothoracic) and corpora allata.)

Vishnoi, H. S., 1956, pp. 1-18. (India, *Odontotermes obesus,* structure, musculature, and mechanism of feeding apparatus of various castes.)

1956a, pp. 45-46. (India, *Odontotermes obesus,* cephalic musculature.)

Weidner, H., 1955e, *in* Schmidt, H. (Ed.), 1955b, pp. 5-81. (Body structure.)

Zuberi, H. A., 1959, pp. 288-291. (Africa, architecture of brain *Ancistrotermes latinotus* and *A. crucifer* figured.)

1959a, pp. 3341-3343. (Africa, *Trinervitermes tchadensis* structure of brain in relation to polymorphism, brains minor and major soldiers and workers discussed.)

1960, pp. 3506-3508. (Palearctic, structure of brain of *Anacanthotermes ochraceus,* a primitive harvester termite; differences in brains castes.)

NESTS

Aubreville, A., 1959, pp. 21-24. (Africa, Ghana, termitaria aligned on savanna and in brush on plains.)

Banerjee, B., 1956, p. 742. (India, *Odontotermes redemanni,* mounds.)

Barros-Machado, A., 1957, pp. 80-81. (Architecture and evolution of African *Apicotermes* nests.)

Boyer, P., 1956, pp. 95-103. (Africa, tropical, action of termitaria on certain soils, *Bellicositermes natalensis, B. rex. Thoracotermes brevinotus.*)

1956a, pp. 105-110. (Africa, tropical, the ingredients of the termitarium of *Bellicositermes natalensis.*)

Coaton, W. G. H., 1958, pp. 1-112. (South Africa, *Hodotermes mossambicus* and *Microhodotermes viator* mounds, soil dumps, nest system.)

De la Rüe, E. A., Bourlière, F., and Harroy, J. P., 1957, pp. 27, 48, 100, 127, 139, 148, 151. (Tropics, tree nests in Panama, mushroom-shaped nests West Africa, magnetic nests *Amitermes meridionalis,* Australia; in savannas in Guinea their mass per unit surface area is equal to one-half entire microfauna, earthworms excepted; eat humus. Influence flora and fauna soils by mining, mounds *Bellicositermes rex* 130 to 1,600 cu. yd. in volume, bring up clay from lateritic stratum, upward transport of clay.)

Desneux, J., 1956, pp. 1-12. (Africa, atypical subterranean nests *Apicotermes lamani.*)

1956a, pp. 92-97. (Africa, *Apicotermes rimulifex* nests.)

1956b, pp. 277-281. (Africa, *Apicotermes lamani,* atypical subterranean nests.)

1958, pp. 281-285. (Africa, *Apicotermes arquieri* double nests.)

1959, pp. 286-292. (Africa, *Apicotermes rimulifex* nest Belgian Congo, ancestral type related to *A. arquieri* and *occultus* while *holmgreni* and *trägårdhi* are still more primitive in morphology and behavior with nests without pores in walls.)

Emerson, A. E., 1956, pp. 248-258. (Regeneration nest structures, ventilation mechanisms, homeostasis of nests.)

Fonseca, J. P. C. da, 1959a, pp. 705-719. (Portuguese Guinea, nests in landscape, various types figured.)

Grassé, P. P., 1958, pp. 189-200. (Brazil, São Paulo, *Cornitermes cumulans,* subterranean nest transformed later into mound nest 1.60 m. high, base diameter 0.95, queen moves about in nest.)

Grassé, P. P., and Noirot, C., 1948, pp. 869-871. (Africa, the climatization of the nest by its inhabitants and the transportation of water.)

1957, pp. 974-979. (French Equatorial Africa, giant mounds.)

1958c, pp. 515-520. (Africa, 3 types nest, *Odontotermes, Bellicositermes, Sphaerotermes,* etc., with and without paraécie, habitacle, exoécie, or large canals to exterior not communicating with nest proper; habitacle, where population assembles and true royal cell; paraécie, open space isolates habitacle. Nests of soil chiefly clay cemented with saliva, royal cell, macerated vegetation in fungus garden. *Sphaerotermes* royal cell constructed of excrement, no fungus garden, absence of partition of habitacle.)

Harris, W. V., 1954-1955, p. 35. (Africa, Angola, *Apicotermes* nests.)

1956, pp. 261-268. (Eastern Africa, mound building.)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands.)

Hartwig, E. K., 1956, pp. 629-639. (Africa, *Trinervitermes,* population distribution in nests.)

Jongen, P., and Oosten, M. van, 1956, p. 247. (Africa, Ubangi soil of a mound nest.)

Kalshoven, L. G. E., 1956, pp. 269-272. (Java, *Macrotermes gilvus,* inner structure mounds.)

Kevan, D. K. McE., 1956, pp. 498-499. (SE. Ethiopia, Ogaden, massive termitaria.)

Leleup, N., 1955, pp. 374-375. (Africa, Belgian Congo.)

1960, pp. 197-206. (Africa, Belgian Congo, types nests described.)

Noirot, C., 1959, pp. 179-184. (Vietnam, nests *Macrotermes gilvus* common in paddy fields of Mekong plain, Cambodge, inundated several months of year, architecture nests compared with those of other regions; fungus gardens supply food reserves during floods.)

1959a, pp. 259-269. (Vietnam, Cambodge (Indochina), *Globitermes sulfureus* builds intricate nest, modified in rice marshland. Soil, excrement (ligneous), and wood fragments (cellulose) used in nest building, earth exterior, inner wall excrement, more internal regions replaced by vegetal material. Wood fragments for food reserve.)

Pathak, A. N., and Lehri, L. K., 1959, pp. 87-90. (India.)

Rand, A. L., and Brass, L. J., 1940, pp. 358. (New Guinea, Mabadauan savannas southern New Guinea very large pinnacled nests 3 ft. in height, characteristic feature, plate 33.)

Schmidt, R. S., 1955, pp. 344-356. (Africa, *Apicotermes* nests important ethological material.)

1955a, pp. 157-181. (Idem, evolution nest building.)

1958, pp. 76-94. (Africa, *Apicotermes trägårdhi,* evolution of nest-building, most primitive lack wall perforations, shagreen, internal arrangement cellular.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus* mound nests 2 ft. high, 25 to 50 years old.)

Vishnoi, H. S., 1955, pp. 143-144. (India, *Odontotermes obesus,* royal cell with unusually large openings.)

1955a, p. 291. (India, *Odontotermes obesus* mounds.)

Weidner, H., 1955a, pp. 201-207. (Africa, Angola, nest of *Apicotermes machodoensis,* n. sp.)

Weidner, H., *in* Schmidt, H. (Ed.), 1955b, pp. 82-120. (Nests, Tropics, phylogeny *Apicotermes* nests; nests in temperate regions, tubes.)

NUTRITION

Alibert, J., 1960, pp. 4205-4206. (France, *Kalotermes flavicollis* trophallactic exchanges between sexual and larvae in young and more aged colonies.)

Bready, J. K., 1960, pp. 43-44. (U.S., studies 3 kinds microorganisms that interfere with termite diet. Methods eliminating protozoa, fungi, and bacteria—latter with antibiotics.)

Gay, F. J., Greaves, T., Holdaway, F. G., and Wetherly, A. H., 1955, pp. 1-60. (Australia, food preferences.)

Henry, T. R., 1958, p. 45. (Canal Zone, Panama, eat lead, thrive on arsenic.)

Lund, A. E., 1960a, pp. 40, 42, 44. (U.S., studies relationship termites and fungi. *Reticulitermes flavipes* and *virginicus* capable attacking sound yellow pine. Nutritional needs. Degrees compatibility specific fungi with termites, some have definite antagonistic influence.)

Pence, R. J., 1956b, pp. 238-240. (*Reticulitermes hesperus* prefers black dyed wood.)

1957, pp. 44, 58. (Stucco and cement digested by *Reticulitermes hesperus.*)

Schmidt, H., 1956a, pp. 115-125. (Organs and biology nutrition.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* eat decayed stems plants, cow pats, decayed wood, 20,000 termites devour 500 times own volume in one year.)

1957, pp. 373-390. (South Africa, *Kalotermes durbanensis* prefers newsprint paper.)

Tracey, M. V., and Youatt, G., 1958, pp. 70-72. (Australia, cellulase and chitinase in two species of Australian termites.)

OBITUARY

Anonymous, 1960f, p. 46. (Karl Hassler, 1898-1960.) (Fumigation to control termites in U.S.)

Bullock, T. H., 1947, pp. 483-484. (S. F. Light, 1886-1947.)

Conklin, E. G., 1951, pp. 433-434. (Harold Heath, 1868-1951.)

Cronin, J. E., 1960, p. 25. (Hermann von Schrenk, 1873-1953.) (Experiments on soil poisons and wood preservatives.)

Pemberton, C. E., 1960, pp. 332-333. (Otto Hermann Swezey, 1869-1959.)

1960a, pp. 182-185. (Otto Hermann Swezey, 1869-1959.) (Notes on termites in Hawaii from 1914-1954.)

Snyder, T. E., Graf, J. E., and Smith, M. R., 1961, pp. 68-73. (William M. Mann, 1886-1960.) (Collected termites on expedition to Tropics, described new termitophiles.)

Snyder, T. E., Wetmore, A., and Porter, B. A., (1959) 1960, pp. 1231-1232. (James Zetek, 1886-1959.) (Termite tests in the Canal Zone, Panama.)

PARASITES

Buchli, H., 1960, pp. 1320-1321. (France, ectoparasite *Antennopsis gallica* on *Reticulitermes lucifugus, santonensis,* out of 20 young colonies, 15 are dead 11 to 13 months after foundation.)

1960a, pp. 3365-3367. (Madagascar, *Antennopsis grassei* parasite on *Neotermes amplus, N. desneuxi,* and *Glyptotermes longiceps,* also on eggs.)

Dieuzeide, R., 1930, pp. 569-571. (North Africa, Tyroglyphid *Caloglyphus* with *Reticulitermes.*)

Gallo, F., 1955, pp. 134-142. (Italy, *Tyrolichus casei* parasitic mite attacking laboratory colonies *Kalotermes flavicollis* and *Reticulitermes flavipes.*)

Oudemans, A. C., 1928, p. 313. (Acarine, *Caloglyphus feytaudi,* n. sp., parasite of *Reticulitermes lucifugus,* North Africa and Spain.)

Pérez, C., 1908, p. 631. (France, *Duboscquia lezeri,* new microsporidian parasite of *Termes lucifugus.*)

Séguy, E., 1935, p. 181. (China, *Hylemyia cana,* Muscid, *Idia flavipennis,* Calliphorid, *Termes fukiensis*? nests, *Reticulitermes fukiensis.*)

1953, p. 9. (Morocco, Calliphoridae: *Rhynchoestus weissi,* Maroc saharien, ectoparasite *Hodotermes ochraceus.*)

1955, pp. 166-177. (Madagascar, Calliphorid, *Rhynchomyia anterotes,* n. sp., parasite of *Coarctotermes clepsydra;* records of 4 other species associated with termites.)

Senior-White, R., et al., 1940, pp. 188-189, 192-194, 197. (British India, Diptera, *Borbororhina bivittata* attracted to freshly opened *Eutermes* mounds, also *Stomorhina luteigaster.* Calliphoridae: *Stomorhina discolor, Stomorhina lunata* beneath termite infested cow dung, Telinkheri, Nagpur, from white ants nest).

Toumanoff, C., and Toumanoff, T. C., 1959, pp. 216-218. (France, epizootic due to *Serratia marcescens, "Reticulotermes santonnensis."*)

PHYLOGENY

Emerson, A. E., 1960, pp. 1-28. (Oriental, Malagasy, and Australian regions, phylogeny Nasutitermitinae, separate origin nasute soldier in two major branches; imago-worker mandibles valuable in taxonomy. Subfamily arose in Neotropical region; *Subulitermes* branch, paralleling *Nasutitermes* branch, had spread to all tropical regions by mid-Cretaceous time. No species from Papuan region. Imago-worker dentition trend toward proportional enlargement apical teeth compared to first marginal tooth. Vestigial mandibles of soldier have lost apical points in *Subulitermes.*)

1960a, pp. 1-21. (Africa, phylogeny 4 new genera on *Subulitermes* branch Nasutitermitinae, from Belgian Congo.)

1960b, pp. 1-49. (Africa, Belgian Congo, phylogeny 6 new genera Termitinae.)

PHYSIOLOGY

Clark, E. W., and Craig, R., 1953, pp. 101-107. (U.S., calcium and magnesium content in the haemolymph of adult *Zootermopsis angusticollis.*)

Grégoire, C., 1957, p. 9. (Canal Zone, Panama, *Cryptotermes,* coagulation haemolymph pattern 1, inception of plasma in shape of islands of coagulation around hyaline hemocytes.)

Howell, D. E., 1960, pp. 12, 14, 16. (U.S., some chlorinated hydrocarbons, etc., may enter insect body in more than one way; oil solutions act more quickly than water, nervous system affected by DDT, etc.; inhibition of enzymes by parathion, etc., organophosphates.)

Jucci, C., 1958, pp. 475-479. (Italy, resistance of termites to insecticides.)

Roeder, K. D. (Ed.), 1953, pp. 94, 130, 277, 307, 323-324, 337-338, 344, 385, 482, 667, 677, 697, 748, 751-753, 755, 757, 761, 765, 768-770, 774-777, 779, 827, 853. (Termite physiology.)

POPULATION

Desneux, J., 1956, pp. 1-12. (Africa, *Apicotermes lamani,* coordination of collective work of workers in nest construction; atypical subterranean nests illustrated.)

Hartwig, E. K., 1956, pp. 629-639. (Africa, population distribution *Trinervitermes* nests.)

Heinzelin, J. de, 1955, pp. 1-37. (Africa, tropical, termite populations.)

Lüscher, M., 1955a, pp. 289-307. (Africa, Ivory Coast and Uganda, *Macrotermes natalensis,* 2 million population large mound.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* 40,000 individuals in mound 12 in. high in winter, probably never exceeds 50,000.)

PREDATORS

Anonymous, 1957e, p. 20. (U.S., Washington, D.C., Zoo, damage to photo file by termites, control by *Tamandua.*)

Beier, M., 1930, pp. 44-48. (West Africa, pseudoscorpions, *Pilanus pilatus* and *pilifer* in termite nests.)

Brackbill, H., 1955, pp. 260-261, 282. (U.S., birds and termites, flying, species of *Reticulitermes.*)

Calaby, J. H., 1956a, pp. 93-96. (West Australia, food habits of *Myobatrachus gouldi,* white anteater.)

1960, pp. 79-80. (W. Australia, desert frogs feeding on termites.)

1960a, pp. 143-146. (SW. Australia, marsupial "numbat" (*Myrmecobius*) eats *Coptotermes acinaciformis,* lives in hollow eucalyptus logs—small banded anteater.)

1960b, pp. 183-207. (SW. Australia, marsupial numbat (*Myrmecobius f. fasciatus*) feeds on termites and ants.)

Chamberlin, R. V., 1925, pp. 35-44. (Canal Zone, Panama, Barro Colorado Island, chilopods (centipedes) found with termites: *Cryptops zeteki* with *Mirotermes panamaensis, Cryptops* sp. with *Obtusitermes biformis, Physida nuda* with *Leucotermes tenuis, Cupipes ungulatus* with *Eutermes* sp., *Orphnaeus brevilabiatus* with *Nasutitermes columbicus* and *Anoplotermes parvus,* probably all predators.)

1926, p. 10. (Canal Zone, Panama, centipede *S.* (*Schendylotyn*) *integer* Chamberlin in nest of *Anoplotermes gracilis* Snyder.)

1944, p. 187. (New Hebrides, centipede *Mecistocephalus consocius,* n. sp., with *Kalotermes* (*Neotermes*) *sanctaecrucis.*)

De la Rüe, E. A., Bourlière, F., and Harroy, J. P., 1957, pp. 147, 151. (Tropics, in Africa ants *Megaponera* and *Pallothyreus;* in savannas anteaters, aardvark and pangolin.)

Gregg, R. E., 1958, pp. 111-121. (Madagascar, *Metapone madagascarica* and *emersoni,* ants in rotten wood with termites.)

Guido, A. S., and Ruffinelli, A., 1958, p. 919. (Montevideo, predaceous wasp (*Cryptocheilis* sp.) paralyzes *Nasutitermes.*)

Henry, T. R., 1958, pp. 21, 49. (*Tamandua;* snakes Typhlopidae and Glauconidae prey on termites, snakes eat eggs and young.)

Hunt, R., 1958, p. 58. (U.S., San Diego, Calif., dermestids *Trogoderma ornatum* scavengers on dead *Kalotermes minor.*)

Krantz, G. W., 1958, pp. 127-131. (U.S., Oregon, Diplogynid mite *Lobogyniella trägårdhi* associated with *Zootermopsis angusticollis.*)

Main, A. R., and Calaby, J. H., 1957, pp. 222-223. (NW. Australia, termites as food of frogs.)

Odhiambo, T. R., 1958, pp. 167-175. (Africa, Uganda, hemipteron, reduviid (*Acanthaspis petax*) in mounds.)

Roonwal, M. L., 1958a, pp. 77-100. (India, rats in Assam, anteaters, lizards, birds.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* at time of swarm few survive predators, in nests red and white mites, solpugid.)

Spencer, G. J., 1957, p. 13. (British Columbia, *Zootermopsis angusticollis* winged eaten by Bonaparte's gulls.)

Von Porat, C. O., 1894, p. 25. (Cameroon, centipede in tunnels termite hills.)

Weidner, H., 1955a, pp. 201-207. (Africa, Angola, struggle between soldier *Pseudacanthotermes militaris* and soldier of a forest ant *Dorylus* (*Typhlopone*) *fulvus dentifrons.*)

1957, p. 109. (Germany, Hamburg, carabid larvae as enemy of termites, *Reticulitermes flavipes* preyed on by *Harpalus aeneus* and *Pterostichus vulgaris?*)

Werner, F., 1935, p. 470. (Africa, Portuguese Guinea, whipless whipscorpion *Paracharon caecus* in termite nest.)

PROTOZOA

Ansari, M. A. R., 1955, p. 62. (Pakistan, Lahore, Mastigophora: Retortamonidae, *Retortamonas termitis, Amitermes beaumonti,* Panama.)

Chakravarty, M. M., and Banerjee, A. K., 1956, pp. 35-44. (India, holomastigotid and trichonymphid flagellates from an Indian *Heterotermes.*)

Cleveland, L. R., 1955, pp. 511-542. (U.S., hormone-induced sexual cycles of flagellates, unusual behavior of gametes and centrioles of *Barbulanympha.*)

1958, pp. 47-62. (U.S., factual analysis of chromosomal movement in *Barbulanympha,* depends on number and position of poles.)

1958a, pp. 63-68. (U.S., movement of chromosomes in *Spirotrichonympha* to centrioles instead of the ends of central spindles.)

1958b, pp. 105-115. (U.S., photographs of fertilization in the smaller species of *Trichonympha.*)

1958c, pp. 115-122. (U.S., photographs of fertilization in *Trichonympha grandis,* a protozoan in *Cryptocercus,* difference in fusion gametes.)

1960, pp. 326-341. (General, the centrioles of *Trichonympha* from termites and their function in reproduction.)

Cleveland, L. R., and Burke, A. W., 1956, pp. 74-77. (Effects of temperature and tension on oxygen toxicity for protozoa of *Cryptocercus.*)

Cleveland, L. R., and Nutting, W. L., 1954, pp. 785-786. (U.S., protozoa as indicators of developmental stages in molting of the roach *Cryptocercus.*)

1955, pp. 485-513. (Suppression of sexual cycles and death of protozoa of *Cryptocercus* [*punctulatus*] resulting from change of hosts during molting period.)

De Mello, I. F., 1952-1954, pp. 127-133. (Brazil, *Stephanonympha havilandi* from intestine of *Cryptotermes havilandi,* an African termite introduced into Brazil.)

Dogel', V. A., 1956, *in* Poltev and Pavel'eva (Ed.), 1956, pp. 47-62. (Protozoan symbionts of termites and their general biological significance in life of their hosts.)

Georgévitch, J., 1929. (Yugoslavia, intestinal fauna termites.)

1931. (Yugoslavia, flagellates termites.)

Grassé, P. P., 1959b, pp. 482-483. (Chromosomes of protozoa, symbionts of termites, in small zooflagellates the chromosome interphases are recognizable in the nuclear fluid, having the appearance of vesicules limited by a thin membrane. There is neither a filament nor structure in the interior of the chromosome vesicule.)

Grimstone, A. V., 1959, pp. 480-482. (U.S., cytoplasmic organization in *Trichonympha,* symbiont flagellates in *Zootermopsis angusticollis,* functional significance parabasal apparatus, membrane of saccules may contain enzyme system responsible for synthesizing the polysaccharide.)

Gutierrez, J., 1956, pp. 39-42. (Metabolism of cellulose-digesting symbiotic flagellates of the genus *Trichonympha* from *Zootermopsis.*)

Ionescu, M. A., 1959, pp. 112-115. (Rumania, *Reticulitermes lucifugus,* flagellates, hypermastigines—*Spirotrichonympha flagellata, S. segmentata, S. crinita, Trichonympha agilis, Trichonympha agilis,* var. *danubica, Trichonympha agilis,* var. *japonica, T. chattoni, T. serbica, Holomastigotes elongatum.*)

Ionescu, M. A., and Murgoci, A., 1949, pp. 618-623. figs. 2-4. (Rumania, *Reticulitermes lucifugus* intestinal fauna, protozoan *Spirotrichonympha crinita,* n. sp., *Trichonympha agilis,* var. *danubica.*)

1950, p. 1. (Rumania, *Reticulitermes lucifugus,* intestinal fauna.)

Lavette, A., 1959, pp. 474-476. ("Phosphatase" acids in symbiotic flagellates of termites.)

Noirot, C., and Noirot-Timothée, C., 1959, pp. 775-777. (*Termitophrya,* n. gen., new type of ciliate infusoria commensal of certain termites, *T. africana* in posterior intestine *Jugositermes tuberculatus* workers, Oubangui-Chari, or Gabon. Other species *Termitophrya* occur in three Apicotermitinae: *J. tuberculatus* Emerson, *Rostrotermes cornutus* Grassé, *Trichotermes villifrons* Sjöst., and in Termitinae: *Pericapritermes chiasognathus* Sjöst. of Gabon and *P. urgens* Silv. of the Ivory Coast.)

Nutting, W. L., 1956, pp. 83-90. (Reciprocal protozoan transfaunations between the cockroach *Cryptocercus* [*punctulatus*] and the termite *Zootermopsis* [*angusticollis*].)

Nutting, W. L., and Cleveland, L. R., 1954, p. 747. (U.S., effects of transfaunations on the sexual cycles of the protozoa of the roach *Cryptocercus.*)

1954a, p. 786. (Effects of reciprocal transfaunations on protozoa of the roach *Cryptocercus* and the termite *Zootermopsis.*)

1955, pp. 485-513. (Suppression of sexual cycles and death of the protozoa of *Cryptocercus* [*punctulatus*] resulting from change of hosts during molting period.)

1958, pp. 13-37. (Effects of glandular extirpations on *Cryptocercus* and the sexual cycles of its protozoa.)

Ritter, H. T. M., 1956, pp. 209-210. (Biology certain intestinal associates of *Reticulitermes flavipes.*)

Roonwal, M. L., 1958a, pp. 77-100. (India, intestinal flagellates.)

Saleem, M., 1955, pp. 34-39. (Pakistan, 2 new genera of hypermastigote flagellates from *Archotermopsis wroughtoni.*)

Schmidt, H., 1956c, pp. 269-275. (Intestinal flagellates of termites.)

1960a, pp. 261-263. (Associations termites and microorganisms.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* protozoan *Nyctotherus silvestrianus* in alimentary canal, not numerous, probably unimportant in digestion cellulose.)

1957, pp. 373-390. (South Africa, *Kalotermes durbanensis,* exposure to temperature 36° C. for 24 hr. has little effect on protozoa, but −10° C. for 2 to 3 hours harmful.)

RACKET

Anonymous, 1956e, pp. 1-4. (National Better Business Bureau report on Dry-Cure Engineering Co.; summary of Hunsberger's claims that termites cannot eat wood and comments by entomologists.)

1956h, pp. 1-3. (Supplemental report to Anon., 1956e.)

1957k, p. 1. (Refutes Hunsberger's claim that termites cannot eat wood.)

1959d, pp. 1-4. (National Better Business Bureau warns against termite quackery, scare tactics, and recommends National Pest Control Association's advice on how to purchase wisely.)

Snyder, T. E., 1956a, p. 26. (Warning against rackets in termite control.)

RADIATION

Alibert, J., 1959, pp. 1040-1042. (France, radioactive phosphorus as an aid in the study of trophallactic exchanges, *Calotermes flavicollis.*)

Anonymous, 1960d, p. 28. (Hawaii, Honolulu, wood soaked with radioactive isotope solution; "hot" wood eaten, showed how fast food travels through colony, how various castes fed.)

Bletchly, J. D., and Fisher, R. C., 1957, p. 670. (England, cobalt-60 kills eggs powder post beetles by exposure to 4000 röntgens 1 to 4 days after hatching, resistance increases rapidly as develop; larval development arrested by irradiation at 8000 röntgens; same dosage adults, no fertile eggs. Tests on all stages outside of wood.)

Dick, W. E., 1957, pp. 1-50. (U.S., wood borers treated by dosage 1000 curies cobalt-60.)

Gösswald, K., and Kloft, W., 1958, pp. 743-745. (Radioactive isotopes in the study of colony life of insects.)

Kurir, von A., 1958a, pp. 84-87. (Austria, *Reticulitermes flavipes,* eradication with cobalt-60 or strontium-90 radioactive ashes in soil in areas not thickly populated, as Hallein, but not in Hamburg, Germany—radioactive isotopes would be dangerous.)

1959, pp. 101-104. (Austria, *Reticulitermes flavipes,* eradication by irradiation, cobalt-60 or strontium-90 suggested.)

Metcalf, R. L. (Ed.), 1957, pp. 81-146. (Use of radioisotopes in pesticide research; radioactive insecticides, tagging.)

1958, pp. 183-206. (Isotope dilution techniques for determination pesticide residues.)

REARING

Hendee, E. C., 1937, *in* Galtsoff, et al., 1937, pp. 275-278. (U.S., rearing of dampwood termites in laboratory, rotten wood in containers; drywood termites, wood with 10% moisture minimum; subterranean termites, moist grooved wood in glass jars with soil.)

Osmun, J. V., 1956, pp. 141-143. (Rearing method for subterranean termites, *Reticulitermes flavipes.*)

1956a, p. 21. (Rearing of subterranean termites, *Reticulitermes flavipes.*)

Pence, R. J., 1955, pp. 28-30. (Easy-to-build termite houses.)

1957b, pp. 238-240. (*Reticulitermes hesperus* maintained for long periods in end-slotted moisture gradient test tubes set in battery jars, moisture 97.5% optimum.)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* observation nests—portions of mound in plaster of paris, sheet cork with cells.)

1957, pp. 373-390. (South Africa, *Kalotermes durbanensis,* artificial nests, glass tubes, plaster of paris with sawdust. Wooden nests.)

REGENERATION

Emerson, A. E., 1956, pp. 248-258. (Africa, regenerative behavior—nest structure.)

RESISTANT WOODS

Anonymous, 1953t, p. 70. (Australia, Canberra, *Syncarpia laurifolia, Eucalyptus crebra, E. tereticornis, paniculata, micrantha, grandis* resistant.)

1956i, p. 67. (Australia, Canberra, *Eucalyptus rostrata, propinqua, punctata, saligna, eugenioides, sieberiana;* plastics, polystyrene unsaturated polyesters, epoxylenes, and phenolic laminates, polyvinyl chloride and cellulose acetate become susceptible when plasticized.)

1957h, pp. 1-15. (U.S., Mississippi State Highway Dept. guard rail posts, native red cedar round posts (1937-1955) 60% perfect; 1939-1953, 85%; 1949-1953, 85%. Western red cedar (1938-1947) 25% perfect. Black locust (1938-1955) 85% perfect.)

1958h, p. 66. (Australia, Canberra, order decreasing resistance: *Eucalyptus rostrata, E. propinqua, E. punctata, E. saligna, E. eugenioides, E. sieberiana* to *Coptotermes lacteus* and *Nasutitermes exitiosus.* Extracts from black bean *Castanospermum australe* have antitermitic effect. Plastics thin films polyethylene, polyvinylidene chloride, and polyvinyl chloride penetrated by termites. Cable sheathings of polyvinyl chloride containing fractional percentages of aldrin and dieldrin immune, permanence not known.)

1958l, pp. 113-119. (U.S., FHA, California redwood, foundation grade, tidewater red cypress, 100% heartwood.)

1959q, pp. 1-15. (U.S., Mississippi State Highway Dept. guard rail posts, native red cedar round posts, 8 to 10 in. in diameter, 1937-1955 and all other tests naturally resistant woods closed as of 1957 report.)

1959s, p. 66. (Western Australia, tests commercial timbers underway.)

Asenjo, C. F., Amoros-Marin, L., 1958, p. 183. (Puerto Rico, resistance mahogany wood (*Swietenia mahogani*) to *Cryptotermes brevis.*)

Asenjo, C. F., et al., 1958, pp. 185-195. (Puerto Rico, resistance mahogany wood (*Swietenia mahogani*) to *Cryptotermes brevis.*)

Bavendamm, W., 1955, *in* Schmidt, H. (Ed.), 1955b, pp. 245-306. (Natural resistance of woods to termites, alphabetical and systematic—by family lists woods of world.)

Gay, F. J., and Wetherly, A. H., 1958a, pp. 1-13. (Australia, hardboards of *Juniperus* stock.)

Gösswald, K., 1956, pp. 65-70. (Europe, *Calotermes flavicollis,* laboratory testing resistant woods.)

Harris, W. V., 1956b, pp. 1-13. (Field tests for resistance.)

1958, pp. 161-166. (East Africa, *Cryptotermes* spp., resistant woods.)

Herfs, A., 1956, pp. 2-5. (*Reticulitermes lucifugus* test on *Larix* wood.)

Jacobson, M., 1958, pp. 1-299. (Extractives render wood resistant.)

Jenkins, C. F. H., 1959, pp. 117-123. (Western Australia, jarrah (*Eucalyptus marginata*), native pine (*Callitris* spp.), jam (*Acacia acuminata.*)

Martínez, J. B., 1957, pp. 1-15. (Canary Islands, *Cryptotermes brevis,* resistant woods.)

Rudman, P., and Da Costa, E. W. B., 1958, pp. 1-8. (Australia, Canberra, resistance to decay, role toxic extractives silver top ash, *Eucalyptus sieberiana.*)

Rudman, P., Da Costa, E. W. B., Gay, F. J., and Wetherly, A. H., 1958, pp. 721-722. (Australia, tectoquinone not solely responsible for durability in teak—*Tectona grandis.*)

Sandermann, W., and Dietrichs, H. H., 1957, pp. 281-297. (Research on termite resistant woods, Germany.)

Schmidt, H., 1960, pp. 59-63. (Germany, test of sawdust of different woods.)

Schultze-Dewitz, G., 1958, pp. 248-251. (Germany, natural resistance of endemic hardwoods to European termites.)

Wolcott, G. N., 1957, pp. 259-311. (Puerto Rico, *Cryptotermes brevis,* natural resistance woods.)

1958, pp. 417-421. (Puerto Rico, extractives from Osage orange, substance 1, and tetrahydroosajin greater value; pinosylvin (Scots pine), taxifolin (Douglas fir), Venezuelan and Trinidad *Ryania speciosa* wood toxic, chlorophorin from African iroko preservatives.)

REVIEWS

ANONYMOUS, 1959c, p. 22. (U.S., California, review of Prevention and Control of the Western Subterranean Termite. Ebeling and Pence, Univ. California Agric. Exper. Stat., Extens. Serv. Circ., 469, 1958. Construction, design, soil poisoning, treated lumber.)

1959i, p. 20. (Review of Advances in Pest Control Research. R. L. Metcalf, 1957-1958, Pest Control, vol. 27, No. 9, p. 20. Sept.)

1959l, pp. 19, 22, 24. (U.S., statistics on wood preservation, 15% decline in 1958 from 1957. Tanalith gained 1%, Osmosalts 20%.)

ROONWAL, M. L., 1956a, pp. 454-455. (South Africa, review of Dwellers in Darkness, Skaife, 1955, London.)

ROZEN, H. J., 1958, p. 127. (U.S., review of Protection against Decay and Termites in Residential Construction, 1956. Building Research and Advisory Board, Nat. Acad. Sci., Nat. Res. Counc., Rep. No. 448, May 10, 1956.)

SCHEFER-IMMEL, V., 1960, p. 128. (Europe, review of Zur Laboratoriumprüfing von Textilien auf Termitenfestigkeit mit *Kalotermes flavicollis* Fabr., Gösswald and Kloft, 1959, Entomologica. Laboratory tests termite-proofing textiles.)

SNYDER, T. E., 1957f, p. 294. (U.S., California, review of The Biology of Colony Formation in *Reticulitermes hesperus* Banks, F. M. Weesner, 1956. Laboratory and field studies, factors that influence production and suppression soldiers, influence of source of alates on types of variation in colonies.)

1959b, p. 50. (U.S., comparison of FHA Minimum Property Standards, Anon., 1958l, with BRAB reports, Dillon 1956 and 1958, on prevention attack by termites and decay to residences.)

VARLEY, G. C., 1956, pp. vii-viii. (South Africa, review of Dwellers in Darkness, S. H. Skaife, 1955. *Amitermes atlanticus* 15% CO_2 in nest; food rotten cellulose; 12 workers first year; population 40,000 in nest 1 ft. high; caste origin due to extrinsic causes; laboratory cultures maintained.)

SECRETIONS

HRDÝ, I., and NOVÁK, V. J. A., in press. (Czechoslovakia, contribution to the question of the nonspecificity of the exohormones.)

JUCCI, C., 1956, pp. 283-284. (Italy, endocrinal gland has a secretion important in differentiation of castes.)

KARLSON, P., and BUTENHAND, A., 1959, pp. 49-51. (Pheromones (ectohormones) of termites, refers to Grassi and Sandias, Grassé, et al., Light and Lüscher, substance produced by reproductives used to influence colony members.)

LAMBINET, F., 1959, pp. 163-177. (France, *Calotermes flavicollis,* mandibular gland consists of 2 types secretory cells, large and small, latter degenerate after molting; gland at its maximum among functional reproductives.)

LÜSCHER, M., 1959, pp. 55-56. ("Pheromones," ectohormone secretion acts through mouth, active substances of functional reproductives inhibit production supplementary reproductives.)

LÜSCHER, M., and MÜLLER, B., 1960, p. 503. (*Kalotermes* and *Zootermopis,* a trail-forming secretion.)

NOIROT, C., 1957, pp. 743-745. (France, *Calotermes flavicollis,* neurosecretion and sexuality.)

VERRON, H., 1957, pp. 25-30. (France, *Calotermes flavicollis,* olfaction plays part in reciprocal attraction between different individuals, nymphs very responsive to smell other nymphs, especially as number increases, neoteinics most sensitive to smell other nymphs, no sex difference, soldiers least sensitive.)

1960, pp. 2931-2932. (France, *Calotermes flavicollis,* perception of odors.)

SENSE ORGANS

DENIS, C., 1958, pp. 171-188. (France, *Calotermes flavicollis,* development neurosensorial organs on legs, after each molt number increases, regression number and size sensorial organs accompanies development pseudoergates.)

1958a, pp. 240-247. (France, *Calotermes flavicollis,* cytology terminal nerves in course ontogeny.)

1959, pp. 712-713. (*Calotermes flavicollis,* evolution peripheral sense cellules.)

Richard, G., 1957, pp. 107-111. (France, *Calotermes flavicollis,* chordonotal organs on antennae.)

Verron, H., 1957, pp. 25-30. (France, *Calotermes flavicollis,* olfaction takes part in reciprocal attraction between different individuals in colony. Larvae very responsive to smell and density of grouping; nymphs 7th instar exhibit higher level of response, especially to grouping of 15 to 20 individuals. Neoteinics give best response to smell of larvae, but not as good to differences of density. Soldiers are least sensitive, interest toward larvae but only for groups of 20 or more.)

SHIELDS

Anonymous, 1958f, p. 4. (U.S., Georgia, termites circumvent even properly installed shields. H. C. Smith, Chief Architect FHA, Atlanta, estimates 90% Georgia's shielded FHA homes 2½ years and older now infested.)

1958l, pp. 113-118. (U.S., FHA recommendations.)

Dillon, R. M. (Ed.), 1956, pp. 1-60. (U.S., metal shields, design, material, installation.)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands.)

Sapp, D. R., 1960, p. 68. (U.S., Gainesville, Fla., termite control operator eliminates FHA 5-year warranty by pretreating with soil poisons and installing cheap shields.)

SOIL POISONS

Anonymous, 1953t, p. 70. (Australia, Canberra, creosote and 5% pentachlorophenol failed as soil poisons after 5 years' test.)

1956d, pp. 1-78. (U.S., clinical memoranda on economic poisons.)

1957i, pp. 30, 32, 34. (U.S., Nat. Pest Control Assoc. now recognizes ethylene dibromide as soil fumigant, gives use instructions; warns against methyl bromide.)

1957n, pp. 19-20. (U.S., pest control operators certification board for soil pretreatment.)

1958, pp. 36, 49-50. (U.S., Texas, demonstration of slabtreating.)

1958b, p. 48. (U.S., Indiana, Purdue Univ. pretreatment tests include granules size of coarse sand, chlorinated hydrocarbons.)

1958h, p. 66. (Australia, Canberra, against *Nasutitermes exitiosus,* 5% DDT failed after 7 years; against *Coptotermes lacteus,* 5% pentachlorophenol and 5% DDT failed after 6 years.)

1958i, pp. 1-7. (U.S., Forest Service recommendations.)

1958l, pp. 112-118. (U.S., FHA recommendations.

1958o, p. 63. (Australia, Canberra, against *Nasutitermes exitiosus* as soil poisons lindane, chlordane, and tetrachlorobenzene have given complete protection for 3 years; against *Coptotermes lacteus,* dieldrin and chlordane have given complete protection for 4 years, and aldrin and tetrachlorobenzene for 3 years. Similar tests against a termite complex in the Riverina, pentachlorophenol, sodium pentachlorophenate, chlordane and creosote have given complete protection for 5 years. After 2 years weathering chlordane, lindane, aldrin and dieldrin used in surface treatments were still effective.)

1959, pp. 17-19. (U.S., Forest Service recommendations.)

1959e, p. 50. (U.S., "chlorohepton" soil poison said to combine chlordane with heptachlor.)

1959g, p. 62. (U.S., California, termite control operator "not responsible" for death customer following treatment chlordane, latter not registered as "ultra-hazardous.")

1959h, p. 58. (U.S., combination of aldrin and dieldrin to compete with Orkin's combination of chlordane and heptachlor as soil poisons.)

1959j, pp. 30, 32, 34. (U.S., Kentucky, Fort Campbell, 1958-1961, preconstruction termite control specifications, cost estimates on inside and pad, stud, and outside soil pretreatments, monthly payments, consulting engineer coordinated work, 3 operators, crew 8 to 10 laborers housed on job site. Soil poison 6.6% dieldrin water solution, 550 gal. applied each housing unit, pump 50 gal. per min. First application after footings poured, in trench 12 in. wide, 8 in. deep, 1 gal. per 4 linear ft., ⅓ at bottom, ⅔ applied to backfill as replaced, tamped with air compressor. Chemical applied around all pipes and ducts. All exposed soil or pad treated, 1 gal. per 10 sq. ft. Slab areas covered with gravel after treatment, then polyethylene vapor barrier, next steel reinforcement, finally concrete poured. After houses constructed, soil adjacent to outside foundation treated in 6-in.-wide, 12-in.-deep trench, 4 gal. to 10 linear ft. No responsibility for retreats. Insurance, thorough preparation, and supervisor on job at all times essential.)

1959s, p. 66. (Western Australia, soil treatment tests have been continued and all chemicals mentioned in 1958 report remain effective.)

1960b, pp. 23-25. (U.S., St. Louis, Mo., Getz exterminators pretreats house 80% full basement and 20% crawl space. 0.3% dieldrin solution in trench with rodding. 2¼ gal. per 5 linear ft., backfill treated, surface soil sprayed 1 gal. per 10 sq. ft. Debris removed.)

1960c, p. 25. (U.S., in Memphis, Tenn., pretreatment with soil poisons costs 40% of cost control in slab houses, 5% less than correction in crawl space houses; in Oklahoma City 25% less.)

1960e, pp. 44, 58. (U.S., Oklahoma, 19 termiticides are approved as soil poisons including chemicals that have been eliminated by Federal agencies for ineffectiveness or other reasons.)

1960h, pp. 54, 62, 64-65. (U.S., H. R. Johnston (Forest Service) warns to discontinue downward trend in reducing concentrations of soil poisons for economic reasons. Many pest control operators feel Federal Housing Administration's concentrations for soil poisons are too low. In the Canal Zone, Panama, twice as much insecticide required for same results as in Mississippi; high rainfall may have bearing. Ethylene dibromide an effective soil fumigant in California for 4 years; Bill Butz (Purdue) stated when a residual chlorinated hydrocarbon is used with a fumigant, the residual will not reach as far as the fumigant will to get the initial toxicity. Joe Kahn (Purdue) stated research shows that ethylene dibromide will not move through the soils of midwestern United States because of the texture and compactness of these soils.)

Beesley, J., 1957, pp. 1-3, 3-4, 4-6. (Australia, Melbourne, treated soil barriers, sodium arsenite, chlordane, dieldrin, benzene hexachloride.)

Bollen, W. B., Roberts, J. E., and Morrison, H. E., 1958, pp. 214-219. (U.S., Oregon, variation in toxic effect in soil led to discovery after 21 months nearly half aldrin lost, significant amount recovered as dieldrin.)

Boswell, V. R., et al., 1955, pp. 1-59. (U.S., Washington, New Jersey, Illinois, and Georgia, investigations 1950-1953 on injury to plants by soil insecticides and residuals, varies with soil type.)

Briegleb, P. H., 1954, pp. 73-76. (U.S., Mississippi, Forest Service tests.)

Butts, W. L., 1961, pp. 44-52. (U.S., termite resistance may crop up at any time.)

Byerly, T. C., 1960, pp. 1-4, *in* U.S. Dept. Agric., ARS, Publ. 20-9, 1960. (U.S., use heptachlor severely limited by fact that under some conditions resulted in small residues of its epoxides.)

Coaton, W. H., 1958, pp. 1-112. (South Africa, *Hodotermes mossambicus* and *Microhodotermes viator,* sodium fluosilicate grass bait less toxic to grazing animals than sodium arsenite.)

Conley, B. E., 1958, p. 18. (U.S., first aid for poisoning.)

Dean, L. A., 1960, pp. 63-69, *in* U.S. Dept. Agric., ARS, Publ. 20-9, 1960. (U.S., persistence of organic substances in soil depends on physical, chemical, or biological processes.)

Dillon, R. M. (Ed.), 1956, pp. 1-60. (U.S., Forest Service tested and approved soil poisons, proprietary poisons, percentages, dosages for various types houses, where to apply.)

Ebeling, W., and Pence, R. J., 1958, pp. 207-211. (U.S., California, laboratory evaluation insecticide-treated soils against *Reticulitermes hesperus.*)

Eno, C. F., 1958, pp. 348-351. (U.S., effect of insecticides in soil and germination and yield plants, especially chlorinated hydrocarbons.)

Ferrero, F., 1959, pp. 30-31. (France, Banyuls, Eastern Pyrenees, *Calotermes flavicollis* damages grapevines. Many have to be replaced each year. DDT, HCH (BHC), heptachlor, and aldrin have been used but without success. Dieldrin used as a dust (20% of active material) or a suspension with 1.5 l. of dieldrin per 100 l. of water has given effective control when the soil was thoroughly treated especially around the roots and the dust or spray was applied under pressure. Wounds in the grapevine stock should be dusted. This method is a curative rather than preventive method. Control of the adults before flight would prevent new colonies from forming. Sealing galleries would prevent flight and use of an attractant for the adults should furnish means for capturing the adults. These termites attack not only the woody grapevine stocks but also other woody plants.)

Foster, A. C., et al., 1956, pp. 1-36. (U.S., rapid deterioration chlorinated hydrocarbons in soil, at dosages used, residues will not accumulate in soil to the extent of impairing growth of plants.)

Gannon, N., and Bigger, J. H., 1958, pp. 1-2. (U.S., Illinois, conversion aldrin and heptachlor to their epoxides in soil. Aldrin converted to dieldrin more rapidly than heptachlor to heptachlorepoxide, hence toxicity due to dieldrin, heptachlor exceeded quantity epoxide but latter more toxic, hence epoxidation advantageous increasing both toxicity and residual effect.)

Gillespie, B. B., 1959, p. 34. (U.S., Indiana, topical application and laboratory soil tests, former showed aldrin and dieldrin most toxic, then heptachlor and chlordane, higher dosage required for *Reticulitermes flavipes* than for *R. hageni;* latter showed aldrin and heptachlor most toxic, then dieldrin and chlordane, no difference between species termites.)

Gunther, F. A., and Blinn, R. C., 1955, pp. 1-708. (Analysis of insecticides and acaricides.)

Heal, R. E., 1957, pp. 73-76. (U.S., chemicals in termite control.)

1957a, pp. 118-120. (U.S., chemicals in built-in protection.)

Hetrick, L. A., 1956, pp. 28-29. (U.S., *Reticulitermes flavipes,* organic insecticides, benzene hexachloride and chlordane decreasing speed action.)

1957, pp. 316-317. (Benzene hexachloride effective more than 10 years in sandy soil, *Reticulitermes flavipes.*)

1957a, pp. 343-348. (Evaluation new chemicals, *Reticulitermes flavipes.*)

India Ministry Food and Agric., 1958, p. 748. (India, treating soil with chemicals.)

Johnston, H. R., 1956, pp. 1-8. (U.S., Mississippi, and Canal Zone, Panama, tests soil poisons.)

1958, pp. 9, 11-16. (Mississippi and Canal Zone, 10- to 13-year tests.)

1958a, pp. 423-431. (Mississippi and Canal Zone, tests soil poisons (chlorinated hydrocarbons most effective.)

1959, p. 32. (Mississippi and Canal Zone, tests of soil poisons: aldrin 0.5%, 100% effective after 9 years; BHC (benzene hexachloride) 0.8% gamma isomer, 80% after 10 years; chlordane 1%, 100% after 10 years; DDT 5%, 90% after 11 years; dieldrin 0.5%, 100% after 9 years. Heptachlor promising; duration increased by increased concentration.)

1960, pp. 44-45. (U.S., Mississippi, volatilization, vaporization, evaporation, and temperature major factors in disappearance of termiticides from soil. Types soil important, 96% heptachlor applied to mucky soil remained, after 56 days only 45% in sandy soil. Alternate wetting and drying causes chemical to disappear rapidly.)

1960a, pp. 1-6. (Tests of soil poisons in Mississippi and the Canal Zone, Panama. Later data than 1956 report, chlorinated hydrocarbons most effective.)

1961, pp. 40, 42. (U.S., Mississippi, breakdown of chemicals in soil includes decomposition, alkalies decompose benzene hexachloride, iron DDT; volatilization is evaporation, is big factor instability. Chemicals with high vapor pressure evaporate more rapidly. Temperature and formulation affect volatilization, as do soil types, moisture, rate application, alkalinity or acidity of soil.)

Johnston, H. R., and Osmun, J. V., 1960, pp. 62-63. (U.S., Forest Service and Purdue Univ. tests show soil poisoning effective, but narrow margin exists between protection and no protection, standards of formulation and dosages should not be lowered.)

Katz, H., 1958, p. 49. (U.S., soil near old woody shrubs should have nearby soil treated with aqueous solution toxicant.)

1958a, p. 6. (U.S., termites will not live in soil so alkaline that chlordane or dieldrin would break down, but might survive in soil alkaline enough to destroy DDT.)

1961, pp. 40, 43. (U.S., paradichlorobenzene and naphthalene, old standbys, will suppress posttreatment swarmers, but not used for long-time control, based on A. E. Lund's tests and commercial use.)

1961a, pp. 9, 11-12, 64. (U.S., treatment of gravel fill material more important than treatment of soil, 1 gal. toxicant per 10 sq. ft. Weight of toxicant/volume of soil more exact, degree wetness of soil will vary dosage.)

Kiigemagi, U., Morrison, H. E., Roberts, J. E., and Bollen, W. B., 1958, pp. 193-204. (U.S., Oregon, aldrin, dieldrin, and heptachlor gave good control of *Scutigerella immaculata* in some field tests, not in others. Where not successful, rapid decline in soil of all three compounds.)

LICHTENSTEIN, E. P., 1959, pp. 31-32. (U.S., factors affecting termite resistance: soil types; application rate; presence or lack of cultivation; soil temperature, soil moisture; soil microorganisms affect persistence of insecticide; persist longer: in soils high organic content, high application rate, noncultivated, low temperature, dry soil, sterilized soils.)

1959a, pp. 40, 42, 56. (U.S., factors affecting insecticide persistence in various soils: soil type, soil temperature, moisture, microorganisms, chemical application rate, chemical conversion in soil.)

LICHTENSTEIN, E. P., BECK, S. D., and SCHULZ, K. R., 1956, p. 936. (U.S., colorimetric determination of lindane in soils and crops.)

LICHTENSTEIN, E. P., DE PEW, L. J., ESHBAUGH, E. L., and SLEESMAN, J. P., 1960, pp. 136-142. (Midwestern U.S., amount organic matter within a particular soil type and climatic conditions of area major factors affecting persistence of DDT, aldrin, and lindane in soils, DDT most persistent, lindane least, all disappeared most rapidly in Kansas experiment soils.)

LICHTENSTEIN, E. P., and MEDLER, J. T., 1958, pp. 222-226. (U.S., Wisconsin, alfalfa treated with heptachlor and aldrin at rates ¼ to ⅛ lb. per acre, 7 days after treatment both were recovered at rate of 0.1 part per million by chemical analysis. 2 weeks after treatment no heptachlor found, 3 weeks after treatment no aldrin found.)

LICHTENSTEIN, E. P., and POLIVKA, J. B., 1959, pp. 289-293. (U.S., top dressings (turf soils), 15% of applied chlordane recovered after 12 years by chemical analysis, 12% by bioassay. 11 years after application, 41% BHC of applied dosage recovered by chemical analysis, 8% by bioassay. After 9 years no heptachlor recovered by analysis, but 4 to 5% by bioassay. Most aldrin had disappeared during 4 years, part converted to dieldrin to extent 8 to 10% of applied dosage.)

LICHTENSTEIN, E. P., and SCHULZ, K. R., 1958, pp. 848-849. (U.S., colorimetric determination of heptachlor in soils and crops.)

1959, pp. 118-124. (U.S., lindane broke down, within 2 weeks, to nontoxic compound, aldrin converted to dieldrin, more dieldrin formed in a sandy loam soil and in soils treated at lower concentrations and at higher temperatures.)

1959a, pp. 124-131. (U.S., 3½ years after treatment 1.43 times more DDT, 4.25 times more aldrin, and 8.45 times more lindane were recovered from a muck soil than from Miami silt loam. Temperature important factor. No loss in frozen soil. Loss 16 to 27% at 6° C. of aldrin and heptachlor, only 2 to 14% persisted at 46° C. after 56 days.)

1960, pp. 192-197. (U.S., aldrin readily transformed into dieldrin in wet, nonautoclaved Carrington loam, less rapidly in muck soil; amounts aldrin and dieldrin recovered equal 16 months after treatment in field. In soils containing low number microorganisms (autoclaved loam, Plainfield sand), or in dry soils amount dieldrin found small. Heptachlor applied to Carrington loam persisted longer than aldrin, but amount of heptachlorepoxide formed smaller than that of dieldrin. Lindane most persistent in dry soil and least in wet, nonautoclaved soil.)

LUND, H. O., 1960, pp. 32, 44, 36. (U.S., Georgia, tests show termites will tunnel up through foundation voids. When treated with dieldrin, aldrin, and chlordane emulsions, tunnels were only built over 0.002% of chlordane after 7 weeks, over the lowest concentrations of aldrin or dieldrin or 0.02% chlordane after 9 months.)

MALINA, M. A., KEARNY, J. M., and POLEN, P. B., 1959, pp. 30-32. (U.S., determination chlordane in air of habitations treated for insect control.)

MARTÍNEZ, J. B., 1958, pp. 1-29. (Spain, arsenic and chlorinated hydrocarbons used as soil poisons.)

METCALF, R. L., 1955, pp. 1-402. (Organic insecticides.)

METCALF, R. L. (Ed.), 1957, pp. 1-523. (Chemistry, uses, hazards in insect pest control, references, etc.)

1958, pp. 1-426. (Application pesticides, isotope dilution for determination residues, spread, insect resistance, etc.)

MILSUM, J. N., 1959, pp. 425-428. (World, termites attacking mango controlled by 20 lb. 5% chlordane dust per acre.)

NELSON, J. A., 1960, p. 5. (U.S., editorial, 5-year guarantee for soil poisoning discriminatory, 10 years experience proves it effective, other approved methods not inspected as to proper installation.)

Newsam, A., and Rao, B. S., 1957, p. 98. (Malaya, aldrin preferred, less costly, dieldrin superior, chlordane less persistent, attack on rubber trees by *Coptotermes curvignathus*.)

1958, pp. 209-215. (Malaya, chlordane, aldrin, dieldrin effective, prevent reattack.)

Osmun, J. V., 1956b, p. 29. (U.S., laboratory techniques for evaluation effect soil insecticides on *Reticulitermes flavipes*.)

1957, pp. 9, 11-12, 16, 19, 48. (Better control through research.)

1957a, pp. 592-593. (Responses *Reticulitermes flavipes* to certain insecticides.)

1958, pp. 23-24, 56. (Ethylene dibromide as fumigant in different types soil, factors affecting dispersion in soil, subslab.)

Parcher, J. V., and Means, R. E., 1959, pp. 29-30, 32. (U.S., characteristics of soils, cohesion, plasticity, strength, void ratio, loads on sand, clay, shrinking and swelling.)

1959a, pp. 57-58, 60. (U.S., chemical application, structural safeguards, penetration soils, soaking for coarse-grained soil, pressure injections for fine-grained soils, effect of building on water content of clay and dry soils.)

1959b, pp. 50, 52, 54. (U.S., texture reveals permeability, cohesionless soils—sand, gravel, silt; cohesive—clay, latter low permeability. Moisture content, macroscopic structure.)

Powell, J. M., Jr., 1959, pp. 20, 22, 24. (U.S., National Assoc. Homebuilders state 5-year warranty required for soil poisoning by FHA unreasonable since not required for other 4 methods termite control, builder responsible. FHA requires guarantee because work cannot be checked. Guarantee should be removed or pretreatment dropped.)

1960, pp. 32, 42, 44. (U.S., Baton Rouge, La., southern builder believes home owner should have responsibility, recommends pipes for later retreatment.)

Rhode Island Dept. Agric. and Conservation, Div. Entomology and Plant Industry, 1958, pp. 1-4, (U.S., Rhode Island, soil poisoning against subterranean termites.)

Sapp, D. R., 1960, p. 68. (U.S., Gainesville, Fla., termite control operator eliminates 5-year warranty for soil poisoning by pretreating and also installs cheap shields to satisfy FHA; 90% buildings pretreated around Gainesville.)

Shepard, H. H., 1958, pp. 1-355. (Effect chemicals on physiology insects, technique for tests, screening, etc.)

Shepard, H. H. (Ed.), 1960, pp. 1-250. (Methods of testing soil insecticides, chap. 6, W. E. Fleming.)

Smith, M. W., et al., 1956, pp. 34, 36, 38, 42. (U.S., what effect soil texture has on penetration and retention chemicals.)

1957, pp. 36, 38, 40. (U.S., new approaches to "sub" treatment of slab houses.)

Spitz, W. J., 1958, pp. 38, 40, 43, 51. (U.S., Texas, complete coverage by drilling under slab from side, chlordane emulsion.)

U.S. Dept. Agric., ARS, 1960, pp. 1-221. (U.S., nature and fate of chemicals applied to soils, plants, and animals.)

Ward, J. C., 1958, pp. 14-16. (U.S., use pesticides with care.)

Westlake, W. E., and San Antonio, J. P., 1960, pp. 105-115, *in* U.S. Dept. Agric., ARS, Publ. 20-9, 1960. (U.S. degradation and products formed of chlorinated hydrocarbons and organic phosphorus compounds. Persistence.)

Young, W. R., and Rawlins, W. A., 1958, pp. 11-18. (U.S., New York, relative persistence heptachlor in 4 different soil types, Dunkirk sandy loam, silt loam, and silty clay loam and muck, not significant, rapid losses, especially in soil surfaces exposed to sun, less from emulsion than from wettable powder, will not accumulate to dangerous levels in cultivated soils.)

Zavon, M. R., 1958, pp. 9-12. (U.S., are comparative toxicities meaningful—today's pesticides?)

Zimmern, A., 1957, pp. 32, 34, 36, 50. (U.S., soil penetration by chemicals.)

SOUND

Blandford, H. F., 1881, p. 32. (Sound-producing ants, Termitidae sound producing).

Bristowe, W. S., 1924, pp. 475-504. (Sound-producing Termitidae.)

1925, pp. 640-641. (Sound-producing Termitidae.)

De Baisieux, P., 1938, pp. 79-302. (Blattoidea: Isoptera, p. 124, scoloparia on femora and tibiae termites from Congo, chordonotal organs register vibrations.)

Fotheringham, J., 1881, p. 55. (Sound-producing Termitidae.)

FRINGS, M., and FRINGS, H., 1960, p. 101. Bibliography of sound-producing and sound-receiving termites.)

GIBB, G., 1859, pp. 121-130. (Sound production by Canadian insects.)

GRAVELY, F. H., 1915, pp. 483-539. (India, sound-producing termites.)

SUPERORGANISM

LÜSCHER, M., 1958c, pp. 48-65. (Colony as an organism.)

TAXONOMY

AHMAD, M., 1955, pp. 25-27. (East Pakistan, *Microtermes pakistanicus*, n. sp., soldier.)

1955a, pp. 202-264. (West Pakistan, Keys, *Neotermes pishinensis*, n. sp.; *Microcerotermes baluchistanicus*, n. s.p., *M. sakesarensis*, n. sp., *M. longignathus*, n. sp.; *Eremotermes neoparadoxalis*, n. sp., *E. malki*, n. sp.; *Amitermes paradentatus; Angulitermes hussaini*, n. sp.; etc.)

1958, pp. 33-118. (Key to Indomalayan termites, 176 of 394 species.)

1958a, pp. 119-198. (Key to Indomalayan termites, 218 of 394 species.)

AHMAD, M., and KHAN, M. A., 1955, pp. 28-30. (Pakistan, imago *Kalotermes beesoni.*)

ANONYMONS, 1959, pp. 17-19. (Number species in world (2,100) and in Smithsonian collection (1,322).)

BECKER, G., 1955, pp. 393-404. (Italy, Sicily, *Kalotermes flavicollis, fuscicollis*, n. var.)

BRADLEY, J. C., 1946, pp. 111-126. (Classification termites.)

CALABY, J. H., and GAY, F. J., 1956, p. 20. (*Coptotermes raffrayi* reduced to subspecies of *acinaciformis.*)

COATON, W. G. H., 1955, pp. 109-136. (Africa, Belgian Congo, *Neotermes aburiensis*, soldier, *N. collarti*, n. sp., *N. lepersonneae*, n. sp.; *Glyptotermes ueleensis*, n. sp., etc.)

1958, pp. 1-112. (South Africa, synonymy *Hodotermes mossambicus, Microhodotermes viator.*)

EMERSON, A. E., 1956a, pp. 98-101. (Africa, Katanga, *Apicotermes rimulifex*, n. sp.)

1956b, pp. 1-31. (Africa, *Apicotermes gurgulifex*, n. sp., *A. holmgreni*, n. sp., *A. aburiensis* transferred to *Allognathotermes.*)

1959, pp. 1-42. (Africa, new combinations, *Firmitermes abyssinicus, ?F. tripolitanus; Hoplognathotermes subterraneus, ?H. submissus; Acutidentitermes osborni*, n. sp., sold.; *Duplidentitermes furcatidens, D. jurioni*, n. sp., sold., *D. latimentonis*, n. sp., sold.; *Heimitermes moorei*, n. sp., sold.)

1960, pp. 1-28. (Oriental, Malagasy and Australian regions, new genera related to *Subulitermes*. Oriental region: *Leucopitermes*, n. gen., type species *leucops* Holmgren, Malacca, sold., work. *Aciculitermes*, n. gen., type species *aciculatus* Haviland, Sarawak, imago, sold., work. *Ceylonitermellus*, n. gen., type species *hantanae* Holmgren, Hantana, Ceylon, imago, sold., work. *Oriensubulitermes*, n. gen., type species *inanis* Haviland, Malaya, sold., work.; *O. inaniformis* (Holmgren), n. comb. Malagasy region: *Malagasitermes*, n. gen., type species *milloti* Cachan, Madagascar, sold., work. Australian region: *Occultitermes*, n. gen., type species *occultus* Hill, N. Terr., Australia, imago, sold. *Macrosubulitermes*, n. gen., type species *greavesi* Hill, N. Queensland, Australia, imago, sold.; *M. perlevis* (Hill), new combination, Port Darwin, N. Terr., Australia, sold. *Australitermes*, n. gen., type species *dilucidus* Hill, Queensland, Australia, sold.)

1960a, pp. 1-21. (Africa, Belgian Congo, new genera and species on *Subulitermes* branch Nasutitermitinae: *Verrucositermes*, n. gen., type species *tuberosus*, n. sp., Leopoldville, imago (king), sold. *Afrosubulitermes*, n. gen., type species *congoensis*, n. sp., Stanleyville, sold., work. *Postsubulitermes*, n. gen., type species *parviconstrictus*, n. sp., Yangambi, imago (queen), sold., work. *Tarditermes*, n. gen., type species *contracolor*, n. sp., Camp Putnam (on Epulu River), imago, sold.)

1960b, pp. 1-49. (Africa, Belgian Congo, 6 new genera of Termitinae: *Nitiditermes*, n. gen., type species *berghei* Keyberg, imago (king), sold., work., close to *Lepidotermes*. *Mucrotermes*, n. gen., type species *osborni*, n. sp., near Camp Putnam, sold., work., close to *Procubitermes*. *Furculitermes*, n. gen., type species *winifredae*, n. sp., Camp Putnam, imago (queen), sold., work., close to *Euchilo-*

termes; other species, *F. hendrickxi,* n. sp., Camp Putnam, sold.; *F. brevilabius,* Camp Putnam, imago (queen), sold.; *F. cubitalis,* n. sp., Stanleyville, sold., work.; *F. soyeri,* n. sp., Keyberg, sold., work.; *F. parviceps,* n. sp., Camp Putnam, sold., work.; *F. longilabius,* n. sp., Camp Putnam, sold., work; *F. brevimalatus,* n. sp., Stanleyville, sold., work. *Pilotermes,* n. gen., type species *langi,* n. sp., near Camp Putnam, imago, sold., work., close to *Basidentitermes. Profastigitermes,* n. gen., type species *putnami,* n. sp., Camp Putnam, sold. *Forficulitermes,* n. gen., type species *planifrons,* n. sp., Sona Mpangu, sold., work., not close to *Basidentitermes.*)

Emerson, A. E., and Banks, F. A., 1957, pp. 1-17. (Revision Neotropical genus *Armitermes, A. brevinasus,* n. sp., *A. latidens,* n. sp., *A. parvidens,* n. sp., *A. snyderi,* n. sp., *A. spissus,* n. sp., redescription *A. silvestrii.*)

Esaki, T., 1956, p. 87. (*Hodotermopsis japonica* imago.)

Gay, F. J., 1956, pp. 207-213. (Australia, *Ahamitermes pumilus* winged; *Paracapritermes hesperus,* n. sp., queen and sold.; *Termes iridipennis,* winged and sold.)

Gesell, S. G., 1959, pp. 1-6. (U.S., some wood-boring insects mistaken for termites.)

Ghidini, G. M., 1955, pp. 69-82. (Africa, Ethiopia, Sagan-Omo, *Bellicositermes jeanneli, goliath* distinguishing characters; *Microtermes vadschaggae* var. *grasséi,* n. n. for var. *dubius* Grassé preocc.; figured *Termes* (*Cyclotermes*) *maledictus, Trinervitermes eldirensis.*)

Grassé, P. P., and Noirot, C., 1955a, pp. 345-388. (Africa, *Allognathotermes ivoriensis,* n. sp.; *Coxotermes,* n. gen., *C. boukokoensis,* n. sp.; *Heimitermes,* n. gen., *H. laticeps,* n. sp.; *Jugositermes tuberculatus,* queen.)

Harris, W. V., 1956a, pp. 926-937. (Africa, French Cameroons, *Microcerotermes progrediens* alate female; *Pericapritermes amplignathus,* n. sp., sold.; *Odontotermes silvaticus,* n. sp., sold.; etc.)

1957a, pp. 421-433. (Southwest Arabia, *Amitermes stephensoni,* n. sp., *A. harleyi,* n. sp., sold.; *Eremotermes sabaeus,* n. sp., sold.; *Trinervitermes arabiae,* n. sp., sold.$^{1-2}$.)

1957c, pp. 20-32. (Malaya, list of species, Kalotermitidae, Rhinotermitidae, Termitidae, field key to sold., heads and mandibles, figured for some.)

1958a, pp. 59-60. (Solomon Islands, *Schedorhinotermes browni* n. sp., sold., Guadalcanal.)

1958c, pp. 3-26. (Belgian Congo, *Crenetermes fruitus,* n. sp., winged, sold., Lusinga; *Thoracotermes lusingensis,* n. sp., winged, sold., Lusinga; *Cubitermes muneris,* winged, *C. oblectatus,* n. sp., winged, sold., Lusinga; *Noditermes festivus,* n. sp., winged, sold., Kenia; *Microtermes upembae,* n. sp., winged, Riv. Lupiala, 15 species listed.)

1960, pp. 17-21. (East Africa, *Odontotermes montanus,* n. sp., sold., Kenya; *O. lacustris,* n. sp., winged, sold., Northern Rhodesia; *O. flammifrons* (Sjöstedt), Northern Rhodesia, Nyasaland.)

1960b, pp. 253-256. (*Eremotermes nanus,* n. sp., soldier, Sudan; *Termes melindae,* n. sp., soldier, British Honduras.)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands, 12 species listed, key to sold.)

Hunt, R., 1958, p. 31. (U.S., how to distinguish Embioptera from termites.)

Karaman, Z., 1954, pp. 21-30. (Yugoslavia, *Reticulitermes lucifugus* and *Calotermes flavicollis,* key to separate.)

Khan, M. A., and Ahmad, M., 1955, pp. 28-30. (Pakistan, *Kalotermes beesoni* winged.)

Krishna, K., 1956, pp. 1-5. (Malaya, *Coptotermes sepangensis,* n. sp., sold., *C. bentongensis,* n. sp., sold.)

Kushwaha, K. S., 1960a, pp. 54-65. (India, chaetotaxy of *Odontotermes assmuthi,* soldier.)

Machado, A. de.B., 1959, pp. 205-207. (*Apicotermes,* Africa, concept of ethological species.)

Mathur, R. N., 1960, pp. 79-85. (South India, *Glyptotermes nigrifrons,* n. sp., sold., nymph.)

Mathur, R. N., and Chhotani, O. B., 1959, pp. 40-53. (India, revision *Stylotermes,* description *S. fletcheri* Holmgr. and Holmgr. and *S. bengalensis,* n. sp., sold., work., Darjeeling, West Bengal.)

Mathur, R. N., and Sen-Sarma, P. K., 1958, pp. 233-241. (India, *Anacanthotermes rugifrons,* n. sp., sold. and work., key.)

1958a, pp. 1-9. (India, imago *Globitermes audax, Microcerotermes burmanicus, Odontotermes parvidens.*)

1959a, pp. 66-78. (India, *Emersonitermes thekadensis,* n. gen., n. sp., sold., work., South India: Thekaday (Travancore), close to *Subulitermes; Trinervitermes nigrirostris,* n. sp., winged, sold. (major, intermediate), Madras; *Nasutitermes beckeri,* n. sp. (Baini Prashad and P. K. Sen-Sarma) described elsewhere.)

1960, pp. 79-85. (South India, *Glyptotermes nigrifrons,* n. sp., sold. and nymphs, Madras, type sold., Forest Research Inst., Dehra Dun.)

1961, pp. 401-406. (Tinnevelly Distr., So. India, *Angulitermes acutus,* n. sp., sold. and workers.)

Moszkowski, L. I., 1955, pp. 15-41. (Madagascar, *Cryptotermes kirbyi,* n. sp.)

Noirot, C., 1955, pp. 139-150. (Angola, *Macrotermes angolensis,* n. sp., sold.$^{1-2}$; *Basidentitermes trilobatus,* n. sp., winged, sold.$^{1-2}$; *Pericapritermes machadoi,* n. sp., sold.; *Coarctotermes brunneus,* n. sp., sold.)

Obenberger, J., 1955, pp. 576-637. (Theories classification, systematic section Isoptera.)

Oldroyd, H., 1958, p. 225. (Family Termopsidae.)

Rhode Island Dept. Agric. and Conservation, Div. Entomology and Plant Industry, 1955, pp. 1-4. (U.S., how to tell ants from termites.)

Roonwal, M. L., and Bose, G., 1960, pp. 38-39. (India, Rajasthan, *Psammotermes rajasthanicus,* n. sp., sold. (holotype), work., first record of genus for India.)

Roonwal, M. L., and Chhotani, O. B., 1959, pp. 325-326. (Southern India, new species *Odontotermes, kulkarni,* sold. and work., Bijapur; *meturensis,* sold., work., Metur Dam.)

1959a, pp. 1967-1968. (India, *Anoplotermes,* n. sp., first record in India, to be described elsewhere.)

1959b, pp. 57-68. (India, further descriptions of *Odontotermes kulkarnii* and *O. meturensis.*)

1960a, p. 701. (Assam, India, *Anoplotermes shillongensis,* n. sp.)

1960b, pp. 143-144. (India, soldier caste found in Mysore in *Speculitermes cyclops sinhalensis* places genus in Amitermitinae.)

Roonwal, M. L., and Krishna, K., 1955, pp. 143-152. (Ceylon, *Coptotermes gaurii.*)

Roonwal, M. L., and Sangal, S. K., 1960, pp. 1-22. (India, near Dehra Dun, *Odontotermes obesus,* variability in size of soldier mandibles.)

Roonwal, M. L., and Sen-Sarma, P. K., 1956, pp. 1-38. (India and Burma, new species and subspecies, *Parrhinotermes khasii, Macrotermes serrulatus hopini, Hypotermes nongpriangi, Hospitalitermes blairi,* and *Parrhinotermes* new for India.)

1958, pp. 1-406. (India and Burma, *Eremotermes dehraduni,* n. sp., and *Indotermes maymensis,* n. sp., in new family Indotermitidae.)

Sands, W. A., 1956, pp. 83-84. (Africa, Gold Coast, *Mimeutermes edentatus,* n. sp., sold.)

1957, pp. 13-24. (Soldier mandibles Nasutitermitinae, specific difference in some genera, lend support to Ahmad's phylogenetic conclusions, with minor exceptions.)

1957a, pp. 1-28. (East Africa, revision Nasutitermitinae.)

1959, pp. 127-156. (Ethiopian Region, *Amitermes,* 13 species, 3 new, keys, distribution map, *Amitermes acinacifer,* n. sp., sold., Kenya; *A. importunus,* n. sp., sold., Nyasaland; *A. truncatidens,* n. sp., winged, sold., Tanganyika; description winged species known only from soldiers.)

Snyder, T. E., 1955h, p. 30. (U.S., need funds for Isopterist, U.S. Nat. Mus.)

1955i, p. 300. (Bolivia, *Anoplotermes brucei,* n. sp., winged.)

1956d, pp. 189-202. (Keys to termites West Indies, Bahamas, Bermuda.)

1957a, p. 352. (Panama, *Neotermes setifer,* n. sp., winged.)

1957d, pp. 81-82. (Bolivia, *Rugitermes laticollis,* n. sp., winged.)

1957g, pp. 42, 44. (U.S. and Europe, death thinning out ranks world's foremost isopterists.)

1958, pp. 229-231. (Philippines, *Glyptotermes franciae* and *magsaysayi,* n. sp., sold. and winged and sold., keys to Philippine species.)

1959c, pp. 313-321. (Venezuela, new species, *Neotermes araguaensis,* winged *Anoplotermes franciscoi,* winged, *Velocitermes bolivari,* sold.$^{1-2}$, ?winged, keys to Venezuelan species.)

Snyder, T. E., and Francia, F. C., 1961, in press. (Keys to Philippine termites.)

Thurich, L., 1960, pp. 145-160. (Palearctic, comparative morphological studies of sold. of *Reticulitermes* from Europe and the Near East.)

Weidner, H., 1955, pp. 63-68. (Anterior Asia, *Microcerotermes gabrielis,* n. sp., winged and sold.)

1955a, pp. 201-207. (Africa, Angola, *Apicotermes machodoensis,* n. sp.)

1955b, pp. 247-254. (Types in Zool. Mus. Hamburg, 98 species listed.)

1955e, *in* Schmidt, H. (Ed.), 1955b, pp. 5-81. (Systematic, keys to families, genera.)

1956a, pp. 55-105. (Africa, Angola, *Synacanthotermes angolensis,* n. sp., *Odontotermes* (*O.*) *chicapenensis,* n. sp., *Pericapritermes minimus,* n. sp., keys.)

1958, pp. 4-16. (Iraq, keys to winged, sold.)

1960a, pp. 43-70. (Afghanistan, Iran, Iraq distribution, descriptions and keys to winged and sold. of *Anacanthotermes ahngerianus, baeckmannianus, macrocephalus, murgabicus, septentrionalis, ubachi, vagans; Heterotermes indicola; Reticulitermes clypeatus, lucifugus; Amitermes vilis; Angulitermes dehraensis; Microcerotermes diversus, gabrielis.*)

WILKINSON, W., 1958, pp. 109-115. (West Africa, *Kalotermes spinicollis,* n. sp., imago, sold., Nkpoku; *K. exsertifrons,* n. sp., imago, sold., Nkpoku.)

1959, pp. 61-72. (East Africa, *Kalotermes sylvaticus,* n. sp., winged, sold., Uganda, Kenya; *K. angulatus,* n. sp., winged, sold., Tanganyika; *Neotermes aridus,* n. sp., winged, sold., Kenya; *Glyptotermes ignotus,* n. sp., winged, sold., Uganda.)

WILLIAMS, R. M. C., 1956, p. 128. (East Africa, erratum Williams, 1954, Proc. Roy. Ent. Soc. London (B), vol. 23, pp. 215-227, figs. 2 and 5, pp. 218 and 225 transposed, fig. 2, *Noditermes wasambaricus,* fig. 5, *Cubitermes umbratus.*)

TEMPERATURE

ANONYMOUS, 1958h, p. 66. (Australia, Canberra, in hardwood forests presence large colony *Coptotermes frenchi* results in increased temperature within infested tree, maximum increase occurs in "nursery" region.)

1960x, pp. 41-42. (U.S., Wisconsin, evolutionary change, termites more frequent in northern U.S.; termites can become winter- or cold-hardy. In tests, termites collected in summer entered "cold stupor" at 38° F.; collected in late August and September, survived temperature near 38° for 2 months longer. Termites in soil in December in upper 6 in. soil, same depth as frost line.)

HUFF, G. E., 1959, p. 61. (U.S., Indianapolis, Ind., subterranean termites in refrigerated display case, moisture in bottom due to leak.)

PESSON, P., 1959, pp. 77-79. (General, temperature habitats never fall below 15° C., go below ground to escape cold or heat, regulate temperature nests.)

SKAIFFE, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* temperature in mounds less than surrounding air.)

1957, pp. 373-390. (South Africa, *Kalotermes durbanensis,* temperature exposure 36° C. for 24 hr. not harmful but −10° C. for 2 to 3 hr. harmful to protozoa.)

TERMITOPHILES *

BOYER, P., 1956, pp. 111-113. (Africa, *Bellicositermes natalensis,* relation between intestinal flora and soil.)

BRITON, E. B., 1957, pp. 1-185. (Australian chafers, Scarabaeidae: Melolonthinae.)

DIEUZEIDE, R., 1930, pp. 569-571. (North Africa, Tyroglyphid *Caloglyphus* with *Reticulitermes.*)

FERNANDO, W., 1957, pp. 81-84. (Ceylon, *Sphecophila ravana,* n. sp., cockroach in colony *Coptotermes ceylonicus.*)

HINDWOOD, K. A., 1959, pp. 1-36. (Australia, birds in termite nests, 23 species kingfishers, 13 species parrots, 4 trogons, 2 puffbirds, a jacamar, and a cotinga.)

KISTNER, D. H., 1958, pp. 1-198. (Africa, Belgian Congo, India, Staphylinidae, p. 84, *Typhloponemya khandalae,* n. sp., with *Odontotermes* (*O.*) *obesus;* p. 88, *T. termitophilus* (Wasm.) with *Cubitermes fungifaber,* accidental, probably guest of ants *Dorylus;* p. 107, *Odontoxenus butteli* (Wasm.) with *Odontotermes* (*Hypotermes*) *obscuriceps;* p. 108, *O. transfuga* (Wasm.) with *Odontotermes* (*O.*) *obesus; O. longesetosus* (Cameron); *O. proximus* (Cameron); p. 110, *O. brevi-*

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* Fauna and flora of nests including symbiotic forms, as well as casual seekers of shelter; some may be predacous on the host termites, or parasites.

cornis (Cameron); *O. termitophilus* Wasm.) with *Odontotermes* (*O.*) *obesus;* p. 112, *O. triarticulatus* (Kemner) with *Odontotermes* (*O.*) *javanicus; O. ceylonicus* (Wasm.) with *Odontotermes* (*O.*) *redemanni;* p. 113, *O. eutermitis* (Wasm.) with *Trinervitermes biformis; O. peradenyiae* (Wasm.) with *Odontotermes* (*O.*) *redemanni; O. splendidus* (Wasm.) with *Odontotermes* (*Hypotermes*) *obscuriceps. Odontoxenus* more primitive than myrmecophile *Doryloxenus,* not found with *Odontotermes* in Africa, transfer to *Odontotermes* after genus reached India during Miocene extension of grasslands.)

Leleup, N., 1955, pp. 374-375. (Africa, Belgian Congo, beetles and flies.)

1960, pp. 197-206. (Africa, Belgian Congo, morphological classification insects found in nests.)

Reichensperger, A. von, 1956, pp. 81-91. (Africa, Congo, new species Coprinae.)

1957, pp. 323-324. (Africa, a new species of Coprinae.)

Salmon, J. T., 1941, p. 348. (Collembolan *Sinella termitum,* Australia, New Zealand.)

Schmitz, H., 1954, pp. 514-519. (Africa, Belgian Congo, Phoridae, *Aenigmatistes* and *Termitostroma,* n. gen.)

1955, pp. 33-60. (Africa, Angola and SW. Africa, 6 new phorid termitophiles.)

1955a, pp. 229-239. (Africa, phorid, *Thaumatoxena,* n. sp.)

1955b, pp. 48-66. (Africa, Belgian Congo, *Termitomyia,* n. sp.)

Seevers, C. H., 1957, pp. 1-334. (Termitophilous Staphylinidae, world, host relationships, phylogeny, classification, maps distribution.)

1960, pp. 825-834. (New termitophilous Staphylinidae of zoogeographic significance, Madagascar *Spirachthodes* first Old-World genus with exudatory abdominal appendages shared only with neotropical *Spirachtha.*)

Skaife, S. H., 1955, pp. 1-134. (South Africa, *Amitermes atlanticus,* sarcophagid fly *Termitometopia skaifei,* n. gen., n. sp.; springtail Collembola *Cyphoderus arcuatus;* white mite *Termitacarus cuneiformis,* red mite *Cosmoglyphus kramerii;* green protea beetle cetonid *Trichostetha fascicularis* scavenger beneath mounds; solpugid; termites *Microcerotermes malmesburyi, Termes winifredae* live in outer parts mounds, former not true inquiline.)

Torrealba, J. F., and Riccardi, B., 1941, p. 248. (Venezuela, Zaraza, *Triatoma* group not found in termite nests.)

Womersley, H., 1939, p. 174. (South Australia, *Sinella termitum.*)

TOXICOLOGY

Anonymous, 1952, pp. 1-45. (U.S., fire and explosion hazards of thermal insecticidal fogging; experiences; safety precautions; flammability chemicals, toxicity, impede fire extinguishing.)

1956d, pp. 1-78. (U.S., clinical memoranda on economic poisons, aldrin, allethrin, benzene hexachloride, chlordane, chlorothion, DDT, demeton, dieldrin, diazinon, dilan, kerosene, parathion, sodium fluoroacetate, toxaphene, warfarin, xylene; formulae, formulation, uses, routes of absorption, physiological action, dangerous acute and chronic doses in man, signs and symptoms of poisoning in man, laboratory findings, pathology, differential diagnosis, treatment, reporting.)

1959, p. 62. (U.S., California, termite control operator "not responsible" for death customer following treatment chlordane, latter not registered as "ultrahazardous.")

1959r, pp. 1-21. (U.S., toxicity dieldrin to man.)

1960, pp. 9-11. (U.S., precautions in pesticide usage; 75% accidents occurred among children less than 10 years old, 90% under 5. Less than 0.9 persons per hundred thousand population die due to pesticides. 65% of accidental adult deaths due to failure to read label. Protective clothing, creams, gloves, masks, respirators. Residues, allergies, 1 min. of precautions may save life.)

1960n, pp. 51, 54-56. (U.S., safety in termite control.)

1960s, p. 10. (U.S., Georgia, South Carolina, and Arkansas, homes commercially treated with 1% chlordane; samples air collected 2 weeks to 6 months after treatment, living portions homes treated for termites contained no chlordane.)

Beechem, H. A., 1955, pp. 36, 50. (U.S., methyl bromide left in applicator near lethal dosage for 20 min. in auto, operator recovered.)

Conley, B. E., 1958, p. 18. (U.S., first aid for poisoning.)

Du Bois, K. P., and Geiling, E. M. K., 1959, pp. 1-313. (U.S., textbook of toxicology.)

Gaines, T. B., 1960, p. 88. (Compares toxicology /LD_{50} values and symptomatology/ of 42 pesticides and 2 metabolites of DDT administered by single dose orally and dermally to Sherman strain adult rats. Includes chlorinated hydrocarbons, organic phosphates, and a group of miscellaneous pesticides.)

Hayes, W. J., 1959, p. 891. (Reports on a survey of human illnesses during antimalaria spray program in Kenya, Tanganyika, Indonesia, India, and Iran. Based on this and pertinent literature concludes that hazard of dieldrin is proportional to degree of exposure as determined by concentration of spray, area of bare skin, duration of contact, and lack of personal hygiene.)

1960, pp. 379-404. (Safety records newer compounds good because of careful labeling in the United States. Safety should be improved in all countries. Investigation required of those exposed to many times greater dosages than the general public.)

Ingle, L., 1956, pp. 1-11. (U.S., toxicity aldrin, chlordane, DDT, dieldrin, endrin, heptachlor, lindane, methoxychlor, toxaphene: acute oral and dermal lethal dosages, tests on animals, case histories man.)

Kerr, S. H., and Brogden, J. E., 1960, p. 19. (U.S., relative acute oral doses of parathion and malathion compared with DDT. Acute dermal toxicity higher than oral—takes more to kill. Toxicity of most insecticides given in Florida Agric. Res. Inst. Exten. Ent. Mimeogr. No. 10, rev. Apr. 1, 1960.)

Knipling, E. F., 1960, pp. 28-36, *in* U.S. Dept. Argic., ARS, Publ. 20-9, 1960, pp. 1-221. (U.S., soil insecticides for control termites. Insecticides responsible for fewer accidental deaths than are many other household chemicals.)

Lehman, A. J., 1951, pp. 122-133. (Acute toxicity of 86 pesticides. Single dose oral toxicity to rats, with symptomatology.)

1952, pp. 3-9. (Dermal toxicity of pesticides. Single 24-hr. exposures of rabbits to 39 pesticides, and multiple exposures of rabbits to 35 of these, with toxicity values and symptomatology.)

Mellan, I., and Mellan, E., 1956, pp. 1-150. (Symptoms and antidotes for poisons—soil poisons, wood preservatives.)

Metcalf, R. L. (Ed.), 1957, pp. 1-38. (Health hazards in use of pesticides; manufacture and distribution; user; medical control, treatment; accidental poisoning; residues in food.)

National Acad. Sci.—National Res. Counc., Div. Medical Sci., 1954, pp. 1-16. (Safe handling of pesticides employed in public health.)

National Safety Counc., 1960, in Safety Education, 1960, pp. 1-4. (Safe use of pesticides in home and garden.)

Negherbon, W. O., 1959, pp. 1-854. (A compendium of information including toxicological data for insecticides. Arranged alphabetically, mostly by chemical names, occasionally by trade names, each section includes a general statement; physical and chemical properties; toxicological data; pharmacology, pharmacodynamics, and physiology; symptoms; phytotoxicity; toxicity for insects; precautions.)

Pesticides Regulation Branch, U.S. Dept. Agric., 1960, pp. 1-5. (Pesticides can be used safely, read and heed the label, causes of accidents, precautions.)

School Public Health, Univ. Michigan, 1954, pp. 1-50. (Industry and public health points of view of toxicology. Pest control operational hazards and precautionary measures, discussion hazards.)

Sollman, T., 1957, p. 48. (Treatment of poisoning, pp. 172-181; insecticides and pesticides, specific chemicals; see index.)

Stilwell, H., 1960, pp. 34-36, 76-78. (U.S., dangers to man in use of chlorinated hydrocarbons as insecticides on the farm; advocates congressional investigation.)

U.S. Public Health Service, 1956, p. 78. (General summary of available toxicological data on pesticides, with symptomatology and suggestions for treatment of poisoning.)

1960, p. 31. (Entire U.S. Lists location, telephone number, and officer to be contacted at Poison Control Centers, facilities which provide to the medical profession on a 24-hr. daily basis information concerning the prevention and treatment of accidents involving ingestion of or contact with poisonous or potentially poisonous substances. Treatment is available at most of the centers.)

1961, pp. 1-38, idem, revised, April.

Ward, J. C., 1958, pp. 14-16. (U.S., use pesticides with care.)

USES IN INDUSTRY, ARTS, AND RELIGION

Treat, I., 1957, p. 40. (Africa, Abyssinia, Somali huts built of red-brown earth taken from termite mounds, ant-proof and hard as mortar.)

WOOD PRESERVATION

Allouard, P., 1956, pp. 96-97. (France, protection wood against termites and decay by simple cheap methods.)

Anonymous, 1953t, p. 70. (Australia, Canberra, low percent pentachlorophenol, 0.75% dry weight of board, added to local hardboard resistant to termites.)

1954d, pp. 68-69. (Australia, plywood made from karri (*Eucalyptus diversicolor*) termite-proofed by dipping in sodium pentaborate or mixture zinc chloride and arsenic pentoxide before bonding; aldrin superior to chlordane or dieldrin as preservative.)

1956, pp. 1-4. (U.S., availability of pressure-treated lumber, list localities, pictorial sampling, list lumber companies.)

1956a, pp. 1-22. (U.S., how to prevent decay and termite damage in houses.)

1956b, pp. 1-24. (U.S., how to build homes that will outlive the mortgage.)

1956i, p. 67. (Australia, Canberra, plastics resistant to termites, polystyrene, unsaturated polyesters, epoxylenes, and phenolic laminates, polyvinyl chloride and cellulose acetate become susceptible when plasticized.)

1957g, pp. 1-26. (U.S., Mississippi State Highway Dept., southern yellow pine stakes, coal tar creosote 1934-1957, 100% perfect; pentachlorophenol 1938-1957, 100% perfect; chemonite 100% perfect; crewood, 1933-1957, 90%, 1934-1957, 100%; osmosar, 1935-1951, 0%.)

1957h, pp. 1-15. (U.S., Mississippi, State Highway Dept., southern yellow pine square posts, coal tar creosote 1931-1957, 90% perfect; 1933-1953, 100%; 1938-1957, 95%; 1939-1957, 100%; Douglas fir square posts, 1944-1957, coal tar creosote, 100%.)

1958e, pp. 16-19. (U.S., 1957 industry production 6.5% increase over 1956, which was 4% over 1955; volume 274.5 million cu. ft., 95% treated products pressure treated, lumber and timber increased 2%, creosote used for 80% all material, pentachlorophenol 13%.)

1958f, p. 4. (U.S., Georgia, all large lumber users, responsible for maintenance properties, use treated wood, homeowners ignorant and not concerned until now.)

1958h, p. 66. (Australia, Canberra, surface treatments with creosote, sodium arsenite, chlordane, dieldrin and pentachlorophenol have given at least 2 years' protection against *Nasutitermes exitiosus.*)

1958l, pp. 113-119. (U.S., FHA minimum property standards, protection against termites and decay, treated lumber alternate control method.)

1956o, p. 63. (Australia, as surface treatment pentachlorophenol effective for 3 years against *Nasutitermes exitiosus,* other materials failed after 2 years.)

1959j, pp. 30, 32, 34. (U.S., Kentucky, Fort Campbell, pretreatment studs for outside walls, dipped up to 4 ft. high in 5% oil solution pentachlorophenol solution dyed red, rest of studs sprayed.)

1959l, pp. 19, 22, 24. (U.S., 15% decline in treated lumber products (41.7 million cu. ft.) from 1957; fire-retardant treatment showed a 13% increase from 7.8 million bd. ft. to 8.9 million. Use liquid preservatives declined 41.5 million gal. or 18%, solid declined 5%. Straight creosote declined 14% (14 million gal.); creosote petroleum solutions declined 26%, creosote and coal tar declined 18%. Volume creosote-pentachlorophenol solutions rose from 300,000 gal. in 1957 to 2.3 million gal. in 1958. Use pentachlorophenol dcereased 3%; water-borne preservatives, except for Tanalith and Osmosalts, declined 1% for Celcure, 40% for Boliden salt. Tanalith gained 1%, Osmosalts 20%. Creosote or solutions were used for 76% of all material treated, pentachlorophenol for 16%, all other preservatives for 8%. 95% material pressure treated. Lumber and timbers treated declined 7%. Creosote and creosote solutions used for 50% total. Volume treated with Tanalith increased 3%, with pentachlorophenol increased less than 1%, with Osmosalts increased 48%. Treatment piles declined 10%, plywood increased 55%, highway posts 9%. Fire-retardant treatments for lumber and plywood in-

cluded 1,019,963 lb. of Minalith; 705,042 lb. Protexal and Pyresote; 232,062 lb. chromated zinc chloride, 98,063 lb. of other chemicals.)

1959m, pp. 12-14, 16. (U.S., Jacksonville, Fla., building constructed of untreated lumber in 1954, inspected by VA badly damaged by decay. Hidden value of house built in 1956 of pressure-treated lumber. Cost allowed in mortgage loan and loan insurance, protected against both termites and decay, estimated in U.S. Dept. Agriculture's Wood Handbook at 500 million dollars per year.)

1959o, pp. 6-7. (U.S., Augusta, Ga., home damaged by termites, protection pressure-treated lumber.)

1959p, pp. 1-24. (U.S., Jackson, Miss., State Highway Dept., open grain southern yellow pine, coal tar creosote, 16 lb. per cu. ft., 1934-1959, 100% perfect; pentachlorophenol 5%, 10.72 lb. per cu. ft., 1938-1959, 100% perfect; chemonite 1938-1959, 100% perfect.)

1959q, pp. 1-15. (U.S., Mississippi State Highway Dept., yellow pine square posts, coal tar creosote 1931-1959, 90% effective; 1939-1957, 100% perfect—test closed; 1938-1959, 95% perfect; 1938-1957, 100% perfect—test closed; Douglas fir round posts, coal tar creosote, 1944-1959, 100% perfect.)

1959s, p. 66. (Western Australia, dip-diffusion treatments of *Pinus radiata* with sodium arsenite or fluoroborate-chromium-arsenic mixture protect against *Coptotermes* as best available pressure treatments. Chlordane or white arsenic added to glue line of karri plywood at all levels effective against termites. Plastic, gypsum plaster boards and insecticide treated hardboards with small additions of aldrin or dieldrin effective. Both dense and "no-fines" concrete termite-proofed by adding small amount dieldrin. Surface treatments with 5% pentachlorophenol only effective wood preservative against *Nasutitermes exitiosus* after 3 years. Tests of more than 30 types of plastic-covered, lead-sheathed, or bitimum-served cables have been under way against *Mastotermes* at Rollingstone, Queensland.)

1960a, pp. 14-17. (U.S., 3 types houses, basement, crawl-space, slab-on-ground, (1) limited protection: for basement houses, pressure preserved sills (cost $20 to $40 more); for crawl-space houses, pressure preserved lumber in substructure (cost $120-$150 more); for slab-on-ground houses, pressure preserved sills, plates, sleepers, columns, studs, porch lumber. (2) full protection: pressure preserve all framing lumber, cost 2% total price. Sills must be preserved, condensation leads to decay, settling. Shields repudiated, become racket, no protection against decay. Soil poisoning only short-term protection, will not prevent decay. Pressure-treated wood safest.)

1960j, p. 4. (U.S., homes up to 45 years old prove pressure-treated lumber provides most efficient protection.)

1960m, p. 4. (U.S., properly pressure-preserved lumber most effective protection against decay and termites, low cost insurance. For limited protection, cost $20 to $40 for average-sized home in areas where termites and decay range from slight to moderate; where range from moderate to heavy (28 States and D.C.) $120-$150. For full protection necessary in 8 States, especially in Florida and California, use pressure-treated lumber from sills to roof boards, cost 2 to 2½ percent additional.)

1960c,[1] pp. 20, 24. (Hawaii, termites controlled by use pressure-treated wood and kiln drying, local plants, Wolman salts for lumber and plywood, pentachlorophenol for millwork and trim, 80% wood treated Douglas fir, 10% Philippine mahogany.)

Barnacle, J. E., 1959, pp. 1-3. (Australia, a pole test against *Mastotermes darwiniensis*.)

Becker, G., 1958, pp. 123-142. (Germany, organic solvents; preparations added to glues, especially Kaurit glue, successful in protecting against termites in Tropics.)

Behr, E. H., 1960, pp. 9-10, 12, 14, 16, 19-20. (U.S., describes wood rots, how to treat, types of preservatives, penetration.)

Blew, J. O., Jr., 1956, pp. 1-7. (U.S., comparison wood preservatives in stake tests.)

1957, pp. 1-48. (U.S., comparison wood preservatives in stake tests.)

1958, pp. 1-8. (U.S., comparison wood preservatives in stake tests.)

1959, pp. 1-8. (U.S., comparison wood preservatives in stake tests. Mississippi, Wisconsin, Louisiana, Florida, Canal Zone, Panama, superficial treatments by dipping and brushing with coal tar creosote and petroleum oils containing copper naph-

thenate, zinc naphthenate, phenyl mercury oleate have added a few months to 4 years to the life of untreated stakes. Some water-borne preservatives have provided less protection than standard preservative oils, when retentions have corresponded to commercial usage, others compare favorably.)

1960, pp. 1-8. (U.S., In Mississippi stakes impregnated with 0.2 lb. fluor chrome arsenate phenol (Tanalith) per cu. ft. had an average life of 10 years; stakes pressure treated with the fire-retarding formulation containing ammonium phosphate and ammonium sulfate lasted 2 to 3 years; with these salts plus borax and boric acid stakes lasted 6 years; copper naphthenate is more effective than zinc naphthenate; stakes pressure treated with phenyl mercury oleate in naphtha have lasted 5 to 9 years. In Canal Zone, Panama, stakes pressure treated wtih chromated zinc arsenate (Boliden salt) 0.33 lb. per cu. ft. had an average life of 9 years, while those with 1.0 lb. had an average life of 15.3 years; stakes treated with 0.6 lb. per cu. ft. of Tanalith had an average life of 14 years; 5% solution of pentachlorophenol in light fuel oil—5-10 lb. per cu. ft. have lasted 14 years; 8 to 16 lb. per cu. ft. of coal tar creosote have lasted over 13 years.)

1961, pp. 1-8. (Mississippi, stakes pressure treated with ammonium phosphate and sulfate lasted on the average 2-3 years. With these salts plus borax and boric acid the life on an average was 4 years.)

Blew, J. O., Jr., and Johnston, H. R., 1956, pp. 272-281. (International termite exposure test, 22d progress report.)

1957, pp. 225-234. (International termite exposure test, 23d progress report.)

Blew, J. O., Jr., and Kulp, J. W., 1956, pp. 1-13. (U.S., Mississippi, comparison wood preservatives in post study.)

1957, pp. 1-16. (U.S., Mississippi, comparison wood preservatives in post study.)

1958, pp. 1-14. (U.S., Mississippi, comparison wood preservatives in post study.)

1959, pp. 1-14. (U.S., Mississippi, comparison wood preservatives in post study, untreated southern yellow pine posts installed from 1936-1938 had an average life of 3.3 years. Untreated longleaf pine posts installed in 1949 had an average life of 2.3 years, those treated with No. 2 fuel oil or Wyoming residual petroleum oil retention 5 to 7 lb. per cu. ft. have an average life of 8 to 9 years. Of southern yellow pine posts, installed from 1936-1941, treated with borax-boric acid all failed after 20 years, average life 10.6 years. Posts treated with the following preservatives have had failures totaling less than 10% and should last 33 years or longer on an average: water gas tar; 50-50 solution of creosote–crankcase oil (latter may contain chlorinated naphthalenes which injure cattle on contact); tetrachlorophenol 4.8% in crankcase oil; pentachlorophenol 3% and 4.8% in crankcase oil; copper sulfate and sodium arsenate applied by double diffusion and zinc meta arsenite. Posts in test in 1936-1941 treated with other preservatives have an estimated average life of 13 to 32 years.)

1960, pp. 1-16. (U.S., Mississippi, posts treated with the following preservatives (installed from 1936-1941) have had failures totaling 10% or less, should last 36 years or longer on an average; water gas tar; 50-50 solution of creosote—crankcase oil; pentachlorophenol 3% and 4.8% in crankcase oil; copper sulfate and sodium arsenate applied by double diffusion and zinc meta arsenite. Posts treated with other preservatives have an estimated average life of 13 to 35 years.)

1961, pp. 1-14. (U.S., Mississippi, experimental untreated southern yellow pine posts installed from 1936 to 1938 at the Harrison Experimental Forest, Saucier, Miss., had an average life of 3.3 years. Untreated longleaf pine posts installed in 1949 had an average life of 2.3 years, while those treated with a No. 2 fuel oil and with Wyoming residual petroleum oil have an estimated average life of 5 and 8 years, respectively. Of southern yellow pine posts installed from 1936 to 1941, those treated with borax-boric acid have all failed with an average life of 10.6 years and those treated at the groundline and top with Osmoplastic have all failed after an average life of 11.2 years. Posts treated with the following preservatives and installed from 1936 to 1941 have had failures totaling 10 percent or less of the number installed and should last 38 years or longer on an average. Pentachlorophenol, 3% and 4.8% in crankcase oil; copper sulfate and sodium arsenate applied by double diffusion; and zinc meta arsenite. Posts in tests in 1936 to 1941 treated with other

preservatives have an estimated average life of 8 to 37 years.

Brown, G. E., and Alden, H. M., 1960, pp. 434-438. (U.S., pentachlorophenol and sodium pentachlorophenate to protect particle board.)

Bulman, R. A., 1959, p. 15. (Africa, protection buildings by efficient wood preservatives for timber.)

Carr, D. R., 1957, pp. 1-19. (New Zealand, decay and subterranean termites not as injurious as native drywood termite *Calotermes brounii.* Boric acid treatment satisfactory for weather boards but not for wood in contact with ground. Pressure treatments with coal tar creosote, 5% pentachlorophenol, zinc and copper naphthenates or boric acid used in New Zealand.)

Chapman, A. W., 1958, pp. 1-9. (U.S., Ferox process for insulation boards.)

Clagg, C. F., and Keck, C. B., 1960. (Hawaii, *Coptotermes formosanus* entered and damaged commercially pressure-treated lumber.)

Clements, W. B., 1956, pp. 18-20, 31-34. (U.S., Florida, termite damage increasing due to scarcity virgin timber, turpentining, poor construction, land clearing and slab construction. Treated lumber will protect.)

Dillon, R. M. (Ed.), 1956, pp. 1-60. (U.S., protection against decay and termites in residential construction, Nat. Acad. Sci.—Nat. Res. Counc. for FHA.)

1958, pp. 1-33. (Addendum A, all structural lumber must be treated to give full protection against termites.)

Ebeling, W., and Pence, R. J., 1958a, pp. 1-16. (U.S., California, treating all rough lumber in house would add 3% to cost, or less expensive, treat all wood up to and including subfloor, cost 10 cents per sq. ft.)

Gay, F. J., Greaves, T., Holdaway, F. G., and Wetherly, A. H., 1955, pp. 1-60. (Australia, method maintaining laboratory colonies *Nasutitermes exitiosus, Coptotermes lacteus,* and *C. acinaciformis.*)

1957, pp. 1-31. (Australia, field testing techniques.)

Gay, F. J., Harrow, K. M., and Wetherly, A. H., 1958, pp. 1-14. (Australia, antitermite comparative studies in laboratory, value over 1.09%, boric acid, zinc chloride, 1.8%, "Tanalith U," 0.90%.)

Gay, F. J., and Wetherly, A. H., 1958, pp. 1-14. (Australia, antitermite value some chlorinated naphthalenes and phenols, low percentages 1 to 2.16% did not give complete protection.)

1958a, pp. 1-13. (Australia, hardboards with 0.75% by weight pentachlorophenol or 0.9% arsenious oxide resistant.)

Gösswald, K., and Kloft, W., 1959, pp. 268-278. (Germany, termite proofing textiles, laboratory tests with *Kalotermes flavicollis.*)

1959a, pp. 257-278. (Idem.)

Graf, J. E., 1956, pp. 16-17 (Canal Zone, Panama, Barro Colorado Island, wood-preservative tests.)

Halsted, C. T., 1958, pp. 116-117. (U.S., termite proofing plywood.)

Harris, W. V., and Brown, E. S., 1958, pp. 737-750. (Solomon Islands.)

Hartman, C. F., 1960, pp. 1-7. (U.S., fire-retardant lumber is an ancient building material, Greeks used vinegar in 4th century B.C.; ammonium sulfate and ammonium phosphate combination patented in 1893 by Max Bachert in New York City. Combination chromated zinc chloride with fire retardant salts patented in 1935 by Protexol Corp. Control by liberated water of crystallization, creation glazed surface, emission noncombustible smothering gas, creation clinkerlike charcoal, insulation against flame. Discussion various tests, such as tunnel, etc.)

Hatfield, I., 1958, pp. 36, 38, 40, 42, 44, (U.S., most economical combined fungicide and wood insect control chemical —pentachlorophenol, "Woodtreat TC," 10% pentachlorophenol by weight oil in water emulsion, coating for wood, penetration equal to 20 brush coatings.)

Hatfield, I., and Allen, R. van, 1956, pp. 32, 34, 78. (U.S., Woodtreat TC, containing pentachlorophenol.)

Hopkin, M. S., 1958, p. 15. (Africa, life of buildings prolonged by efficient wood preservation.)

Hrdý, I., 1959, pp. 193-207. (Raising the resistance of wood-fiber boards by the use of pentachlorophenol, sodium pentachlorophenate, trichlorobenzene, and lindane.)

In press. (Czechoslovakia, methods of laboratory testing of the resistance of materials against termite attack.)

Hunt, R. W., 1960, pp. 1211-1212. (U.S., Southern California, damage to buildings by *Kalotermes minor* surpassing that

caused by either subterranean termites or decay. Use of even small amount wood preservatives worth while; copper component desirable.)

Isherwood, H. R., 1957, pp. 32-33. (U.S., pressure-treated wood in home mechanical termite control.)

Jackson, W. F., 1957, pp. 49-50. (Malaya, termite resistance test on resin-bonded wood waste containing BHC.)

Klem, G. G., 1957, pp. 20A-21A. (U.S., new method for testing.)

Lund, A. E., 1957, pp. 363-367. (U.S., accelerated study, wood preservatives retentions—water-borne—used to determine approximate threshold killing concentrations for subterranean termites.)

1958, pp. 1-9. (U.S., relationship subterranean termite attack to varying retentions water-borne preservatives, from 0.500 lb. per cu. ft. for copper–zinc compound to 0.031 lb. per cu. ft. for copper–arsenic preservative.)

1959, pp. 220-223. (U.S., Douglas fir plywood treated resistant.)

Lund, H. O., 1959, pp. 533-534. (U.S., Georgia, laboratory tests prove *Reticulitermes flavipes* can build tubes over wood treated by pressure or soaking with creosote, osmose salts, Wolman salts, and copper naphthenate.)

1960, pp. 32, 34, 36. (U.S., Georgia, tests show termites can tunnel over wood freshly treated with creosote, copper naphthenate, Wolman salts, osmose salts within a month; or over wood treated 24 months with pentachlorophenol; 16 months with copperized chromated zinc chloride.)

1961, pp. 63-64. (U.S., termites built tunnels to top of wood treated with Osmose in 9 days; over creosoted wood in 19 days; wood protected with copper naphthenate spanned in 27 days; with Wolman salts 28 days; copperized chromated zinc chloride 16 months; with pentachlorophenol 24 months.)

Martínez, J. B., 1952, pp. 1-550. (Conservation of wood, studies of oleaginous antiseptics.)

Mellan, L., and Mellan, E., 1956, pp. 1-150. (Dictionary of poisons, wood preservatives included.)

Merrick, G. D., 1955, pp. 319-352. (U.S., quantity of wood treated and preservatives used in 1954, 250.7 million cu. ft., 14% less than in 1953.)

1956, pp. 289-320. (U.S., 3% more treated wood used in 1955 than in 1954.)

1957, pp. 281-314. (U.S., industry production in 1956 4% over 1955.)

1958, pp. 259-293. (U.S., 16.6 million cu. ft., or 6.5% more wood treated in 1957 than in 1956, use creosote increased 4%, pentachlorophenol decreased 9%.)

1959, pp. 253-287. (U.S., in 1958 volume wood treated the smallest in many years, a decrease of 15% from 1957, only 232.8 million cu. ft., a decrease of 41.7 million cu. ft. from 1957. Use of liquid preservatives declined 18%. Creosote decreased 14%, creosote petroleum 26%, creosote coal tar 18%, creosote pentachlorophenol solutions increased to 2.3 million gal., pentachlorophenol decreased 3%. Water-borne preservatives decreased except Tanalith and Osmosalts, former increased 1%, latter 2%. Creosote or creosote solutions used for 76% of all treated wood, pentachlorophenol 16%; others 8%. 95% treatments by pressure. Preservative-treated lumber and timber decreased 7%.)

1960, pp. 249-283. (U.S., the volume of wood products treated by the wood-preserving industry in 1959 was 214.5 million cu. ft., a decrease of 18.5 million cu. ft. or almost 8% from 1958, and to the lowest level since 1935. Changes from 1958 are: poles +6%, crossties −29%, lumber and timbers +13%, fence posts +6%, piles −9%, switch ties −33%, cross arms +6%, miscellaneous +3%.

The use of liquid preservatives decreased 12 million gal. or 6%, while the use of solids increased 3.8 million lb., or 18%

The use of creosote decreased 7%, creosote in pentachlorophenol-creosote solutions more than tripled; the use of pentachlorophenol increased nearly 19%; the use of all water-borne preservatives except Minalith increased.)

Meyer, F. J., and Spalding, D. H., 1958, pp. 1-10. (U.S., treatments for fiberboard, hardboard, particle board.)

Moore, R. F., 1958, pp. 6, 8. (U.S., New Orleans, La., $60,000 plantation home, southern yellow pine, umbrella roof, well above ground, wood pressure preserved with 8 lb. pentachlorophenol per cu. ft., Ricciuti Associates.)

Page, R. H., 1958, pp. 7, 14. (U.S., Georgia, Georgia Forestry Commission and U.S. Forest Service adopt recommendations

in "Wood preservation in home construction.")

Putnam, R. B., 1957, pp. 360-362. (U.S., how and what to specify in the preservative treatment of wood for buildings.)

Reid, L., 1955, pp. 1-2. (U.S., build in decay insurance, 10 tips to avoid decay.)

Roberts, L., 1957, p. 496. (U.S., propolis—bee glue—vs. wood preservation for beehives.)

Sandermann, W., 1955, *in* Schmidt, H. (Ed.), 1955b, pp. 208-244. (Chemical basis wood protectants for use against termites and methods application.)

Selbo, M. L., 1960, pp. 10-14. (U.S., laminated timbers properly glued with resorcinol or phenyl resorcinol adhesives and adequately treated with a suitable preservative effective; treating wood after glueing most practical, with certain species—preservatives feasible to glue already treated lumber. Tanalith showed least interference with bonding.)

Shepard, H. H. (Ed.), 1960, pp. 1-250. (U.S., testing resistance chemically-treated textiles to insect damage, chap. 7, M. M. Walton and H. H. Shepard.)

Snyder, T. E., 1956b, p. 18. (Canal Zone, Panama, Barro Colorado Island, 30-year test proves treated wood building is termite proof.)

1956c, pp. 20, 22. (Summary results "International Termite Exposure Test.")

Stolloy, I., 1958, pp. 1-6. (U.S., treatments, particle board, to increase resistance to fungi and termites.)

Tamblyn, N., Da Costa, E. W. B., and Gay, F. J., 1959, pp. 1-8. (British Commonwealth, Australia, most effective momentary dipping process for plywood sodium pentaborate, zinc chloride–arsenic mixture.)

Tu, T., 1957, pp. 13-18. (Formosa, blue camphor oil effective wood preservative.)

Wakeman, C., 1959, p. 12. (U.S., Los Angeles, Calif., pressure-treated sills and structural framing (Douglas fir) protects house against termites and decay.)

Wolcott, G. N., 1955a, pp. 115-149. (Puerto Rico, organic repellents tested against *Cryptotermes brevis*.)

1956, pp. 85-86. (Puerto Rico, 1% pentachlorophenol protects wood against drywood termite attack for more than 11 years.)

ZOOGEOGRAPHICAL REGIONS: AUSTRALIAN

Anonymous, 1953t, p. 70. (Australia.)
1954d, pp. 68-69. (Australia.)
1956i, p. 67. (Australia.)
1958h, p. 66. (Australia.)
1958n, pp. 2-10. (Australia.)
1958o, p. 63. (Australia.)
1959s, p. 66. (Australia.)

Barnacle, J. E., 1959, pp. 1-3. (Australia.)

Beesley, J., 1957, pp. 1-3, 4-6. (Australia, Melbourne.)

Briton, E. B., 1957, pp. 1-185. (Australia.)

Calaby, J. H., 1956, pp. 89-92. (Western Australia.)
1956a, pp. 93-96. (Western Australia.)
1956b, pp. 111-124. (Western Australia.)
1960, pp. 79-80. (Western Australia.)
1960a, pp. 143-146. (SW. Australia.)
1960b, pp. 183-207. (SW. Australia.)

Calaby, J. H., and Gay, F. J., 1956, pp. 19-39. (Western Australia.)
1959, pp. 211-223. (Australia.)

Carr, D. R., 1957, pp. 1-19. (New Zealand.)

Casimir, M., 1957, pp. 68-78. (Australia.)

Emerson, A. E., 1960, pp. 1-28. (Australia.)

Gay, F. J., 1955, pp. 58-59.
1956, pp. 207-213.
1957, pp. 86-91.
1960, pp. 228-231. (Australia.)

Gay, F. J., Greaves, T., Holdaway, F. G., and Wetherly, A. H., 1955, pp. 1-60. (Australia.)
1957, pp. 1-31. (Australia.)

Gay, F. J., Harrow, K. M., and Wetherly, A. H., 1958, pp. 1-14. (Australia.)

Gay, F. J., and Wetherly, A. H., 1958, pp. 1-14. (Australia.)
1958a, pp. 1-13. (Australia.)
1959, pp. 26-28. (Australia.)

Greaves, T., 1959, pp. 114-129. (Australia.)

Harris, W. V., 1955a, pp. 12-13. (Australia.)

Hindwood, K. A., 1959, pp. 1-36. (Australia.)

Jenkins, C. F. H., 1960, pp. 117-123. (Western Australia.)

McKeown, K. C., and Calaby, J. H., 1958, pp. 462-465. (Australia.)

Main, A. R., and Calaby, J. H., 1957, pp. 216-228. (NW. Australia.)

Miller, D., 1956, pp. 477-478. (New Zealand.)

Morgan, F. D., 1959, pp. 155-195. (New Zealand.)

New South Wales Dept. Agriculture, Entomological Branch, 1958, pp. 1-19. (Australia, N. S. Wales.)

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- Wilson, H. B., 1959, pp. 35, 37, 39, 41, 43, 45, 47-49, 51, 53, 89-91, 93-95. (Australia.)
- Womersley, H., 1939, p. 174. (South Australia.)
- Zondag, R., 1959, pp. 15-17. (New Zealand.)

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  - 1956a, pp. 105-110. (Tropical.)
  - 1956b, pp. 111-113. (Tropical.)
  - 1956c, pp. 801-803.
  - 1958, pp. 479-482.
  - 1958a, pp. 488-490.
- Bulman, R. A., 1959, p. 15. (Africa.)
- Coaton, W. G. H., 1955, pp. 109-136. (Belgian Congo.)
  - 1958, pp. 1-112. (South Africa.)
  - 1960, pp. 6-9. (South Africa.)
  - 1961, pp. 39-54. (Africa.)
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Charles D. and Mary Vaux Walcott Research Fund

COMPARISON OF TEKTITE SPECIMENS FROM EMPIRE, GEORGIA, AND MARTHA'S VINEYARD, MASSACHUSETTS

(WITH SIX PLATES)

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COMPARISON OF TEKTITE SPECIMENS FROM EMPIRE, GEORGIA, AND MARTHA'S VINEYARD, MASSACHUSETTS[1]

By ROY S. CLARKE, Jr.,[2] and MAXWELL K. CARRON[3]

(With Six Plates)

INTRODUCTION

The recent find of a tektite at Gay Head, Martha's Vineyard, Mass., has been reported by Kaye, Schnetzler, and Chase (1961). This specimen, representing a possible new occurrence of tektites, was generously submitted by the finders to us for laboratory study. The Martha's Vineyard tektite (USNM 2082) arrived when we were completing study of a tektite from Empire, Ga. (USNM 1396), which has been at the U. S. National Museum since 1938. A similarity between these two specimens was immediately suggested by their close agreement in color, density, and magnetic properties. Further study of the Martha's Vineyard tektite established that a truly remarkable similarity does exist. This report presents new physical and chemical data and photographs for both of these specimens. The possible significance of the unexpected nature of these data and the ambiguous conclusion to which they lead are discussed. Either this new group of tektites has much more uniform properties than would be expected, or else there is room to doubt their authenticity.

ACKNOWLEDGMENTS

The authors are indebted to a number of their colleagues who have supported and contributed to the studies presented here. Most of these workers are cited at appropriate places in the text. Frank E. Senftle, Irving Friedman, and E. C. T. Chao, of the U. S. Geological Survey, should receive special mention, as they have had an active interest in this work since its inception. Their suggestions, criticisms, and experimental observations are included below. Paul D. Low-

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[1] Publication authorized by the Director, U. S. Geological Survey.

[2] U. S. National Museum, Smithsonian Institution.

[3] U. S. Geological Survey, Washington 25, D. C.

man, Jr., of the National Aeronautics and Space Administration, and E. P. Henderson, of the Smithsonian Institution, have generously shared their knowledge of tektite specimens and literature with the senior author in many helpful discussions.

PREVIOUS WORK

The initial identification of tektites from Georgia was made by E. P. Henderson of the Smithsonian Institution's Division of Mineralogy and Petrology. Two specimens (USNM 1396) were submitted for examination and an identification was made during 1938. Confirmation of Georgia as an area of tektite occurrence has been reported by Barnes and Bruce (1959). Bruce (1959) has published a general discussion of tektite finds in Georgia, and included in his paper are photographs of several specimens. Cohen (1959) has discussed Georgia tektites with particular reference to their similarity to moldavites and bediasites. His paper includes a compilation of physical properties and spectrochemical data. Senftle and Thorpe (1959) have measured the magnetic susceptibility and intensity of magnetization for the Georgia tektite and for a number of other tektites, and have discussed the significance of these measurements. Reynolds (1960) and Gentner and Zähringer (1960) have measured potassium-argon ages for the major tektite groups. These data show that Georgia tektites and bediasites are of similar age, but that moldavites are much younger. Stair (1955a, 1955b, 1956) has published the absorption spectra and a photomicrograph of this same Georgia specimen. He also gives a photograph of a second Empire, Ga., tektite. The measurements reported in the literature on Georgia tektites by all the workers cited above have been made on portions of one specimen, USNM 1396.

The only previous experimental work using material from the Martha's Vineyard tektite other than a chemical analysis reported by Kaye et al. (1961) is that of Pinson and Schnetzler (1960). These authors have determined rubidium and strontium contents and strontium isotope ratios.

MORPHOLOGY AND INTERNAL STRUCTURE

The two tektite specimens with which we are particularly concerned have both similarities and striking differences in gross morphology. Plate 1 is a direct-light photograph of (A) the Empire, Ga., and (B) the Martha's Vineyard, Mass., tektites. Plates 2 and 3 are photographs of these specimens after ammonium chloride smoking to bring out surface features. All photographs of the Martha's Vineyard tektite show the complete object before removal of material for analysis. Over half of the Empire, Ga., specimen has been consumed in experimental studies, and plate 1, A, shows the remaining portion of this specimen. Plate 2 shows the front and back surfaces of this specimen after it had been cut to remove a slice for study. The distance between halves approximates the material that has been removed.

Plates 5 and 6 are previously unpublished photographs of other Georgia tektites. They were furnished to the authors by E. P. Henderson and are included here as background material. Plate 5, A and B, are photographs of a second Empire, Ga., specimen (also having catalog number USNM 1396), a complete individual that is preserved in the collection of the U. S. National Museum. A tektite from Plainfield, Ga., belonging to G. A. Bruce is shown in plate 5, C and D. Plate 6, B, shows a tektite found near Osierfield, Ga., lent by A. S. Furcron, of the Georgia Geological Survey. Dimensions of these tektites are given in table 1.

TABLE 1.—*Approximate size and weight of specimens*

Locality	Length of longest axis *cm.*	Length perpendicular to longest axis *cm.*	Maximum thickness *cm.*	Weight *g.*	Illustrated in—
Empire, Ga.[a]	~6.5	~3.5	~1.0	>25	Pl. 2
Empire, Ga.	3.3	2.7	1.4	13.4	Pl. 5, A, B
Plainfield, Ga.	3.5	2.9	0.9	11.2	Pl. 5, C, D
Osierfield, Ga.	4.7	4.4	0.6	17.8	Pl. 6, B
Martha's Vineyard, Mass.	5.3	3.9	1.0	17.8	Pl. 3

[a] Lengths given were estimated from photographs of cut specimen, and thickness was measured on remaining portion of specimen.

The most striking feature of the four Georgia tektites is their disklike shape; three are nearly circular. These specimens are rather uniformly covered with many shallow pits and grooves which produce generally smooth surfaces and edges. The disk shapes and general surface features are suggestive of the moldavites. Disk shapes are known among moldavite specimens but are rare among the other tektite groups (Suess, 1900; Barnes, 1940; Baker, 1959).

The Martha's Vineyard specimen appears to be a sector of a roughly circular disk about 3 inches in diameter. The smooth fracture surfaces on the sides of the specimen imply that it has been broken from a parent mass after formation of its surface features. The deeply serrated edge of the Martha's Vineyard specimen is different from anything that has been observed on Georgia tektites,[4] and it is an uncommon feature of tektites in general. The surface relief is also much more pronounced for this specimen. It has sharp ridges on the top and bottom surfaces and particularly on the serrated edge. These sharp, relatively unabraded features imply that the Martha's Vineyard tektite has not been transported far by normal geologic processes subsequent to sculpturing. An unsual feature of this specimen is that the edge pattern appears to be radial, while the surface pattern on the interior of the disk appears to be concentric (pl. 3, A).

There is a remarkable similarity between the Martha's Vineyard specimen and a photograph of a moldavite published by F. E. Suess (1900, pl. V, fig. 5b). Our specimen appears, at first glance, to be a part of this specimen studied long ago by Suess. However, this apparent duplication is due to the fact that Suess's photograph is enlarged. His figures 5a and 5c show this tektite at natural size. It is obvious that the Martha's Vineyard tektite must have come from a parent of greater diameter than Suess's specimen.

It has been stated above that the Martha's Vineyard tektite is apparently a part of a larger disk-shaped object, probably 3 inches (7.6 cm.) in diameter. If this assumption is valid, the parent body of this specimen was larger than any disk-shaped tektite of which we are aware. The hypothetical parent tektite would have a diameter-to-thickness ratio of 7.6, which is greater than that of any tektite known to us. Even if a 2-inch diameter is assumed, this tektite would still have a very high ratio, approximately 5. The Osierfield, Ga., tektite (pl. 6, B, and table 1), with a ratio value of 7, is the only other tektite we know of in this range.

The internal structure and inclusions in the Empire, Ga., and Martha's Vineyard specimens are shown in the accompanying photomicrographs. Plate 4, A, is a photomicrograph taken with white transmitted light of a slice 0.25 cm. thick cut radially from the Martha's Vineyard tektite. Plate 4, B, is of the same area using plane polarized light, crossed nicols. Plate 4, C and D, are photographs of a slice 0.07 cm. thick of the Empire, Ga., tektite. If allowance is made for the differences in thickness between the two sections, the similarity in pattern and character of inclusions is apparent. Some of these inclusions are well outlined and are of lower index of refraction than the surrounding glass. They show wavy extinction and have not been positively identified. Barnes (1940) has proposed that similar inclusions in bediasites are lechatelierite. Sparsely distributed small round

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[4] Bruce, G. A., personal communication, 1960.

and elongated bubble cavities are also present, appearing in the photomicrographs as dark spots.

Pronounced flow structure, or flow lines, indicative of inhomogeneity within the glass, appears in both specimens. This structure is revealed by variation in index of refraction resulting presumably from minor compositional differences (pl. 4, A and C). Strain is also present in these glasses and is associated both with the flow structure and inclusions. This strain is evident from the anisotropism that is observed in the sections with plane polarized light, crossed nicols (pl. 4, B and D).

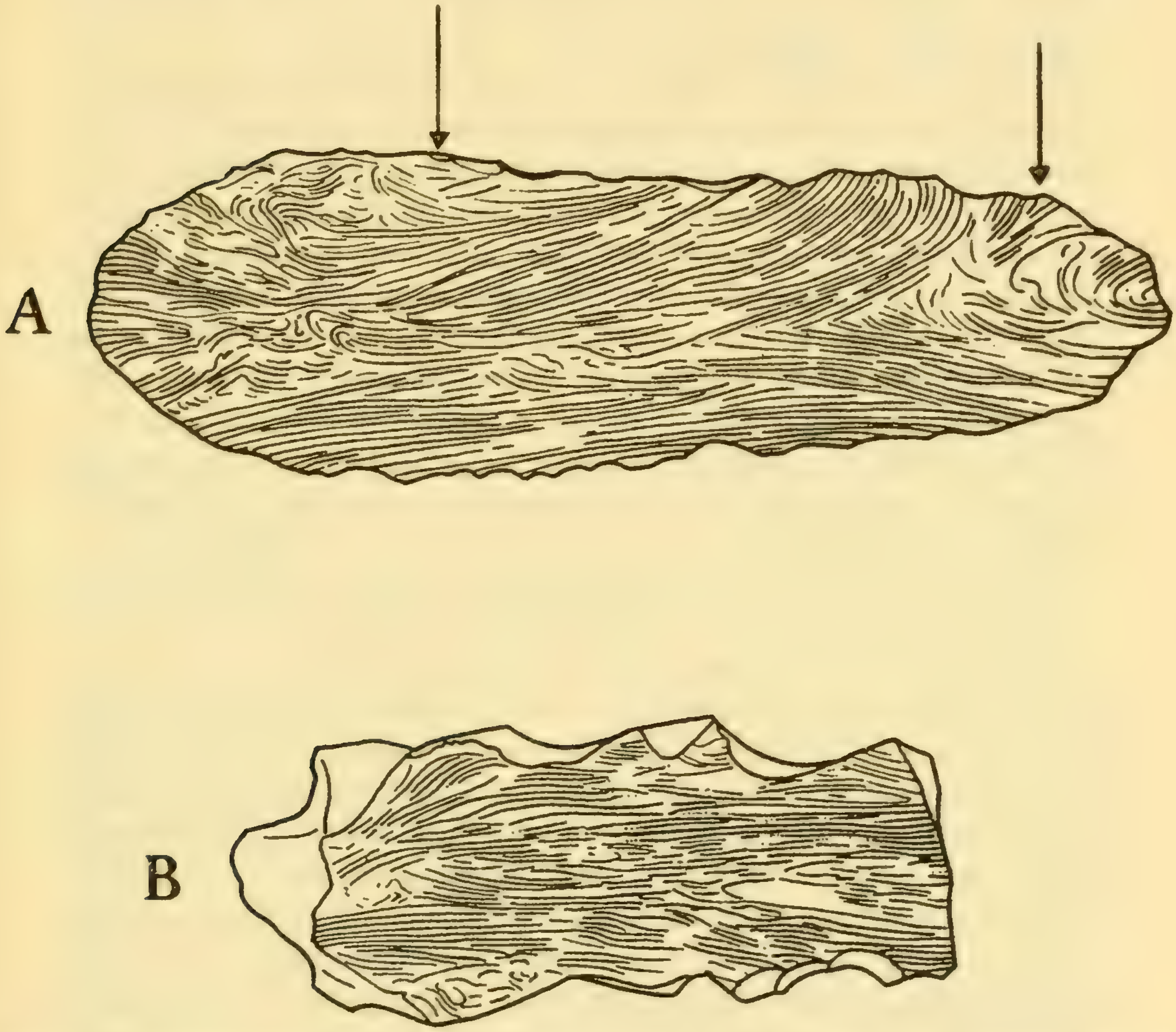

Fig. 1.—Flow structure diagram prepared from slice of (A) Empire, Ga., tektite, and (B) Martha's Vineyard, Mass., tektite. × 3.

The flow structure of both specimens here studied in detail conforms quite well to the surface of the specimens. In figure 1 are given flow structure drawings prepared from a projected image of the sections used in making the photomicrographs (pl. 4). Figure 1, A, is of a section from the flat end of the Georgia tektite specimen (pl. 1, A). The slice from which figure 1, B, was prepared was taken several millimeters in from the left broken edge of the Martha's Vineyard specimen positioned as in plate 1, B, extending approximately two-thirds of the way into the specimen and parallel to that edge. This relationship of surface to flow structure is unusual for tektites in general (Barnes, 1940; Baker, 1959).

The present external surfaces of these specimens are essentially secondary features due largely to chemical etching. Indeterminant factors such as the original shape of the specimen, the susceptibility of its various parts to chemical attack, the nature of the chemical environment and the time through which it has acted, and mechanical effects, combined to produce the present surface features of these tektites. The main surface features, pitting and grooving, have no obvious relation to the internal structure of the material. Tektite surface pits are sometimes referred to as bubble cavities, but it is unlikely that bubbles within the glass were responsible for the pitting on the tektites we studied. It has been mentioned above that the bubbles present in the sections were small and sparsely distributed (pl. 4). Their concentration in the medium and their individual diameters are both minute when compared to the surface pits.

The internal flow structure, however, is related directly to delicate striae that are readily observable as a secondary surface feature on these specimens. The striae frequently occur where the flow structure is truncated by the specimen surface and undoubtedly result from slight differences in susceptibility to chemical attack. The left-hand piece of the Empire, Ga., tektite shown in plate 2, A, exhibits striation which is of particular interest because it indicates the extent to which flow structure conforms to the surface of the specimen. The striae follow the edge of the specimen and suggest that the flow structure pattern based on the section (fig. 1, A) holds in a general way for the complete specimen. The arrows in figure 1, A, indicate areas where the U-shaped striae on the surface of the specimen (fig. 1, A) terminate.

Striae are obvious on the surfaces of the Martha's Vineyard tektite (pl. 3, A and B) and especially on the serrated edge (pl. 3, C). The concentric external pattern is consistent with the flow structure illustrated from the section (fig. 1, B). The second Empire, Ga., tektite (pl. 5) is a striking example of surface expression of internal structure. The more irregular pattern on this tektite probably indicates a more contorted flow structure. Surface striation of this type is also present on the Plainfield (pl. 5, C and D) and Osierfield (pl. 6, B), Ga., specimens and can be seen in the photographs.

Plate 6, A, is an enlargement of a small area of the surface of the Plainfield, Ga., specimen. It shows several features that are common to all the specimens with which we are concerned and one feature that is peculiar to this specimen. The latter is an apparently glassy mass, or protuberance, that projects from the bottom of a surface cavity (pl. 6, A; and slightly to left of center in pl. 5, C). This protuberance is firmly attached to the body of the specimen and apparently resulted from chemical attack on a volume of glass containing an inclusion or inhomogeneity of more resistant composition. No measurements of properties or composition of this protuberance were possible as the owner desired to maintain the specimen intact.

All these tektites show what appear to be several generations of surface pits, a feature particularly apparent on close examination of plate 6, A. Around the top edge of the cavity containing the protuberance there are four outlined depressions, apparently the remnants of previous pits that have grown together and been largely obliterated by the younger central pit. The photograph also shows numerous examples of pits within pits, and pits overlapping pits. A particularly interesting pattern can be seen in the lower right-hand corner of plate 6, A. A raised, rather white area is surrounded by five distinctly outlined grayish areas that seem to have been formed as a result of enlargement of pits. This feature and the glassy protuberance described above provide direct evidence that the internal composition of the material has at least a limited control on the surface features that develop. A number of very small pits possibly could have resulted from bubbles within the glass, but it is impossible to identify any of these from the photograph.

To summarize: Study of the detailed morphology of these specimens supports the idea that chemical weathering, controlled to a slight extent by variations in composition of the material, is the main agent responsible for the formation of these surface features. We find no evidence either in the gross shapes or on the surfaces of these specimens that suggests a history of aerodynamic shaping.

PHYSICAL PROPERTIES

A comparison of some of the physical properties of the two specimens is given in table 2. All the properties listed are remarkably similar.

Density measurements were made by weighing the suspended specimens in air and in carbon tetrachloride of accurately known density at the temperature of measurement. The resulting bulk density figures of 2.330 for the Georgia tektite and 2.332 for the Martha's Vineyard tektite agree within the limit of error of the measurement (estimated to be 0.002 g./cm.^{3}). These density figures are slightly lower than the lowest specific gravity figure (2.334) given by Barnes (1940) for bediasites and are in the middle of the range of density figures (2.303 to 2.367 g./cm.^{3}) he gives for moldavites. Conversion of Barnes's specific-gravity values to densities is not possible because of insufficient data. The difference between our values and his lowest bediasite value could be more apparent than real. The close agreement of density values for the two specimens under study combined with their chemical compositions (table 4) confirms the impression obtained from transparent sections that bubble size and distribution in the two materials are the same.

TABLE 2.—*Comparison of physical properties of the Martha's Vineyard and Georgia tektites*

Property	Georgia tektite (USNM 1396)	Martha's Vineyard tektite (USNM 2082)
Color	Light olive green	Light olive green
Weight (g.)	11.4[a]	17.76[b]
Index of refraction	1.485±0.003[c]	1.4852±0.0004[d]
Density (g./cm.^{3})	2.330	2.332
Magnetic susceptibility (e.m.u./g.)	3.6×10^{-6}[e]	3.90×10^{-6}[f]
Magnetization	0[e]	0[f]

[a] Remaining portion of specimen.
[b] Complete specimen.
[c] Determined by I. Friedman, U. S. Geological Survey.
[d] Bulk index determined by E. C. T. Chao, U. S. Geological Survey.
[e] From Senftle and Thorpe (1959).
[f] Determined by A. Thorpe, U. S. Geological Survey.

The index of refraction of both the Martha's Vineyard and Georgia tektites is 1.485. This value is slightly less than the smallest value ($N_{Na}=1.488$) given by Barnes (1940) for bediasites and in the middle of the range ($N_{Na}=1.4798$ to 1.4961) he gives for moldavites. Barnes (1940, pp. 522-523) has used the Gladstone and Dale relationship to plot index of refraction and density data to show relationships of these data for the various tektite groups and other natural glasses. The data for the Martha's Vineyard and Georgia tektites give a specific refractivity of 0.208, which falls in the moldavite area of Barnes's plot, outside of the area where moldavites and bediasites overlap.

Magnetic data for a number of tektites and other glasses have been obtained and discussed by Senftle and Thorpe (1959). The magnetic susceptibility values depend both on the total amount of iron present and the proportion of oxidized to reduced iron. The Martha's Vineyard and Georgia tektites contain approximately the same total iron (table 4). The slightly higher proportion of oxidized iron in the Martha's Vineyard tektite is consistent with the slightly higher magnetic susceptibility value observed for this specimen. The magnetic susceptibility values for the Georgia and Martha's Vineyard tektites fall in the range between the highest moldavite value (3.0×10^{-6} e.m.u./g.) and the lowest bediasite value (4.2×10^{-6} e.m.u./g.) reported by Senftle and Thorpe (1959). The zero magnetization value, a value which is typical for tektites in general, is interpreted to mean essentially complete solution of iron in the tektite glass. These observations are indicative of a history of high-temperature treatment during formation of the glass.

ABSORPTION SPECTRA

The spectral transmission of a number of tektites, including the Empire, Ga., specimen, in the ultraviolet, visible, and near infrared regions of the spectrum (300 to 5,000 millimicrons) has been reported by Stair (1955a, 1955b, 1956). Cohen (1958) has given absorption spectra for a number of tektites in the region 300 to 2,600 millimicrons. He points out that his curves and Stair's are in agreement for the region they treat in common, and that the Empire, Ga., tektite curve agrees particularly well with that of moldavites. Cohen (1958) interprets these curves as being consistent with the high ferrous to ferric iron ratio observed in chemical data on tektites (table 4), while Stair (1955a) tentatively interprets them as indicative of high ferric iron.

A new determination of the absorption spectrum of the Empire, Ga., tektite, along with that of the Martha's Vineyard spectrum, is given in figure 2. These curves are directly comparable to those of Cohen and were obtained by using a Cary Model 14 recording spectrophotometer.[5] Highly polished specimen slice surfaces were prepared, using 0- to 2-micron diamond powder followed by magnesium oxide.[6] The Georgia tektite slice used for the photomicrograph in plate 4, C and D, was further polished and used for the absorption measurement. Masks with identical light transmission areas slightly

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[5] Dr. Walter Shropshire, Jr., Division of Radiation and Organisms, Smithsonian Institution, did the instrumental work in obtaining these curves.

[6] Grover C. Moreland, Division of Mineralogy and Petrology, U. S. National Museum, Smithsonian Institution, prepared the polished slices.

smaller than the smallest specimen were prepared for use in the sample and reference beam of the spectrophotometer. A blank correction was determined by measuring the absorbance with the masks in position previous to mounting the specimens.

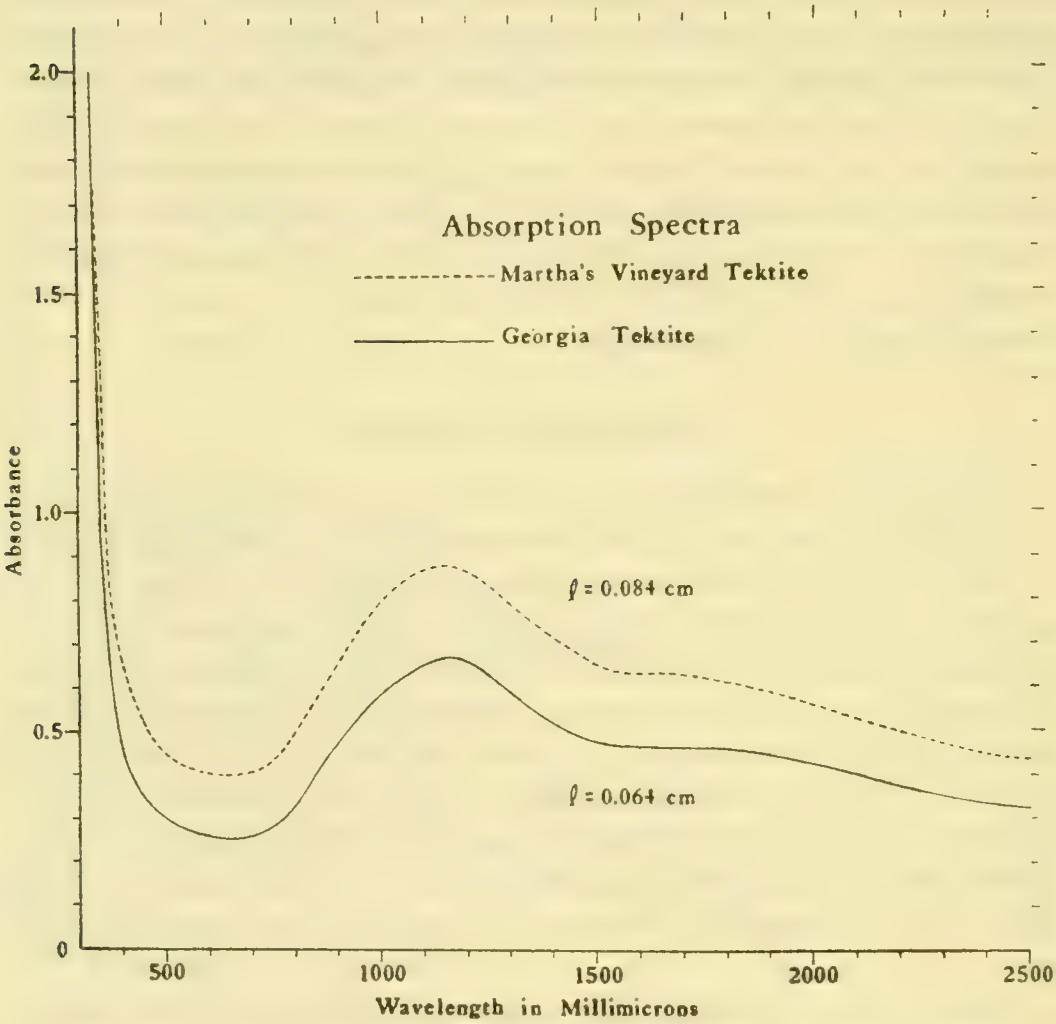

FIG. 2.—Absorption spectra of the Empire, Ga., and Martha's Vineyard, Mass., tektite specimen.

The curves in figure 2 are essentially identical. The greater absorption of the Martha's Vineyard slice can be attributed to sample thickness, suggesting that these two materials adhere to Lambert's law and have the same extinction coefficient.

SPECTROGRAPHIC AND CHEMICAL ANALYSES

Semiquantitative spectrographic analyses of both tektites are shown in table 3. Assuming that this type of analysis is within a factor of only 2 of the correct value, one can say that the analyses of both specimens are essentially the same with the exception of boron, lead, beryllium, and yttrium. The high boron and beryllium contents are undoubtedly due to contamination. The mortar in which the Martha's Vineyard tektite was ground had previously been used for grinding hambergite, $Be_2(OH)BO_3$, and this probably accounts for the high values for these elements. The high lead and yttrium values could not be accounted for. The following elements were looked for and not found: As, Au, Bi, Cd, Ce, Dy, Er, Eu, Gd, Ge, Hf, Ho, In, Ir, La, Li, Lu, Mo, Nd, Os, Pd, Pr, Pt, Re, Rh, Ru, Sb, Sm, Ta, Tb, Th, Tl, Tm, W, Zn. Only elements to which the method is sensitive in

TABLE 3.—*Semiquantitative spectrographic analysis*[a] *of the Georgia and Martha's Vineyard tektites*

Element	Georgia tektite[b] *percent*	Martha's Vineyard tektite[b] *percent*
Si	M	M
Al	7	7
Fe	1.5	1.5
Mg	0.3	0.3
Ca	0.3	0.3
Na	0.7	0.7
K	1.5	1.5
Ti	0.15	0.3
Mn	0.07	0.07
Ag	0.00007	0.00007
B	0.003	0.015
Ba	0.03	0.03
Be	0.0003	0.003
Co	0.0015	0.0015
Cr	0.0007	0.0007
Cu	0.0007	0.0007
Ga	0.0003	0.0003
Nb	0.0015	0.0007
Ni	0.0015	0.0015
Pb	0.00015	0.007
Sc	0.0007	0.0007
Sn	0.0007	0.0007
Sr	0.007	0.007
V	0.007	0.007
Y	0.0015	0.007
Yb	0.00015	0.00015
Zr	0.015	0.015

[a] Figures are reported to the nearest number in the series 7, 3, 1.5, 0.7, 0.3, 0.15, etc., in percent. These numbers represent midpoints of group data on a geometric scale. Comparison of this type of data with that obtained by quantitative methods shows that the assigned group includes the quantitative value about 60 percent of the time.

[b] Analyst: Helen W. Worthing, U. S. Geological Survey.

amounts of 0.01 percent or less are included in this list. The analytical procedure used has been described in detail by Waring and Annell (1953).

The chemical analyses of both specimens are essentially the same (table 4). The analysis reported here for the Martha's Vineyard tektite also agrees equally well with the independent analysis of a different part of the same specimen given by Kaye et al. (1961).

TABLE 4.—*Chemical analyses of the Georgia and Martha's Vineyard tektites*

Elemental oxide	Georgia tektite[a] *percent*	Martha's Vineyard tektite[b] *percent*
SiO_2	80.54	80.6
Al_2O_3	11.21	11.3
Fe_2O_3	0.33	0.4
FeO	2.40	2.2
CaO	0.61	0.7
MgO	0.65	0.7
MnO	0.05	0.05
Na_2O	1.16[c]	1.1
K_2O	2.38[c]	2.4
H_2O^-	None	<0.1
H_2O^+	0.02	<0.1
TiO_2	0.43	0.5
Total	99.78	99.9

[a] Analyst: M. K. Carron, U. S. Geological Survey.
[b] Analyst: R. S. Clarke, Jr., Smithsonian Institution.
[c] Analyst: W. W. Brannock, U. S. Geological Survey.

A gravimetric chloride determination was also done on a small sample of the Georgia tektite. The figure of 0.03 percent chloride obtained represents a limiting value. Chloride could not be present in a concentration greater than this, but the true value could be considerably less. The analysis of the Martha's Vineyard specimen is reported to only one decimal place because of the small size of sample used for analysis.

The chemical data on the Georgia and Martha's Vineyard glasses (table 4) fit quite well into the general pattern of tektite analyses as presented by Barnes (1940) in his review of this subject. The high silica, high alumina, high ferrous to ferric iron ratio, and the excess of potassium oxide over sodium oxide are all typical of tektite analyses. The moldavites are the only tektite group that have silica contents as high as those obtained in our analyses, and moldavites are the group most similar in physical and morphological character to our material. It is of interest to compare Barnes's moldavite analyses in some detail to the new data. Barnes's analysis No. 5 was excluded from the comparison because of its atypical ferrous to ferric iron ratio and the possibility that this reflects either a peculiar oxidizing history for this specimen or analytical error.

Only two of the nine moldavite analyses have a higher silica content (82.3, 82.7 percent SiO_2) than the new analyses, and two have essentially the same value (80.5, 80.7 percent SiO_2). The remaining analyses range from 77.8 to 80.0 percent SiO_2. The total iron for the new analyses is within the range given for moldavites, but our analyses suggest an appreciably higher proportion of Fe_2O_3 (seven of the moldavite analyses report only FeO). A recent moldavite analysis given by Vorobbev (1960) has a total iron in the expected range with a ferrous-ferric ratio similar to that obtained for the Martha's Vineyard and Empire, Ga., material. Our analyses show a lower proportion of CaO in the alkaline earth fraction, and the total $CaO+MgO$ is only about half of that observed for the moldavites. The total alkalies are within the range given by Barnes, but the proportion of Na_2O is considerably higher. The ratio of percent K_2O to percent Na_2O is smaller on the average by a factor of slightly greater than 3. These observations relating to chemical composition establish that the Georgia and Martha's Vineyard glasses are significantly different from moldavite glass as we understand it today.

The similarity of composition shown by our analyses seems to be extended in the recent publication by Barnes (1960) of a chemical analysis of a light green tektite from Fayette County, Tex. Its composition is very close to that of the Georgia and Martha's Vineyard material. Minor differences are a slightly higher SiO_2 and a higher proportion of Na_2O in the combined alkalies. These differences are so small that they suggest a relationship between this specimen and the two we have studied. Barnes (1960) also states that this material contains no bubbles and is significantly different from bediasites.

Ehmann (1960) has reported on a study of nickel-iron ratios in tektites and other glasses. Neutron activation analysis was used to determine accurate Ni values, and tektites were observed to have $Ni/Fe(\times 10^4)$ values ranging from 4.7 to 57, with a moldavite having a value of 10. It is interesting that the value of this ratio is 9 for the Martha's Vineyard, Mass., and Empire, Ga., specimens calculated on the basis of our semiquantitative spectrographic Ni value of 0.0015 percent.

DISCUSSION

The physical and chemical properties given here for the glasses from Martha's Vineyard, Mass., and Empire, Ga., show a remarkable and unexpected similarity. The measured physical properties show no significant differences. The pattern of compositional similarity shows variations for only four of the elements detected. This observed similarity is a significant observation that requires further examination.

The chemical data in the tektite literature would not lead one to expect such close similarity of properties for two specimens selected at random from widely separated geographic points. In his comprehensive paper Barnes (1940) gives bulk chemical analyses taken from the literature for 43 specimens from the three major tektite groups (24 indochinites, 10 moldavites, 9 australites). No two of them suggest agreement comparable to that which has been observed for the Martha's Vineyard and Empire, Ga., specimens. These analyses demonstrate that considerable natural variation of chemical composition exists within the same group of tektites. Larger variations are observed from one tektite group to another. Barnes also points out that compositional variations, as indicated by index of refraction measurements, are observed for different portions of the same specimen.

The explanation of this observed similarity would seem to lie in one of two areas. The first possibility is that our understanding of tektite specimens and their occurrence is based on inadequate and fragmentary data, so that the observed coincidence is actually an event of reasonable probability. The second possibility, and one that should not be too casually dismissed, is that we are dealing with artificial materials of related origin. Regardless of which explanation pertains, it is obvious that this problem requires further detailed study.

There is little room for doubt that the major tektite groups, such as australites, indochinites, and moldavites, are geologic occurrences, the results of natural processes. Georgia tektites have been placed in the tektite category largely on the basis of analogy, as these glass objects have similar chemical and physical properties to known tektites. However, the total number of specimens that have been found in Georgia is very small in comparison to the large number that have been found for the major groups. Weights of specimens are not available, but certainly the total for all the 12 reported Georgia finds (Bruce, 1959) must be only some fraction of a pound. Detailed observations relating these few specimens to their geologic environment have not been recorded and seem not to have been made. The situation with regard to the Martha's Vineyard specimen, a unique find so far for this region, is equally unsatisfactory.

A general similarity in appearance between moldavites and Georgia tektites has been frequently noted. This similarity, as was suggested earlier, also holds true in the same very broad sense for the Martha's Vineyard tektite. However, similarity to one class of objects does not preclude similarity to another class. In fact, the Martha's Vineyard tektite shows an interesting similarity to the bottom of a bottle now in the collections of the Smithsonian Institution (USNM 58.115A). This olive-green bottle was probably made in Keene, N. H., in the second quarter of the 19th century.[7] The chemical composition of this bottle is undoubtedly quite different from that of the Martha's Vineyard tektite. Its index of refraction is greater than 1.50, and under the microscope this grain appears to be ordinary unstrained bottle glass. However, the radius of curvature, the periodicity of the radial pattern along the curved edge, and the circular pattern in from the edge (see fig. 3) of the Martha's Vineyard speci-

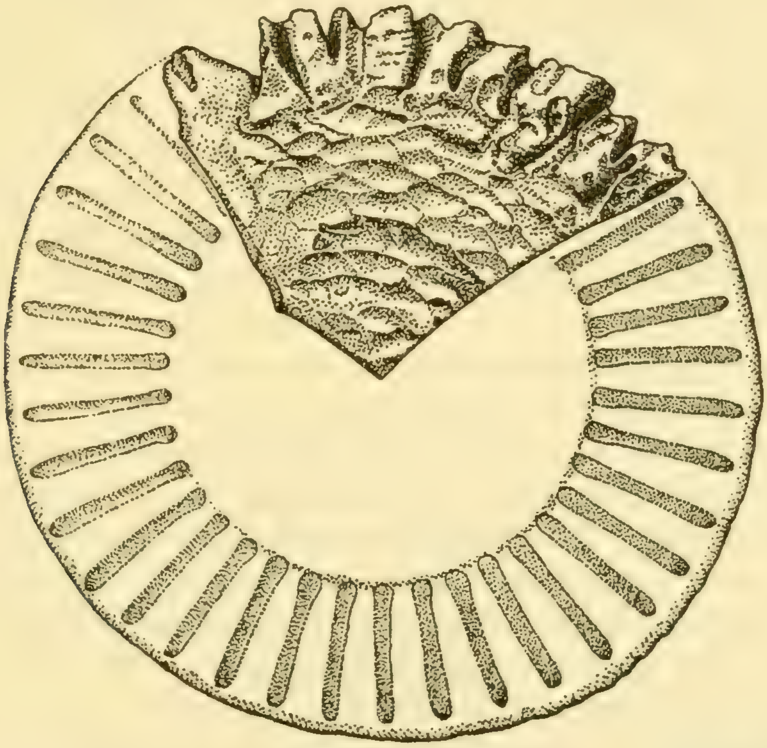

FIG. 3.—Scale drawing of bottom of a bottle from Smithsonian Institution collection (cat. No. 58.115A) with Martha's Vineyard tektite superimposed. The bottle was probably made in Keene, N. H., during the period from 1825 to 1850.

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[7] Paul V. Gardner, Division of Ceramics and Glass, U. S. National Museum, Smithsonian Institution, oral communication.

men are suggestive of the mold from which the Keene, N. H., bottle must have been made.

An argument commonly used to support a natural rather than artificial origin for tektites is based on the relatively high temperatures required to melt glass of tektitic composition. We have difficulty attaining these temperatures today; therefore, we are apt to conclude unjustifiably that these temperatures must have been unattainable in the fairly recent past. However, there is evidence that leads one to doubt this reasoning. An example is given in the studies of Hubbard, Jenkins, and Krumrine (1952), in which they compare the properties of modern commercial glasses to Amelung glasses. These antique glasses were made in the large factory of Johann Friedrich Amelung near Frederick, Md., in the years around 1800. Hubbard et al. report that these old glasses ". . . had working temperatures considerably higher than any of the modern commercial glasses studied, with the exception of fused silica and Vycor." They further noted considerable difficulty in working these glasses after heating to 1500°C., the highest temperature to which they cared to take Globar furnaces.

Glass has been a common item in commerce along the east coast of the United States since the early Colonial period, and it is a byproduct of many industrial and manufacturing operations. There is a possibility that starting with the proper raw materials—perhaps by accident—glass of the composition of the Georgia and Martha's Vineyard tektites could have been formed in this still difficultly attainable high-temperature range. Had Precambrian feldspar or other geologically old materials been included among the raw materials from which this peculiar glass was made, another difficulty could possibly be reconciled. Conceivably the mysterious process that formed the glass could have produced a product that retained sufficient radiogenic argon-40 to give the approximately 30-million-year ages that have been reported in the literature for the Empire, Ga., specimen (Reynolds, 1960; Gentner and Zähringer, 1960). Admittedly, this suggestion is contrary to normal laboratory experience; however, this type of measurement as applied to tektites is too new to be accepted without reservations.

Two criteria are commonly accepted in defining and identifying tektites. The first is that the specimens are of natural occurrence within a given although perhaps not completely delineated geographic area; the second is that they are glasses of an unusual range of chemical compositions, exhibiting characteristic physical properties.

It should be clearly demonstrated that both of the above hold before specimens are accepted as proven tektites. The natural occurrence requirement seems not to have been proven beyond reasonable doubt in the case of Georgia and Martha's Vineyard specimens. Certainly, the history of specimens found to date in these localities is not overwhelming evidence of their natural origin (Bruce, 1959; Kaye et al., 1961).

The data that have been given point to a current weakness in our understanding of tektites. It has not been possible to take two glass objects, found 20 years and 1,000 miles apart, into the laboratory and, after studying their chemical and physical properties, report unequivocally that they are tektites. Had the specimens under study belonged to one of the major recognized tektite groups, and had their properties been fairly typical of that group, a reasonably certain identification could undoubtedly have been made. However, chemical composition apparently separates the specimens from Martha's Vineyard, Mass., and Empire, Ga., from known tektite groups. The specimens have properties that are typical of tektites but not exclusive for tektites. All the properties that we were able to measure have a counterpart in natural or artificial glasses. Further information on these tektites, particularly their field occurrence, is required before a final judgment should be made. A disproportionate amount of laboratory work cannot compensate for the lack of sufficient field data. A typically geological approach is needed for a problem that remains basically a geological problem.

CONCLUSIONS

In the chemical and physical data that have been presented, there is nothing inconsistent with the claim that the Georgia and Martha's Vineyard glasses are tektites—tektites in the sense of the major tektite groups. However, there is likewise nothing in these data to prove categorically that only a natural origin can account for the specimens. Conceivably some type of artificial origin, perhaps an accidental one, is possible. Certainly it would be premature to assume that Martha's Vineyard is a valid tektite locality. The cause of our inability to solve this problem at present—and this seems to apply also to problems concerning the major tektite groups—is the lack of geological evidence relating specimens to their occurrence. Until the occurrence is understood, speculation as to origin lacks foundation.

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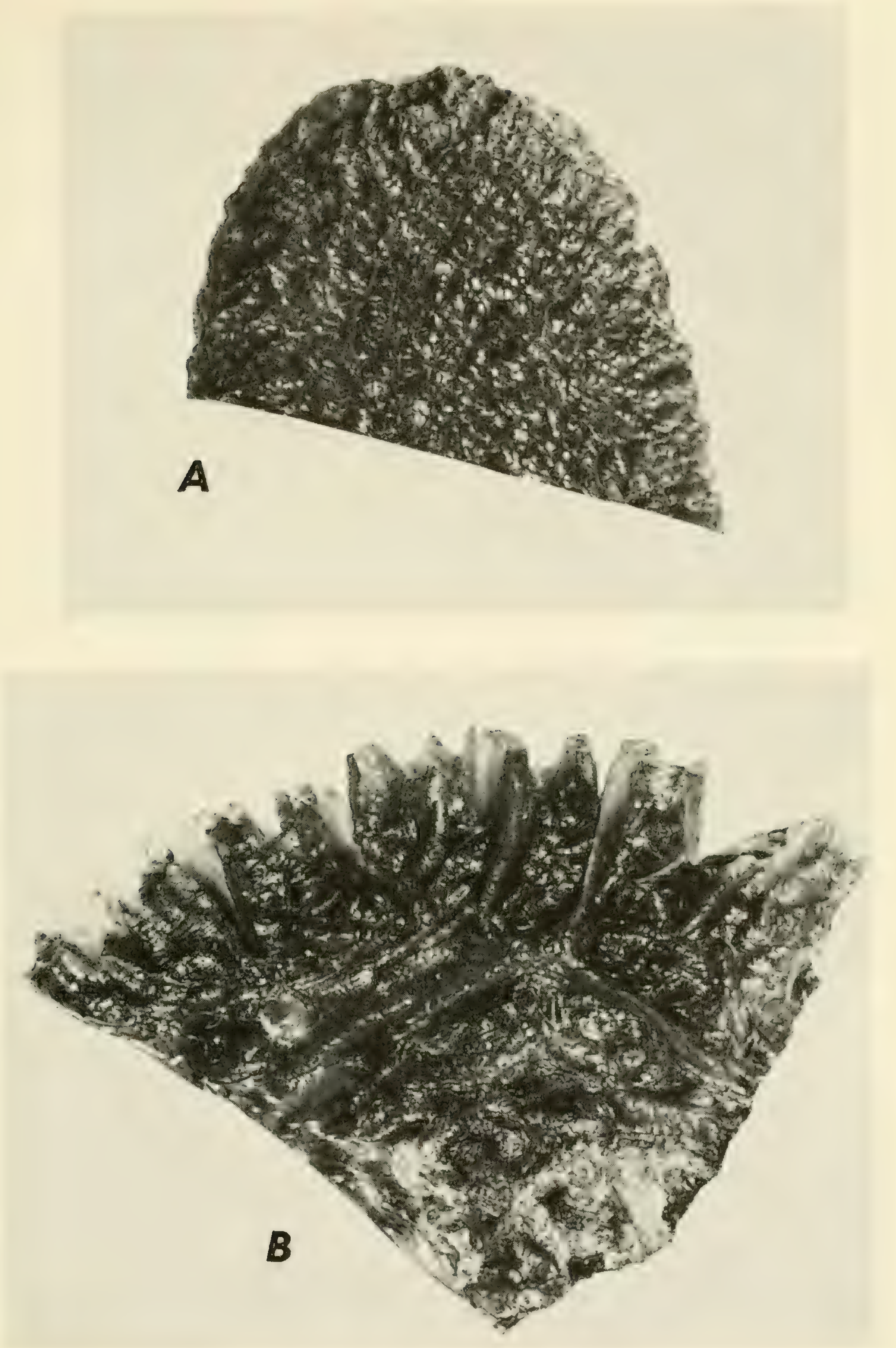
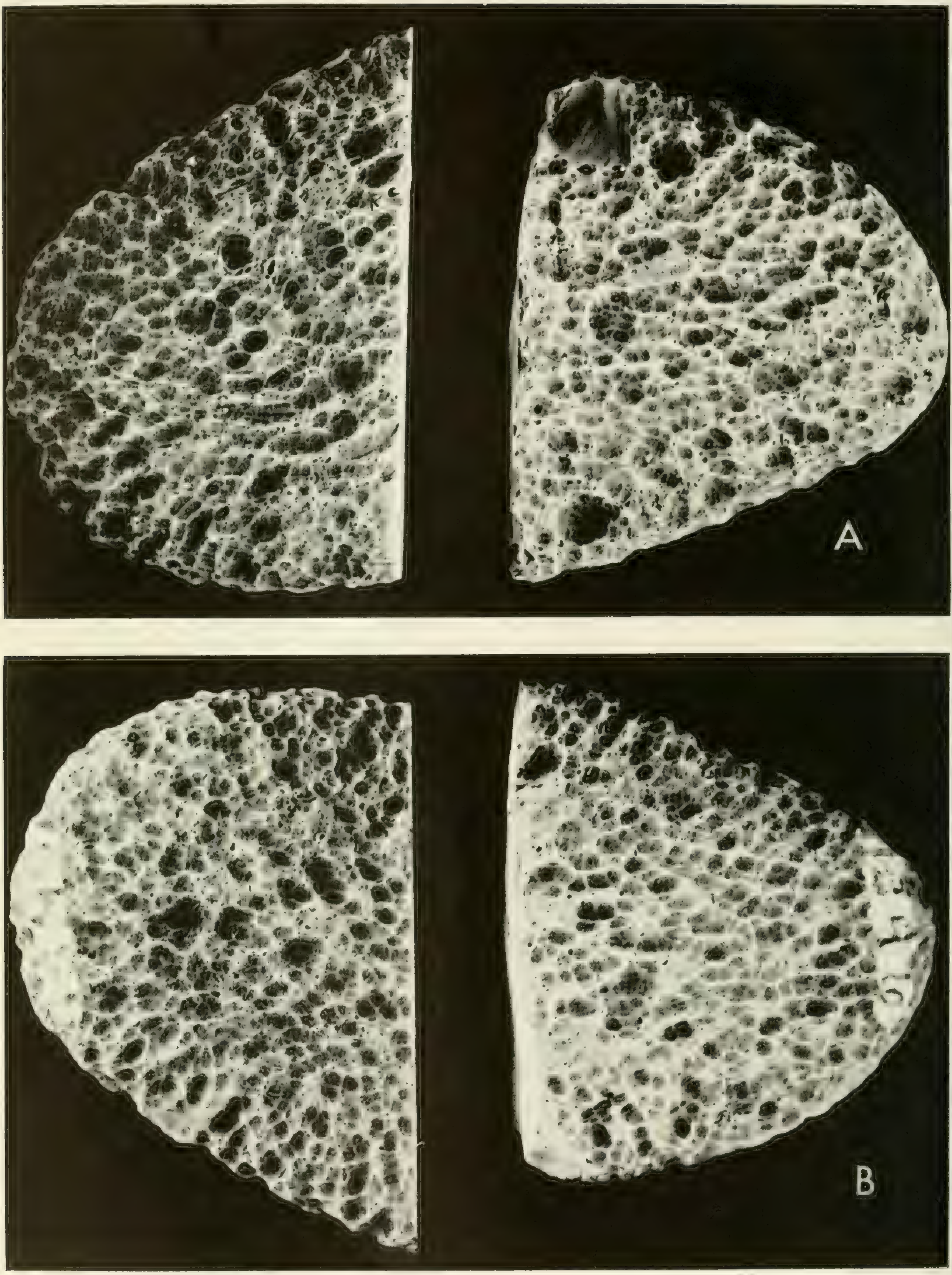
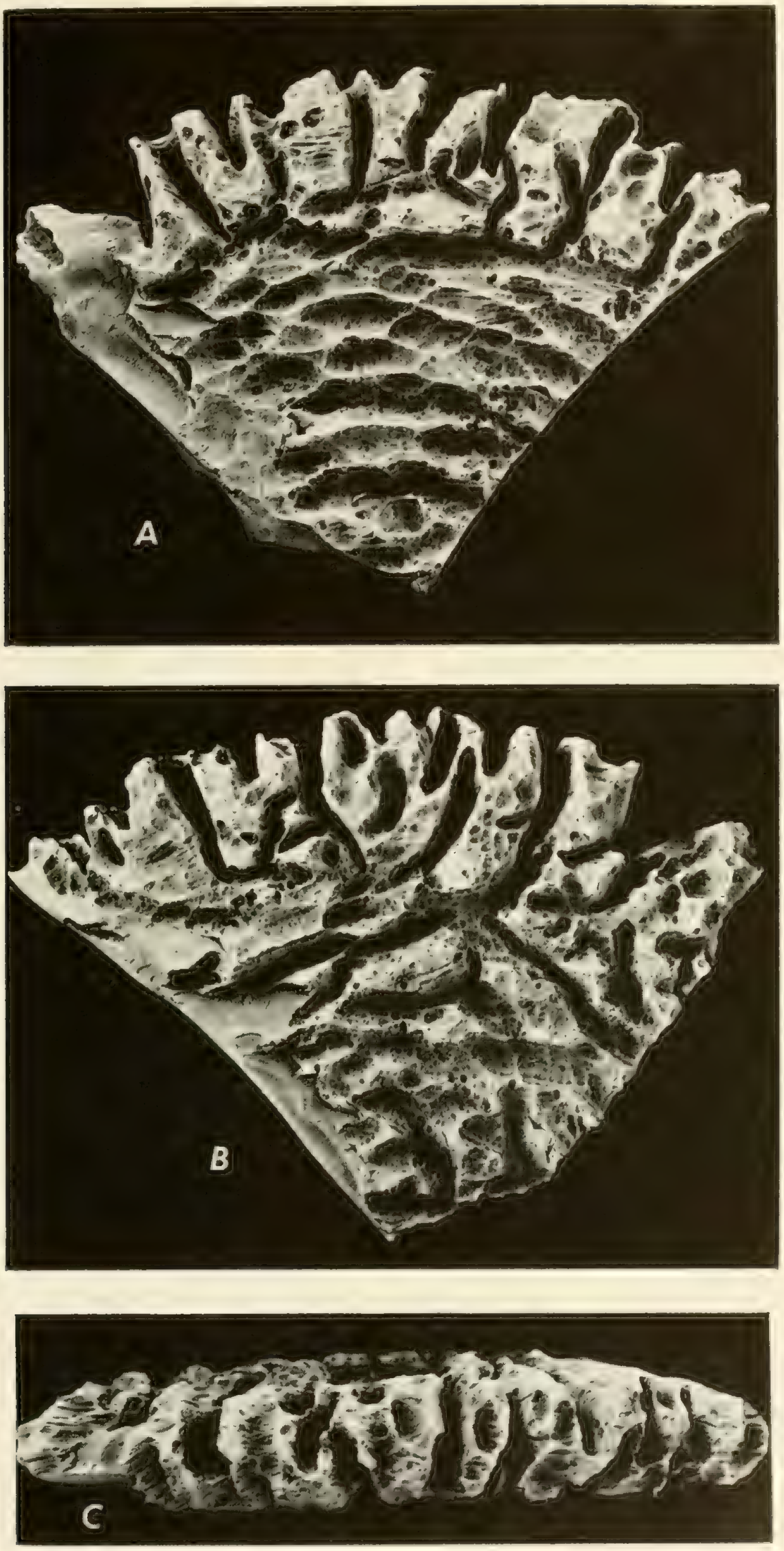


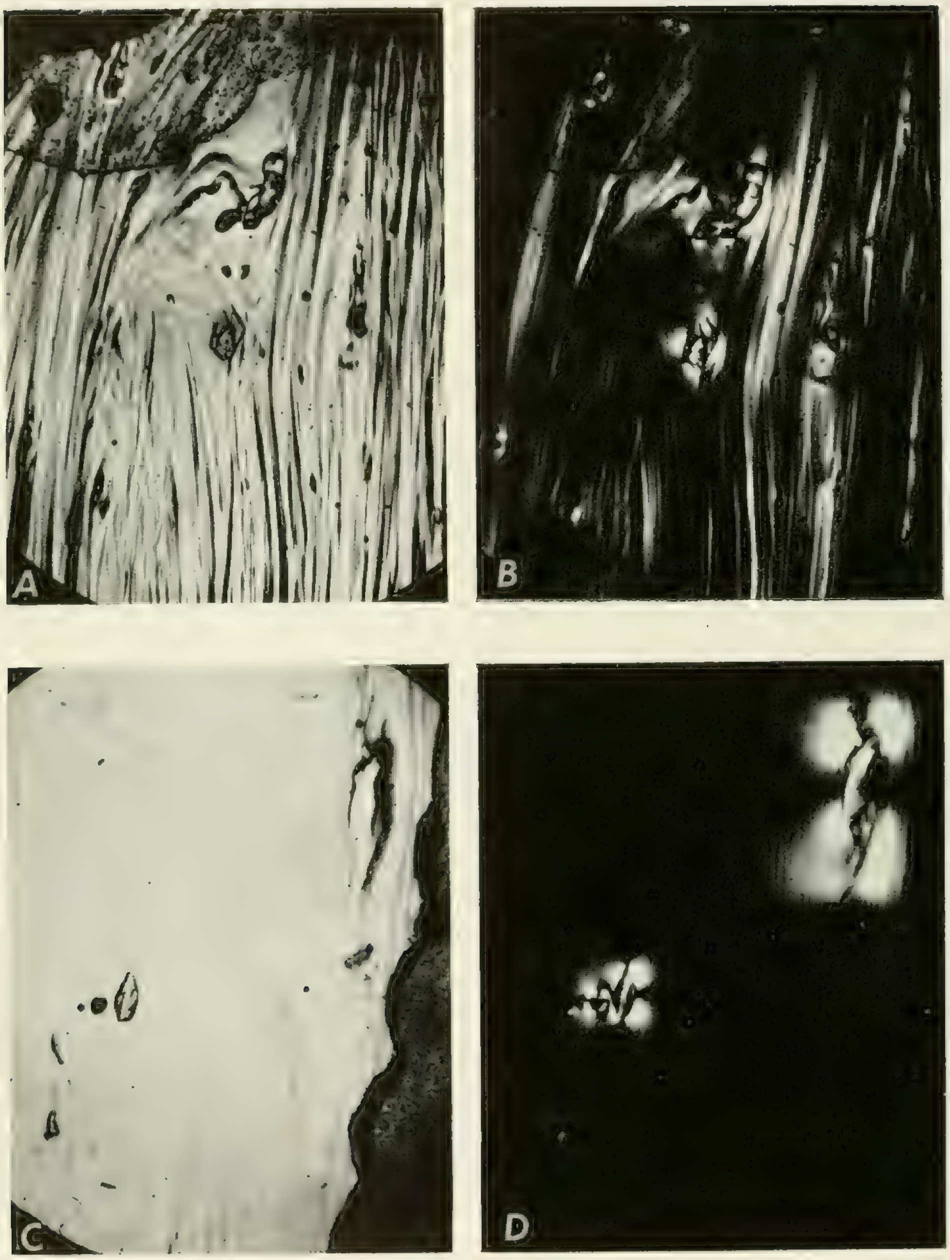
Tektite photographs taken with direct lighting. A, Tektite from Empire, Ga., USNM 1396, × 2. B, Tektite from Martha's Vineyard, Mass., USNM 2082, × 2.



Empire, Ga., tektite after slicing to remove material for analysis. The specimen has been smoked with ammonium chloride to bring out surface features. USNM 1396, × 2.

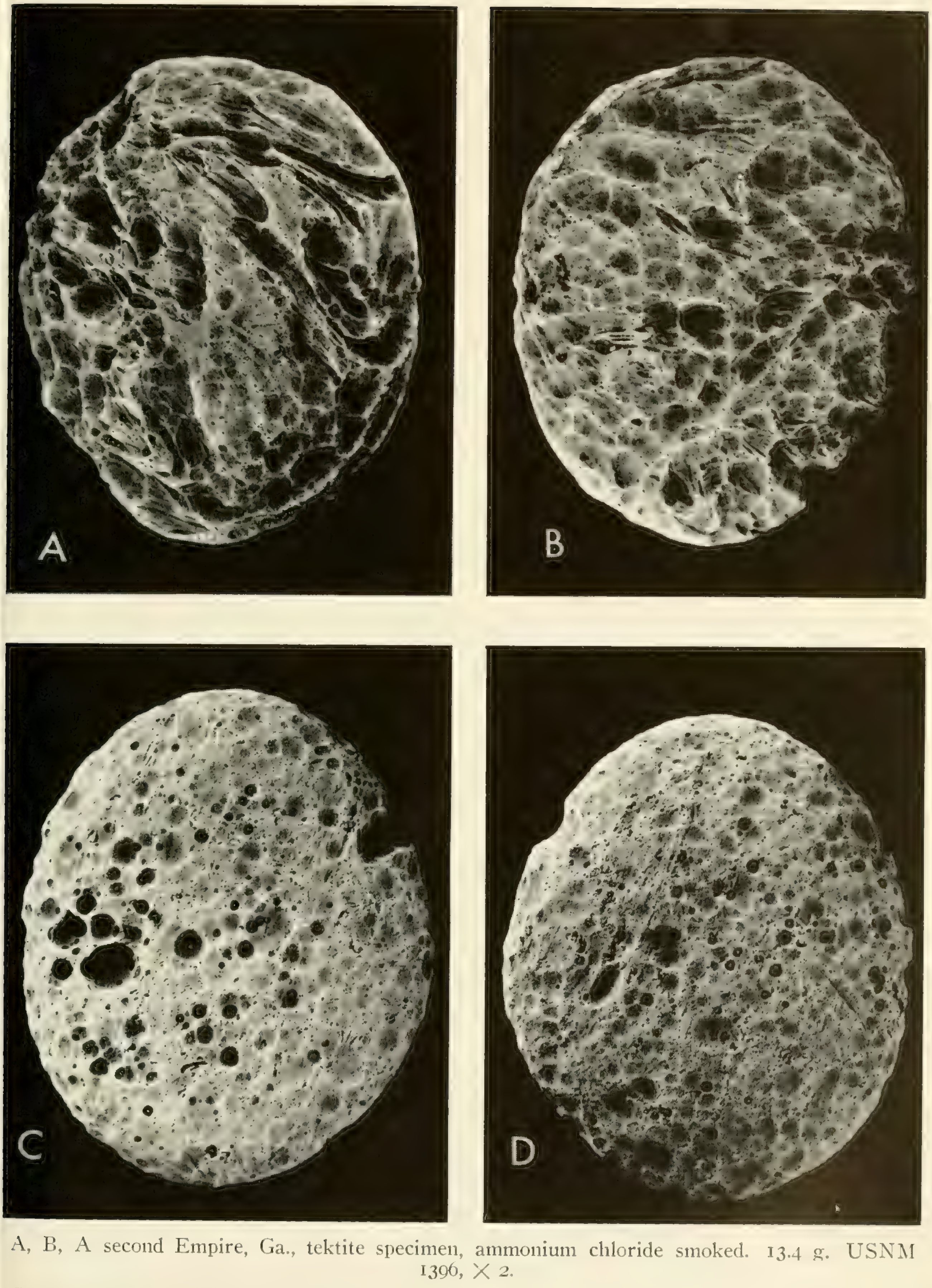


Martha's Vineyard, Mass., tektite photographed after ammonium chloride smoking. 17.8 g. USNM 2082, × 1½. B, Surface opposite that shown in A. C, Photographed down deeply serrated edge.



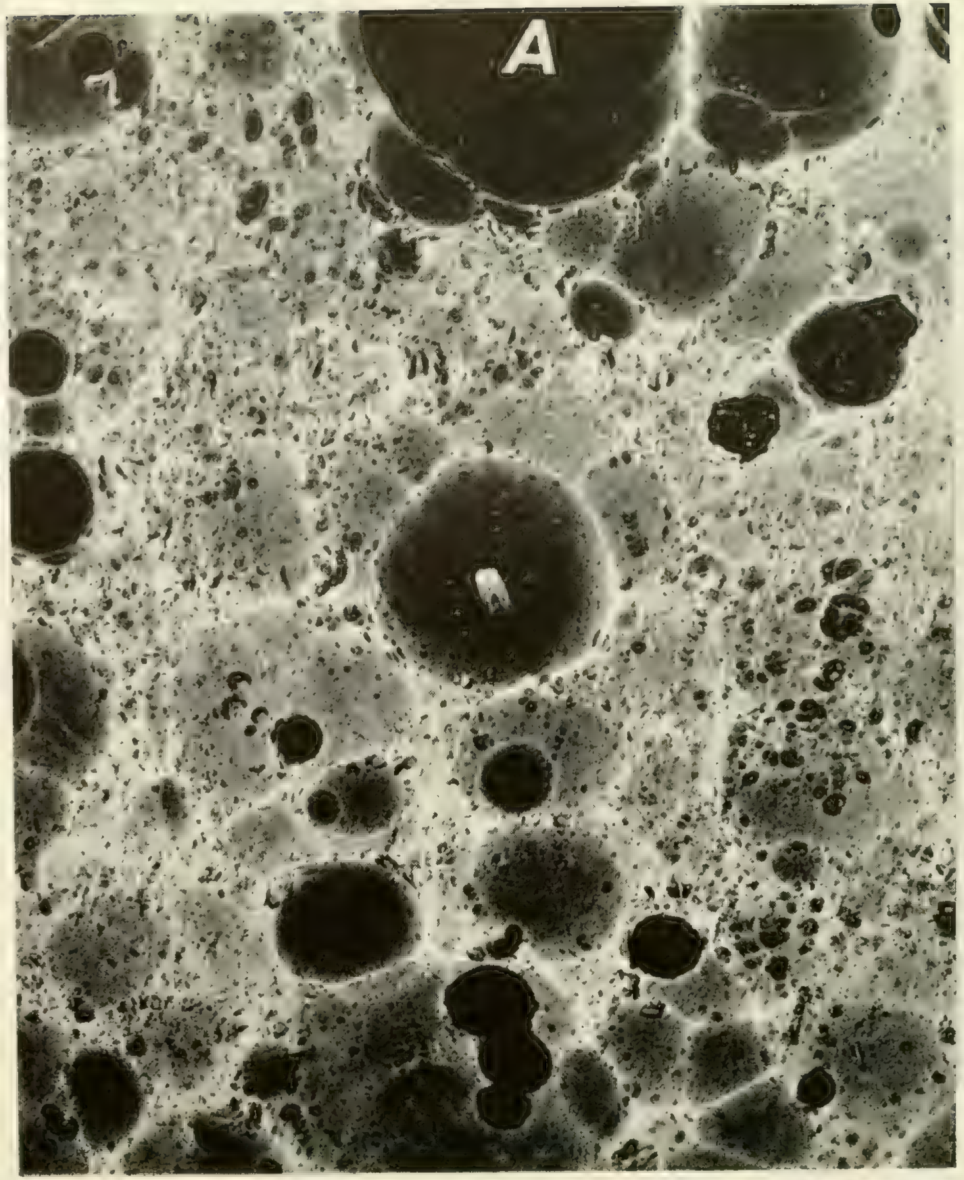
A, B, Photomicrograph of a 0.25-cm. slice of Martha's Vineyard tektite, × 10. A, White transmitted light; B, crossed nicols.

C, D, Photomicrograph of a 0.07-cm. slice of the Empire, Ga., tektite, × 10. C, White transmitted light; D, crossed nicols.

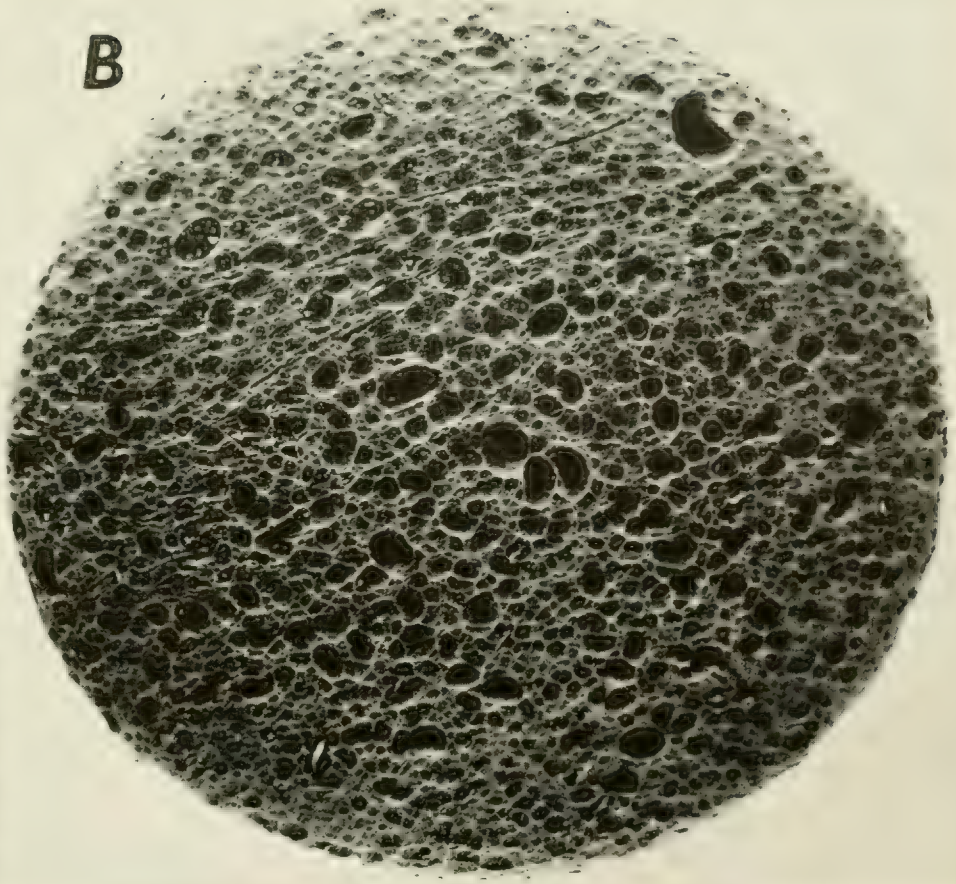


A, B, A second Empire, Ga., tektite specimen, ammonium chloride smoked. 13.4 g. USNM 1396, × 2.

C, D, Plainfield, Ga., tektite, ammonium chloride smoked. Property of G. A. Bruce. 11.2 g. × 2.



A, Details of small area of Plainfield, Ga., specimen, ammonium chloride smoked. × 10.



B, Osierfield, Ga., tektite, ammonium chloride smoked. Property of Georgia Geological Survey, lent by A. S. Furcron. 17.8 g. × 2.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
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Roebling Fund

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A LONG-RANGE TEMPERATURE FORECAST

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GENERAL COMMENTS

I quote the opening paragraph of my recent paper "A Long-Range Forecast of United States Precipitation"[1]: "A hidden family of harmonic regular periods exists in weather. The periodic members of this family persist with unchanged lengths for scores of years. By determining their average forms and amplitudes for intervals of a thousand months, successful forecasts may be made for years to come; or backcasts may be made for former years and compared to former events. Agreement of such backcasts with the records warrants confidence in future forecasts."

In the publication cited correlation coefficients ranging between +52 and +69 percent were found over the interval 1950-58 between prediction and observation. Positive coefficients of correlation, as I will show, also subsist between temperature forecasts and events for the same interval. Examples appear herein as figures 1, 2, 3.

While *very nearly normal weather* must obviously average closer to the normal values than to my forecasts, the case is quite different for extremes of weather. Extremes in precipitation range from 50 to 200 percent away from the normals. It is to be able to anticipate weather of this unusual kind that good forecasts are financially valuable. As an example I give the following computations based on tables 10 and 14 of Publication 4390:

Cincinnati results from table 10

From 108 months, 1950-58, from forecast, 27%	mean departures from normal,	29%
From 56 months within 25% of normal, from forecast, 26%	do.	14%
From 52 months over 25% from normal, from forecast, 27%	do.	47%
From 20 months over 48% from normal, from forecast, 31%	do.	58%

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[1] Smithsonian Misc. Coll., vol. 139, No. 9, Publ. 4390, Mar. 23, 1960.

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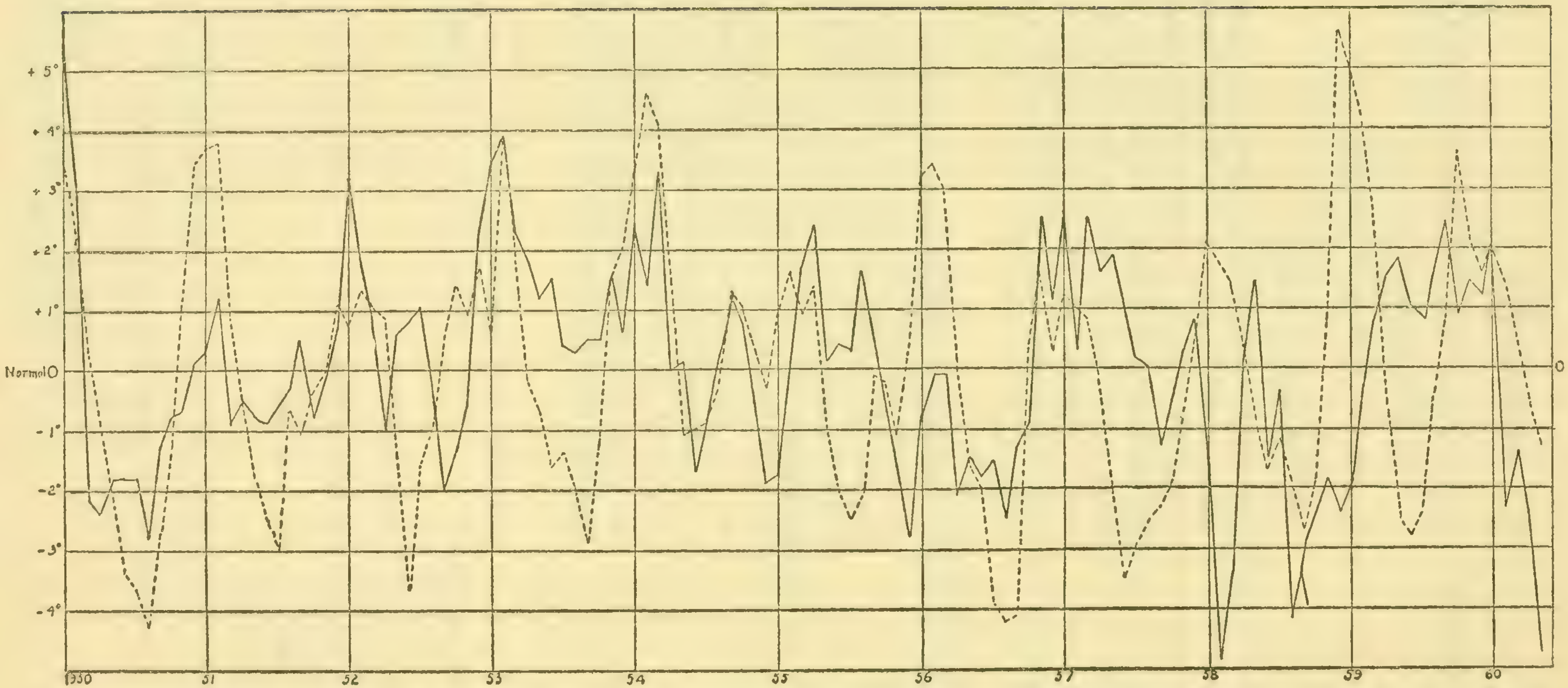

FIG. 1.—Washington temperatures. Dotted lines, forecast; solid lines, observed. Although amplitudes differ, features are seldom displaced a month. Forecast from records for 1870-1956, with 3-month smoothing.

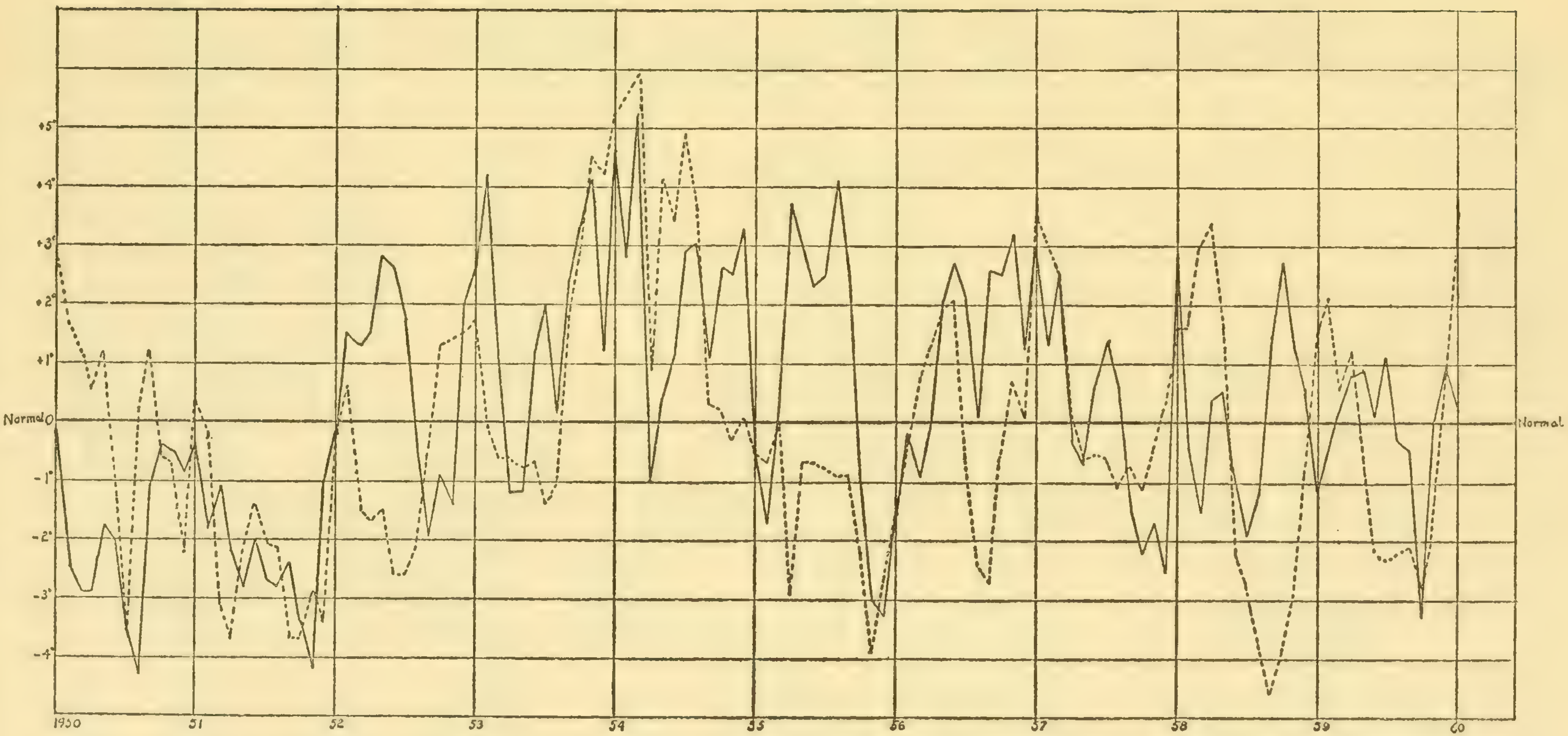

FIG. 2.—Omaha temperatures. Dotted lines, forecast; solid lines, observed. Note 1951, 1952-54, 1954-56, 1957, the great swings predicted. Based on records for 1870 through November 1956, with 3-month smoothing.

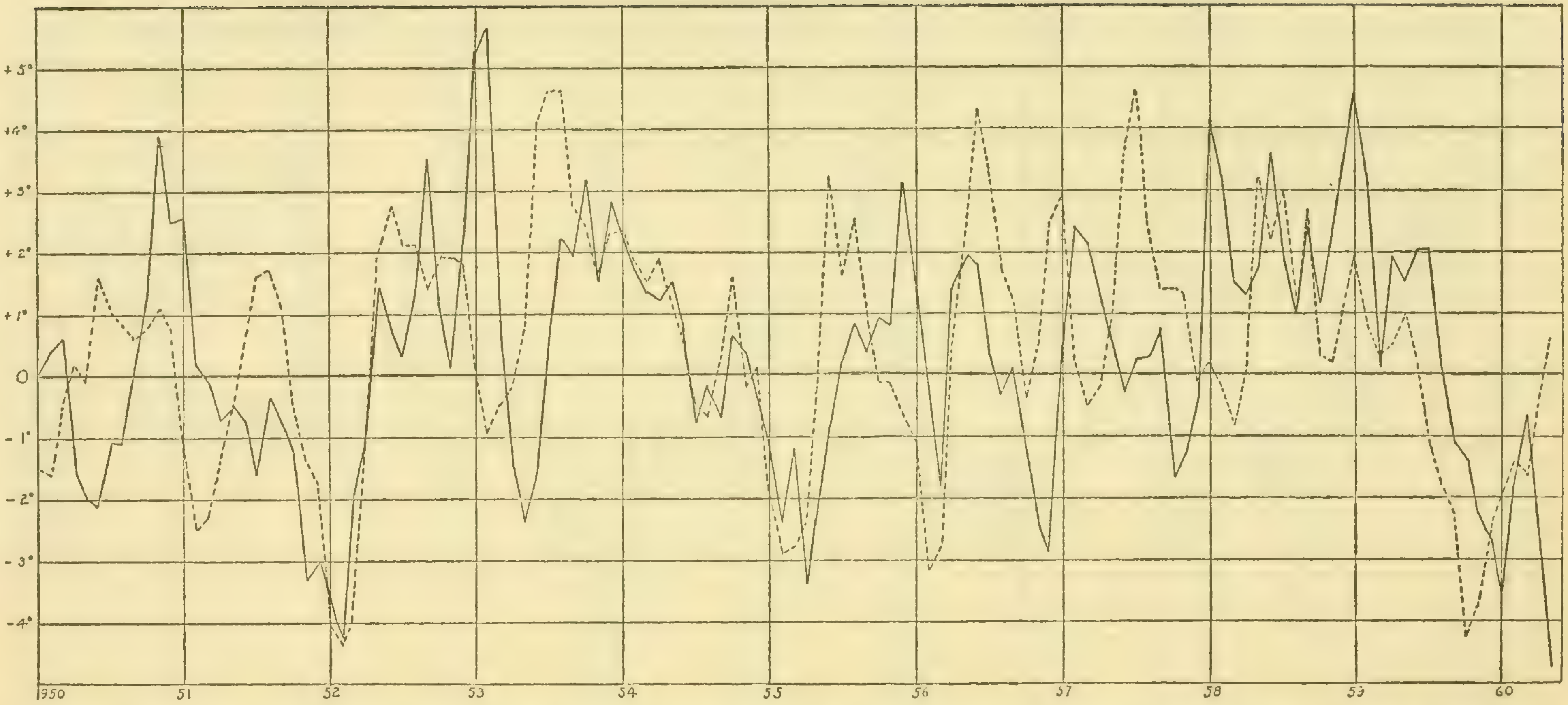

FIG. 3.—Salt Lake City temperatures. Dotted lines, forecast; solid lines, observed. Though amplitudes differ, note check of great swings, with features seldom displaced. Forecast from records for 1870-1956, with 3-month smoothing.

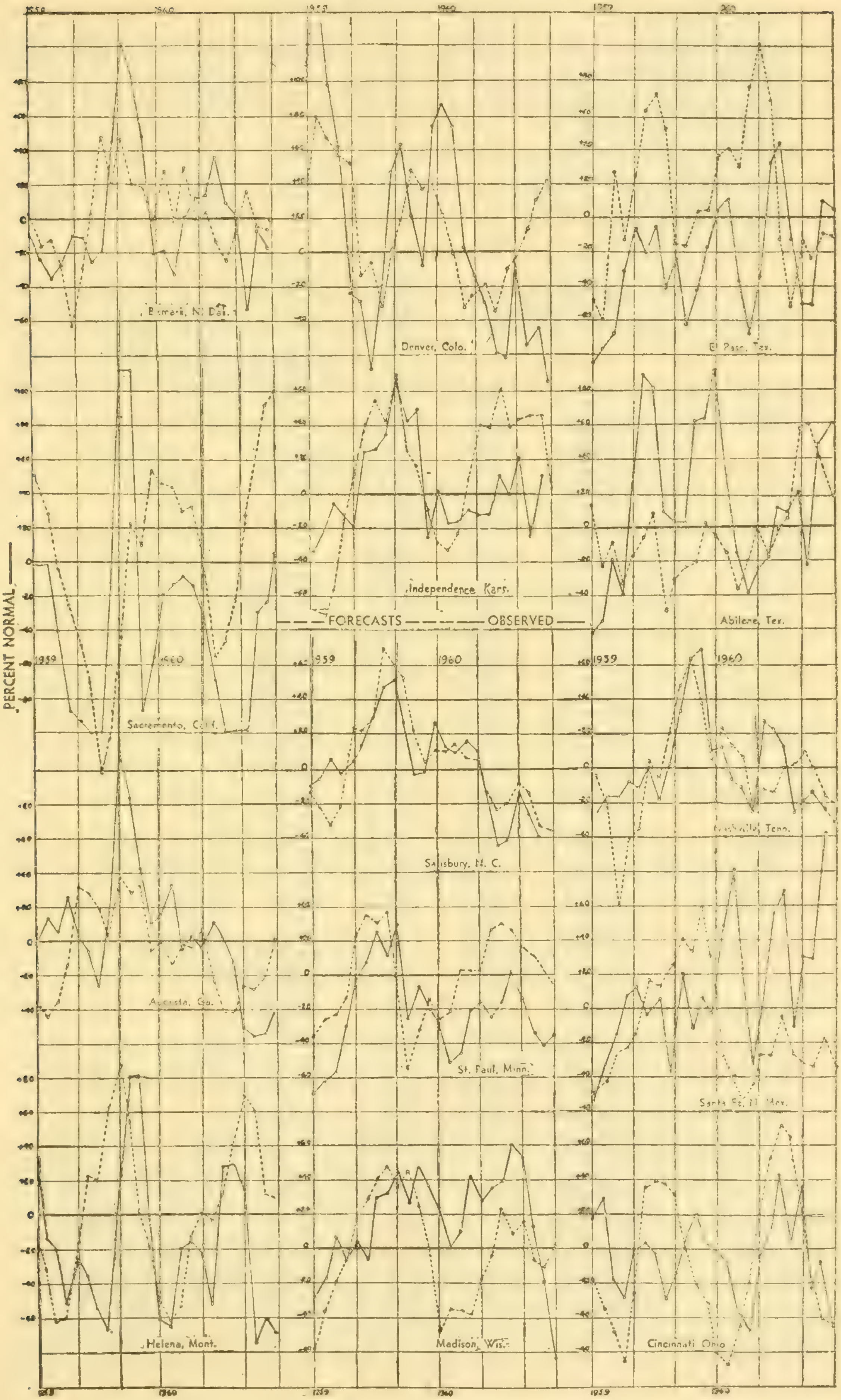

FIG. 4.—Precipitation forecast (dotted lines) and observed (solid lines) from records of 1870-1956.

Cincinnati results from table 14

From 27 four-month periods, 1950-58, from forecast, 26.6%	mean departures from normal,	25%
From 14 periods within 25% from normal, from forecast, 27.7%	do.	13%
From 13 periods over 25% from normal, from forecast, 23%	do.	38%
From 6 periods over 38% from normal, from forecast, 27.5%	do.	47%

TABLE 1.—*Forecasts of precipitation 1950-58 and 1959-60. Departures from normal (1950-58) and percent average deviation from mean departures*

		Groups of deviation from normal				
Station	Interval	0-25	26-50	51-75	76-100	>100
Abilene	1950-58	13±25	36±39	61±34	84±21	....
	1959-60	11±29	37±25	58±60	......	....
Augusta	1950-58	12±23	37±36	58±51	81±70	....
	1959-60	10±31	34±38	......	......	....
Bismarck	1950-58	11±24	34±31	66±57	97±44	....
	1959-60	9±24	36±31	......	......	....
Cincinnati	1950-58	13±24	39±30	56±44	80±17	....
	1959-60	18±19	39±35	64±48	......	....
Denver	1950-58	13±33	39±34	61±30	......	....
	1959-60	13±35	38±38	60±37	......	....
El Paso	1950-58	12±19	40±43	65±32	90±51	112±97
	1959-60	13±37	34±55	65±73	......	....
Helena	1950-58	12±21	35±31	58±40	82±21	....
	1959-60	12±36	......	59±49	......	....
Independence ..	1950-58	13±26	37±33	59±42	81±45	....
	1959-60	13±18	38±30	63±37	......	....
Madison	1950-58	13±27	35±36	64±28	......	....
	1959-60	13±37	39±32	......	......	....
Nashville	1950-58	12±23	35±25	63±30	100±42	....
	1959-60	11±16	37±26	......	......	....
Sacramento	1950-58	11±47	37±43	62±52	80±51	108±55
	1959-60	14±53	37±67	59±56	......	....
Salisbury	1950-58	12±24	33±31	60±36	......	....
	1959-60	17±15	33±17	61±19	......	....
Santa Fe	1950-58	11±37	39±45	61±57	81±54	135±103
	1959-60	17±33	35±41	......	......	....
St. Paul	1950-58	11±29	35±44	77±69	......	....
	1959-60	11±32	30±28	......	......	....
Mean	1950-58	12±27	37±36	62±43	86±42	118±85
Mean/12	1950-58	1	3	5	7	10
A.D./27	1950-58	1	1.3	1.6	1.6	3.0
Mean	1959-60	13±30	36±36	61±47	% above 75	87±89
Mean/13	1959-60	1	3	5	" "	7
A.D./30	1959-60	1	1.2	1.6		3.0

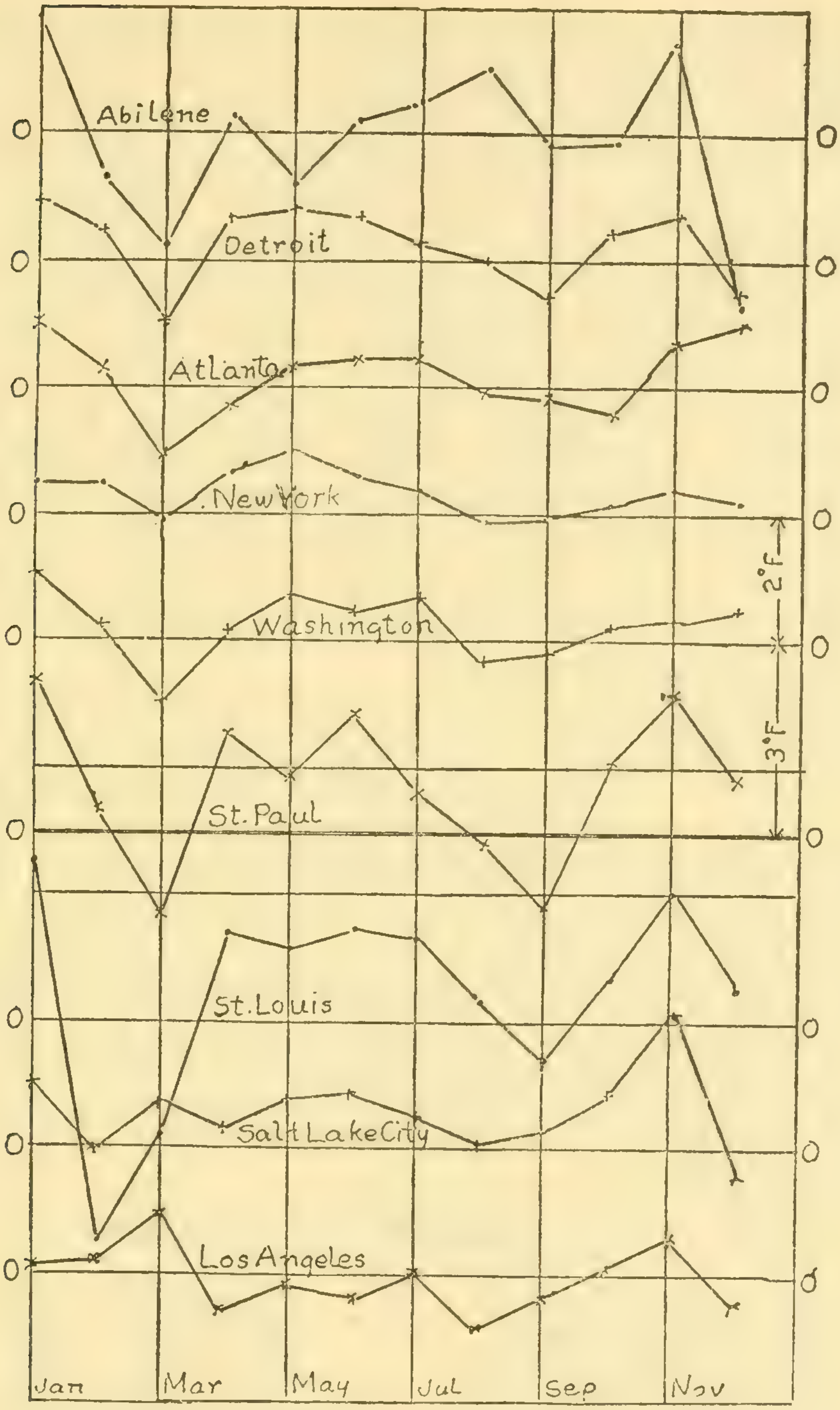

FIG. 5.—Normal temperatures, sunspots few minus sunspots many.

In table 1 I compare an analysis for 14 stations over the interval 1950-58 with an analysis for the same stations for the interval 1959-60. The mean results for the two intervals are almost identical. They show that forecasts three years after the last month (November 1956) used in their basis are just as good as earlier forecasts. Further support for this thesis will be found by inspection of figure 4.

These results show about as good agreement of forecasts with observed precipitation for extreme departures as for usual departures.

This recommends my forecasts to those whose interests demand foreknowledge of wide departures from the normal. A second recommendation arises from the fact, which may be verified by inspection of figures 1, 2, 10, and 11 of Publication 4390, that large trends in departures from normal precipitation, continuing over several years, may be tolerably forecasted. Third, as far as time has elapsed, results remain encouraging. In figure 4 and table 1 I give evidence that during the 24 months of 1959 and 1960, three years after November 1956, (the latest record used in the forecast) a strong correlation (about 50 percent) between forecast and event was observed.

In preparing temperature forecasts or precipitation forecasts, as explained in my paper "A Long-Range Forecast of United States Precipitation," it is necessary to compute new monthly normals from the published records. These new normals relate respectively to the years when the Wolf sunspot numbers are greater, and to the years when they are less than 20.

To illustrate the need for taking account of sunspot frequency in normals of weather records, and to show interesting features of the difference between stations in their relations to sunspot frequency, I give figure 5. It shows the difference in percentage of normal temperature between times of sunspots less and more than 20 Wolf numbers for the 12 months of the year. There is a partial similarity among the graphs, but Salt Lake City and Los Angeles behave rather differently from the other eight. It will be noted that ranges of 2° or even 3° F. occur for some cities, which are ignored in usual monthly normals where sunspot frequency is neglected.

The following dates may be used to separate SS > 20 and SS < 20 groups of months:

TABLE 2.—*Intervals of high and low sunspot numbers*[2]

SS > 20	
July 1857-Aug. 1865	Mar. 1868–Apr. 1875
Jan. 1880–July 1886	May 1891–Nov. 1898
July 1903–Mar. 1910	Jan. 1915–July 1921
Apr. 1925–May 1931	Mar. 1935–May 1942
Mar. 1945–Jan. 1953	May 1955–(May 1962)
SS < 20	
Jan. 1854–June 1857	Sept. 1865–Feb. 1868
May 1875–Dec. 1879	Aug. 1886–Apr. 1891
Dec. 1898–June 1903	Apr. 1910–Dec. 1914
Aug. 1921–Mar. 1925	June 1931–Feb. 1935
June 1942–Feb. 1945	Feb. 1953–Apr. 1955

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[2] Table 2 and remarks thereon, unfortunately omitted from Publ. 4390, are here quoted from "Solar Energy," vol. 2, No. 1, June 1958.

In the use of tables of periods in weather for forecasting beyond 1957, it is necessary to make extrapolations from the preceding tables of dates. This is done (of course with marginal uncertainty) by averaging the intervals (given above) in months SS>20 and SS<20, and assuming that future intervals will be approximately the same as these averages. The uncertainty will usually not lead to important errors of forecasts, for generally the curves representing SS > 20 and SS < 20 for the periods are similar for a given period and differ but a few months, or even not at all, in phases. I use for future dates: for SS > 20, 84 months, for SS < 20, 52 months.

To avoid being misled by sudden large jumps between consecutive monthly departures, the departures from these new normals are smoothed by 3-month consecutive means. Owing to unpredictable lags in the phases of the harmonic periods, it is necessary, as explained in the paper just cited, to divide the record data into special groups, depending on the time of the year, the prevalence of sunspots, and the secular march of time. This requires that 220 tables should be computed for the forecast of temperature at each station, just as in the precipitation forecasts of Publication 4390.

This large task requires electronic computation. It was done for the 10 temperature stations and for the 32 precipitation stations by Jonathan Wexler of Tempe, Ariz. In order to avoid new procedure in programming the electronic computer for temperature, I directed him to convert recorded temperatures, published in Fahrenheit degrees, into absolute temperatures Fahrenheit by adding 491.7° minus 32°, or 459.7°. Departures from the monthly normals were then computed in percentages, as was done with the precipitation values.

For instance, the normal temperature for June at Detroit for years of sunspots greater than 20 Wolf numbers is 67.8° F. Subtracting 32° and adding 491.7° it becomes 527.5° abs. F. The observed temperature of Detroit for June 1950 was 68.1° F. Similar steps make it 527.8° abs. F. Its ratio to normal June temperature is $527.8 \div 527.5 = 1.0006$. All this rearranging was done with the electronic computer. In the subsequent computations we used the differences from 1.0000 as far as the fourth decimal place. These differences ranged for the most part between +150 and −80, corresponding to a range of 2.3 percent of the absolute temperature, or about 11.5° F.

Readers interested in further details of the method are referred to my paper "A Long-Range Forecast of United States Precipitation" (Publication 4390) and other references cited therein. Temperature forecasts are somewhat less satisfactory than the precipitation forecasts. For while the range of percentages of normal precipitation goes from 0 to 1,000 or more, the entire range of absolute temperature is only about 2.3 percent. The *accidental* fluctuations of temperature bear a much larger proportion to range than the accidental fluctuations of precipitation. Hence, correlation coefficients between forecasted and observed temperature, though always positive, are always smaller than those between forecasted and observed precipitation. While the 32 cities forecasted for precipitation, 1950 to 1958, all yielded positive correlation coefficients with the events ranging between 50 and 70 percent, the correlations on temperature for 10 cities, forecasted 1950 to 1958, ran as follows: Detroit +16 percent; Los Angeles +22 percent; Atlanta +32 percent; and the other 7 stations all ranged between +40 and +50 percent.

My forecasts of temperature and precipitation rest on one fact and one assumption. The fact is that a harmonic family of regular periods exists in solar radiation and in weather. The assumption is that if this family of periods is individually and quantitatively determined from weather records, 1870 to 1956, the mean course of these periods will be followed approximately through subsequent years. This assumption may indeed prove wrong when unusual disturbances occur in atmospheric conditions—for example, the volcanoes of Krakatoa and Katmai; the furious bombing during the world wars; atomic bomb tests; the hurricane Donna of September 1960. But tests such as figures 1, 2, 3, 10, 11 of Publication 4390, and those of temperature in this paper, show that generally the assumption is justified. As yet it has not been explained why displacements between forecasts and events in features of weather by 1, 2, or 3 months occasionally are observed. If this difficulty can be overcome, much higher coefficients of correlation will be found between forecasts and events. I plan an investigation of possible causes of this defect.

There is one important difference between my forecasts of precipitation and of temperature. The amplitude of the principal features in precipitation changes was found for all stations to be so nearly the same in forecasts and events that no adjustments were made. Not so with temperature. For all the 10 cities the *amplitudes* of the features of change were obviously *greater in the forecasts* than in the events. I cannot explain why this is so. The forecasts would have been left woefully wrong unless this discrepancy had been corrected.

To make this correction for *scale,* I carefully plotted for each city the curves of forecast and event from 1950 through 1958. Then I measured as best I could the depths of obviously corresponding large depressions of the two curves, and determined their average ratio of amplitudes in forecasts and observations for about a half dozen principal depressions. These ratios, in terms of event divided by forecast, were for most cities between 0.70 and 0.75. Using these average ratios of amplitude of features, I reduced all the forecasts to approximately the same scale of amplitude as the events.

There remained still another correction, but one not puzzling like that for scale. As many have pointed out, temperatures have gradually risen in parts of the United States for a great many years. It would have been quite wrong to make forecasts of temperature for 1950 through 1967 without allowing for this well-established change of *level*. Hence I took the ratio of the sum of monthly departures from normal after correcting for scale, as forecasted from 1950 through 1959, and divided by the corresponding sum for the event. This gave a correction to lift the forecasts bodily by amounts ranging from 0.11 to 0.37 percent for the different cities. Expressed in degrees of temperature, these corrections of *level* range from 0.5° to 1.9° F.

Having by these two necessary corrections adjusted the forecasts to terms justly comparable with the events, I computed the correlation coefficients mentioned above.

RESULTS OF THE INVESTIGATION

First of all, to inspire confidence in the method, which, as I have said, is substantially the same for temperature as for precipitation, I give in figure 4 for 14 of the 32 stations of Publication 4390 a comparison of forecasts and events on precipitation for the 24 months of 1959 and 1960. This interval is several years beyond the latest month, November 1956, used in the basis of the forecasts. Table 1, above, gives for 1959 and 1960 an analysis of the monthly values of forecasts and events in percentage departures from the normal monthly precipitation to be found in column B, table 9, of Publication 4390.

Twelve other precipitation stations gave almost as good correlation as these fourteen stations, except that more cases of displacement of features by one, two, or three months occurred between forecasts and events. Such displacements, frequently noted in my former papers, are as yet impossible to forecast. This is the main defect of my forecasts. It is true that the *amplitudes* of features frequently differ between forecasts and events, but if the main features occur *when predicted,* the moderate difference of amplitudes is not a very serious defect. If one could predict *when* phases of prominent features would be displaced, the correlation between forecasts and events in precipitation would rise from being 40 to 70 percent to lie between 70 and 90 percent.

I have computed the correlation coefficient in precipitation between forecasts and events, 1959 through 1960, combining the results referred to in table 1 for 14 stations. Just as the mean temperatures for the decade 1950 to 1960 differ generally between 0.5° and 2.0° F. from those of the mean values 1870 to 1956, so, too, the mean values of precipitation 1950 to 1961 differ from the mean values 1870 to 1956. Before computing the general correlation coefficients, 1950-58 and 1959-60, for the 14 stations, I have corrected these differences of *level* by lifting or lowering the forecasts bodily. These differences range from zero to 17 percent among the 14 stations. This done, the general correlation coefficient between forecasts and events for the 336 months during 1959 and 1960 available at the time of computing from official records resulted as +47.0 percent.

I am not aware that anyone has ever before predicted the monthly precipitation at 14 definite cities over 2 years of time (in my case 1959-1960) and has achieved a correlation coefficient as high as +47 percent for 24 months, 3 years after the last month used in the basis of his forecast. It seems to me that this marks an important and encouraging advance in long-range forecasting.

Figure 4 shows graphically the results tabulated in table 1. I call attention to cases of displacements of obviously common features in forecasts and events that occurred, and remark that such displacements must obviously have pulled down the value of the correlation coefficient which, notwithstanding, reached +47 percent. These cases are: Cincinnati, 3 months May 1959–April 1960; El Paso, 2 months about June 1960; Helena, 2 months about October 1959 and 2 months about September 1960; Sacramento, 2 months about January 1960.

NUMERICAL TABULATIONS

I was assisted in these tabulations by Mrs. Lena Hill and Mrs. Isobel Windom. Miss M. A. Neill assisted in reading proof. With the electronic computer, Jonathan Wexler furnished 3-month means of absolute temperatures, covering the years 1870 through 1956. We continued them through 1959. Subtracting 459.7°, we expressed them in ordinary Fahrenheit degrees. There were two sets of monthly normals computed covering 1870 through 1956: A for the years when Wolf sunspot numbers were less than 20, B for the years when Wolf sunspot numbers exceeded 20. The dates included in these two categories are given in table 2 and accompanying quotation from the journal "Solar Energy."

Table 3 gives these two sets of normal temperatures in both absolute and ordinary Fahrenheit, applying to the years 1870 through 1956.

TABLE 3.—*Normal monthly temperatures from records 1870-1956 absolute and usual Fahrenheit*

Category A
Wolf sunspot numbers < 20

Category B
Wolf sunspot numbers > 20

	Abilene. 1				Atlanta. 2			
	Absolute		Usual		Absolute		Usual	
	A	B	A	B	A	B	A	B
Jan.	504.9°	503.2°	45.2°	43.5°	504.1°	503.1°	44.4°	43.4°
Feb.	506.9	507.6	47.2	47.9	505.8	505.5	46.1	45.8
Mar.	514.3	516.1	54.6	56.4	511.8	512.9	52.1	53.2
Apr.	524.6	524.3	64.9	64.6	520.7	521.0	61.0	61.3
May	531.2	532.0	71.5	72.3	529.6	529.3	69.9	69.6
June	539.7	539.5	80.0	79.8	536.6	536.2	76.9	76.5
July	543.0	542.5	83.3	82.8	538.6	538.2	78.9	78.5
Aug.	542.9	541.9	83.2	82.2	537.5	537.6	77.8	77.9
Sept.	535.5	535.7	75.8	76.0	532.8	533.0	73.1	73.3
Oct.	525.4	525.5	65.7	65.8	522.4	522.8	62.7	63.1
Nov.	514.1	512.6	54.4	52.9	512.1	511.4	52.4	51.7
Dec.	505.0	505.7	45.3	46.0	505.1	504.1	45.4	44.4

	Detroit. 3				Los Angeles. 4			
	Absolute		Usual		Absolute		Usual	
	A	B	A	B	A	B	A	B
Jan.	485.8°	484.8°	26.0°	25.1°	515.2°	515.1°	55.5°	55.4°
Feb.	485.9	485.4	26.2	25.7	516.2	516.0	56.5	56.3
Mar.	492.6	494.5	32.9	34.8	518.4	517.5	58.7	57.8
Apr.	506.3	505.6	46.6	45.9	519.6	520.2	59.9	60.5
May	518.0	517.2	58.3	57.5	522.4	522.6	62.7	62.9
June	528.2	527.5	68.5	67.8	526.0	526.4	66.3	66.7
July	532.8	532.5	73.1	72.7	530.5	530.5	70.8	70.8
Aug.	530.5	530.5	70.8	70.8	530.7	531.6	71.0	71.9
Sept.	523.2	523.8	63.5	64.1	529.5	529.9	69.8	70.2
Oct.	512.5	512.1	52.8	52.4	525.6	525.6	65.9	65.9
Nov.	499.8	499.1	40.1	39.4	522.2	521.5	62.5	61.9
Dec.	488.9	489.4	29.2	29.7	516.8	517.3	57.1	57.6

	New York. 5				Omaha. 6			
	Absolute		Usual		Absolute		Usual	
	A	B	A	B	A	B	A	B
Jan.	491.8°	491.3°	32.1°	31.6°	483.4°	480.6°	23.7°	20.9°
Feb.	491.8	491.3	32.1	31.6	486.1	485.4	26.4	25.7
Mar.	498.7	498.8	39.0	39.1	495.7	497.6	36.0	37.9
Apr.	509.4	508.7	49.7	49.0	512.6	510.5	52.9	50.8
May	520.6	519.6	60.9	59.9	522.7	522.1	63.0	62.4
June	529.3	528.7	69.6	69.0	532.9	531.6	73.2	71.9
July	534.4	534.0	74.7	74.3	537.9	537.2	78.2	77.5
Aug.	532.6	532.7	72.9	73.0	535.0	534.8	75.3	75.1
Sept.	526.4	526.5	66.7	66.8	525.5	526.5	65.8	66.8
Oct.	516.3	516.2	56.6	56.5	514.9	513.8	55.2	54.1
Nov.	504.9	504.5	45.2	44.8	499.6	497.6	39.9	37.9
Dec.	494.7	494.5	35.0	34.8	487.1	486.7	27.4	27.0

TABLE 3—*continued*

	Category A Wolf sunspot numbers < 20				Category B Wolf sunspot numbers > 20			
	Salt Lake City. 7				St. Louis. 8			
	Absolute		Usual		Absolute		Usual	
	A	B	A	B	A	B	A	B
Jan.	488.8°	487.8°	29.1°	28.1°	493.6°	491.1°	33.9°	31.4°
Feb.	492.9	493.0	33.2	33.3	495.0	494.5	35.3	34.8
Mar.	501.3	500.6	41.6	40.9	502.8	504.6	43.1	44.9
Apr.	509.7	509.4	50.0	49.7	516.6	515.2	56.9	55.5
May	518.2	517.5	58.5	57.8	526.5	525.6	66.8	65.9
June	527.5	526.7	67.8	67.0	536.0	534.5	76.3	74.8
July	536.2	535.7	76.5	76.0	540.3	539.0	80.6	78.3
Aug.	534.3	534.3	74.6	74.6	537.7	537.4	78.0	77.7
Sept.	524.4	524.2	64.7	64.5	529.7	530.3	70.0	70.6
Oct.	512.8	512.0	53.1	52.3	519.0	518.3	58.3	58.6
Nov.	501.2	499.1	41.5	39.4	506.2	504.2	46.5	44.5
Dec.	490.9	491.4	31.2	31.7	495.3	494.8	35.6	35.1

	St. Paul. 9				Washington. 10			
	Absolute		Usual		Absolute		Usual	
	A	B	A	B	A	B	A	B
Jan.	474.0°	471.6°	14.3°	11.9°	495.3°	494.3°	35.6°	34.6°
Feb.	476.5	476.2	16.8	16.4	495.8	495.5	36.1	35.8
Mar.	488.1	489.6	28.4	29.9	502.7	503.6	43.0	43.9
Apr.	506.3	504.8	46.6	45.1	514.0	513.9	54.3	54.2
May	518.5	517.6	58.8	57.9	524.6	523.9	64.9	64.2
June	528.3	526.5	68.6	66.8	532.8	532.4	73.1	72.7
July	533.1	532.4	73.3	72.7	537.2	536.5	77.5	76.8
Aug.	529.7	529.9	70.0	70.2	534.5	534.8	74.8	75.1
Sept.	519.9	521.1	60.2	61.4	528.2	528.3	68.5	68.6
Oct.	509.2	508.1	49.5	48.4	517.2	517.0	57.5	57.3
Nov.	493.4	491.2	33.7	31.5	506.1	505.8	46.4	46.1
Dec.	479.8	479.0	20.1	19.3	496.8	496.4	36.1	36.7

The same 27 harmonic periods were evaluated for temperature forecasts that were used for precipitation forecasts (see Publ. 4390). As stated above, atmospheric changes required division of the monthly temperature records, 1870 through 1956, into 220 groups. Each period was determined in form and amplitude by employing these groups as was described in Publication 4390 and other papers cited therein. Thereby a table of 216 months, 27 columns wide, was formed to cover the interval 1950 through 1967. The columns were added together across the table to make a single column of temperature forecasts for each city for the years 1950 through 1967. This column was designated "Σ." A parallel column designated "Obs" contained the observed temperatures of 108 months, 1950 through 1959. Both columns were representative, not of absolute Fahrenheit degrees of temperature, but of percentages of the normals A and B of table 3. One might regard them as flowing functions, $1+X$ and $1+Y$, times the normal temperatures A and B, where X and Y are flowing variables, each ranging from -80 to $+150$ ten-thousandths.

Taking the mean $1+X$ and the mean $1+Y$, used as multipliers of the normals A and B, these normals could be transferred into new normals suited to the atmospheric conditions prevailing from 1950 through 1959. By assumption these new normals were usable in the forecasts from 1960 through 1967. But, as stated above, it was found that neither in *scale* nor in *level* did the new normals from X agree with the new normals from Y. To make the Σ values fairly comparable with the Obs values, a *scale* correction to Σ was first determined. This was done as stated above by plotting Σ and Obs from 1950 through 1959, and obtaining the mean ratio of amplitudes of some half-dozen principal obviously common features of the two curves. After this adjustment of scale a level correction to Σ was computed. This was the ratio of the sums of scale-corrected Σ to the unchanged Obs for the years 1950 through 1959. Applying it, the two variables became justly comparable. As thus reconciled, the new final normal absolute temperatures were tabulated, and then they were reduced to ordinary Fahrenheit by subtracting 459.7°. In this form the new normals, which are assumed to be suited to the atmospheric conditions 1950 through 1967, are given in table 4.

Subtracting the new normals from the two reconciled columns of Σ and Obs we obtained the monthly march of Obs from 1950 through 1959, and that of Σ from 1950 through 1967. The march Σ after 1960 represents the forecast of chief interest. But the comparative marches of Σ and Obs 1950 through 1959 gives the evidence on which a judgment of the probable value of the forecast 1960 through 1967 principally depends.

For convenient general views of the predicted march of temperature, I give in table 6 4-month mean values of the forecasted departures from normal 1950 through 1967, together with 4-month means of the observed departures from normal 1950 through 1959. From a comparison of these 10 years a judgment may be formed of the worth of the forecast after 1959.

As further evidence of the value of the forecast I give in table 7 the average discrepancy between forecast and event 1950 through 1959 and the average algebraic mean difference to show that the corrections for scale and level combined closely reconciled forecast and event.

TABLE 4.—*Normal temperature corrected for scale and level to suit interval 1950 through 1959*

	Abilene		Atlanta		Detroit		Los Angeles		New York	
	A	B	A	B	A	B	A	B	A	B
Jan.	45.8°	44.1°	45.2°	44.1°	27.2°	26.2°	56.8°	56.7°	33.9°	33.4°
Feb.	47.8	48.5	46.9	46.6	27.3	26.8	57.8	57.6	33.9	33.4
Mar.	55.2	57.0	52.8	54.0	33.9	35.9	60.0	59.1	40.8	40.9
Apr.	65.5	65.2	61.8	62.1	47.8	47.0	61.2	61.8	51.6	50.7
May	72.1	72.9	70.7	70.4	59.5	58.7	64.1	64.2	62.8	61.8
June	80.6	80.4	77.7	77.3	69.7	69.0	67.6	68.0	71.6	70.0
July	84.0	83.5	79.7	79.3	74.3	73.9	72.1	72.1	76.7	76.3
Aug.	83.9	82.9	78.6	78.7	72.0	72.0	72.3	73.2	74.9	74.0
Sept.	76.4	76.5	73.9	74.1	64.7	65.3	71.1	71.5	68.6	68.7
Oct.	66.3	66.4	63.5	63.9	54.0	53.6	67.2	67.2	58.5	58.4
Nov.	55.0	53.5	53.2	52.5	41.2	40.5	63.8	63.1	47.1	46.7
Dec.	45.9	46.6	46.2	45.2	30.3	30.8	58.4	58.9	36.7	36.6

	Omaha		Salt Lake City		St. Louis		St. Paul		Washington	
	A	B	A	B	A	B	A	B	A	B
Jan.	23.9°	21.1°	29.3°	28.3°	34.5°	32.0°	15.0°	12.6°	37.5°	36.5°
Feb.	26.6	25.9	33.4	33.5	35.4	35.4	17.5	17.2	38.1	37.7
Mar.	36.2	38.1	41.9	41.2	43.7	45.5	29.1	30.6	44.9	45.8
Apr.	53.2	51.1	50.3	50.0	57.5	56.1	47.4	45.9	56.3	56.2
May	63.3	62.7	58.8	58.1	67.4	66.5	59.6	58.7	66.9	66.3
June	73.5	72.2	68.1	67.3	76.9	75.4	69.4	67.6	75.1	74.7
July	78.5	77.8	76.8	76.3	81.2	79.9	74.2	73.5	79.5	78.8
Aug.	75.6	75.4	74.9	74.9	78.6	78.3	70.8	71.0	76.8	77.1
Sept.	66.1	67.1	65.0	64.8	70.6	71.2	61.0	62.2	70.5	70.6
Oct.	55.5	54.4	53.4	52.6	59.9	59.2	50.3	49.2	59.5	59.3
Nov.	40.1	38.1	41.8	39.6	47.1	45.1	34.4	32.2	48.3	47.0
Dec.	27.6	27.2	31.4	31.8	36.2	35.7	20.8	20.0	39.0	38.5

TABLE 5.—*Forecast of temperature departures from normal 1950 through 1959 from 3-month running means*

	Abilene, Tex.			Atlanta, Ga.			Detroit, Mich.			Los Angeles, Calif.			New York, N. Y.		
1950	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ
Jan.	+3.2°	+2.9°	—0.3°	+3.5°	+5.4°	+1.9°	+2.6°	+2.8°	+0.2°	—1.5°	—3.5°	—2.0°	+2.0°	+4.0°	+2.0°
Feb.	+1.4	+1.7	+0.3	+0.6	+3.9	+3.3	+1.0	—0.2	—1.2	—0.6	—2.5	—1.9	+2.2	+1.5	—0.7
Mar.	+0.7	+0.2	—0.5	—1.5	—0.9	+0.6	+0.5	—3.9	—4.4	+0.8	—0.2	—1.0	+0.5	—2.2	—2.7
Apr.	+1.2	—1.1	—2.3	—0.1	—1.6	—1.5	+0.6	—4.1	—4.7	+0.4	—0.5	—0.9	—1.5	—3.3	—1.8
May	+2.7	—0.9	—3.6	+2.8	—0.3	—3.1	+0.1	—2.5	—2.6	—0.6	—0.9	—0.3	—3.2	—2.5	+0.7
June	+1.5	—1.3	—2.8	+2.0	+0.3	—1.7	+0.3	—1.5	—1.8	—0.8	—0.8	0.0	—2.1	—1.2	+0.9
July	+0.9	—2.4	—3.3	+1.2	—1.3	—2.5	—0.5	—1.0	—0.5	—1.4	—0.8	+0.6	—3.5	—1.7	+1.8
Aug.	—1.4	—2.7	—1.3	+0.3	—2.4	—2.7	0.0	—2.5	—2.5	—0.6	—1.3	—0.7	—2.1	—1.5	+0.6
Sept.	—0.1	—0.1	0.0	—1.1	—1.0	+0.1	+0.7	—0.6	—1.3	—0.2	—0.9	—0.7	—1.8	—1.3	+0.5
Oct.	—0.7	+0.9	+1.6	—2.8	—1.9	+0.9	+0.9	—1.3	—2.2	+0.8	+0.1	—0.7	—1.1	—0.2	+0.9
Nov.	+0.1	+0.6	+0.5	+2.9	—2.5	—5.4	+0.5	—2.2	—2.7	+1.3	+2.0	+0.7	+1.1	+0.5	—0.6
Dec.	—1.9	—1.0	+0.9	—1.5	—2.8	—1.3	+0.3	—2.5	—2.8	+2.5	+0.9	—1.6	+3.2	+0.9	—2.3
1951															
Jan.	—1.0°	—0.7°	+0.3°	—2.7°	—0.8°	+1.9°	+0.2°	—0.9°	—1.1°	+2.7°	+0.3°	—2.4°	+3.3°	+1.5°	—1.8°
Feb.	—2.3	—0.2	+2.1	—2.0	+0.4	+2.4	+0.8	+1.0	+0.2	+2.4	—0.4	—2.8	+2.7	+2.3	—0.4
Mar.	—1.4	—0.7	+0.7	—1.5	—0.7	+0.8	+0.6	0.0	—0.6	+0.9	—0.6	—1.5	+0.5	+1.7	+1.2
Apr.	—1.6	—0.8	+0.8	—3.9	—1.1	+2.8	—0.5	+0.1	+0.6	—0.2	—0.5	—0.3	—0.1	+0.7	+0.8
May	—1.8	—0.6	+1.2	—2.0	—0.7	+1.3	—1.6	—0.6	+1.0	—0.4	—1.3	—0.9	—1.3	—0.1	+1.2
June	—0.6	+0.6	+1.2	+0.1	—0.1	—0.2	0.0	—0.6	—0.6	—1.4	—0.6	+0.8	—0.8	+0.1	+0.9
July	+1.3	+1.6	+0.3	—1.5	+0.8	+2.3	—0.2	—1.7	—1.5	—1.6	—0.8	+0.8	—1.9	—1.4	+0.5
Aug.	+1.1	+2.2	+1.1	+1.5	+0.5	—1.0	—0.3	—2.4	—2.1	—1.4	—0.6	+0.8	—0.3	—0.1	+0.2
Sept.	—0.5	+2.4	+2.9	—0.6	+1.1	+1.7	—0.6	—1.3	—0.7	—1.2	—0.2	+1.0	—0.9	—0.7	+0.2
Oct.	—2.6	—0.2	+2.4	—0.7	—1.4	—0.7	+0.2	—2.5	—2.7	—1.2	0.0	+1.2	—1.1	—1.5	—0.4
Nov.	0.0	0.0	0.0	—1.2	—0.6	+0.6	—0.7	—2.2	—1.5	—0.6	—1.4	—0.8	—0.1	—0.2	—0.1
Dec.	—0.5	+1.8	+2.3	—0.2	+0.7	+0.9	+0.1	—1.6	—1.7	+0.4	—3.3	—3.7	+1.8	+0.7	—1.1

(continued)

TABLE 5.—*continued*

	Abilene, Tex.			Atlanta, Ga.			Detroit, Mich.			Los Angeles, Calif.			New York, N. Y.		
	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ
1952															
Jan.	0.0°	+4.2°	+4.2°	+1.5°	+3.1°	+1.6°	+1.2°	+1.1°	—0.1°	+0.7°	—2.4°	—3.1°	+2.1°	+2.8°	+0.7°
Feb.	—0.8	+2.6	+3.4	+1.8	+1.5	—0.3	+1.3	+1.3	0.0	+0.2	—2.0	—2.2	+1.8	+1.8	0.0
Mar.	—1.3	—0.5	+0.8	0.0	—0.3	—0.3	+1.8	+1.0	—0.8	—0.4	—1.1	—0.7	+1.6	+1.8	+0.2
Apr.	—1.1	—1.9	—0.8	—0.1	—0.5	—0.4	+1.1	—0.3	—1.4	—0.8	—0.7	+0.1	—0.7	0.0	+0.7
May	+0.1	0.0	—0.1	—1.0	+2.0	+3.0	—0.5	+1.7	+2.2	—1.2	—0.2	+1.0	—1.8	+1.0	+2.8
June	+0.9	+0.9	0.0	+1.2	+3.1	+1.9	—2.8	+1.4	+4.2	—2.1	+0.1	+2.2	—2.7	+1.7	+4.4
July	+0.6	+3.4	+2.8	+0.5	+2.4	+1.9	—3.5	+1.8	+5.3	—1.6	—0.4	+1.2	—2.4	+1.2	+3.6
Aug.	+3.5	+2.0	—1.5	+0.3	—0.2	—0.5	—2.1	+0.3	+2.4	—0.7	+1.3	+2.0	+0.3	+1.7	+1.4
Sept.	+2.5	+1.0	—1.5	+0.6	—4.3	—4.9	—1.9	—2.4	—0.5	—0.4	+1.1	+1.5	+1.0	—1.4	—2.4
Oct.	+1.9	—1.8	—3.7	+1.3	—4.5	—5.8	—1.3	—1.4	—0.1	—0.6	—0.5	+0.1	+1.1	—0.7	—1.8
Nov.	+2.2	—1.9	—4.1	+1.6	—4.7	—6.3	—0.7	+0.1	+0.8	—1.8	—2.3	—0.5	+0.9	—0.2	—1.1
Dec.	+2.2	+1.5	—0.7	+1.6	+0.5	—1.1	+0.3	+3.4	+3.1	—0.9	—1.0	—0.1	+2.0	+2.6	+0.6
1953															
Jan.	+0.1°	+2.3°	+2.2°	—0.7°	+0.7°	+1.4°	—0.1°	+4.3°	+4.4°	+0.7°	+0.7°	0.0°	+2.6°	+3.4°	+0.8°
Feb.	+4.4	+4.6	+0.2	+2.8	+1.7	—1.1	+1.3	+4.4	+3.1	+0.8	+1.3	+0.5	+2.1	+3.6	+1.5
Mar.	+2.8	+1.5	—1.3	—0.9	0.0	+0.9	—0.7	+1.9	+2.6	—0.1	—0.9	—0.8	+0.3	+1.9	+1.6
Apr.	+2.8	+1.1	—1.7	—2.6	+0.7	+3.3	—1.7	0.0	+1.7	—1.0	—1.2	—0.2	+0.2	+0.3	+0.1
May	+2.1	+1.6	—0.5	—3.8	+0.3	+4.1	—2.8	—1.0	+1.8	—1.6	—1.2	+0.4	—0.4	—0.4	0.0
June	+0.3	+2.3	+2.0	—4.6	+0.7	+5.3	—3.3	0.0	+3.3	—1.0	+0.6	+1.6	—1.8	—0.5	+1.3
July	—1.1	+1.5	+2.6	—3.3	0.0	+3.3	—1.7	+0.8	+2.5	—1.0	+0.1	+1.1	—2.2	—0.1	+2.1
Aug.	—4.3	—0.1	+4.2	—2.4	—0.8	+1.6	—1.4	+0.3	+1.7	—0.7	+0.1	+0.8	—1.5	0.0	+1.5
Sept.	—5.3	0.0	+5.3	—2.6	—0.3	+2.3	+0.7	+1.5	+0.8	+0.1	—0.2	—0.3	—1.2	+0.8	+2.0
Oct.	—4.9	—0.3	+4.6	—3.5	—0.5	+3.0	—0.1	+1.9	+2.0	+1.6	+0.3	—1.3	+0.2	+1.4	+1.2
Nov.	—2.1	—1.5	+0.6	—1.5	—0.9	+0.6	+1.4	+3.1	+1.7	+2.6	+0.8	—1.8	+1.6	+2.5	+0.9
Dec.	—2.0	—1.5	+0.5	+0.1	—1.0	—1.1	+0.6	+1.9	+1.3	+2.1	—0.2	—2.3	+1.9	+1.4	—0.5

1954															
Jan.	+0.1°	+1.9°	+1.8°	—0.9°	+0.2°	+1.1°	+2.1°	+2.9°	+0.8°	+1.7°	+1.7°	0.0°	+2.0°	+2.6°	+0.6°
Feb.	+1.3	+2.3	+1.0	+2.2	+1.1	—1.1	+2.5	+1.6	—0.9	+1.5	+0.7	—0.8	+2.1	+1.4	—0.7
Mar.	+4.4	+3.9	—0.5	+2.5	+2.4	—0.1	+2.7	+2.7	0.0	+1.6	+1.0	—0.6	+3.3	+2.7	—0.6
Apr.	+4.2	—0.1	—4.3	+0.7	—0.8	—1.5	—1.1	—1.2	—0.1	+1.6	—1.2	—2.8	+0.9	—0.6	—1.5
May	+4.0	+0.5	—3.5	+1.7	—0.8	—2.5	+0.5	—0.5	—1.0	+0.7	—0.2	—0.9	+0.6	—1.1	—1.7
June	+1.8	0.0	—1.8	+0.9	—1.3	—2.2	+2.1	—2.1	—4.2	—1.1	+1.4	+2.5	+0.9	—2.2	—3.1
July	+2.3	+2.1	—0.2	+4.3	+2.2	—2.1	+4.7	+0.1	—4.6	—1.3	+1.8	+3.1	+1.2	—1.9	—3.1
Aug.	+2.4	+3.0	+0.6	+4.5	+3.3	—1.2	+4.2	—1.3	—5.5	+0.2	+2.3	+2.1	+0.2	—2.1	—2.3
Sept.	+1.4	+2.4	+1.0	+5.2	+2.9	—2.3	+3.2	—0.3	—3.5	+1.1	+0.2	—0.9	+2.3	—0.8	—3.1
Oct.	+1.0	+1.7	+0.7	+2.6	+0.3	—2.3	+2.1	+0.3	—1.8	+0.8	+0.1	—0.7	+2.3	—0.2	—2.5
Nov.	+0.2	+1.4	+1.2	+1.7	—1.8	—3.5	—1.1	—0.1	+1.0	+0.3	—0.8	—1.1	+1.7	0.0	—1.7
Dec.	—0.8	+0.9	+1.7	0.0	—2.6	—2.6	—1.3	—0.4	+0.9	+0.3	—1.0	—1.3	—0.4	—1.7	—1.3
1955															
Jan.	—1.1°	+0.8°	+1.9°	+1.8°	—1.2°	—3.0°	+0.8°	+3.3°	+2.5°	0.0°	—1.4°	—1.4°	—0.9°	—1.2°	—0.3°
Feb.	—1.8	+0.4	+2.2	+0.6	+0.8	+0.2	+1.0	+4.0	+3.0	—0.7	—0.9	—0.2	—0.9	—0.8	+0.1
Mar.	—1.9	+1.9	+3.8	+0.3	+2.7	+2.4	+1.6	+6.5	+4.9	—1.4	+0.2	+1.6	—0.5	+0.8	+1.3
Apr.	—3.4	—2.4	+1.0	+2.2	+3.3	+1.1	—0.7	+3.6	+4.3	—0.8	+0.1	+0.9	—0.8	+1.0	+1.8
May	+1.0	+1.3	+0.3	+0.5	+0.7	+0.2	+1.2	+2.9	+1.7	—0.9	—0.8	+0.1	—0.9	+0.2	+1.1
June	+2.7	—0.2	—2.9	—1.0	—0.7	+0.3	+1.5	+2.5	+1.0	—1.5	—1.4	+0.1	—0.5	+1.8	+2.3
July	+1.5	—0.9	—2.4	+0.1	—1.1	—1.2	+2.0	+2.7	+0.7	—1.9	—0.3	+1.6	—2.0	+1.1	+3.1
Aug.	+0.5	+0.4	—0.1	—0.5	+0.8	+1.3	+1.0	+2.9	+1.9	—1.8	+1.1	+2.9	—1.6	+2.5	+4.1
Sept.	+0.1	+0.6	+0.5	—0.4	+0.2	+0.6	+0.6	+1.7	+1.1	—1.0	+0.7	+1.7	—1.1	+0.9	+2.0
Oct.	—0.5	+0.4	+0.9	—0.3	—0.9	—0.6	0.0	—0.4	—0.4	—0.5	—0.4	+0.1	—0.8	—0.9	—0.1
Nov.	—2.4	—0.4	+2.0	—1.6	—1.9	—0.3	0.0	—1.6	—1.6	—0.2	—2.7	—2.5	—0.5	—2.7	—2.2
Dec.	—3.3	—0.8	+2.5	—0.5	—2.1	—1.6	—0.6	—2.0	—1.4	—0.2	—2.0	—1.8	+0.3	—3.3	—3.6

(continued)

TABLE 5.—*continued*

	Abilene, Tex.			Atlanta, Ga.			Detroit, Mich.			Los Angeles, Calif.			New York, N. Y.		
	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ
1956															
Jan.	—3.2°	—0.9°	+2.3°	+0.9°	+0.1°	—0.8°	+1.0°	—0.6°	—1.6°	+0.3°	—2.7°	—3.0°	+2.1°	—1.2°	—3.3°
Feb.	—1.4	—0.1	+1.3	+2.0	+0.6	—1.4	+1.6	—0.7	—2.3	+0.1	—1.3	—1.4	+1.8	—0.1	—1.9
Mar.	—1.5	—0.4	+1.1	+3.0	+1.1	—1.9	+2.7	—1.2	—3.9	—0.9	—2.1	—1.2	+2.2	—0.7	—2.9
Apr.	—0.9	+1.1	+2.0	+0.3	+0.3	0.0	+1.2	—2.7	—3.9	—2.0	—0.5	+1.5	+0.6	—3.5	—4.1
May	—0.1	+2.2	+2.3	—1.0	+0.1	+1.1	+0.7	—1.3	—2.0	—1.4	—0.4	+1.0	—0.4	—2.4	—2.0
June	+1.3	+3.4	+2.1	+0.6	+0.5	—0.1	—1.1	—1.6	—0.5	—2.9	+0.5	+3.4	+0.9	—1.7	—2.6
July	+2.3	+2.8	+0.5	+0.1	+0.4	+0.3	—1.3	—0.8	+0.5	—1.7	+0.1	+1.8	—1.9	—1.5	+0.4
Aug.	+3.7	+2.2	—1.5	+0.4	—0.2	—0.6	—1.9	—2.8	—0.9	—1.0	+1.1	+2.1	—1.9	—2.0	—0.1
Sept.	+2.8	+2.6	—0.2	—0.7	+0.2	+0.9	—2.4	—0.7	+1.7	+0.9	+1.0	+0.1	—2.1	—1.7	+0.4
Oct.	+1.1	+1.1	0.0	0.0	—1.1	—1.1	—1.0	—0.3	+0.7	+1.9	+2.8	+0.9	+0.5	—1.3	—1.8
Nov.	—0.8	+1.4	+2.2	+1.3	+2.7	+1.4	0.0	+2.8	+2.8	+2.2	+1.7	—0.5	+1.1	+1.7	+0.6
Dec.	+1.8	+0.2	—1.6	—1.0	+2.9	+3.9	—1.5	—0.2	+1.3	+1.7	+0.9	—0.8	—0.6	+0.3	+0.9
1957															
Jan.	+1.0°	+2.3°	+1.3°	0.0°	+3.6°	+3.6°	—1.1°	+1.8°	+2.9°	+2.3°	+0.1°	—2.2°	+1.2°	+0.3°	—0.9°
Feb.	+0.6	+0.7	+0.1	—1.1	—0.4	+0.7	+0.8	+0.5	—0.3	+3.1	—0.2	—3.3	+2.1	+0.5	—1.6
Mar.	—0.4	—0.3	+0.1	—2.9	—2.6	+0.3	—0.3	+2.3	+2.6	+3.5	0.0	—3.5	+1.4	+2.8	+1.4
Apr.	—1.3	—3.6	—2.3	—3.4	+2.2	+5.6	—0.7	+0.3	+1.0	+3.2	—0.4	—3.6	+0.9	+1.8	+0.9
May	—0.5	—3.6	—3.1	—5.0	+0.4	+5.4	—1.6	—0.2	+1.4	+1.7	—0.5	—2.2	—1.6	+2.5	+4.1
June	—0.8	+0.4	+1.2	—2.5	+0.5	+3.0	—1.8	—1.2	+0.6	—0.4	+0.2	+0.6	—2.5	+3.1	+5.6
July	+2.2	+0.7	—1.5	—0.8	—0.3	+0.5	—2.5	—1.0	+1.5	—1.1	+0.4	+1.5	—1.9	+1.3	+3.2
Aug.	+3.7	—1.4	—5.1	+2.6	+0.8	—1.8	—2.8	—1.6	+1.2	—1.5	—0.2	+1.3	—3.3	+1.6	+4.9
Sept.	+3.1	—1.6	—4.7	+2.2	—0.8	—3.0	—2.2	—2.0	+0.2	—1.0	—1.4	—0.4	—3.1	—0.3	+2.8
Oct.	+1.3	—3.9	—5.2	+0.7	—4.5	—5.2	—3.7	—1.3	+2.4	—0.6	—2.2	—1.6	—1.5	+1.1	+2.6
Nov.	+0.6	—1.7	—2.3	+0.3	+1.2	+0.9	—3.0	+0.4	+3.4	—0.4	—0.7	—0.3	+0.5	+2.1	+1.6
Dec.	+1.1	—0.9	—2.0	—0.5	+1.5	+2.0	—0.9	+1.4	+2.3	—1.0	+0.5	+1.5	+1.0	+2.2	+1.2

1958															
Jan.	+0.6°	—0.8°	—1.4°	—1.5°	—5.2°	—3.7°	+0.3°	+0.2°	—0.1°	+0.6°	+2.0°	+1.4°	+2.9°	—0.7°	—3.6°
Feb.	—1.7	—1.1	+0.6	—2.3	—8.8	—6.5	—0.3	—0.7	—0.4	+1.5	+2.4	+0.9	+3.8	—2.2	—6.0
Mar.	—0.9	—5.9	—5.0	—0.8	—4.2	—3.4	+0.8	0.0	—0.8	+1.0	+1.3	+0.3	+2.5	—1.3	—4.8
Apr.	—0.4	—4.7	—4.3	+0.1	+0.3	+0.2	+0.7	+0.8	+0.1	+0.1	+1.1	+1.0	+1.1	—0.4	—1.5
May	+1.3	—1.1	—2.4	+2.0	+0.3	—1.7	+0.7	—0.9	—1.6	—0.8	+1.9	+2.7	+1.0	—1.4	—2.4
June	+1.3	+0.2	—1.1	—0.5	—0.3	+0.2	—1.2	—2.3	—1.1	—1.4	+0.3	+1.7	—0.8	—0.9	—0.1
July	+0.1	+1.0	+0.9	—0.2	—0.5	—0.3	—1.6	—2.5	—0.9	—1.6	—0.3	+1.3	—3.0	—0.8	+2.2
Aug.	—2.0	+0.1	+2.1	—1.3	+0.2	+1.5	—0.8	—1.1	—0.3	—1.6	—0.3	+1.3	—1.4	+1.3	+2.7
Sept.	—1.6	—1.1	+0.5	—2.5	—0.1	+2.4	—0.5	0.0	+0.5	—1.0	+2.3	+3.3	—2.3	—0.7	+1.6
Oct.	—3.3	—1.1	+2.2	—4.2	—1.9	+2.3	—0.6	+1.1	+1.7	—0.2	+2.4	+2.6	—1.5	—0.2	+1.3
Nov.	—3.1	—1.9	+1.2	—1.2	+4.0	+5.2	+0.9	+3.4	+2.5	+1.7	—3.2	—4.9	+1.1	—2.4	—3.5
Dec.	—1.5	—2.1	—0.6	+1.9	—2.6	—4.5	+2.1	+1.2	—0.9	+1.8	+2.4	+0.6	+3.3	—2.1	—5.4
1959															
Jan.	+0.1°	—2.3°	—2.4°	+3.3°	—1.9°	—5.2°	+4.2°	+0.1°	—4.1°	+1.6°	+2.1°	+0.5°	+4.5°	—3.2°	—7.7°
Feb.	—0.2	—1.4	—1.2	+1.0	+1.1	+0.1	+3.0	—2.5	—5.5	+1.2	+2.6	+1.4	+3.6	—1.3	—4.9
Mar.	—0.4	—1.6	—1.2	+1.0	—2.8	—3.8	+2.5	—1.3	—3.8	—0.3	+2.3	+2.6	+3.1	+0.1	—3.0
Apr.	—1.5	—0.5	+1.0	+1.3	+0.8	—0.5	+1.3	+0.2	—1.1	—1.6	+3.2	+4.8	+1.1	+1.6	+0.5
May	—2.1	—0.6	+1.5	+0.5	+1.7	+1.2	+0.7	+1.0	+0.3	—2.5	+2.1	+4.6	—1.0	+2.2	+3.2
June	—2.6	—1.2	+1.4	+0.1	—0.7	—0.8	—0.3	+1.6	+1.9	—2.0	+2.0	+4.0	—1.2	+2.5	+3.7
July	—0.4	—1.7	—1.3	—0.6	—0.2	+0.4	—0.7	+4.7	+5.4	—2.0	+1.8	+3.8	—2.2	+1.3	+3.5
Aug.	+0.5	—1.0	—1.5	+1.1	+1.8	+0.7	+0.2	+2.3	+2.1	—2.6	+3.9	+6.5	—1.4	+2.7	+4.1
Sept.	+0.6	—0.1	—0.7	+2.1	—0.8	—2.9	+0.4	+1.7	+1.3	—0.8	+1.9	+2.7	—1.8	+1.7	+3.5
Oct.	—2.0	—2.5	—0.5	+2.5	+0.9	—1.6	+1.3	—1.1	—2.4	0.0	+2.8	+2.8	+1.4	+0.2	—1.2
Nov.	—1.4	—2.4	—1.0	+0.2	—0.7	—0.9	+0.5	—0.4	—0.9	+0.9	+2.8	+1.9	+1.4	+0.2	—1.2
Dec.	—0.4	—1.3	—0.9	—1.6	+1.0	+2.6	+0.7	+1.0	+0.3	+0.8	+1.0	+0.2	—0.8	+0.5	+1.3

(*continued*)

TABLE 5.—*continued*

	Omaha, Nebr.			Salt Lake City, Utah			St. Louis, Mo.			St. Paul, Minn.			Washington, D. C.		
	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ
1950															
Jan.	+3.5°	—0.5°	—4.0°	—2.1°	—0.2°	+1.9°	+3.2°	+3.9°	+0.7°	+0.6°	—1.8°	—2.4°	+3.8°	+5.2°	+1.4°
Feb.	+1.8	—2.7	—4.5	—2.3	+0.2	+2.5	+1.5	+0.8	—0.7	—1.4	—4.1	—2.7	+2.3	+2.8	+0.5
Mar.	+1.3	—3.2	—4.5	—1.1	+0.3	+1.4	—0.1	—2.9	—2.8	—1.7	—5.2	—3.5	+0.2	—2.2	—2.4
Apr.	+0.5	—3.4	—3.9	—0.4	—1.9	—1.5	—0.3	—2.8	—2.5	—1.2	—6.0	—4.8	—1.0	—3.1	—2.1
May	+1.2	—2.1	—3.3	—0.6	—2.2	—1.6	—1.1	—1.5	—0.4	+1.0	—3.8	—4.8	—2.6	—2.0	+0.6
June	—1.0	—2.4	—1.4	+1.2	—2.4	—3.6	—2.7	—1.0	+1.7	+0.7	—2.2	—2.9	—3.9	—1.8	+2.1
July	—0.6	—4.0	—3.4	+0.5	—1.5	—2.0	—2.8	—3.4	—0.6	—1.0	—2.0	—1.0	—4.2	—1.8	+2.4
Aug.	—0.3	—4.7	—4.4	+0.3	—1.5	—1.8	—1.8	—4.3	—2.5	—0.9	—2.0	—1.1	—4.9	—2.9	+2.0
Sept.	+1.3	—1.4	—2.7	+0.2	+1.0	+0.8	—0.9	—1.1	—0.2	+0.6	+0.3	—0.3	—3.1	—1.4	+1.7
Oct.	—0.7	—0.7	0.0	+0.4	+2.0	+1.6	+0.1	—1.4	—1.5	0.0	—0.1	—0.1	—1.5	—0.9	+0.6
Nov.	—0.6	—0.7	—0.1	+0.8	+3.6	+2.8	+1.0	—2.3	—3.3	—0.8	—2.6	—1.8	+2.2	+0.4	—1.8
Dec.	—2.0	—2.4	—0.4	+0.4	+2.4	+2.0	+2.7	—3.8	—6.5	—0.6	—4.9	—4.3	+3.9	+0.1	—3.8
1951															
Jan.	+0.4°	—0.6°	—1.0°	—2.1°	+2.5°	+4.6°	+0.7°	—1.7°	—2.4°	+0.6°	—3.2°	—3.8°	+4.2°	+0.3°	—3.9°
Feb.	—0.2	—2.0	—1.8	—3.3	0.0	+3.3	+0.5	—1.2	—1.7	—0.9	—3.9	—3.0	+4.3	+1.2	—3.1
Mar.	—1.2	—3.3	—2.1	—3.1	—0.4	+2.7	—1.4	—2.7	—1.3	—1.9	—4.0	—2.1	+1.0	+0.2	—0.8
Apr.	—2.4	—4.0	—1.6	—2.2	—1.0	+1.2	—3.2	—2.5	+0.7	—2.2	—3.4	—1.2	—0.7	—0.7	0.0
May	—2.6	—3.1	—0.5	—0.1	—0.8	—0.7	—3.8	—1.8	+2.0	—0.5	—1.1	—0.6	—2.3	—1.0	+1.3
June	—1.7	—2.3	—0.6	—0.3	—1.1	—0.8	—4.4	—0.9	+3.5	—2.1	—0.3	+1.8	—2.9	—0.9	+2.0
July	—2.4	—3.0	—0.6	+1.2	—1.9	—3.1	—4.2	—1.3	+2.9	—3.0	—2.5	+0.5	—3.4	—0.7	+2.7
Aug.	—2.5	—3.1	—0.6	+1.4	—0.7	—2.1	—2.8	—2.2	+0.6	0.0	—3.4	—3.4	—0.8	—0.3	+0.5
Sept.	—4.2	—2.7	+1.5	+0.6	—1.2	—1.8	—1.3	—1.7	—0.4	+0.3	—3.1	—3.4	—1.3	+0.4	+1.7
Oct.	—4.2	—3.8	+0.4	—1.1	—1.6	—0.5	0.0	—3.5	—3.5	—1.2	—4.3	—3.1	—0.4	—1.0	—0.6
Nov.	—3.2	—4.4	—1.2	—3.1	—3.4	—0.3	0.0	—2.2	—2.2	—3.5	—3.5	0.0	+1.0	+0.9	—0.1
Dec.	—1.1	—3.6	—2.5	—3.5	—3.0	+0.5	+1.0	—0.6	—1.6	—1.8	—3.2	—1.4	+1.4	+0.6	—0.8

1952															
Jan.	+0.1°	+0.5°	+0.4°	—5.0°	—4.0°	+1.0°	+2.2°	+3.0°	+0.8°	+0.9°	+1.2°	+0.3°	+0.8°	+3.1°	+2.3°
Feb.	+0.7	+1.3	+0.6	—5.5	—4.6	+0.9	+2.3	+2.4	+0.1	+1.6	+0.8	—0.8	+1.4	+1.7	+0.3
Mar.	—1.7	+1.1	+2.8	—2.7	—3.8	—1.1	+0.2	+0.5	+0.3	0.0	+2.3	+2.3	+1.1	+0.7	—0.4
Apr.	—1.9	—1.8	+0.1	—1.7	—1.3	+0.4	—1.6	—1.3	+0.3	—1.4	—0.1	+1.3	+0.8	—1.1	—1.9
May	—1.7	+2.2	+3.9	+1.0	+1.6	+0.6	—3.2	+2.5	+5.7	—0.3	+2.1	+2.4	—2.9	+0.4	+3.3
June	—2.9	+2.3	+5.2	+2.5	+0.4	—2.1	—3.3	+3.7	+7.0	—2.0	+0.7	+2.7	—4.2	+0.7	+4.9
July	—3.0	+1.4	+4.4	+1.9	0.0	—1.9	—2.3	+3.5	+5.8	—2.0	+0.5	+2.5	—1.8	+1.0	+2.8
Aug.	—2.4	—0.7	+1.7	+1.8	+1.0	—0.8	—0.2	+0.6	+0.8	—1.5	—0.5	+1.0	—0.6	—0.3	+0.3
Sept.	—0.5	—2.2	—1.7	+1.1	+3.2	+2.1	+0.2	—1.4	—1.6	—0.2	—1.8	—1.6	+0.6	—2.2	—2.8
Oct.	+1.4	—1.2	—2.6	+1.6	+0.9	—0.7	+1.5	—0.5	—2.0	+0.9	—0.4	—1.3	+1.6	—1.5	—3.1
Nov.	+1.6	—1.6	—3.2	+1.7	—0.1	—1.8	+2.0	+0.1	—1.9	+1.4	+0.7	—0.7	+2.0	+0.3	—1.7
Dec.	+1.7	+0.9	—0.8	+1.7	+2.2	+0.5	+2.8	+2.6	—0.2	+3.3	+3.7	+0.4	+2.0	+2.2	+0.2
1953															
Jan.	+2.1°	+2.4°	+0.3°	+0.3°	+5.0°	+4.7°	+3.2°	+3.6°	+0.4°	+2.9°	+2.8°	—0.1°	+0.6°	+3.3°	+2.7°
Feb.	—0.2	+4.0	+4.2	—1.6	+5.4	+7.0	+1.9	+4.9	+3.0	0.0	+2.4	+2.4	+4.0	+3.6	—0.4
Mar.	—0.6	+0.9	+1.5	—1.2	+0.4	+1.6	+0.8	+1.5	+0.7	—1.0	—1.1	—0.1	+2.0	+2.2	+0.2
Apr.	—0.5	—1.5	—1.0	—0.8	—2.8	—2.0	+0.3	0.0	—0.3	—1.1	—1.7	—0.6	—1.7	+1.6	+3.3
May	—1.0	—1.5	—0.5	+0.3	—3.7	—4.0	—0.9	+0.2	+1.1	—2.8	—2.0	+0.8	—0.9	+1.0	+1.9
June	—0.8	+0.9	+1.7	+4.1	—1.9	—6.0	—1.1	+2.4	+3.5	—0.8	—0.2	+0.6	—1.9	+1.4	+3.3
July	—1.6	+1.7	+3.3	+4.9	+0.3	—4.6	—0.1	+2.6	+2.7	—0.7	+0.7	+1.4	—1.7	+0.3	+2.0
Aug.	—1.2	+0.8	+2.0	+5.1	+1.9	—3.2	—0.2	+1.8	+2.0	+2.0	+0.6	—1.4	—2.5	+0.2	+2.7
Sept.	+2.0	+2.1	+0.1	+2.5	+1.6	—0.9	+2.1	+2.4	+0.3	+2.8	+3.4	+0.6	—3.3	—0.5	+2.8
Oct.	+3.2	+3.0	—0.2	+2.2	+2.8	+0.6	+4.3	+2.5	—1.8	+6.4	+4.2	—2.2	—1.7	+0.4	+2.1
Nov.	+5.1	+3.9	—1.2	+1.2	+1.2	0.0	+4.1	+2.5	—1.6	+7.8	+4.4	—3.4	+1.7	+1.4	—0.3
Dec.	+4.8	+1.0	—3.8	+1.9	+2.5	+0.6	+3.6	+1.1	—2.5	+5.6	+5.4	—0.2	+2.3	+0.4	—1.9

(*continued*)

Table 5.—*continued*

	Omaha, Nebr.			Salt Lake City, Utah			St. Louis, Mo.			St. Paul, Minn.			Washington, D. C.		
	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ	Forecast Fahr.	Observed	O-F Δ
1954															
Jan.	+5.9°	+4.4°	—1.5°	+2.1°	+2.0°	—0.1°	+1.9°	+3.5°	+1.6°	+5.7°	+3.8°	—1.9°	+3.7°	+2.3°	—1.4°
Feb.	+6.4	+2.6	—3.8	+1.6	+1.5	—0.1	+0.5	+1.8	+1.3	+2.8	+3.0	+0.2	+5.0	+1.2	—3.8
Mar.	+6.6	+5.0	—1.6	+1.2	+1.0	—0.2	—0.2	+4.1	+4.3	+2.8	+4.3	+1.5	+4.4	+3.1	—1.3
Apr.	+1.0	—1.3	—2.3	+1.6	+0.9	—0.7	—0.8	—0.5	+0.3	—1.0	—2.7	—1.7	+1.7	—0.1	—1.8
May	+2.1	+0.1	—2.0	+0.6	+1.2	+0.6	+2.2	+0.5	—1.7	+0.3	—1.8	—2.1	—1.3	—0.1	+1.2
June	+3.8	+0.8	—3.0	—0.6	+0.4	+1.0	+1.9	+0.1	—1.8	+1.4	—1.4	—2.8	—1.1	—1.7	—0.6
July	+5.5	+2.6	—2.9	—1.0	—1.1	—0.1	+2.6	+2.4	—0.2	+3.2	+0.5	—2.7	—0.9	—0.9	0.0
Aug.	+4.0	+2.9	—1.1	—1.4	—0.1	+1.3	+3.3	+3.1	—0.2	+3.3	—0.3	—3.6	—0.4	0.0	+0.4
Sept.	+0.2	+0.8	+0.6	—0.4	—1.0	—0.6	+2.4	+1.7	—0.7	+2.3	—1.4	—3.7	+1.5	+1.1	—0.4
Oct.	+0.2	+2.3	+2.1	+1.3	+0.3	—1.0	+2.2	+1.3	—0.9	+1.8	+0.1	—1.7	+1.1	+0.7	—0.4
Nov.	—0.3	+2.3	+2.6	—0.8	0.0	+0.8	+1.8	+0.2	—1.6	+1.2	+1.4	+0.2	+0.4	—0.6	—1.0
Dec.	—0.3	+3.1	+3.4	—0.3	—2.3	—2.0	+1.2	+0.1	—1.1	+1.0	+2.0	+1.0	—0.4	—2.0	—1.6
1955															
Jan.	—0.5°	—0.6°	—0.1°	—2.5°	—6.2°	—3.7°	—0.8°	+0.1°	+0.9°	—0.8°	—0.2°	+0.6°	+1.0°	—1.3°	—2.3°
Feb.	—0.8	—1.9	—1.1	—3.7	—7.5	—3.8	—0.9	+0.7	+1.6	—3.5	—2.3	+1.2	+1.7	—0.1	—1.8
Mar.	0.0	+0.1	+0.1	—3.8	—6.5	—2.7	—2.4	+2.3	+4.7	—2.9	0.0	+2.9	+1.0	+1.6	+0.6
Apr.	—3.3	+3.4	+6.7	—3.3	—3.7	—0.4	—2.9	+3.2	+6.1	—2.9	+2.5	+5.4	+1.6	+2.2	+0.6
May	—0.8	+2.6	+3.4	+1.4	—2.3	—3.7	—1.1	+1.8	+2.9	+1.2	+4.0	+2.8	—1.3	—0.2	+1.1
June	—0.8	+2.0	+2.8	+3.0	—1.1	—4.1	+0.1	+0.8	+0.7	+0.2	+3.4	+3.2	—2.3	+0.3	+2.6
July	—0.9	+2.2	+3.1	+1.2	—0.1	—1.3	—1.2	+0.8	+2.0	+1.0	+3.4	+2.4	—2.9	+0.3	+3.2
Aug.	—1.0	+3.8	+4.8	+2.3	+0.2	—2.1	—2.0	+2.9	+4.9	—1.5	+3.4	+4.9	—2.4	+1.5	+3.9
Sept.	—1.0	+2.2	+3.2	—0.1	+0.6	+0.7	—0.6	+1.6	+2.2	—1.9	+2.4	+4.3	—0.1	+0.5	+0.6
Oct.	—2.6	—1.3	+1.3	—0.6	—1.2	—0.6	—0.7	—0.1	+0.6	—2.0	—1.5	+0.5	—0.2	—0.8	—0.6
Nov.	—4.4	—3.2	+1.2	—0.5	+0.5	+1.0	—1.8	—1.6	+0.2	—2.9	—4.1	—1.2	—0.2	—1.1	—0.9
Dec.	—3.8	—3.5	+0.3	—1.2	+3.0	+4.2	—0.9	—1.8	—0.9	—2.4	—4.5	—2.1	+0.5	—2.8	—3.3

1956															
Jan.	—1.6°	—1.5°	+0.1°	—1.6°	+1.8°	+3.4°	+0.1°	—0.3°	—0.4°	—0.5°	—3.0°	—2.5°	+3.6°	—1.0°	—4.6°
Feb.	+0.7	—0.4	—1.1	—4.1	+0.5	+4.6	+0.5	+0.2	—0.3	+0.5	—2.0	—2.5	+3.8	—0.2	—4.0
Mar.	+1.0	—1.1	—2.1	—3.8	—2.1	+1.7	+0.9	+0.2	—0.7	+2.5	—3.4	—5.9	+3.4	—0.1	—3.5
Apr.	+1.5	—0.3	—1.8	0.0	+1.1	+1.1	+0.9	—0.1	—1.0	+2.7	—3.1	—5.8	0.0	—2.2	—2.2
May	+2.2	+1.8	—0.4	+2.0	+1.5	—0.5	—1.0	+0.5	+1.5	+2.5	+0.4	—2.1	—2.0	—1.7	+0.3
June	+2.4	+2.4	0.0	+4.3	+1.5	—2.8	—0.7	+0.4	+1.1	+0.4	+0.8	+0.4	—2.3	—1.8	+0.5
July	—0.7	+1.8	+2.5	+3.2	+0.1	—3.1	—1.5	0.0	+1.5	—1.9	+0.9	+2.8	—4.5	—1.6	+2.9
Aug.	—2.7	—0.2	+2.5	+1.4	0.0	—1.4	—0.7	—0.5	+0.2	—2.9	—2.3	+0.6	—4.9	—2.5	+2.4
Sept.	—3.1	+2.3	+5.4	+0.8	—0.2	—1.0	+0.7	+2.2	+1.5	—1.8	+1.1	+2.9	—4.6	—1.4	+3.2
Oct.	—0.7	+2.2	+2.9	—1.0	—1.3	—0.3	+2.1	+2.0	—0.1	—0.5	+1.7	+2.2	+0.4	—1.1	—1.5
Nov.	+0.8	+4.0	+3.2	0.0	—2.5	—2.5	+1.6	+3.2	+1.6	+0.1	+4.3	+4.2	+2.8	+3.4	+0.6
Dec.	+0.2	+1.1	+0.9	+2.5	—3.0	—5.5	+0.2	—0.5	—0.7	+0.3	+1.0	+0.7	+0.3	+1.1	+0.8
1957															
Jan.	+1.9°	+2.7°	+0.8°	+2.8°	+0.8°	—2.0°	+0.6°	+0.8°	+0.2°	+1.5°	+1.5°	0.0	+1.4°	+2.4°	+1.0°
Feb.	+3.5	+1.1	—2.4	—0.2	+2.2	+2.4	+1.6	—0.7	—2.3	+3.3	+3.0	—0.3	+1.2	+0.1	—1.1
Mar.	+1.9	+2.2	+0.3	—1.0	+1.8	+2.8	—1.1	+1.1	+2.2	+3.7	+1.5	—2.2	+0.4	+2.4	+2.0
Apr.	+0.2	—0.6	—0.8	—0.8	—0.2	+0.6	—3.2	—0.7	+2.5	+1.7	—0.3	—2.0	—0.1	+1.4	+1.5
May	—0.7	—1.0	—0.3	+0.5	—1.0	—1.5	—4.0	+0.1	+4.1	+1.2	—0.3	—1.5	—2.4	+2.0	+4.4
June	—0.7	+0.3	+1.0	+3.5	—0.9	—4.4	—3.0	+0.1	+3.1	—1.0	+0.3	+1.3	—4.0	+1.0	+5.0
July	—0.7	+1.1	+1.8	+4.6	—0.1	—4.7	—2.6	+0.5	+3.1	—1.0	+0.9	+1.9	+3.2	+0.1	—3.1
Aug.	—1.3	+0.3	+1.6	+2.2	0.0	—2.2	—0.9	—0.5	+0.4	—1.5	0.0	+1.5	—2.8	—0.1	+2.7
Sept.	—0.9	—1.8	—0.9	+1.1	+0.3	—0.8	—1.3	—2.1	—0.8	—2.0	—1.4	+0.6	—2.7	—1.5	+1.2
Oct.	—1.3	—2.5	—1.2	+1.0	—2.0	—3.0	—1.2	—2.9	—1.7	—2.1	—1.2	+0.9	—3.2	—0.6	+2.6
Nov.	—0.5	+1.5	+2.0	+1.0	—1.5	—2.5	—0.2	—0.2	0.0	+0.4	+1.7	+1.3	+0.2	+1.2	+1.0
Dec.	+0.3	+4.2	+3.9	—0.5	—0.5	0.0	+1.7	+0.9	—0.8	+1.4	+5.2	+3.8	+0.8	+0.8	0.0

(*continued*)

TABLE 5—*concluded*

	Omaha, Nebr.			Salt Lake City, Utah			St. Louis, Mo.			St. Paul, Minn.			Washington, D. C.		
	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ	Fore-cast Fahr.	Ob-served	O-F Δ
1958															
Jan.	+1.8°	+2.6°	+0.8°	—0.2°	+3.8°	+4.0°	+1.0°	—1.9°	—2.9°	+2.8°	+4.4°	+1.6°	+2.4°	—1.9°	—4.3°
Feb.	+1.8	—0.8	—2.6	—0.7	+2.9	+3.6	—0.5	—6.0	—5.5	+2.1	+3.5	+1.4	+1.9	—4.4	—6.3
Mar.	+3.4	—2.7	—6.1	—1.5	+1.2	+2.7	+0.1	—6.0	—6.1	+2.8	+1.0	—1.8	+1.6	—3.5	—5.1
Apr.	+3.8	+0.1	—3.7	—0.5	+1.0	+1.5	—0.4	—2.9	—2.5	+1.5	+2.2	+0.7	+0.3	0.0	—0.3
May	+1.8	+0.2	—1.6	+1.4	+2.8	+1.4	—0.4	—1.6	—1.2	+1.3	—0.1	—1.4	—1.2	+1.7	+2.9
June	—2.5	—0.3	+2.2	+1.9	+3.3	+1.4	—2.5	—2.6	—0.1	—0.7	—1.7	—1.0	—2.0	—1.6	+0.4
July	—3.1	—2.2	+0.9	+2.8	+1.6	—1.2	—3.5	—2.7	+0.8	—0.3	—2.3	—2.0	—1.4	—3.6	—2.2
Aug.	—4.2	—1.3	+2.9	+0.7	+0.7	0.0	—2.8	—1.8	+1.0	+0.4	—0.7	—1.1	—2.2	—4.2	—2.0
Sept.	—5.2	+1.2	+6.4	+2.5	+2.1	—0.4	—2.5	—0.7	+1.8	—2.7	+1.6	+4.3	—3.1	—0.5	+2.6
Oct.	—4.4	+2.4	+6.8	+3.0	+0.8	—2.2	+3.2	+0.7	—2.5	—2.7	+2.7	+5.4	—2.1	—0.1	+2.0
Nov.	—3.3	+2.0	+5.3	+2.1	+2.1	0.0	—1.9	—0.6	+1.3	—2.0	+1.1	+3.1	+1.5	—1.3	—2.8
Dec.	—0.9	+0.3	+1.2	+1.1	+3.1	+2.0	+2.0	—2.5	—4.5	—0.1	—0.9	—0.8	+3.2	—2.5	—5.7
1959															
Jan.	+1.8°	—1.3°	—3.1°	+0.1°	+4.1°	+4.0°	+4.1°	—3.6°	—7.7°	+1.2°	—2.0°	—3.2°	+5.8°	—2.0°	—7.8°
Feb.	+2.4	—0.7	—3.1	+0.4	+2.9	+2.5	+3.9	—1.7	—5.6	+1.3	+0.3	—1.0	+4.7	—0.4	—5.1
Mar.	+0.7	0.0	—0.7	—0.2	+1.5	+1.7	+2.5	+0.4	—2.1	+1.8	+1.6	—0.2	+2.9	+0.9	—2.0
Apr.	+1.4	+0.5	—0.9	+0.1	—0.2	—0.3	+0.9	+1.3	+0.4	+0.2	+2.2	+2.0	—0.8	+1.3	+2.1
May	—0.5	+0.6	+1.1	+0.6	+1.1	+0.5	—0.3	—0.1	+0.2	—2.0	+2.1	+4.1	—2.7	+1.6	+4.3
June	—2.9	—0.2	+2.7	—0.2	+1.8	+2.0	—0.3	+1.6	+1.9	—1.7	+2.0	+3.7	—3.3	+0.9	+4.2
July	—2.6	+0.8	+3.4	—2.0	+1.7	+3.7	+0.2	+0.7	+0.5	—2.0	+2.8	+4.8	—2.8	+0.8	+3.6
Aug.	—2.5	—0.6	+1.9	—2.5	—0.2	+2.3	—0.2	+0.3	+0.5	—0.5	+2.0	+2.5	—0.7	+1.5	+2.2
Sept.	—2.4	—0.8	+1.6	—3.2	—1.3	+1.9	+1.2	+0.6	—0.6	—3.0	0.0	+3.0	+1.0	+2.5	+1.5
Oct.	—3.2	—3.6	—0.4	—5.4	—1.7	+3.7	+1.2	—1.9	—3.1	—3.3	—3.7	—0.4	+4.1	+0.8	—3.3
Nov.	—1.8	—0.2	+1.6	—4.8	—2.5	+2.3	+0.1	—0.5	—0.6	—2.8	—0.4	+2.4	+3.3	+2.3	—1.0
Dec.	+0.4	+0.7	+0.3	—3.0	—2.8	+0.2	+0.3	+0.6	+0.3	—1.6	+2.8	+4.4	+1.9	+1.2	—0.7

TABLE 5a—*Forecast of temperature departures from normal 1960 through 1967 from 3-month running means*

	Abilene, Tex.	Atlanta, Ga.	Detroit, Mich.	Los Angeles Calif.	New York, N. Y.	Omaha, Nebr.	Salt Lake City, Utah	St. Louis, Mo.	St. Paul, Minn.	Washington, D. C.
1960										
Jan.	—1.8°	0.0°	+1.2°	+0.7°	+1.5°	+3.3°	—2.7°	+1.4°	+1.3°	+2.1°
Feb.	+0.1	—0.7	+1.5	+0.8	+1.6	+1.8	—2.0	—2.9	+2.8	+1.6
Mar.	—1.2	—2.0	+0.4	+1.4	+2.4	+2.1	—2.4	+0.5	+3.3	+0.3
Apr.	—0.2	—2.3	+0.9	+1.5	+1.9	—0.4	—1.0	—1.6	+3.2	—0.9
May	+0.3	—1.5	+0.7	+0.8	+0.7	—1.3	+0.2	—2.6	+2.4	—1.6
June	+1.9	+2.1	+0.3	+0.6	+0.9	—0.8	+2.7	—2.1	+1.5	—1.2
July	+1.5	+2.6	—1.3	+0.4	—1.8	—3.1	+3.3	—2.1	+1.2	—0.8
Aug.	+2.2	+1.9	—1.6	+0.3	—1.2	—4.1	+2.2	—2.7	+0.5	—1.9
Sept.	+1.4	+1.2	—0.3	—0.1	—0.4	—3.7	+0.9	—1.2	—2.1	+0.2
Oct.	+0.9	+0.1	+0.3	—0.2	+0.8	—1.2	—0.4	+0.3	—0.6	+1.6
Nov.	+0.2	0.0	+1.4	+0.5	+2.7	+1.0	—0.6	+0.8	+0.1	+4.2
Dec.	+0.4	—2.4	+1.8	+1.2	+1.7	+1.7	—1.7	+1.2	+1.8	+3.6
1961										
Jan.	—0.9°	—2.6°	+1.6°	+1.9°	+3.2°	+1.8°	—2.2°	+1.2°	+0.8°	+2.4°
Feb.	—0.4	+1.7	+1.8	+1.5	+2.5	+2.8	—2.3	+1.6	+1.8	+2.0
Mar.	+0.2	—0.3	+1.3	+0.5	+0.8	+2.0	—2.1	+0.8	+1.8	+1.7
Apr.	+1.8	+1.3	+1.2	—0.7	+1.1	+1.8	—0.7	+1.1	+2.2	+1.3
May	+3.2	+2.4	—0.3	—1.8	—0.1	+2.8	+1.5	+2.2	+3.8	—2.6
June	+4.6	+4.1	—0.2	—2.6	+0.1	+4.0	+2.7	+1.5	+3.7	—2.1
July	+3.3	+3.0	—0.8	—1.8	—2.1	+2.7	+4.0	+1.4	+1.7	—1.3
Aug.	+3.6	+1.6	—0.3	—0.4	—1.1	+1.7	+3.0	+1.3	—0.4	—2.3
Sept.	+3.2	+1.9	—1.0	+0.1	—0.9	+1.1	+1.8	+0.4	—1.7	—1.0
Oct.	+2.8	—0.6	—0.8	+1.0	—0.5	+1.5	—0.1	—0.7	—0.6	—0.1
Nov.	+0.7	+0.2	0.0	+0.9	+1.0	+1.3	—3.0	—0.6	—1.1	+3.4
Dec.	—2.4	+1.1	+1.1	+0.6	+2.3	+1.5	—5.1	+0.1	—0.6	+4.2

(*continued*)

TABLE 5a.—*continued*

1962	Abilene, Tex.	Atlanta, Ga.	Detroit, Mich.	Los Angeles, Calif.	New York, N. Y.	Omaha, Nebr.	Salt Lake City, Utah	St. Louis, Mo.	St. Paul, Minn.	Washington, D. C.
Jan.	—3.1°	+2.4°	+2.5°	+1.2°	+3.2°	+3.2°	—5.4°	+0.5°	+0.7°	+5.5°
Feb.	—2.0	+2.8	+3.9	+0.7	+3.5	+3.6	—4.2	+1.6	—1.4	+4.3
Mar.	—1.1	+3.5	+3.3	—0.1	+1.7	+2.4	—2.8	—0.1	+0.4	+3.8
Apr.	—1.9	+1.1	+1.1	—0.3	0.0	—0.3	—0.7	—1.3	—1.4	—0.6
May	—0.1	—0.4	—0.2	—0.5	—1.9	—1.3	+0.7	—1.1	—0.8	—3.7
June	+2.2	+1.5	—0.5	+0.2	—1.0	+0.1	+1.1	—2.5	—1.5	—2.6
July	+1.9	+3.6	—0.9	+0.1	—0.4	+0.6	+2.2	—1.8	+0.9	—3.6
Aug.	+2.8	+0.4	+0.2	—0.1	—0.7	+1.3	+0.2	—1.7	—0.4	—2.1
Sept.	+2.6	—1.1	+0.4	—0.5	—0.9	+0.2	+0.7	—3.0	—2.2	—2.4
Oct.	+0.4	+0.7	—0.7	+1.0	—0.6	—1.4	+0.2	—1.7	—3.2	—0.8
Nov.	—0.5	+0.2	—0.7	+1.1	0.0	—3.2	+1.3	+0.4	+6.1	—0.7
Dec.	+0.3	+1.5	—0.6	+1.6	+0.8	—4.1	+0.9	+0.8	—2.2	—1.1
1963										
Jan.	—0.5°	—1.5°	—0.1°	+1.5°	—1.3°	—1.9°	0.0°	+0.6°	—1.4°	—1.2°
Feb.	+0.9	—1.4	—1.2	+1.5	—0.8	—0.2	—1.8	—0.6	—1.2	—1.5
Mar.	+0.5	—2.5	—0.4	+0.5	+0.2	+0.9	—0.7	—2.3	—1.8	—1.4
Apr.	+1.0	—2.5	—0.7	—0.4	+0.4	+2.9	0.0	—0.8	+0.2	—0.5
May	+1.2	—4.8	0.0	—0.9	—0.4	+3.8	+1.9	—2.1	+0.4	—1.2
June	+1.1	—4.4	—0.6	—1.6	—1.3	+2.8	+2.7	—1.9	—0.1	—2.5
July	—2.5	—3.8	—2.8	—1.2	—2.7	+0.2	+5.2	—3.1	—2.4	—3.4
Aug.	—4.2	—2.9	—2.9	—0.6	—2.9	—2.0	+5.1	—5.4	—0.5	—3.3
Sept.	—4.2	—3.2	—2.5	+0.2	—1.9	—2.8	+5.1	—5.0	+2.0	—2.7
Oct.	—3.5	—1.7	+0.9	+0.9	—0.4	—2.9	+2.0	—2.3	—2.4	—2.1
Nov.	—1.9	—0.7	+0.9	+1.8	+0.1	—2.5	+0.5	—0.1	—0.3	—0.3
Dec.	—0.1	+1.0	+0.9	+2.4	+0.8	—1.7	—2.0	+1.3	—1.5	+1.0

1964										
Jan.	+1.0°	+2.0°	+1.2°	+2.2°	−0.2°	0.0°	−1.5°	+2.9°	+0.5°	+0.8°
Feb.	+1.8	+4.3	+1.9	+1.1	0.0	+1.4	−3.0	+4.1	+1.7	+0.8
Mar.	+2.4	+3.9	+1.5	−1.7	−0.3	+1.8	−2.1	+4.3	+1.5	+1.0
Apr.	+1.7	+1.6	+0.5	−1.3	0.0	+3.9	−1.9	+3.3	+2.8	+0.4
May	−1.0	−0.5	−0.9	−1.2	+1.0	+1.6	0.0	+0.4	+1.4	+1.2
June	−2.9	−2.6	+0.7	−1.0	+0.9	+1.4	+1.1	−1.1	+4.1	−0.5
July	−4.5	−2.0	+1.5	−1.7	+0.3	+1.3	+0.5	−1.7	+5.9	−0.2
Aug.	−3.4	−0.5	+4.0	−0.9	−0.3	+0.7	+2.3	−1.3	+5.9	−0.6
Sept.	−1.0	+0.3	+2.6	−0.5	−0.8	+1.0	+0.2	+1.1	+7.9	−0.7
Oct.	+1.2	+2.2	+2.9	−0.2	+1.1	+0.7	−1.0	+1.7	−4.2	+0.2
Nov.	+1.1	+1.2	+1.4	+0.2	−0.1	+1.1	+0.8	+1.2	+0.7	−0.4
Dec.	+1.4	+2.2	+1.7	+0.6	+1.9	+0.8	−0.2	+1.6	+0.2	−3.8
1965										
Jan.	+1.8°	+3.2°	+1.3°	+0.2°	+1.6°	+0.7°	−2.3°	+1.5°	−2.1°	+4.7°
Feb.	+1.7	+2.9	+1.6	−0.4	+2.1	+2.4	−2.0	+1.7	−0.8	+5.2
Mar.	+0.6	+2.0	+0.9	−0.5	+1.2	+0.7	−3.2	−0.1	−1.8	+3.2
Apr.	+0.3	+0.4	+0.3	−0.1	+0.4	−0.3	−3.0	−0.9	−0.4	+2.6
May	−2.1	+0.7	−0.3	+0.3	+1.7	−1.3	−1.9	+0.5	−2.1	+1.2
June	+0.6	0.0	−0.8	−0.2	+0.9	−0.8	−0.4	−0.4	−3.1	−1.0
July	+1.2	−2.6	−2.1	−0.1	+0.9	−2.1	+2.8	−2.1	−1.9	−4.0
Aug.	+1.0	−4.6	−3.1	−0.2	−2.3	−2.3	+3.1	−3.5	−2.4	−5.1
Sept.	−0.9	−2.5	−5.0	+1.6	−3.7	−3.0	+3.3	−4.0	−1.7	−4.4
Oct.	−0.6	−0.9	−4.1	+1.8	−2.4	−2.6	+3.6	−2.9	−4.2	−1.6
Nov.	−0.2	+1.7	−3.9	+2.0	−0.6	−3.0	+0.8	−0.6	−1.5	+0.5
Dec.	+0.4	+3.3	−3.7	+1.2	+0.4	−1.9	+0.6	+0.5	−1.4	+1.7

(*continued*)

TABLE 5a.—*concluded*

1966	Abilene, Tex.	Atlanta, Ga.	Detroit, Mich.	Los Angeles, Calif.	New York, N. Y.	Omaha, Nebr.	Salt Lake City, Utah	St. Louis, Mo.	St. Paul, Minn.	Washington, D. C.
Jan.	—0.5°	+2.2°	—4.2°	+1.7°	+0.4°	—2.0°	—0.7°	+1.0°	—0.4°	+3.1°
Feb.	+0.1	+3.3	—0.8	+0.6	+1.5	—2.1	—2.5	+1.5	+0.3	+2.9
Mar.	—2.7	—1.4	—0.7	—0.4	+3.5	—1.7	—2.8	+0.1	—1.8	+0.4
Apr.	—1.2	—2.4	—0.2	—1.6	+2.7	+1.1	—1.2	+0.8	0.0	+3.8
May	—1.0	—5.0	—0.9	—2.1	—0.3	—0.5	+0.2	+0.8	+0.1	+1.1
June	—1.6	—7.8	—1.1	—2.2	—0.3	—1.4	+2.1	+0.7	—0.1	—1.1
July	—0.7	—5.5	—1.5	—2.4	—2.4	—0.2	+4.8	+0.8	—0.6	—3.6
Aug.	—1.7	—4.7	—1.5	—2.3	—2.3	+0.5	+4.2	+0.2	—0.5	—2.1
Sept.	—0.4	—2.2	—1.6	—0.9	—2.5	—0.8	+0.2	—1.9	+0.6	—2.1
Oct.	—0.9	+0.9	+0.2	—0.1	+0.6	+0.7	—0.4	—0.2	+4.8	—0.9
Nov.	—1.1	+3.1	—0.8	+0.8	+0.8	+1.7	—2.3	—0.1	+3.8	+0.8
Dec.	—1.6	—0.2	+0.5	+0.2	+3.4	—0.8	—1.6	+1.0	+2.7	+2.5
1967										
Jan.	—0.9°	—0.8°	+0.4°	+1.0°	+3.2°	+1.9°	—2.0°	+0.7°	+0.6°	+3.1°
Feb.	—1.0	—1.9	—0.1	+1.3	+0.2	+3.5	—1.1	+1.1	+0.9	+2.6
Mar.	+0.7	—0.9	—0.6	+0.7	+1.4	+3.9	+0.2	+0.4	+2.0	+0.6
Apr.	+1.0	—0.5	—1.6	+0.3	—1.6	+1.0	+2.2	—1.0	—0.1	—2.5
May	+2.3	—2.1	—2.4	+0.2	—1.7	+1.0	+4.0	—2.9	—0.8	—3.0
June	+2.5	—1.9	—1.0	+0.8	—0.8	+0.4	+3.5	—2.1	+0.4	—1.8
July	+1.0	—2.2	—2.1	—0.8	—2.6	—0.6	+4.5	—2.5	—0.5	—2.4
Aug.	—0.4	—4.2	—1.9	—2.0	—2.7	—2.3	+2.4	—3.4	—0.2	—1.3
Sept.	—0.6	—3.0	—1.4	—3.2	—3.1	—3.5	—0.4	—2.4	—0.8	—2.6
Oct.	—1.1	—0.6	—0.5	—2.0	—1.6	—2.5	—2.2	—1.3	0.0	—1.4
Nov.	—1.7	+1.6	+0.6	—0.8	+0.8	—1.0	—4.6	—0.6	+0.7	+2.0
Dec.	0.0	+2.9	+2.3	+0.1	+3.8	+0.3	—2.0	+0.3	+0.1	+2.3

As further evidence in justification of this method of very long-range forecasting of temperatures, I give table 8 (p. 37) showing the relative percent numbers of cases when forecasts and events lay on the same and on opposite sides of normal.

As in Publication 4390, I give United States maps (pp. 38-46) showing the 4-month mean departures from normal of the forecast 1960 through 1967. The number of stations is too small to warrant further general comment as to temperatures of the whole country, but a partial view of this may be perceived in these maps. Numbers relate to names as in table 8.

TABLE 6—*Four-month mean temperatures 1950-67 predicted on the level of normals 1950-59*
All based on 3-month running mean data

	Abilene, Tex.			Atlanta, Ga.			Detroit, Mich.			Los Angeles, Calif.			New York, N. Y.		
1950	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ
I	+1.6°	+0.9°	—0.7°	+0.6°	+1.7°	+1.1°	+1.2°	—1.2°	—2.4°	—0.2°	—0.7°	—0.5°	+0.8°	0.0°	—0.8°
II	+0.9	—1.8	—2.7	+1.6	—0.3	—1.9	0.0	—1.9	—1.9	—0.8	—1.0	—0.2	—2.7	—1.7	+1.0
III	—0.6	+0.1	+0.7	—0.6	—2.0	—1.4	+0.6	—1.6	—2.2	+1.1	+0.5	—0.6	+0.3	0.0	—0.3
1951															
I	—0.8	—0.6	+0.2	—2.5	—0.5	+2.0	+0.3	0.0	—0.3	+1.4	—0.3	—1.7	+1.6	+1.6	0.0
II	+0.2	+1.0	+0.8	—0.5	+0.1	+0.6	—0.5	—1.3	—0.8	—1.2	—0.8	+0.4	—1.1	—0.4	+0.7
III	—0.9	+1.0	+1.9	—0.7	0.0	+0.7	—0.2	—1.9	—1.7	—0.6	—1.2	—0.6	—0.1	—0.4	—0.3
1952															
I	—0.8	+1.1	+1.9	+0.8	+1.0	+0.2	+1.4	+0.8	—0.6	—0.1	—1.5	—1.4	+1.2	+1.8	+0.6
II	+1.3	+1.6	+0.3	+0.2	+1.8	+1.6	—2.2	+1.3	+3.5	—1.4	+0.2	+1.6	—1.6	+1.4	+3.0
III	+2.2	—0.3	—2.5	+1.3	—1.1	—2.4	—0.9	—0.1	+0.8	—0.9	—0.7	+0.2	+1.2	+0.1	—1.1
1953															
I	+2.5	+2.4	—0.1	—0.4	+0.8	+1.2	—0.3	+2.6	+2.9	+0.1	0.0	—0.1	+1.3	+2.3	+1.0
II	—0.8	+1.3	+2.1	—3.5	0.0	+3.5	—2.3	0.0	+2.3	—0.1	—0.1	0.0	—1.5	—0.3	+1.2
III	—4.6	—0.8	+3.8	—1.9	—0.7	+1.2	+0.6	+2.1	+1.5	+1.8	+0.2	—1.6	+0.6	+1.5	+0.9
1954															
I	+2.5	+2.0	—0.5	+1.1	+0.7	—0.4	+1.6	+1.5	—0.1	+1.6	+0.5	—1.1	+2.1	+1.5	—0.6
II	+3.4	+1.4	—2.0	+2.8	+0.8	—2.0	+2.9	—0.9	—3.8	—0.4	+1.3	+1.7	+0.7	—1.8	—2.5
III	+0.4	+1.6	+1.2	+2.4	—0.3	—2.7	+0.7	—0.1	—0.8	+0.6	—0.4	—1.0	+1.5	—0.7	—2.2
1955															
I	—2.0	+1.4	+3.4	+1.2	+1.4	+0.2	+0.7	+4.4	+3.7	—0.7	—0.5	+0.2	—0.8	0.0	+0.8
II	+1.6	+0.1	—1.5	—0.2	—0.1	+0.1	+1.4	+2.8	+1.4	—1.5	—0.3	+1.2	—1.2	+1.4	+2.6
III	—1.5	0.0	+1.5	—0.7	—1.2	—0.5	0.0	—0.6	—0.6	—0.5	—1.1	—0.6	—0.5	—1.5	—1.0
1956															
I	—1.8	—0.1	+1.7	+1.5	+0.5	—1.0	+1.6	—1.3	—2.9	—0.6	—1.6	—1.0	+1.7	—1.4	—3.1
II	+1.8	+2.8	+1.0	+0.5	+0.2	—0.3	—0.9	—1.6	—0.7	—1.8	+0.3	+2.1	—0.8	—1.9	—1.1
III	+1.2	+1.3	+0.1	—0.1	+1.2	+1.3	—1.2	+0.4	+1.6	+1.7	+1.6	—0.1	—0.3	—1.1	—0.8
1957															
I	0.0	+0.2	+0.2	—1.8	+0.7	+2.5	—0.3	+1.2	+1.5	+3.0	—0.1	—3.1	+1.4	+1.4	0.0
II	+1.2	—1.0	—2.2	—1.4	+0.4	+1.8	—2.2	—1.0	+1.2	—0.3	0.0	+0.3	—2.3	+2.1	+4.4
III	+1.5	—2.0	—3.5	+0.7	—0.5	—1.2	—2.4	—0.4	+2.0	—0.8	—0.9	—0.1	—0.8	+1.3	+2.1

II	+0.2	0.0	—0.2	0.0	—0.1	—0.1	—0.7	—1.7	—1.0	—1.4	—0.3	+1.1	—1.0	—0.4	+0.6
III	—2.4	—1.5	+0.9	—1.5	—0.2	+1.3	+0.5	+1.4	+0.9	+0.6	+1.0	+0.4	+0.2	—1.4	—1.6
1959															
I	—0.5	—1.4	—0.9	+1.6	—0.7	—2.3	+2.8	—0.9	—3.7	+0.2	+2.5	+2.3	+3.1	—0.7	—3.8
II	—1.2	—1.1	+0.1	+0.3	+0.6	+0.3	0.0	+2.4	+2.4	—2.3	+2.4	+4.7	—1.4	+2.2	+3.6
III	—0.8	—1.6	—0.8	+0.1	+0.1	0.0	+0.7	+0.3	—0.4	+0.2	+2.1	+1.9	0.0	+0.6	+0.6
1960															
I	—0.8			—1.2			+1.0			+1.1			+1.8		
II	+0.5			+1.3			—0.5			+0.5			—0.4		
III	+0.7			—0.3			+0.8			+0.4			+1.2		
1961															
I	+0.2			0.0			+1.5			+0.8			+1.9		
II	+3.7			+2.8			—0.4			—1.6			—0.8		
III	+1.1			+0.6			—0.2			+0.6			+0.7		
1962															
I	—2.0			+2.4			+2.7			+0.4			+2.1		
II	+1.7			+1.3			—0.4			—0.1			—1.0		
III	+0.7			+0.3			—0.4			+0.8			—0.2		
1963															
I	+0.5			—2.0			—0.6			+0.8			—0.4		
II	—1.1			—4.0			—1.6			—1.1			—1.8		
III	—2.4			—1.1			0.0			+1.3			—0.4		
1964															
I	+1.7			+3.0			+1.3			+0.1			—0.1		
II	—2.9			—1.4			+1.3			—1.2			+0.5		
III	+0.7			+1.5			+2.2			0.0			+0.5		
1965															
I	+1.1			+2.1			+1.0			—0.2			+1.3		
II	+0.2			—1.6			—1.8			0.0			+0.3		
III	—0.3			+0.4			—4.2			+1.6			—1.6		
1966															
I	—1.1			+0.4			—1.5			+0.1			+2.0		
II	—1.2			—5.7			—1.2			—2.2			—1.3		
III	—1.0			+0.4			—0.4			0.0			+0.6		
1967															
I	0.0			+1.0			—0.5			+0.8			+0.8		
II	+1.3			—2.6			—1.8			+0.4			—1.9		
III	—0.8			+0.2			+0.2			—1.5			0.0		

(continued)

TABLE 6.—*concluded*

	Omaha, Nebr.			Salt Lake City, Utah			St. Louis, Mo.			St. Paul, Minn.			Washington, D. C.		
	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ	Pred.	Obs.	Δ
1950															
I	+1.8°	—2.4°	—4.2°	—1.5°	—0.4°	+1.1°	+1.1°	—0.2°	—1.3°	—0.9°	—4.3°	—3.4°	+1.3°	+0.7°	—0.6°
II	—0.2	—3.3	—3.1	+0.4	—1.9	—2.3	—2.1	—2.5	—0.4	0.0	—2.5	—2.5	—3.9	—2.1	+1.8
III	—0.5	—1.3	—0.8	+0.4	+2.2	+1.8	+0.7	—2.2	—2.9	—0.2	—1.8	—1.6	+0.4	—0.4	—0.8
1951															
I	—1.1	—2.5	—1.4	—2.7	+0.3	+3.0	—0.8	—2.0	—1.2	—1.1	—3.6	—2.5	+2.2	+0.2	—2.0
II	—2.3	—2.9	—0.6	+0.5	—1.1	—1.6	—3.8	—1.5	+2.3	—1.4	—1.8	—0.4	—2.4	—0.7	+1.7
III	—3.2	—3.6	—0.4	—1.8	—2.3	—0.5	—0.1	—2.0	—1.9	—1.5	—3.5	—2.0	+0.2	+0.2	0.0
1952															
I	—0.7	+0.3	+1.0	—3.7	—3.4	+0.3	+0.8	+1.2	+0.4	+0.3	+1.0	+0.7	+0.5	+1.1	+0.6
II	—2.5	+1.3	+3.8	+1.8	+0.8	—1.0	—2.2	+2.6	+4.8	—1.4	+0.7	+2.1	—2.4	+0.4	+2.8
III	+1.0	—1.0	—2.0	+1.5	+1.5	0.0	+1.6	+0.2	—1.4	+1.4	+0.5	—0.9	+1.5	—0.3	—1.8
1953															
I	+0.2	+1.4	+1.2	—0.8	+2.0	+2.8	+1.5	+2.5	+1.0	+0.2	+0.6	+0.4	+1.2	+2.7	+1.5
II	—1.2	+0.5	+1.7	+3.6	+0.8	—2.8	—0.6	+1.8	+2.4	—0.6	—0.2	+0.4	—1.8	+0.7	+2.5
III	+3.8	+2.5	—1.3	+1.9	+2.0	+0.1	+3.3	+2.1	—1.2	+5.6	+4.4	—1.2	—0.2	+0.4	+0.6
1954															
I	+5.0	+2.7	—2.3	+1.6	+1.3	—0.3	+0.4	+2.2	+1.8	+2.6	+2.1	—0.5	+3.7	+1.6	—2.1
II	+3.8	+1.6	—2.2	—0.6	+0.1	+0.7	+2.5	+1.5	—1.0	+2.0	—0.8	—2.8	—0.9	—0.7	+0.2
III	0.0	+2.1	+2.1	0.0	—0.8	—0.8	+2.0	+0.8	—1.2	+1.6	+0.5	—1.1	+0.6	—0.2	—0.8
1955															
I	—1.1	+0.2	+1.3	—3.3	—6.0	—2.7	—1.8	+1.6	+3.4	—2.5	0.0	+2.5	+1.3	+0.6	—0.7
II	—0.9	+2.6	+3.5	+2.0	—0.8	—2.8	—1.0	+1.6	+2.6	+0.2	+3.5	+3.3	—2.2	+0.5	+2.7
III	—3.0	—2.0	+1.0	—0.6	+0.7	+1.3	—1.0	—0.5	+0.5	—2.3	—1.9	+0.4	0.0	—1.0	—1.0
1956															
I	+0.4	—0.8	—1.2	—2.4	+0.3	+2.7	+0.6	0.0	—0.6	+1.3	—2.9	—4.2	+2.7	—0.9	—3.6
II	+0.3	+1.4	+1.1	+2.7	+0.8	—1.9	—1.0	+0.1	+1.1	—0.5	0.0	+0.5	—3.4	—1.9	+1.5
III	—0.7	+2.4	+3.1	+0.6	—1.8	—2.4	+1.2	+1.7	+0.5	—0.2	+2.0	+2.2	—0.3	+0.5	+0.8
1957															
I	+1.9	+1.4	—0.5	+0.2	+1.2	+1.0	—0.5	+0.1	+0.6	+2.5	+1.4	—1.1	+0.7	+1.6	+0.9
II	—0.8	+0.2	+1.0	+2.7	—0.5	—3.2	—2.6	0.0	+2.6	—0.6	+0.2	+0.8	—3.1	+0.7	+3.8
III	—0.6	+0.4	+1.0	+0.6	—0.9	—1.5	—0.2	—1.1	—0.9	—0.6	+1.1	+1.7	—1.2	0.0	+1.2
1958															
I	+2.7	—0.2	—2.9	—0.7	+2.2	+2.9	—0.1	—4.2	—4.1	+2.3	+2.8	+0.5	+1.5	—2.4	—3.9
II	—2.0	—0.9	+1.1	+1.7	+2.1	+0.4	—2.3	—2.2	+0.1	+0.2	—1.2	—1.4	—1.7	—1.9	—0.2

1959															
I	+1.6°	—0.4°	—2.0°	+0.1°	+2.1°	+2.0°	+2.8°	—0.9°	—3.7°	+1.1°	+0.5°	—0.6°	+3.1°	0.0°	—3.1°
II	—2.1	+0.2	+2.3	—1.0	+1.1	+2.1	—0.2	+0.6	+0.8	—1.5	+2.2	+3.7	—2.4	+1.2	+3.6
III	—1.8	—1.0	+0.8	—4.1	—2.1	—2.0	+0.7	—0.3	—1.0	—2.7	—0.3	+2.4	+2.6	+1.7	—0.9
1960															
I	+1.7			—2.0			—0.6			+2.4			+0.8		
II	—2.3			+2.1			—2.4			+1.4			—1.4		
III	—0.6			—0.4			+0.3			—0.2			+2.4		
1961															
I	+2.1			—1.8			+1.2			+1.6			+1.8		
II	+2.8			+2.8			+1.6			+1.9			—2.1		
III	+1.3			—1.6			—0.2			—1.0			+1.6		
1962															
I	+2.2			—3.3			+0.2			—0.4			+3.2		
II	+0.2			+1.0			—1.8			—0.4			—3.0		
III	—2.1			+0.8			—0.9			—0.4			—1.2		
1963															
I	+0.4			—0.6			—0.8			—1.0			—1.2		
II	+1.2			+3.7			—3.1			—0.6			—2.6		
III	—2.5			+1.4			—1.5			+0.6			—1.0		
1964															
I	+1.8			—2.1			+3.6			+1.6			—0.8		
II	+1.2			+1.0			—0.9			+4.3			0.0		
III	+0.9			—0.1			+1.4			+1.2			+0.7		
1965															
I	+0.9			—2.6			+0.6			—1.3			+3.9		
II	—1.6			+0.9			—1.4			—2.4			—2.2		
III	—2.6			+2.1			—1.8			—2.2			—1.0		
1966															
I	—1.2			—1.8			+0.8			—0.5			+2.6		
II	—0.4			+2.8			+0.6			—0.3			—1.4		
III	+0.2			—1.0			—0.3			+0.7			+0.1		
1967															
I	—2.6			—0.2			+0.3			+0.8			+0.9		
II	—0.4			+3.6			—2.7			—0.3			—2.1		
III	—1.7			—2.3			—1.0			0.0			+0.1		

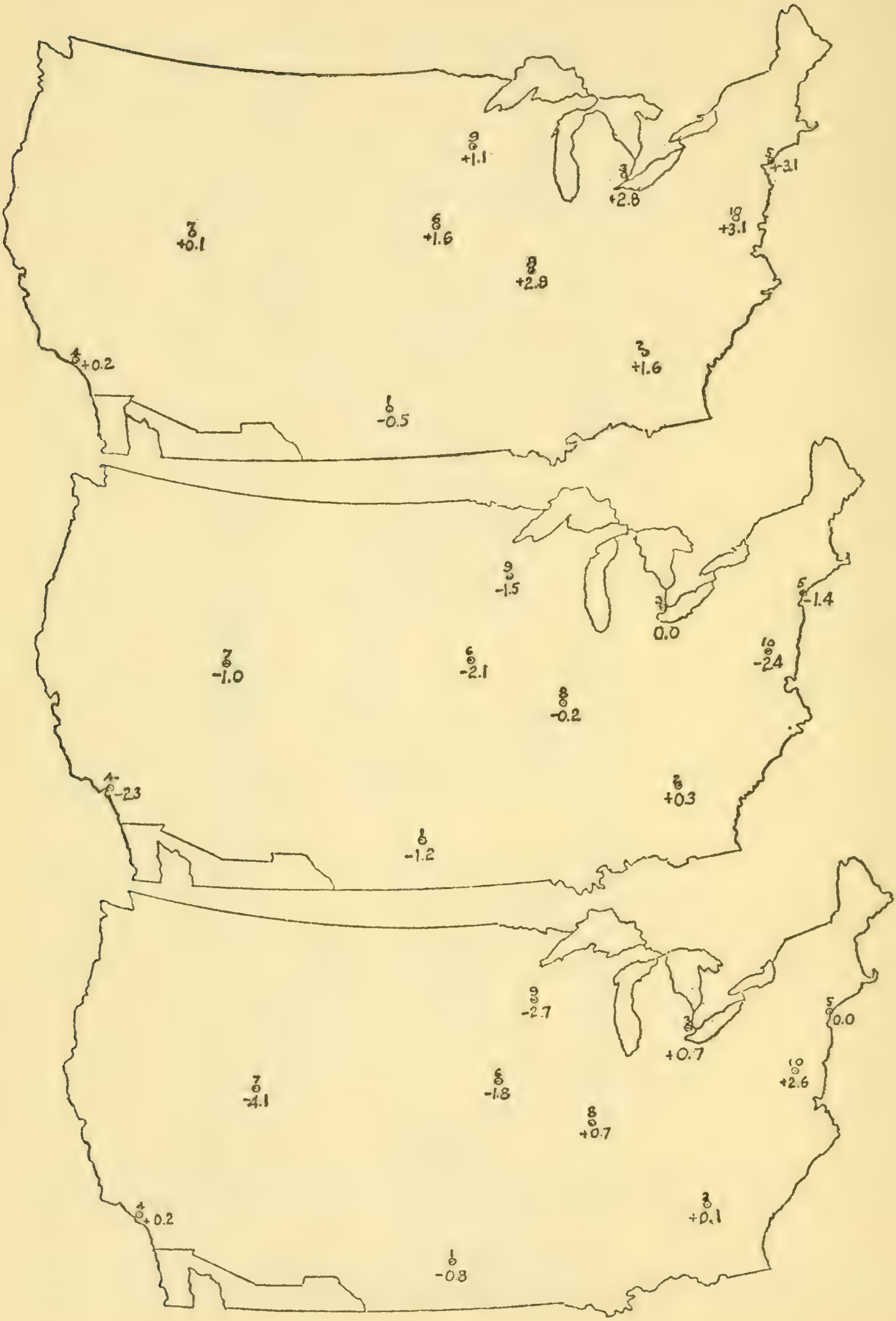
TABLE 7.—*Four-month means of forecast, 1950 through 1958, summed separately, plus and minus, and compared regarding mean algebraic and arithmetical values*

+	−	$\Delta \div 30 = a$		$\Sigma \div 30 = b$		+	−	$\Delta \div 30 = a$		$\Sigma \div 30 = b$	
		Abilene, Tex.						*Omaha, Nebr.*			
21.8°	20.1°	+1.7°	0.06°	41.9°	±1.4°	30.9°	25.5°	+5.4°	0.18°	56.4°	±1.9°
		Atlanta, Ga.						*Salt Lake City, Utah*			
19.6	19.6	0.0	0.00	39.2	±1.3	22.2	26.0	−3.8	0.13	48.2	±1.6
		Detroit, Mich.						*St. Louis, Mo.*			
25.7	24.2	+1.5	0.05	49.9	±1.6	25.5	22.8	+2.7	0.09	48.3	±1.6
		Los Angeles, Calif.						*St. Paul, Minn.*			
19.2	13.7	+5.5	0.18	32.9	±1.1	24.6	26.2	−1.6	0.05	50.8	±1.7
		New York, N. Y.						*Washington, D. C.*			
22.1	24.0	−1.9	0.06	46.1	±1.5	26.2	22.6	+3.6	0.12	48.8	±1.6
		Mean, $\frac{\Sigma a}{10} = +0.03$						Mean, $\frac{\Sigma b}{10} = +1.5$			

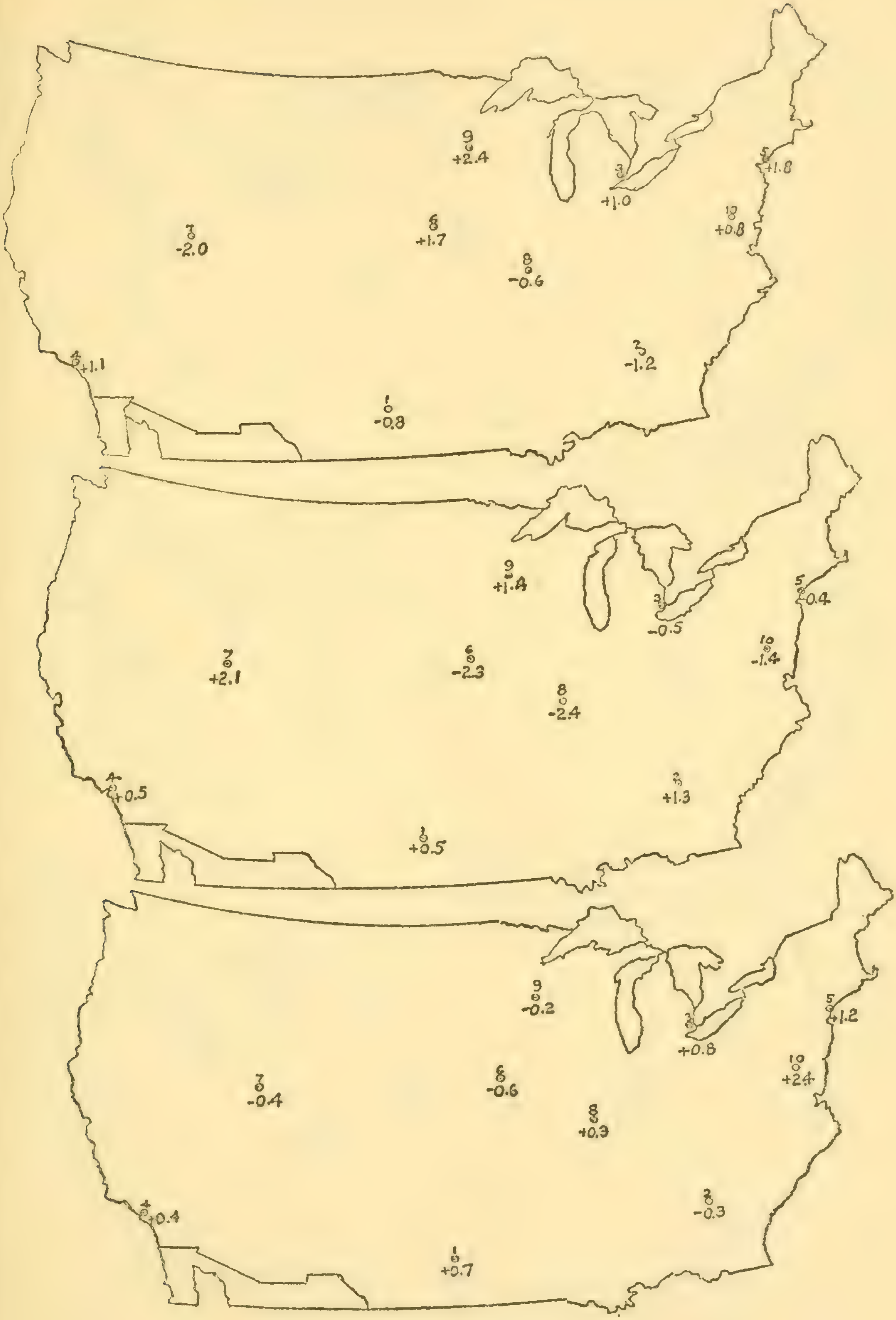
TABLE 8.—*The same and opposite signs of percentages of departure from normal of forecasts and events, 1950 through 1959*

	Percent same	Percent opposite		Percent same	Percent opposite
Abilene, Tex., 1	70	30	Omaha, Nebr., 6	60	40
Atlanta, Ga., 2	61	39	Salt Lake City, Utah, 7	67	33
Detroit, Mich., 3	61	39	St. Louis, Mo., 8	63	37
Los Angeles, Calif. 4	60	40	St. Paul, Minn., 9	68	32
New York, N. Y., 5	56	44	Washington, D. C., 10	64	36

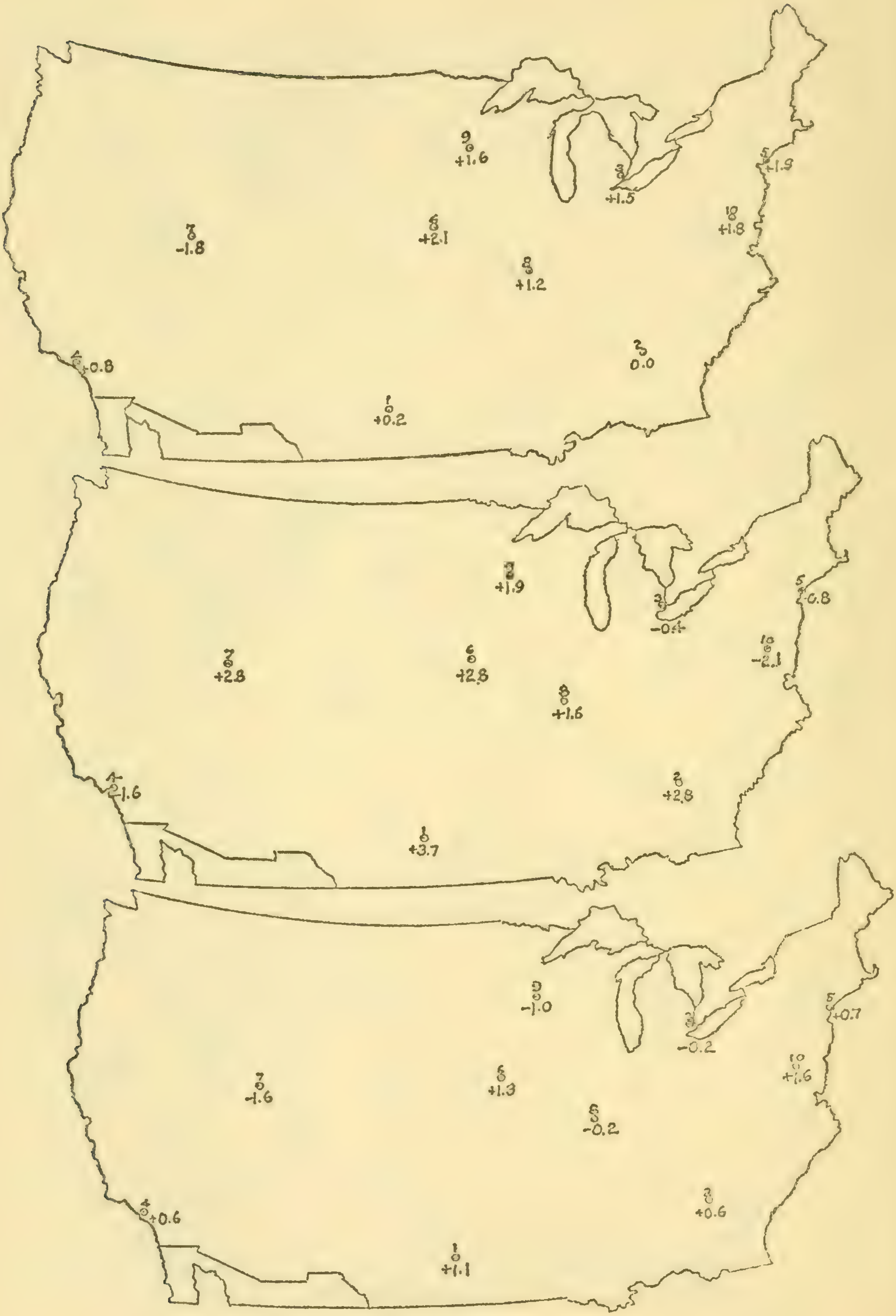
Means: Same 63, opposite 37.


9
+1.1
3
+2.8
5
+3.1
7
+0.1
6
+1.6
10
+3.1
8
+2.8
4
+0.2
3
+1.6
1
-0.5
9
-1.5
3
0.0
5
-1.4
7
-1.0
6
-2.1
10
-2.4
8
-0.2
4
-2.3
2
+0.3
1
-1.2
9
-2.7
3
+0.7
5
0.0
10
+2.6
7
-4.1
6
-1.8
8
+0.7
4
+0.2
3
+0.1
1
-0.8

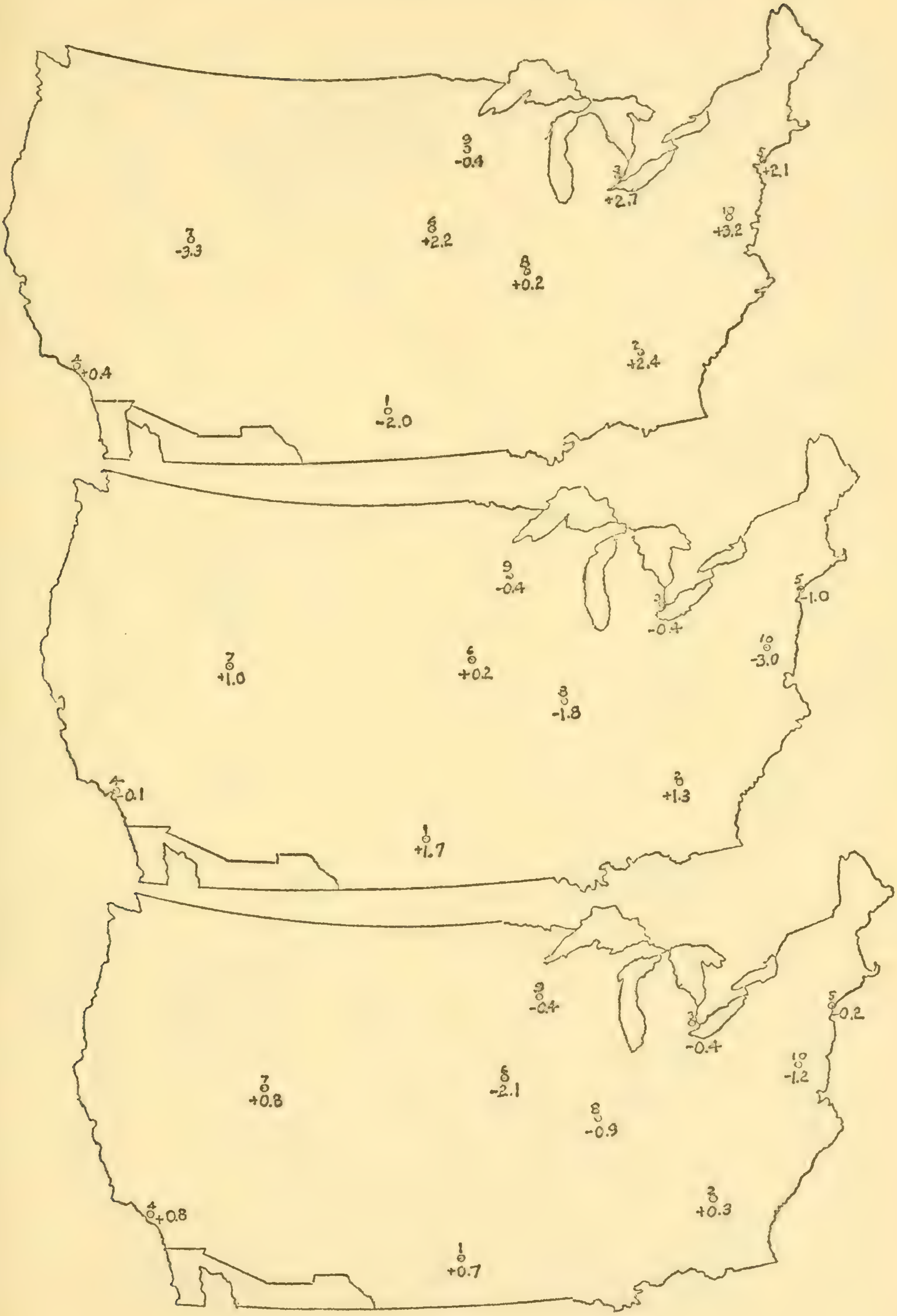
1959


9 +2.4
3 +1.0
5 +1.8
10 +0.8
7 -2.0
6 +1.7
8 -0.6
4 +1.1
2 -1.2
1 -0.8
9 +1.4
3 -0.5
5 0.4
10 -1.4
7 +2.1
6 -2.3
8 -2.4
4 +0.5
2 +1.3
1 +0.5
9 -0.2
3 +0.8
5 +1.2
10 +2.4
7 -0.4
6 -0.6
8 +0.3
4 +0.4
2 -0.3
1 +0.7

1960


9
+1.6
3
+1.5
5
+1.9
10
+1.8
7
-1.8
6
+2.1
8
+1.2
4
+0.8
2
0.0
1
+0.2
9
+1.9
3
-0.4
5
-0.8
10
-2.1
7
+2.8
6
+2.8
8
+1.6
4
-1.6
2
+2.8
1
+3.7
9
-1.0
3
-0.2
5
+0.7
10
+1.6
7
-1.6
6
+1.3
8
-0.2
4
+0.6
2
+0.6
1
+1.1

1961


9
-0.4
3
+2.7
5
+2.1
10
+3.2
7
-3.3
6
+2.2
8
+0.2
2
+2.4
4
+0.4
1
-2.0
9
-0.4
5
-1.0
3
-0.4
10
-3.0
7
+1.0
6
+0.2
8
-1.8
2
+1.3
4
-0.1
1
+1.7
9
-0.4
5
-0.2
3
-0.4
10
-1.2
7
+0.8
6
-2.1
8
-0.9
2
+0.3
4
+0.8
1
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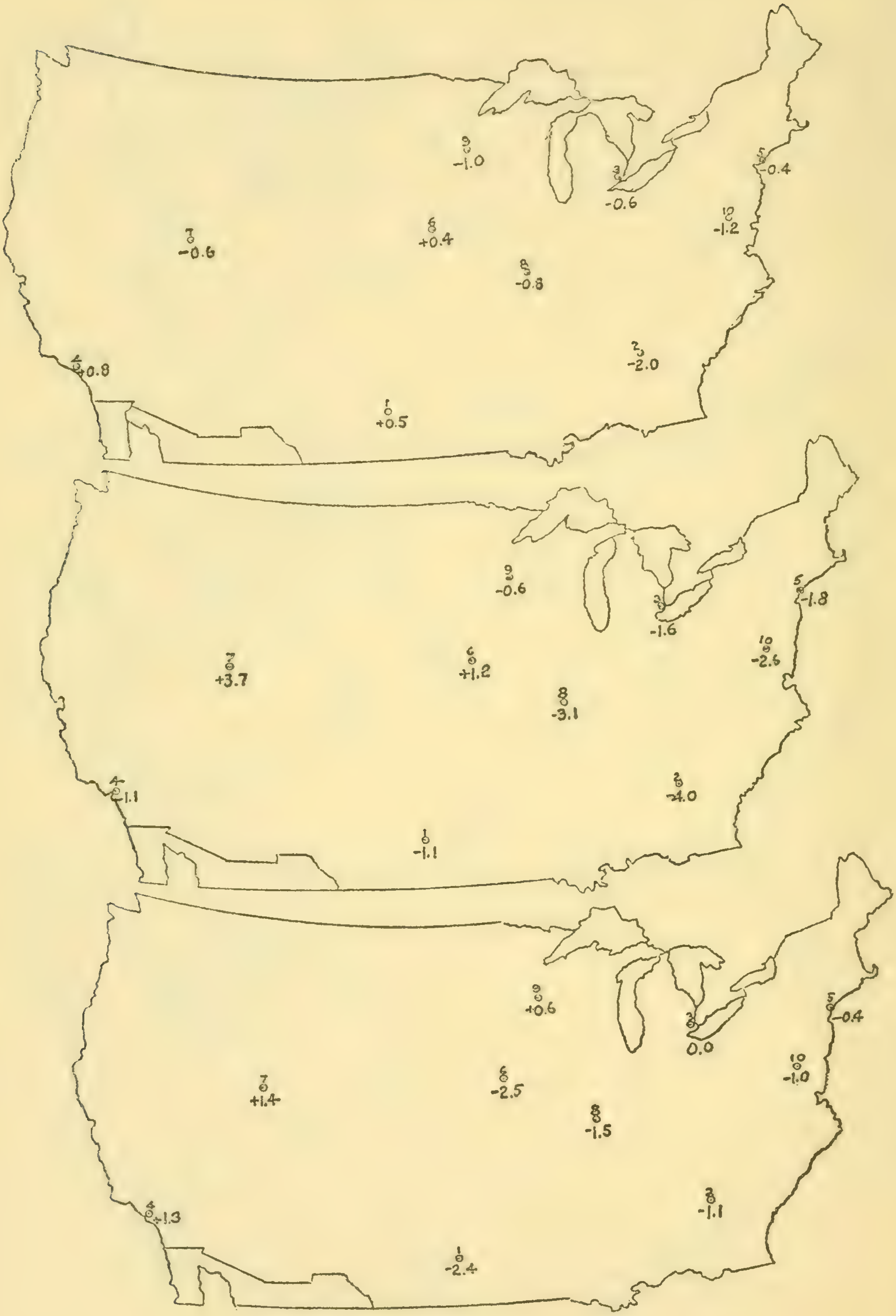
1962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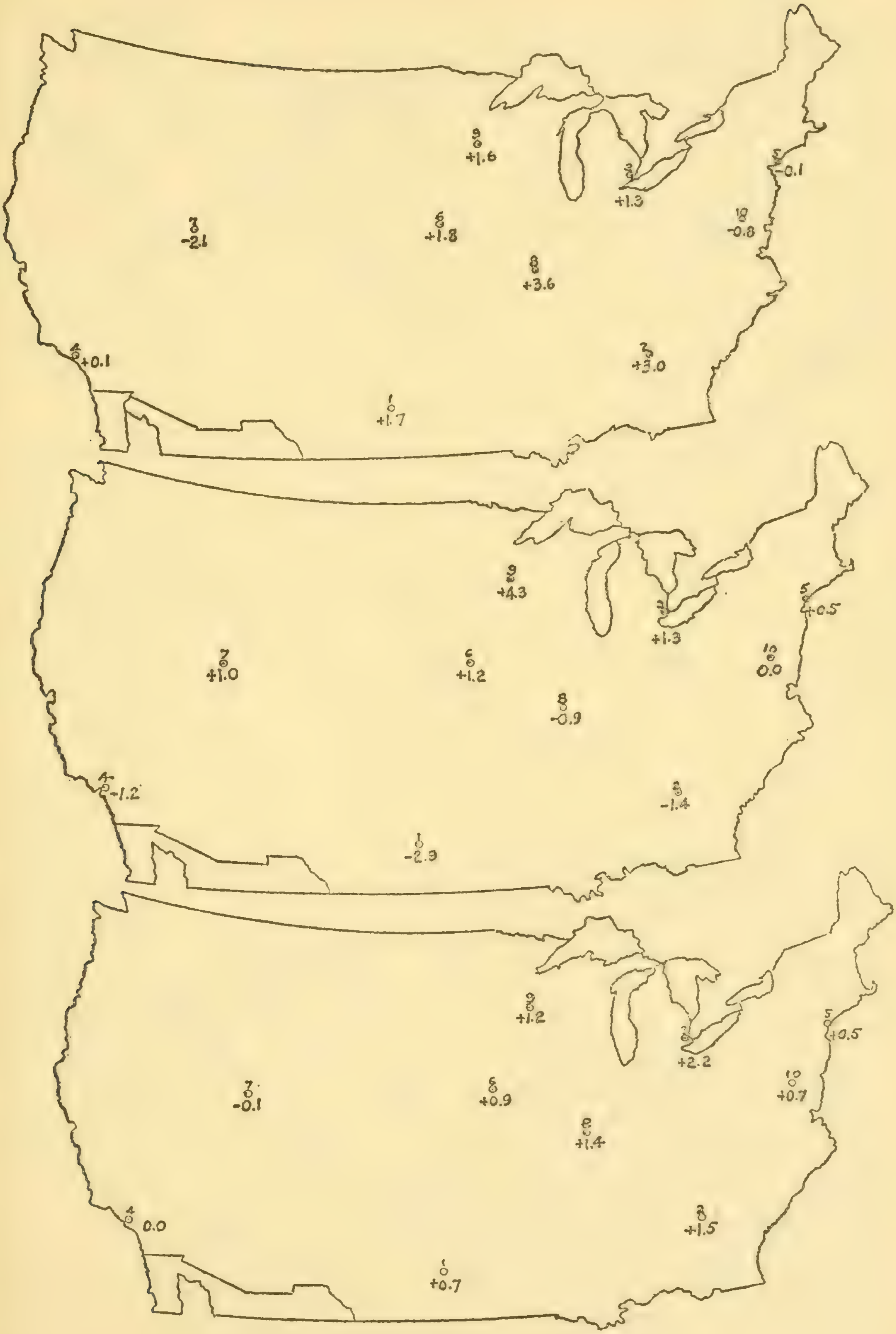
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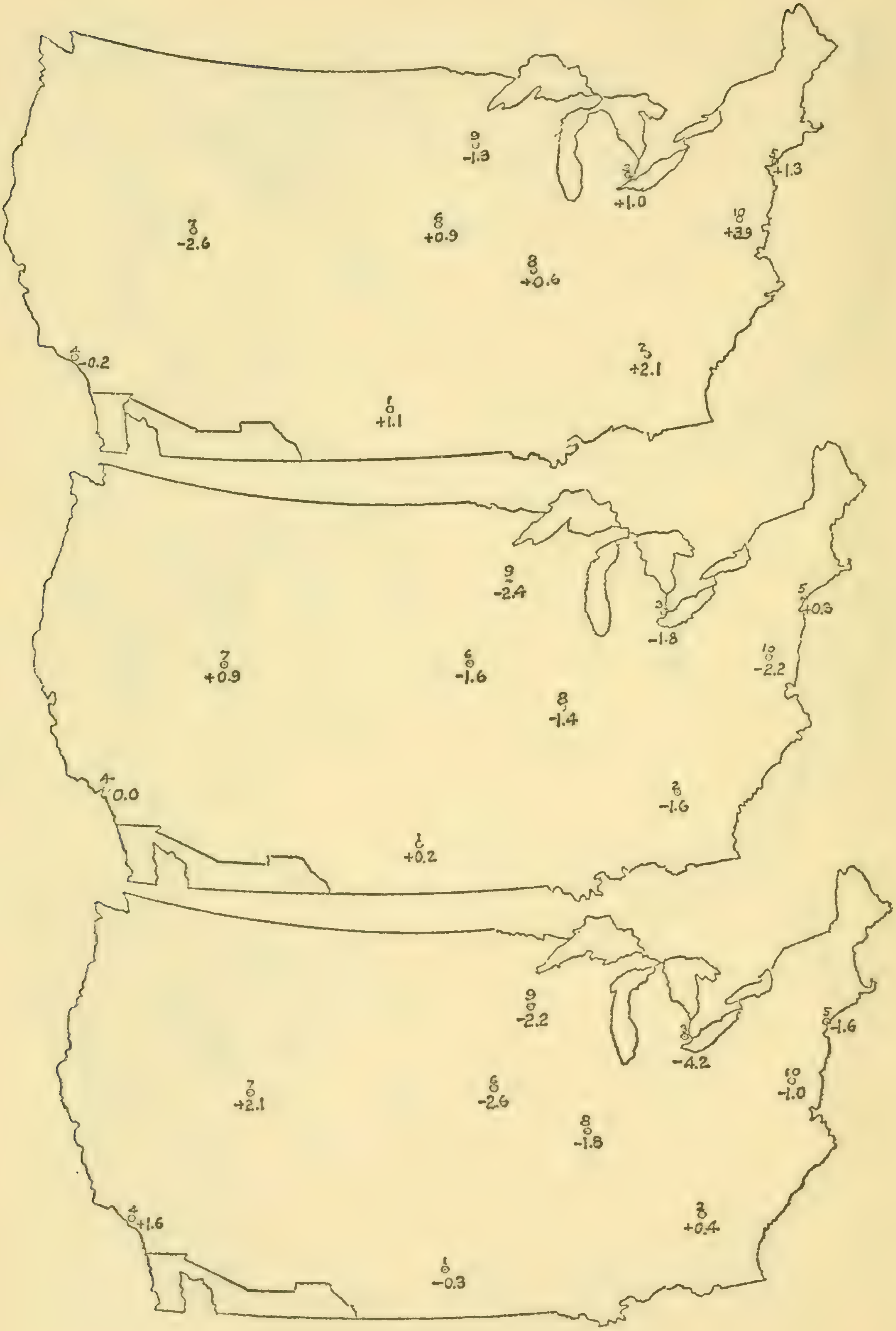
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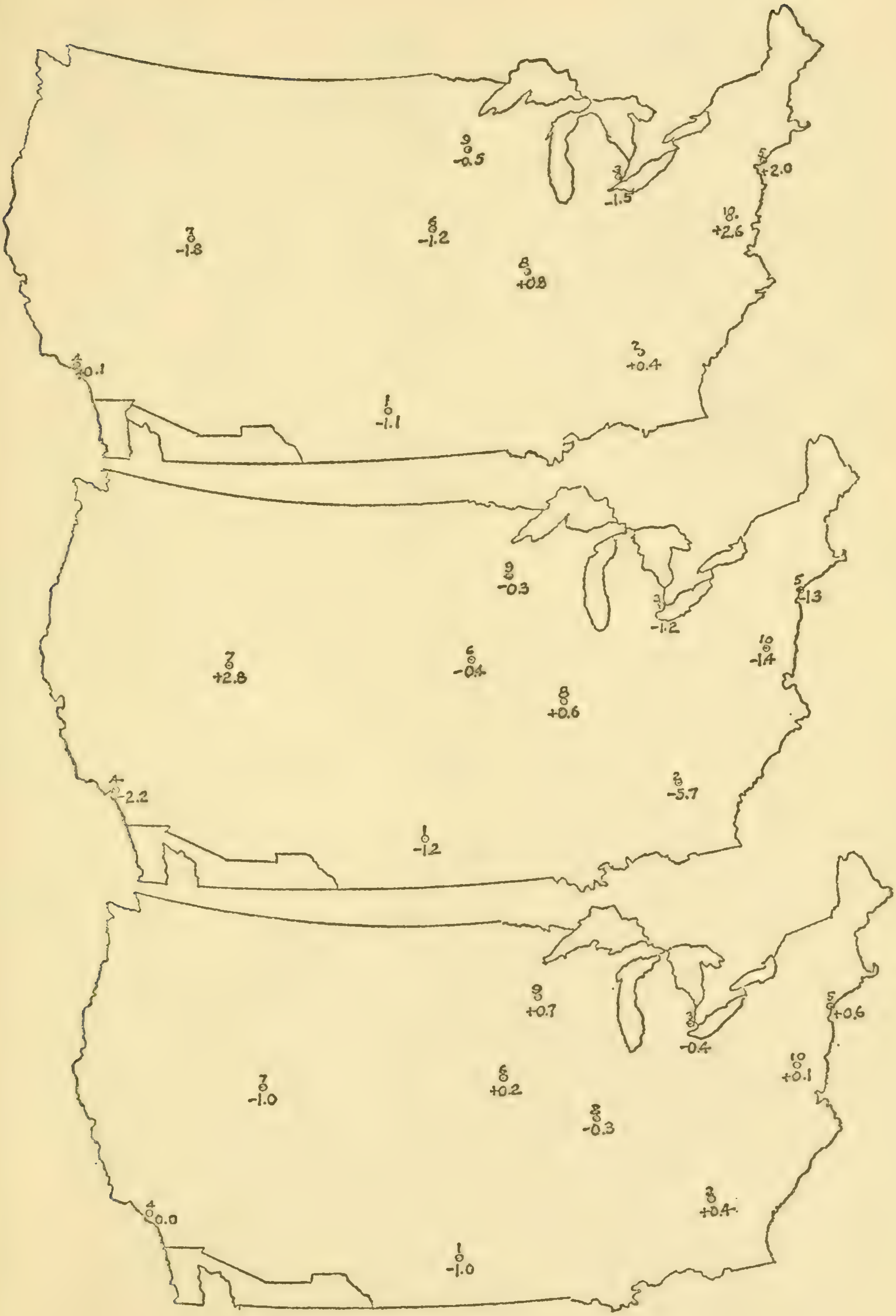
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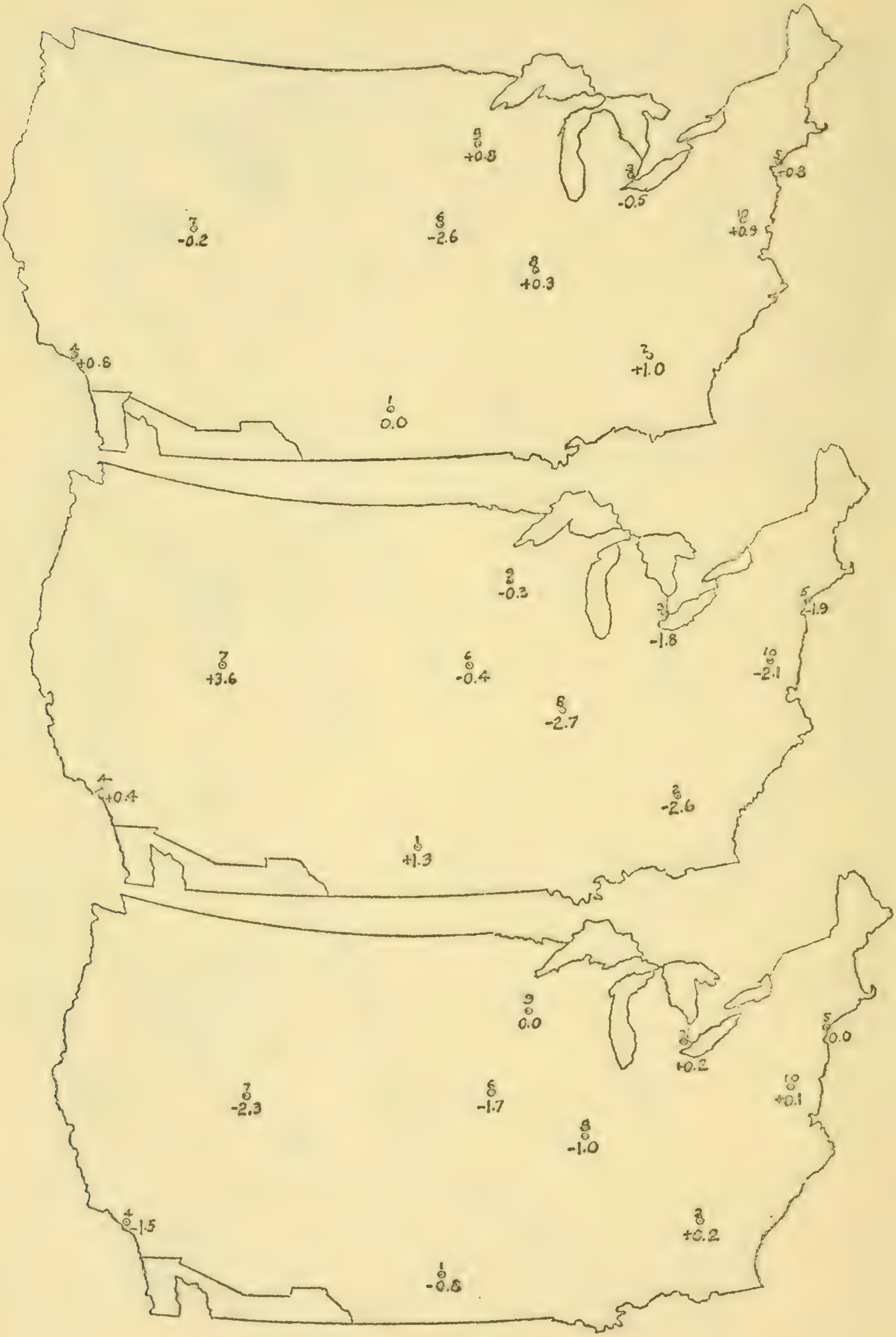
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SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 143, NUMBER 6

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By
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Research Associate
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(Publication 4472)

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FIG. 1.—The celery caterpillar and butterfly, *Papilio polyxenus asterius* Stoll.

THE CATERPILLAR AND THE BUTTERFLY

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INTRODUCTION

The caterpillar and the butterfly are here given the title role because they are a familiar example of those insects in which the young differ so much from their parents that they must go through a reconstruction called a metamorphosis in order to attain their own adult form. So well known, in fact, is the apparent transformation of the wormlike caterpillar into the splendid winged butterfly, and so marvelous does it seem, that it has been taken as a symbol of human resurrection. In ancient Greek the human mind or soul was called *psyche,* and the same name was given to the butterfly, presumably the emancipated soul of the caterpillar. Though the process of resurrection is obscure, and the fact has perhaps not been fully demonstrated, we now know almost the whole story of how the caterpillar appears to become a butterfly. Furthermore, in recent years students of insect metamorphosis have given much attention to the role of hormones in controlling the life of the young insect and the development of the adult. In short, almost the whole of modern studies on insect metamorphosis has been devoted to understanding the change of the larval insect to the adult, or imago.

On the other hand, little attention has been given to the question as to how or why did the young moth or butterfly ever become such a thing as a caterpillar, a creature so different in every way from its parents. It would indeed be a wise butterfly that knows its own child, since probably it has no memory of its own youthful life as a caterpillar. Equally certain is it that the caterpillar has no idea that it will ever be a butterfly.

With most animals, including many insects, the young resemble their parents except in matters of immaturity. Consider the young grasshopper or the young cockroach—they differ from their parents principally in the incomplete development of their wings and the external genital organs. They have no need to fly since they live in the same habitat as their parents, have the same kind of mouth parts, and eat the same kind of food. There is no reason why the young of such insects should be radically different from their parents. They are able to develop gradually into the adult form. Many other insects are in the same class and go through life without any metamorphosis.

Let us suppose now that the adults of some other insects far back in the early days of their evolution adopted a way of feeding that depended on their ability to fly and became structurally adapted to obtaining a special kind of food. If the young of these insects had to inherit the new kind of feeding organs of their parents, being unable to fly, they would be left to starve and the species would die out. To prevent such a calamity the usual laws of heredity have somehow been set aside in such cases, allowing the young insect to undergo an evolution on its own part adapting it structurally to some suitable environment where it could live and grow to maturity. A good example is the dragonfly; the flightless young insect could not catch mosquitoes in the air as do its parents, so it took to the water where plenty of live food was available, and has become structurally so individualized that it now has no resemblance to its parents. Likewise the young mosquito without wings could not practice bloodsucking as does its mother, or the nectar-feeding of its father, so it also became aquatic and has been equipped for its own way of feeding in the water. Adult fleas are wingless, but they have substituted jumping legs for wings and are able to feed on the blood of vertebrate animals. The larval flea thus left where it was hatched has to make the best of the circumstances by feeding on whatever it can find, but its form and mouth parts are suitable to the life it has to lead. The wasps and the bees take care of their helpless larvae, but the young of insects deserted by their parents receive special attention from nature.

Most any of the lower insects undergo some changes at the last moult, such as the completion of the wings and the external genital organs, or a remodeling of the shape and proportions of the body. Such changes may be called "metamorphosis" in a literal sense, but they are merely the final stage of normal adult development. A true metamorphosis involves the discarding of specialized larval characters, which allows the completion of adult development, and differs in degree according to the degree of aberration of the young from the adult structure. Various cases might be cited in which the young insect differs from its parents only in some minor character of its own, which is discarded at the last moult.

A very simple example of metamorphosis due to juvenile specialization is seen in the cicada. The young nymph of the seventeen-year cicada (fig. 2 A) as compared with the adult is more elongate and cylindrical, with the front of the head strongly protruding and rounded, but it has a special juvenile feature in the form of the front legs. These legs are modified for burrowing during the underground life of the nymph, and later (B) for climbing when it comes out of the ground. The under surface of the femur is armed with strong teeth, the tibia is toothed at its end, and the slender, undivided tarsus is freely attached to its mesal surface. At the moult to the adult the cuticle of these larval legs is cast off, and the adult leg (C) appears in the typical mature form. The leg epidermis simply forms two kinds of legs, one for the nymph, the other for the imago, but the nymphal leg is a special adaptation for the nymph.

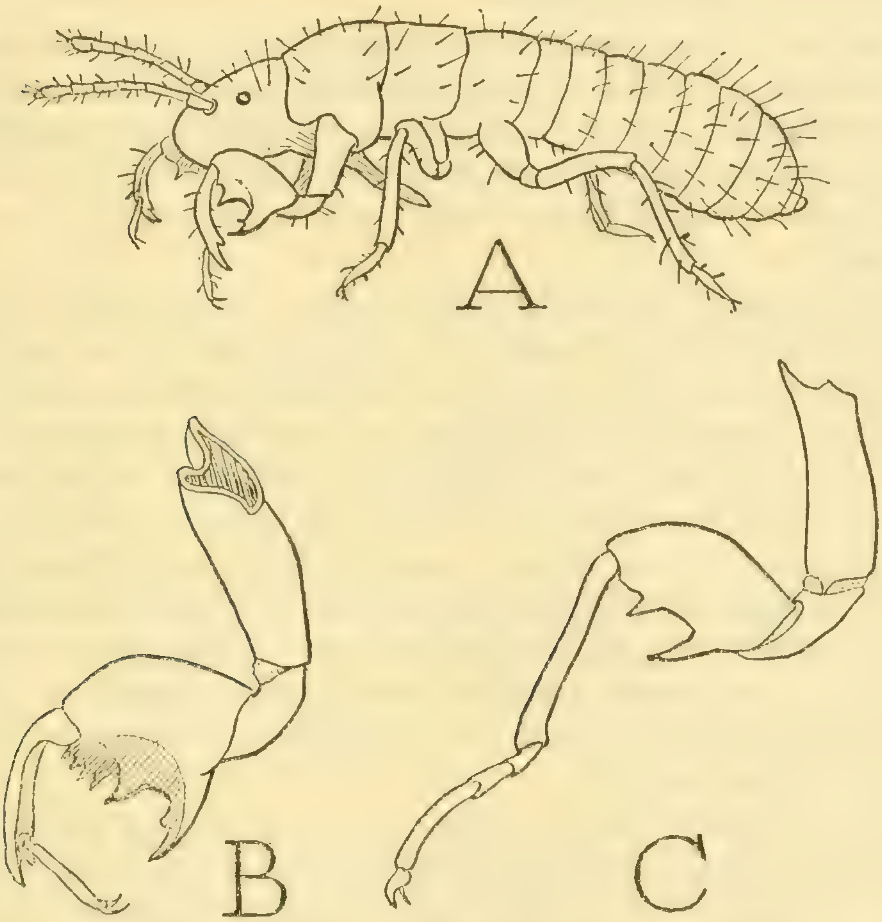

FIG. 2.—Young nymph of the seventeen-year cicada, and change in the front leg from nymph (B) to adult (C).

It would be interesting to know when and how the young cicadas first became adapted to underground life. With most insects of which the young have a special habitat, the female lays her eggs where the young will live. The female cicada, however, following the tradition of her race, inserts her eggs into the stems of trees, suggestive that formerly the young cicadas lived on the trees, as do young aphids and scale insects. At present, the young cicadas simply drop off the trees to the ground, a habit that may have been accidental at first, but gave a better chance of survival. Here, then, is a case where the young insects have deserted their parents, and fortunately became structurally adapted to a subterranean burrowing life. Also in the ground they were able to prolong their lives.

From the case of the cicada it is only a step, though perhaps a long one, to that of the dragonfly in which the young insect has become entirely different from its parents in adaptation to living and feeding in the water, but still it reverts to the adult structure at one moult. The same is true of some other insects, such as the mayflies and the stoneflies.

As this process of independent juvenile specialization is carried still farther in the higher insects, affecting not only the external form but the internal organs as well, many of the larval tissues and organs become so different from those of the adult that they have to be destroyed. The corresponding adult parts are then newly built up, in which case it can hardly be said that the larva is metamorphosed into the imago. It now becomes necessary for a reconstructive stage, or pupa, to intervene between the larva and the fully formed imago, which is liberated by a final moult. The insect is now said to be "holometabolous." The holometabolous insect becomes virtually two distinct animals separated by the pupa, in which one is broken down and the other newly constructed.

Now the question comes up as to how does one egg produce two individuals so different as the larva and the adult may be. This is probably a question for the geneticists to explain, but so far as known to the writer they have not done so. However, since gene mutations affect adult structures, they should produce modifications also in juvenile stages. If a mutation is beneficial to the adult, it can be preserved; when useful *only* to the young insect, it must be discarded at the moult to the imago, but restored to the next larval generation.

Experimentally it has been shown that the egg is potentially both larval and adult, but the fact does not explain how it has come to be so. We can surmise that the egg contains two sets of chromosomes or two kinds of genes, but how did this condition arise only in cases where the young insect could not lead the life of its parents and had to be given a form of its own? In the course of normal development the young animal naturally comes first, so in the case of double development the larval form, whatever it may be, precedes the adult. The larva is the direct development from the egg, but it carries the factors of adult development suppressed temporarily until the larva has completed its growth, which then allow the adult development to proceed.

It may be disputed whether the holometabolous insects represent one or several lines of descent. There is no modern larva that might plausibly be selected as of the type from which the others may have been evolved. Yet all holometabolous larvae have one feature in common, which is the internal development of the wings. Just what essential survival value the endopterous condition may have had is difficult to see, since the young of numerous other insects seem to get along very well with external wing pads. However, whatever may have been the form of the primary holometabolous larva, or why it became endopterous, it seems highly probable that external winglessness was a condition favorable for many potential habitats, and thus led to the great diversification of modern larval structure in adaptation to various ways of living. The association of the endopterous condition of the larva with holometabolism is probably because internal wing rudiments could become fully developed external wings only in a pupal stage.

Of all the holometabolous larvae, the lepidopterous caterpillar is structurally one of the most standardized. Though caterpillars differ in size and details of structure, they never depart from the fundamental caterpillar organization. By way of contrast consider the difference among the Diptera between a mosquito larva and the maggot of a muscoid fly, or in the Hymenoptera the contrast between a sawfly larva and the larva of a wasp or bee. Some function of the caterpillar has demanded a basic uniformity of structure in all species.

In conformity with the principle already discussed that the adult insect is responsible for the structure of the larva, we must look to the moth or butterfly to find the reason for the caterpillar.

EVOLUTION OF THE ADULT

The moths and butterflies are named Lepidoptera because of their scaly wings, but their scales do not make them what they are, any more than do the bright colors that many of them wear. The mosquito has scales on its wings, and some moths have clear wings. The typical lepidopteron is distinguished from all other insects by the possession of a tubular, nonpiercing, maxillary proboscis, coiled beneath the head when not in use (fig. 3 E). The other mouth parts are much reduced or suppressed, and the proboscis limits the diet of the moth or butterfly to readily accessible liquids, which are mostly the nectar of flowers. This fact determines the essential structure not only of the adult lepidopteron, but that of the caterpillar as well. The intake of liquid food necessitates the possession of an efficient sucking apparatus connected with the alimentary canal, while the alimentary canal itself can be much simplified by comparison with that of an insect that feeds on solid food.

Butterflies, it is true, do not feed entirely on nectar; some are able to rasp fruit for the juice, others may suck up sap exuding from trees, or imbibe honeydew from aphids, and they have been seen apparently feeding on carrion and excreta. They all drink water. So far as known, the only digestive enzyme of adult Lepidoptera is invertase. Swingle (1928) reports the presence of only this enzyme in the oriental fruit moth, and in elaborate studies on digestion in various adult Lepidoptera Stober (1927) found no other digestive enzyme than invertase. It appears, therefore, that adult Lepidoptera can digest only cane sugar. When small quantities of starch, fat, or protein (blood) are mixed with their food, these substances, Stober says, remain unchanged in the stomach. Glucose, of course, can be absorbed as obtained in nature. Species with reduced mouth parts that do not feed as adults were found to have no digestive enzymes. It is not known what butterflies seen apparently feeding on carrion or excrement may get from such sources. Possibly the juices contain products of bacterial decomposition that can be directly absorbed as predigested food.

Inasmuch as a few modern moths have vestigial mandibles, there can be little question that present-day Lepidoptera are descended from adult progenitors that fed on solid food. Their adaptation for a liquid diet, therefore, must have been made when the early ancestors of the moths and butterflies renounced solid food for liquids. The proboscis is formed of the maxillary galeae, and is probably not a functional organ of great antiquity, since early stages of its evolution are still preserved in two primitive families, the Eriocraniidae and the Mnesarchaeidae. Except for one doubtful form, fossil Lepidoptera are not known much before the Eocene.

At the time when the Lepidoptera first appeared in evolution, the mutual relationship between flowers and insects had already been established. Flowers had bright colors and probably attractive odors, and their pollen formed a nutritious food for insects. Thus the plants fed the insects, and the insects pollinated the plants.

The Micropterygidae have long been regarded as a primitive lepidopterous family, but taxonomists now assign them to a separate order, the Zeugloptera (Chapman, 1917), which Hinton (1946) contends is more primitive even than the Trichoptera. However, whatever may be the correct classification of the micropterygids, their ancestors must have had some relation to the ancestors of the Lepidoptera, and their modern mouth parts may be taken as an approximate example of the feeding organs of the lepidopterous progenitors. The adult micropterygids have well-developed functional jawlike mandibles. The maxillae (fig. 3 A) are of generalized structure, each organ

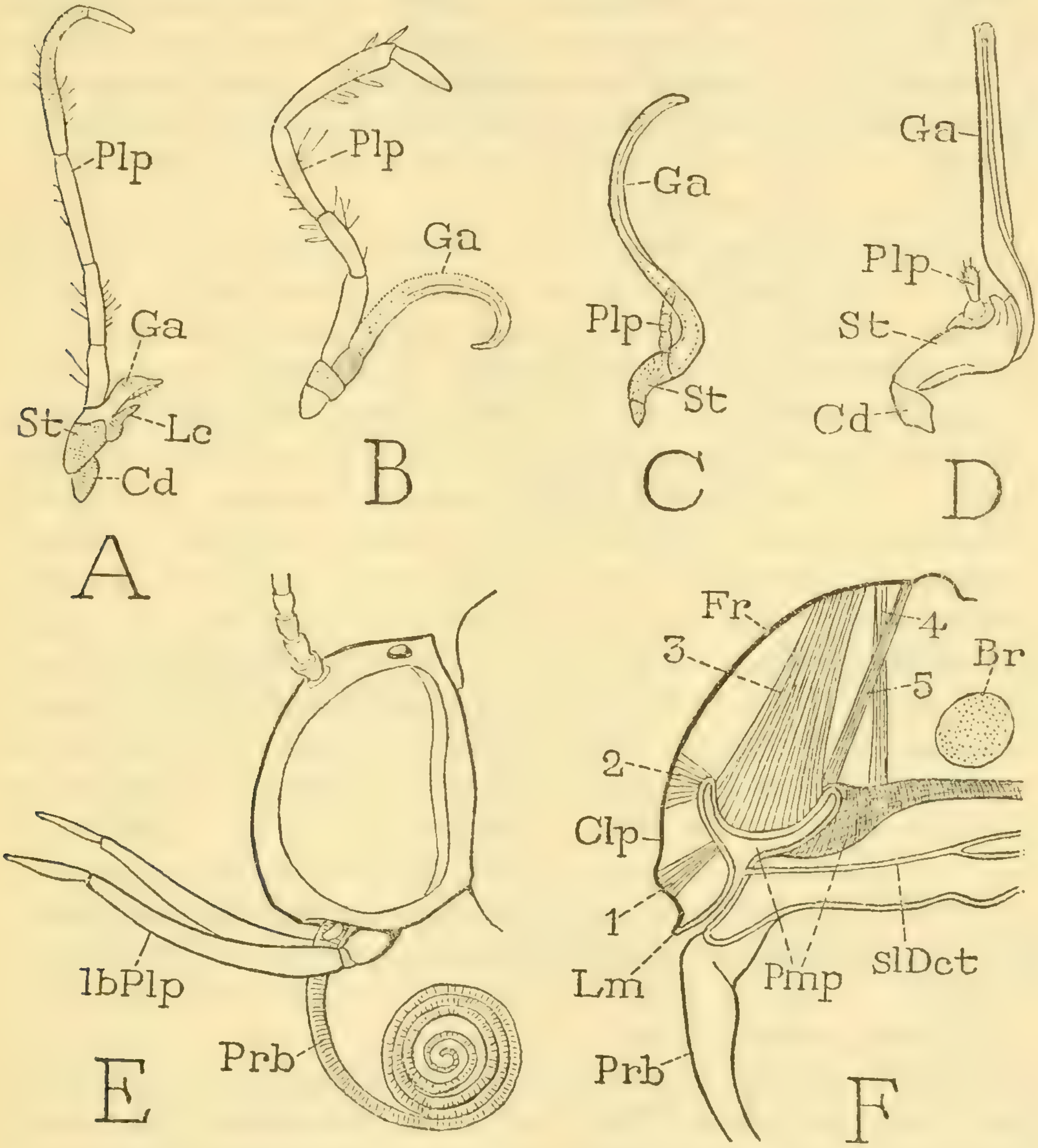

FIG. 3.—Evolution of the lepidopterous proboscis, and the sucking pump (A,B,C, from Tillyard, 1923).

A, Maxilla of *Micropteryx aruncella.* B, Maxilla of *Eriocrania semiperpurella.* C, Maxilla of *Mnesarchaea paracosma.* D, base of a typical, fully developed lepidopterous maxilla. E, Head of *Sanninoidea exitiosa.* F, Section of head of sphinx moth, diagrammatic, showing the sucking pump and its muscles.

having a small, simple lacinia and a galea, and a long 5-segmented palpus. A detailed comparative description of the mouth parts of several micropterygid species is given by Issiki (1931), but he says nothing of the food or feeding habits of the insects. According to Tillyard (1923) the mandibles of *Sabatinca* "work in conjunction with the epipharyngeal and hypopharyngeal brushes and the triturating basket of the hypopharynx as grinders of the minute pollen grains or other fine vegetable matter which form the food of the imago." Hannemann (1956) says the long flexible maxillary palpi are used for bringing the food into the mouth.

If the mandibulate progenitors of the Lepidoptera fed on pollen, they had easy access to nectar, their problem being how to obtain it from the depth of the flower corollas. If, then, some fortunate mutation happened to lengthen the maxillary galeae, the latter may have enabled their possessors to get a taste of nectar. The next step in the evolution of a maxillary proboscis is seen in the modern Eriocraniidae, in which the galea of each maxilla is much elongated, curved, and grooved on its inner surface (fig. 3 B), while the lacinia is entirely suppressed. According to Busck and Böving (1914) in *Mnemonica auricyania* the galeae have marginal serrations that serve to connect them with each other. In the Mnesarchaeidae the galeae are still more lengthened (C), and the maxillary palpi are reduced to three small segments. From the condition in these two primitive lepidopterous families it is but another step in the same direction to the long, coiled proboscis typical of the other Lepidoptera (fig. 3 E), in which the base of the maxilla (D) retains the form it has in the eriocraniids. Along with the development of the proboscis the mandibles underwent a reduction until they became functionless vestiges or disappeared altogether. From an early stage in their evolution, therefore, the Lepidoptera became entirely liquid feeders.

The fully developed proboscis of modern Lepidoptera is a truly remarkable instrument. When not in use it remains tightly coiled beneath the head, but it can be straightened out to its full length for insertion into flowers to serve as a nectar conduit. A detailed study of the structure and mechanism of the proboscis of *Pieris brassicae* has been made by Eastham and Eassa (1955), in which they critically review and correct certain ideas on how the proboscis works expressed by earlier writers.

A proboscis alone could not serve for the ingestion of liquid food; a sucking apparatus must have been developed along with the evolution of the proboscis. In *Micropteryx* it is shown by Hannemann (1956) that the slender oesophagus opens directly from the preoral cavity and that there is no pharyngeal dilatation. All Lepidoptera that feed in the adult stage, however, are provided with a sucking pump in the head connected with the base of the proboscis and continuous into the oesophagus. In a comparative study of the pump, Schmitt (1938) shows that the organ varies somewhat in size and structure in different species, but is always operated by two sets of dilator muscles separated by the frontal ganglion and its brain connectives. The preganglion muscles arise on the clypeal region of the head, the postganglion muscles on the frontal region. The lepidopterous food pump, therefore, is a combination of the preoral cibarium and the postoral pharynx. The same type of pump is described by Srivastava (1957) in *Papilio demoleus,* and is strongly developed in the sphinx moth (fig. 3 F, *Pmp*). Its principal dilator muscles (*3,4,5*) arise on the frons (*Fr*) and are therefore pharyngeal, the anterior muscles (*1,2*) arising on the clypeal region (*Clp*) are cibarial. The sucking pump of the honey bee is also cibario-pharyngeal, but in most sucking insects the pump is entirely cibarial.

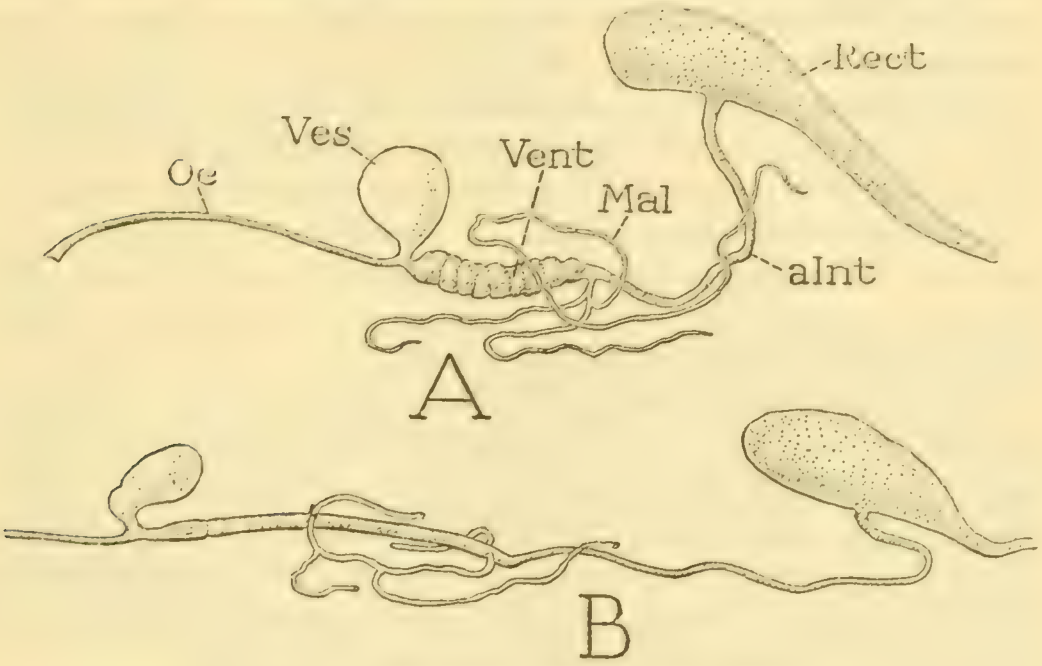

FIG. 4.—Alimentary canal of adult moths.

A, *Malacosoma americanum.* B, *Sanninoidea exitiosa.*
aInt, anterior intestine; *Mal,* Malpighian tubules (not shown full length); *Oe,* oesophagus; *Rect,* rectum; *Vent,* ventriculus; *Ves,* oesophageal vesicle.

In contrast to the highly developed sucking apparatus, the alimentary canal of adult Lepidoptera is much simplified, as might be expected of a nectar-feeding insect. In the moth of the tent caterpillar (fig. 4 A), for example, the oesophagus (*Oe*) is a long slender tube traversing the thorax from the sucking pump in the head to the anterior part of the abdomen, where it joins the stomach, or ventriculus (*Vent*). Just before the stomach the oesophagus bears dorsally a diverticulum in the form of a thin-walled vesicle (*Ves*), which has been supposed to be a reservoir for liquid food, but generally it is found to contain air. The very short ventriculus has no caeca, and its walls are thrown into circular folds. Following the ventriculus is a long, slender intestinal tube (*aInt*), which opens into the under side of a large rectal sac (*Rect*). In a peach borer moth (B) the alimentary canal is an even more slender tube, except for the oesophageal diverticulum and the rectal sac. The alimentary canal of the monarch butterfly *Danais plexippus,* as described by Burgess (1880) under the name *archippus,* and recently figured by Ehrlich and Davidson (1961) differs in no essential way from that of the moths, though the oesophageal diverticulum is half or two-thirds the length of the abdomen. According to Burgess the delicate walls of the diverticulum are well supplied with slender longitudinal and transverse muscle fibers, but the sac contains nothing but air.

Long coiled glands opening by a common duct at the base of the labium have been described or figured in various adult Lepidoptera (see Schmitt, 1938; Srivastava, 1957; Ehrlich and Davidson, 1961). These glands have replaced the larval silk glands, and are presumably salivary in function. In the honey bee larva the silk glands completely break down after spinning, and the salivary glands of the adult are regenerated from anterior remnants of the larval ducts.

The Malpighian tubules arise from the anterior end of the intestine as a pair of tubes varying in length, in some species swollen into bladderlike vesicles. Each primary tubule divides into two, and usually one of these again divides, giving three tubules in all on each side. The tubules may form a tangled mass around the stomach and the intestine, and in some species at least their posterior ends are inserted beneath the muscular coat of the rectum.

It is clear that the basic specialization of adult Lepidoptera is a structural adaptation for feeding on nectar contained in the depths of flower corollas. That sugars are their only food is evident from their lack of digestive enzymes other than invertase. Though nectar was formerly a favorite drink of the gods, it must be a very inadequate diet even for a moth or butterfly. The female at least needs proteins for the production of yolk-filled eggs. Hence it should be the duty of the caterpillar to store up food reserves in its body to supplement its diet in its own adult stage. The tent caterpillar moth, *Malacosoma americanum,* is a species that takes no food in the adult stage, but the ovaries are fully stocked with ripe eggs on emergence of the female, ready to be laid as soon as fertlized. In this case the egg-forming material must have been received from the caterpillar. The lepidopterous caterpillar, therefore, should be a larva primarily constructed for the function of general feeding. According to Stober (1927) it is provided with enzymes for the digestion of sugar, starches, fats, and proteins. Babers and Woke (1937) report that digestive enzymes of the southern armyworm include amylase, maltase, glycogenase, invertase, rennin, lipase, trypsin, and erepsin. The caterpillar is thus evidently equipped to handle any kind of food. It is the dietetic limitation of the adult, therefore, that has brought about the structure of the caterpillar, and the caterpillar is responsible for the life of the adult. An investigation of the caterpillar now will show just how well it has met its obligations.

THE CATERPILLAR

A typical modern caterpillar (fig. 5 A) has a long, soft, cylindrical body of 13 segments, and a sclerotized head. On each side of the head (B) is a group of six small simple eyes. The antennae (*Ant*) are very short, sometimes minute. The mandibles are strong biting-and-chewing jaws (F). On the under side of the head (C) the closely associated labium and maxillae form a prominent lobe containing the silk-spinning apparatus, which opens by a small tapering spinneret (*Spn*) at the end of the labium. The thoracic legs (A) are very short, but each has the usual six segments of an insect leg (D). The abdomen bears generally a series of short, paired, unsegmented appendages, known as *prolegs* (*PrL*), commonly present on segments *III-VI* and *X*.

It is always of interest to know something of the ancestry of any modern animal we are trying to understand, but we know nothing of the nature of the primitive lepidopterous larva. Larvae of the Micropterygidae (fig. 6 A,B) have been described and figured by Chapman (1894) and by Tillyard (1922). They look as much like caterpillars as anything else, and the well-developed mandibles could pass for those of a modern caterpillar. The antennae, however, are long and slender (B,C), and in place of prolegs the larvae have either minute points (A) or more slender processes on the first eight abdominal segments (B), each ending in a single curved claw (D). According to Hinton (1955), these organs lack muscles, and it is unlikely that they are prototypes of the lepidopterous prolegs. Some micropterygid larvae feed in the open and spin silken cocoons.

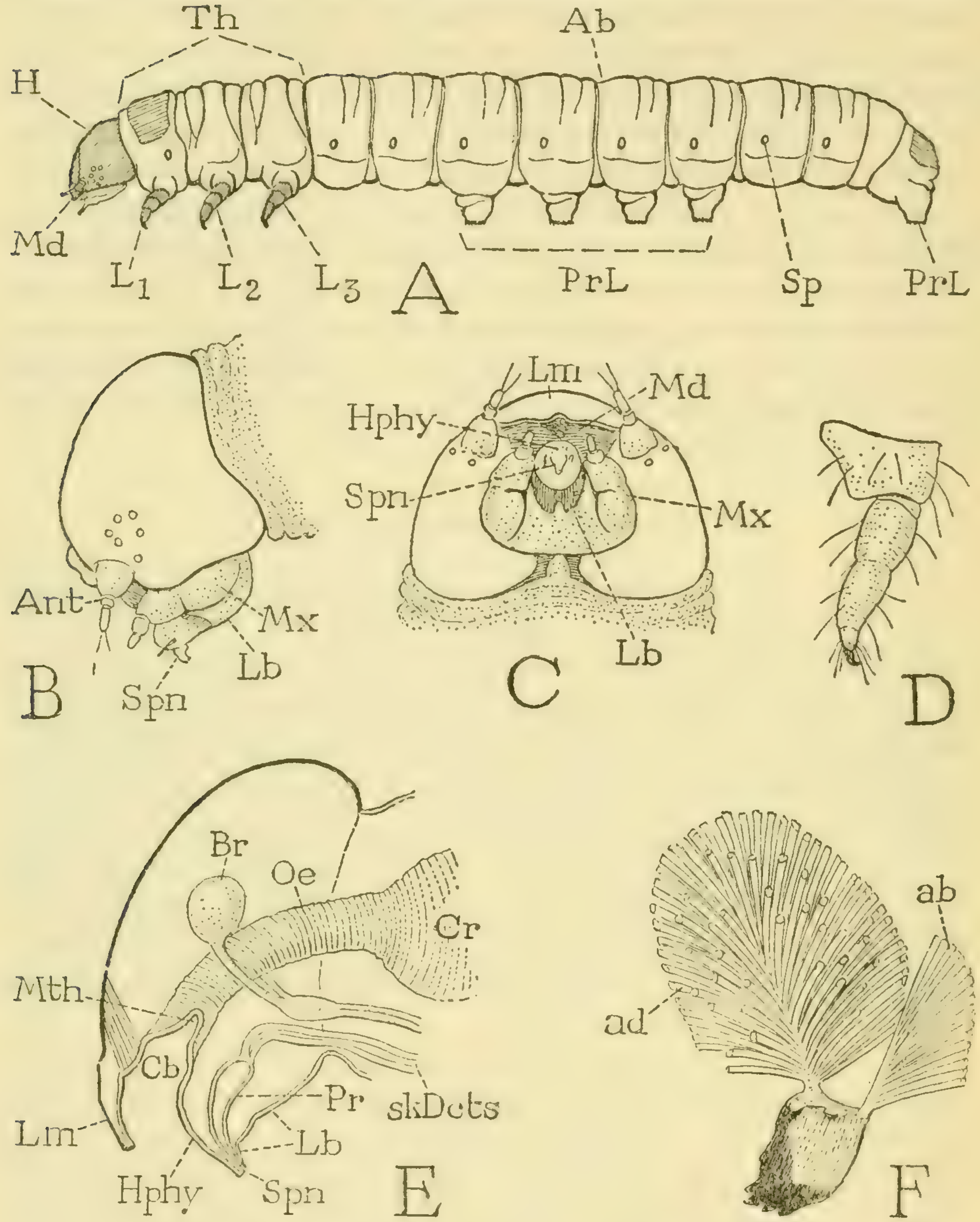

FIG. 5.—External features of a caterpillar.

A, Typical structure of a caterpillar. B, Head of a silkworm, lateral. C, Same, ventral. D, A thoracic leg. E, Longitudinal section of a caterpillar's head, diagrammatic, showing united hypopharynx and labium enclosing the silk press (salivarium). F, Left mandible and muscles of a tomatoworm, anterior.

Ab, abdomen; *ab*, abductor muscle; *ad*, adductor muscle; *Ant*, antenna; *H*, head; *Hphy*, hypopharynx; *L*, thoracic leg; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *PrL*, prolegs; *Sp*, spiracle; *Spn*, spinneret; *Th*, thorax.

A larva of the primitive lepidopterous family Eriocraniidae, *Mnemonica auricyania* (fig. 6 E), as shown by Busck and Böving (1914), has a small head and a simple tapering body of 13 segments, but being a leaf miner it lacks both thoracic and abdominal legs. It is in the Hepialidae that we first encounter a typical caterpillar (F), though in this case a stem borer.

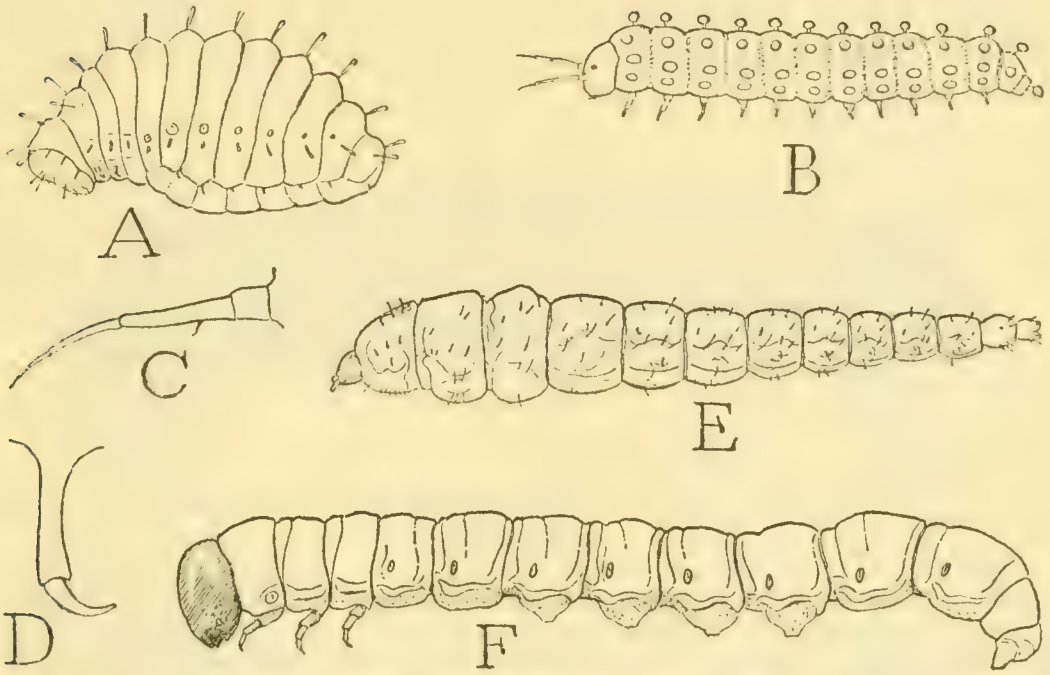

FIG. 6.—Larvae of Micropterygidae and lower Lepidoptera. (A, from Tillyard, 1922; B,C,D, from Chapman, 1894; E, from Busck and Böving, 1914.)

A, *Sabatinca barbarica* (Micropterygidae). B, *Eriocephala calthella* (Micropterygidae). C, Same, antenna. D, Same, abdominal "proleg." E, *Mnemonica auricyanea* (Eriocraniidae). F, *Hepialus* sp. (Hepialidae).

To effectively perform its function of feeding, after the adult had adopted a nectar diet it was first necessary for the caterpillar to have strong biting-and-chewing mandibles, and these it inherited from its ancestors. At the same time it needed a stomach of a size capable of digesting a constant supply of leafy food, and this the modern caterpillar has. Descriptions of the alimentary canal of various caterpillar species may be found in the papers here cited by Bordas (1911), Peterson (1912), Stober (1927), Neiswander (1935), Woke (1941), El-Sawaf (1950), and Teotia and Pathak (1957).

The alimentary canal of a typical caterpillar almost fills the body (fig. 7). Beginning with the pharyngeal region (*Phy*) following the mouth (*Mth*) a narrow oesophagus (*Oe*) curves back through the head and in some species expands in the thorax into a huge, strongly muscular crop (*Cr*). The crop is followed by a long, thick stomach, or ventriculus (*Vent*), occupying half the length of the body, and its walls are thrown into circular folds that evidently allow of much expansion. The proctodaeum (*Proc*) is differentiated into a short pyloric section (*Py*) into which open the Malpighian tubules (*Mal*), a colon, or anterior intestine (*AInt*), and a large pear-shaped rectal sac (*Rect*). Clearly, the caterpillar did not inherit its alimentary canal from its parents (cf. fig. 4). It has been provided with a digestive system adequate to handle all the food it can eat, and there is no limit to its appetite. In a tent caterpillar with a full stomach (fig. 8 A) the latter (*Vent*) may extend from the thorax into the seventh segment of the abdomen. In an individual just after a meal (B) the crop (*Cr*) is expanded to a long sac more than twice its length before eating, and the stomach is correspondingly shortened. Crowell (1943) found that a measured amount of food goes through the alimentary canal of the fifth or sixth instar of the southern armyworm in about 3¼ hours. During resting periods the fore gut is cleared of solid food.

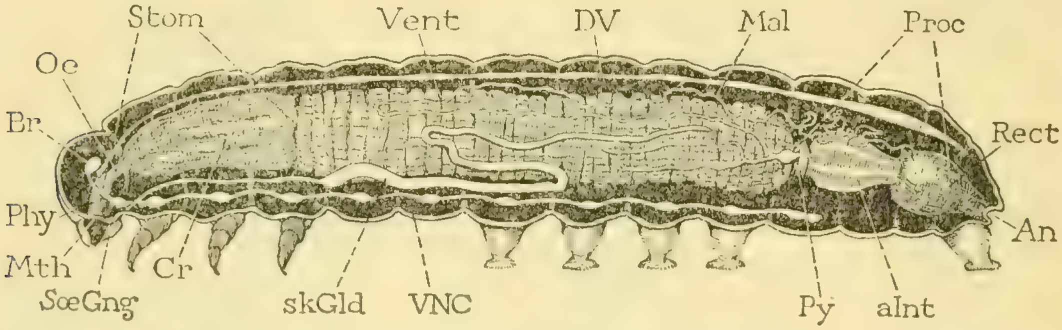

FIG. 7.—Internal organs of a caterpillar, except the fat tissue, exposed from the left side.

aInt, anterior intestine; *An,* anus; *Br,* brain; *Cr,* crop; *DV,* dorsal blood vessel; *Mal,* Malpighian tubules; *Mth,* mouth; *Oe,* oesophagus; *Phy,* pharynx; *Proc,* proctodaeum; *Py,* pylorus; *Rect,* rectum; *skGld,* silk gland; *SoeGng,* suboesophageal ganglion; *Stom,* stomodaeum; *Vent,* ventriculus (stomach); *VNC,* ventral nerve cord.

Experimental studies on the feeding reactions of caterpillars and their senses of smell and taste have been described by Dethier in a series of papers (1937, 1939, 1941a, 1941b). Odor is shown to be the principal factor by which a phytophagous caterpillar recognizes its food plant. The olfactory sense organs are on the terminal segments of the antennae and maxillae. The caterpillar's perception of odor is of very short range, but its head is always close to the feeding surface. In a study of *Papilio* larvae, which feed almost exclusively on umbelliferous plants, Dethier shows that the attractive odor is that of the complex chemical components of the essential oils of the Umbelliferae, which impart a characteristic odor to plants of this family. Caterpillars greedily drink sweet solutions, but give a decisive avoidance reaction to a salt, sour, or bitter solution. Tests on *Apamea velata* and *Malacosoma disstria* gave their sensitiveness to sugars as follows: sucrose, fructose, dextrose, and lactose in decreasing order. The final food test by the caterpillar is the taste of the leaf. The organs of gustation, according to Dethier, are primarily on the epipharynx, but probably also on the hypopharynx. Most young caterpillars do not have to hunt

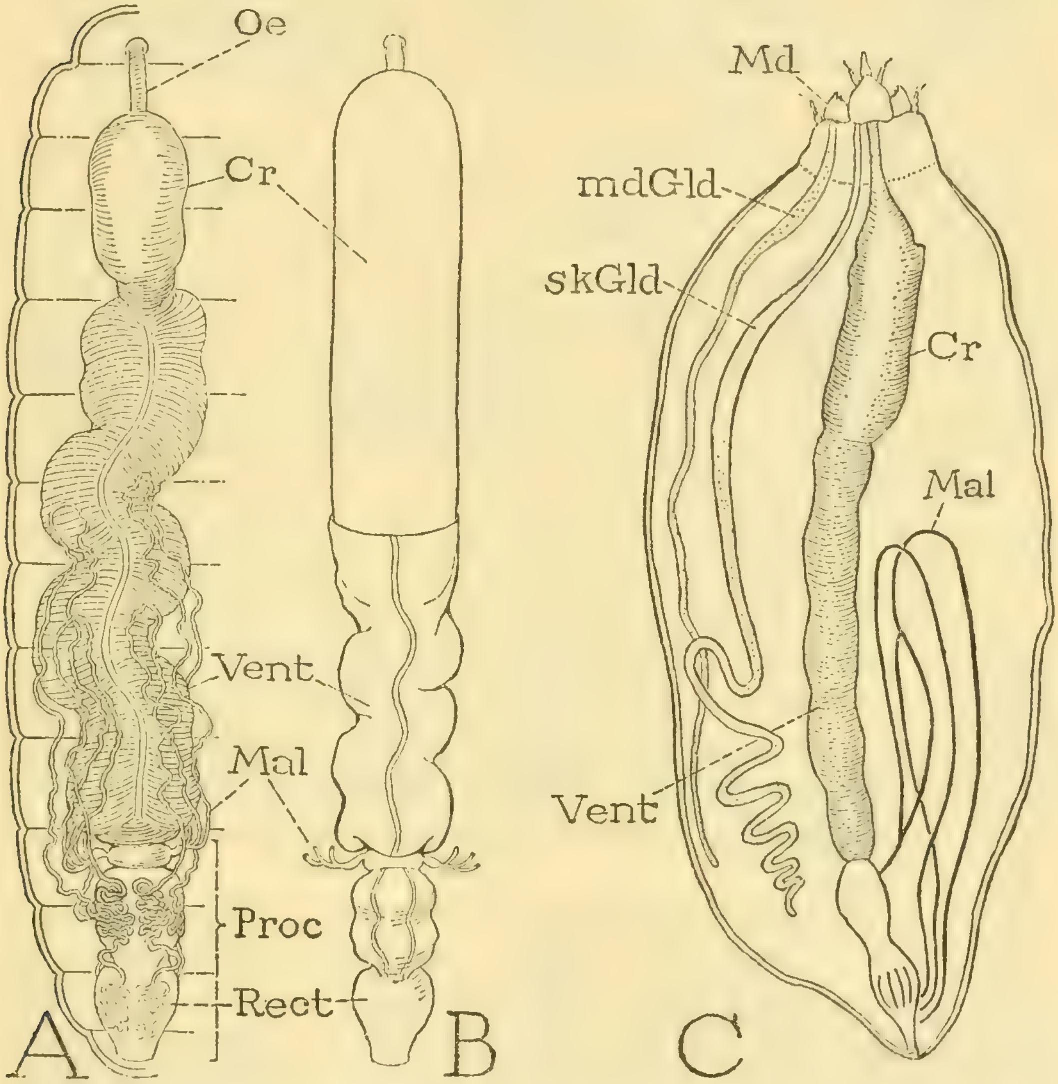

FIG. 8.—Alimentary canal and head glands of caterpillars. Lettering as on figure 7, except *mdGld*, mandibular gland.

A, Tent caterpillar, *Malacosoma americanum*, crop contracted, stomach full of food, greatly extended. B, Same after a period of feeding, crop extended, stomach contracted. C, Caterpillar of *Enarmonia pseudonectis* opened from above, showing alimentary canal, silk gland (*skGld*), and mandibular gland (*mdGld*) of left side (from Teotia and Pathak, 1957).

for their food, because the female moth or butterfly usually deposits her eggs on the proper food plant for the larva.

Since the usual labial salivary glands of other insects are converted into the silk glands of the caterpillar, many caterpillars at least have long tubular mandibular glands (fig. 8 C, *mdGld*). The secretion of these glands might be supposed to have a salivary function, but from analyses that have been made Uvarov (1928) suggests that the secretion may be of an excretory nature.

The cylindrical body of the caterpillar accommodates the large alimentary canal, but the abdomen is too heavy to be held up by the thorax in the manner of adult insects. The reduction of the thoracic legs, therefore, allows the abdomen to follow in line with the thorax, and also brings the mouth parts into close contact with the feeding surface. The prolegs support the heavy abdomen, and serve for holding on tight when the caterpillar is climbing or feeding.

The prolegs occupy the position of the abdominal limb vestiges of the embryo, and for this reason some writers have regarded them as appendages serially homologous with the thoracic legs. In structure and musculature, however, the prolegs have nothing in common with the thoracic legs, and they are not moved in the manner of legs as organs of locomotion. Hinton (1955) has thoroughly discussed the whole subject of larval prolegs, not only in the Lepidoptera but in the other orders as well, and gives cogent reasons for believing that in all cases these legs are secondary adaptive structures of the larva having no relation to former abdominal appendages represented by vestiges in the embryo.

A typical caterpillar proleg (fig. 9 A, G, J) is a short, thick, hollow outgrowth of the body wall ending with a flattened foot lobe known as the *planta,* which is armed with small hooks, or *crochets.* Muscles from the body wall are attached on the base of the leg (figs. 9 E, 10 A), and in some cases within the leg; but the principal proleg muscles are a group of long fibers from the lateral body wall inserted on or near the center of the planta (fig. 9 E). These muscles are plantar retractors. Inasmuch as the Onychophora and Tardigrada have a leg musculature similar to that of the caterpillar's prolegs, Pryor (1951) points out that this type of musculature simply meets the need of a similar mechanism in legs of a similar structure, and can have no phylogenetic significance.

The crochets are arranged in various patterns on the planta in different caterpillar species. Fracker (1930) and Peterson (1948) have made comparative studies of the crochets from a taxonomic standpoint without correlating their arrangement with the habits of

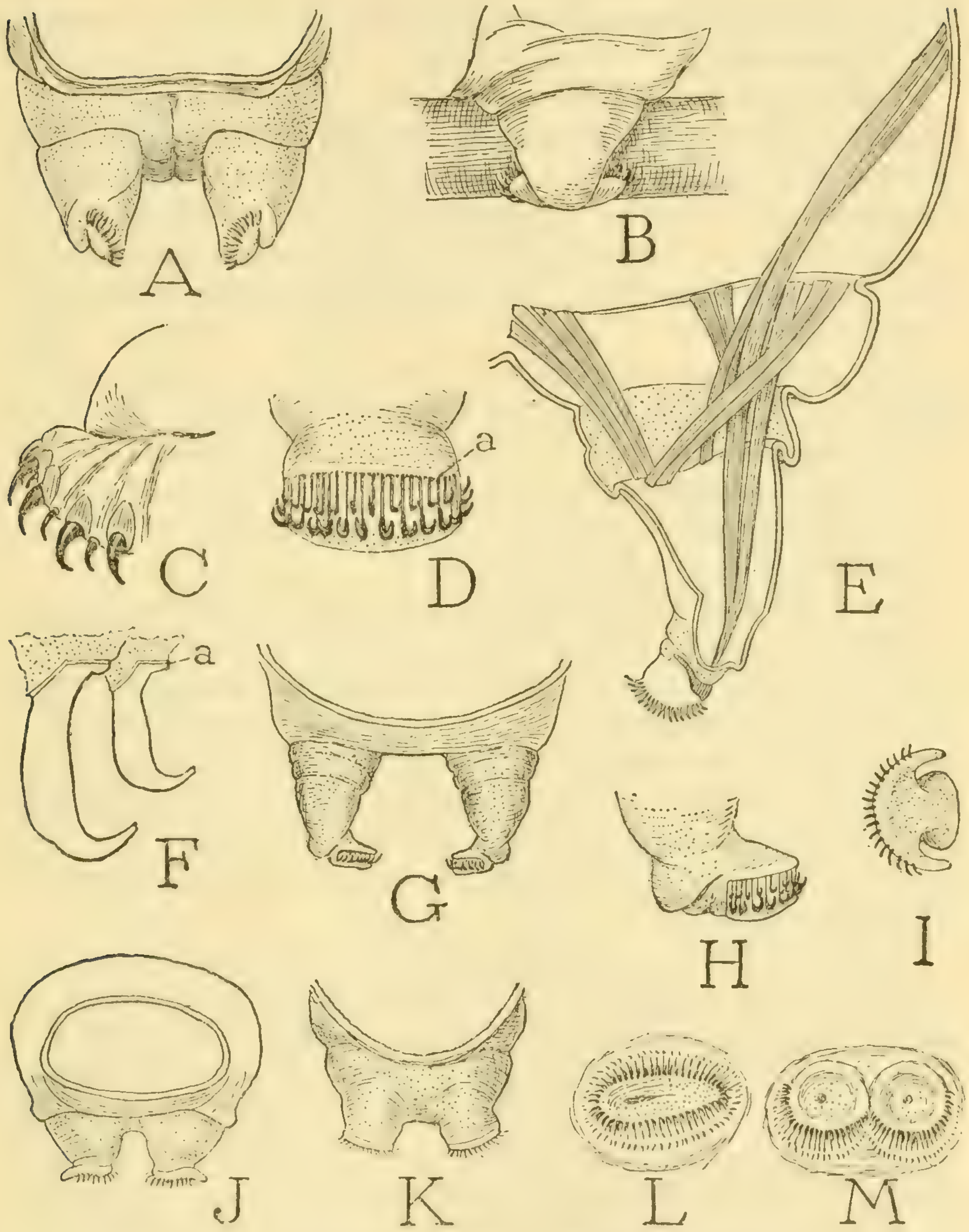

FIG. 9.—Examples of larval prolegs and crochets.

A, Tomatoworm, *Protoparce quinquefasciata*, a pair of prolegs, anterior. B, Same, a proleg clasping a twig. C, Same, part of planta, ventral. D, Same, mesal surface of planta. E, Tent caterpillar, *Malacosoma americanum*, section of proleg, showing muscles. F. Tomatoworm, a pair of crochets, anterior; *a*, articular point on planta (D,*a*). G, Silkworm, *Bombyx mori*, a pair of prolegs, anterior. H, Same, planta more enlarged. I, *Diacrissia virginica*, planta, ventral. J, Same, abdominal segment and prolegs, anterior. K, *Hepialus* sp., pair of median prolegs. L, Same, ventral surface of a median proleg showing crochets. M, Same, crochets of an anal proleg, ventral.

the caterpillars. Hinton (1955) gives a good account of the mechanism of the planta that operates the crochets. Only a few special examples will be given here.

Prolegs typical of climbing caterpillars are well shown by the tomatoworm *Protoparce quinquefasciata* (fig. 9 A). The mesal part of the planta projects as a pad, which, when viewed ventrally (C), appears to be armed with a marginal row of larger upturned hooks and a submarginal row of smaller hooks. On the mesal surface of the pad (D) it is seen that each hook is supported on what appears to be a slender vertical bar in the wall of the planta. Dissection reveals, however, that these apparent bars are the exposed edges of the crochets themselves (F) which are deeply buried in grooves of the plantar surface, and that the visible hooks are only their free outer ends. The wide bases of the crochets are articulated by mesal points (F, *a*) in an even row on the plantar lobe (D). The same type of plantar structure is seen in the silkworm (G, H).

In the resting caterpillar clinging to a twig, the prolegs are kept extended by internal body pressure, or turgor; the crochet-bearing pads are then turned mesally and the claws firmly grasp the support (fig. 9 B). The retractor muscle of the planta is attached laterad of the base of the crochet-bearing lobe, and, as noted by Hinton (1955), a contraction of the muscle turns the lobe downward and disengages the claws. When the caterpillar is crawling, the plantae are successively lifted to allow the prolegs to be carried forward with the extension of their segments.

On flat surfaces or on the ground the crochets probably have little use, the prolegs serving merely as supports for the abdomen. The actively running arctiid caterpillars have very short prolegs (fig. 9 J). In the yellow woolybear *Diacrisia virginica* (fig. 9 I), the crochet-bearing lobe is crescent shaped with a single row of marginal upturned crochets. Some caterpillars are able to walk on glass by pressing the plantae flat against the surface. Presumably a slight contraction of the plantar muscles converts the feet into suction cups. Such caterpillars can adhere to the glass at a steep angle, but they cannot crawl on a vertical glass surface. Probably they maintain a foothold in the same way on the surface of leaves.

A different type of planta is seen in a stem-boring larva of *Hepialus* (fig. 6 F). The short median prolegs (fig. 9 K) end with flat plantar surfaces (L), each bearing a transverse oval series of larger crochets surrounded by an outer series of small crochets. The plantar muscle is attached excentrically on the plantar surface. The anal prolegs have each a pair of plantar discs side by side (M), with crochets only on the anterior margins. Each disc has a central muscle attachment. It is not clear that the arrangement of the crochets here has any relation to the boring habits of the larva, since in other boring species the crochet pattern is highly variable.

The prolegs are clearly very useful structures to the caterpillars as props for the abdomen and for holding on while climbing, but they are not active organs of locomotion. Though usually they are present on abdominal segments *III-VI* and *X*, and are rarely more numerous, they are frequently fewer in number, and in leaf miners may be absent entirely.

A few caterpillars, such as the case makers and the bagworms, walk with the thoracic legs while the body is held erect. To the ordinary free caterpillars, however, both the thoracic and the abdominal legs are of little or no use for progression, and the caterpillars have developed a remarkable motor mechanism for direct movement of the body itself. In addition to crawling and climbing, various caterpillar species have become leaf miners and others bore into the stems or wood of plants or burrow in the ground. Furthermore, most caterpillars are able to twist and turn in all directions, and often, while holding on with the abdominal legs, they raise the anterior part of the body and swing it about in search of new foliage on which to feed. For all these movements the caterpillars have a most elaborate body musculature (figs. 10, 11), which includes the usual dorsal and ventral longitudinal bands of intersegmental muscles, and a complex outer system of small muscles going in various directions against the body wall. Similar muscle patterns in other species are illustrated by Forbes (1914).

The common caterpillar does not walk; as already said it progresses by movements of its body, not by means of its legs. It has therefore evolved a type of motor mechanism that propels it forward while the body is close to the support, and its manner of moving is not that of a worm or a snake. The locomotor movements are best seen on a slender, naked caterpillar, such as a noctuid; the following observations were made on a species of *Heliothis*. When the resting caterpillar is about to move, the thoracic legs may first become active and somewhat stretch the anterior part of the body, but they do not bring up the heavy abdomen. Forward movement is initiated by lifting the posterior end of the body, curving it downward and forward, so shifting the anal prolegs anteriorly to a new grasp on the support. Immediately then the deflected segments contract, straighten, and produce a hump on the back, while the anal legs maintain their hold, though reversed in position. A wave of successive forward contrac-

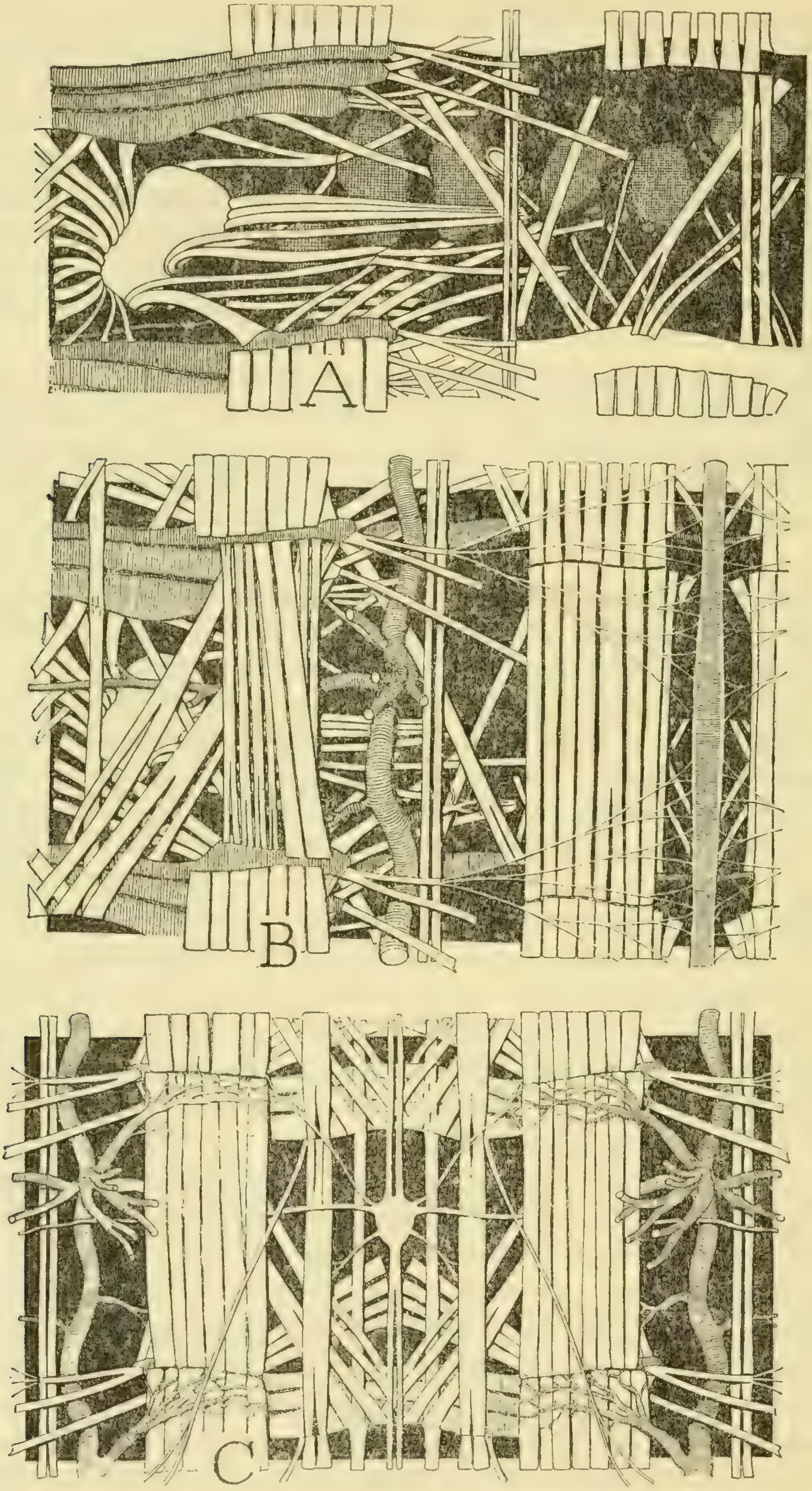

Fig. 10.—(See legend on opposite page.)

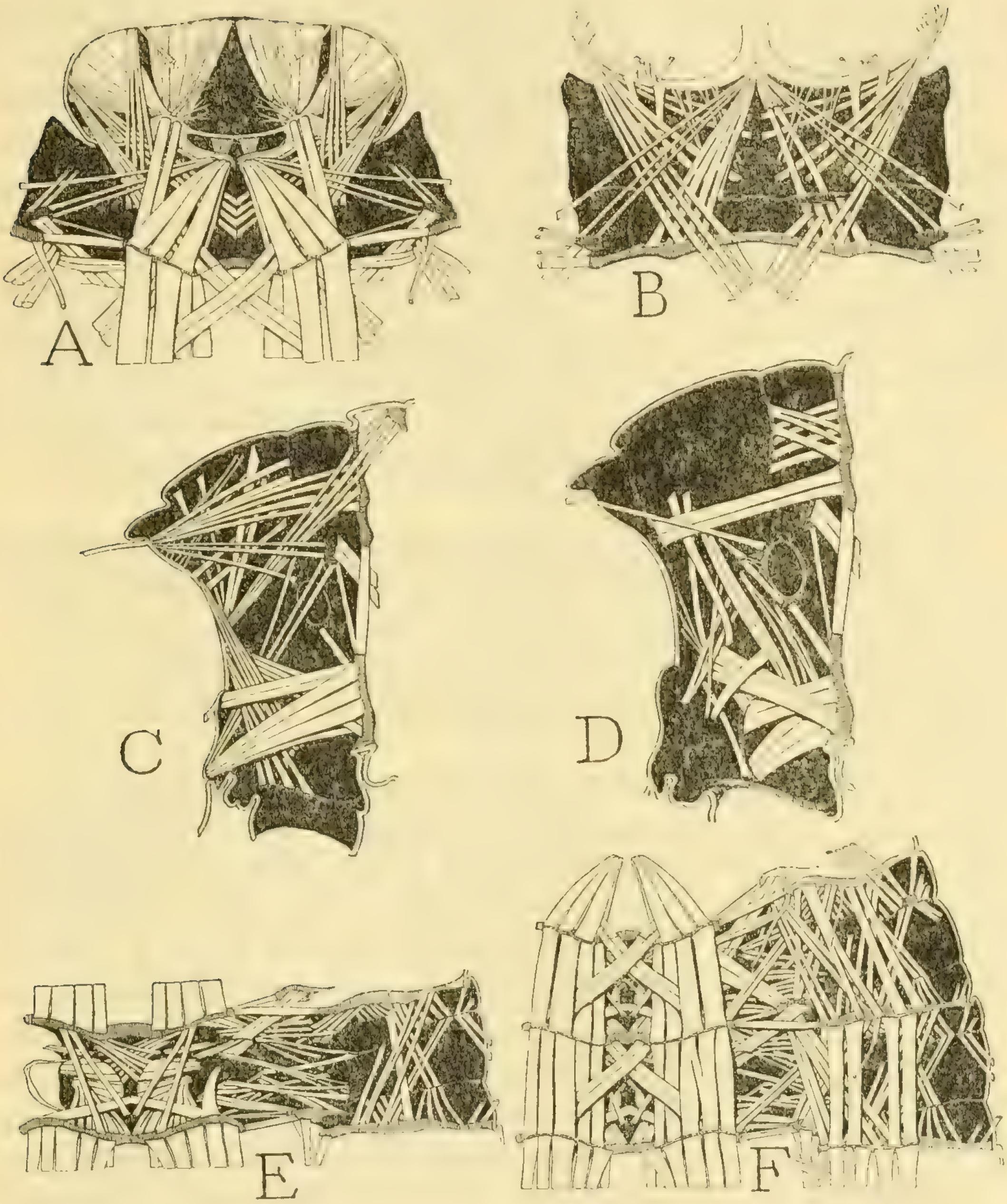

FIG. 10 (See opposite page).—Somatic muscles of the salt marsh caterpillar, *Estigmene acraea.*

A, External muscles of right half of third abdominal segment as seen after removal of longitudinal bands, showing basal muscles of proleg. B, Right half of fourth abdominal segment, ventral longitudinal muscles partly removed. C, Ventral half of fourth abdominal segment.

FIG. 11 (above).—Somatic muscles of the tent caterpillar, *Malacosoma americanum.*

A, Ventral prothoracic muscles of head. B, Dorsal muscles of back of head. C, Right half of prothorax and head muscles. D, Same after removal of head muscles. E, External ventral and right lateral muscles of metathorax. F, Ventral and right external muscles of mesothorax and metathorax.

tion and expansion of the segments now runs rapidly forward through the length of the body. Each segment contracts from the rear and is then expanded anteriorly by the following contraction of the segment in front. Thus the segments successively extend forward, and finally the head is protruded a short distance. At the same time the dorsal hump runs forward like the crest of a wave along the back, lifting successively the prolegs of segments *VI-III* and carrying them forward to a new position; on reaching the thorax the thoracic legs are carried forward in the same manner. The anal legs then again are brought up for a new hold, and the whole series of events is repeated every few seconds. The caterpillar thus progresses at a uniform rate by short forward thrusts of the body. Some species crawl with less exertion, the anal legs being simply moved forward with little humping of the body.

The only contribution of the legs to the locomotion of the crawling caterpillar is the successive forward movement of the anal prolegs. These legs are often more strongly musculated than the others. Their reversal of position as the body advances gives them the appearance of pushing forward, but it is the body moving away from them that alters their slant.

Since the motor force of the caterpillar's movement is the successive *contraction* of the body segments from behind forward, locomotion is produced evidently by the dorsal and ventral bands of longitudinal muscles of segmental length. There being no muscular mechanism of expansion, contraction has been made the effective agent of forward movement, each contracting segment expanding the segment behind in a forward direction. Other writers, as Barth (1937) and Fiedler (1938), have attributed the caterpillar's movement to contraction of the segments without noting the expansion. The locomotor mechanism of the caterpillar is clearly a substitute for leg action, but in no way resembles that of the earthworm. The legless worm moves forward by a compression of the rear part of the body, which extends the anterior part by internal pressure. Nothing of this sort is evident in the caterpillar. The caterpillar's method of locomotion depends on the soft, flexible nature of the integument, and the successive contraction of the longitudinal muscles in individual segments. In a last analysis, therefore, locomotion is controlled by the action of the nervous system in momentarily stimulating the segmental muscles in order from the rear forward.

Barth (1937) terms the locomotor movements of the caterpillar "peristaltic." Peristalsis (Gr. *peristalticos,* clasping or compressing), however, is a propagated series of circular (*peri*) contractions through a tube, such as the oesophagus, that drives the contents of the tube through the lumen. The caterpillar type of movement, on the other hand, is a successive *lengthwise* contraction and expansion of the body segments that gives a forward motion to the tube itself, in this case the caterpillar. Barth, however, makes a detailed analysis of the muscles involved in the progressive movements of the caterpillar. He points out, furthermore, that the preservation of internal pressure, or turgor, is an important factor in maintaining the action of the muscles. This function he ascribes to the outer system of body-wall muscles, which counteracts a dilation of the soft integument of the caterpillar that would otherwise reduce the turgor. The somatic musculature, according to Barth, is thus composed of locomotor muscles and turgor-preserving muscles.

Caterpillars of the Geometridae, the loopers, or measuringworms, have adopted a method of locomotion by which they can progress at a much greater speed than the ordinary caterpillar. In these caterpillars (fig. 12 A) the prolegs of only segments *VI* and *X* are functional organs, the others have been eliminated or greatly reduced in size. Instead of making a short forward step with the anal legs and then extending the body a corresponding distance, the geometrids, while holding to the support with the thoracic legs, bring the prolegs of segment *VI* clear up to the thorax (C), thus throwing the first five abdominal segments into a dorsal loop. Then, retaining their grip by the prolegs, they straighten the body forward and upward, and finally bring it down on the support ready to repeat the action. By this method, with each forward step, the caterpillar advances a distance (*a*) equal to the length of the first five abdominal segments. The rate of progression can be varied; the caterpillar may go along at a leisurely pace but when in a hurry it loops and straightens in rapid succession. According to Barth (1937) the geometrids are not able to crawl in the manner of other caterpillars. In their movements there is no visible contraction and expansion of the body segments.

If the prime function of the caterpillar is feeding and the storage of food reserves in its body as fuel for the pupa or to supplement the sugar diet of the adult, it may be accredited with having fully met its obligations. Almost its entire organization is a reconstructive adaptation for feeding. This is seen in the structure of the mandibles, the long, soft, flexible body, the shortness of the thoracic legs, the presence of prolegs on the abdomen, the great size of the stomach, the abundance of fat tissue for food conservation, the extraordinary development of the muscular system, the body mechanism of locomotion, and the correlated action of the nervous system. All these features are adaptations for procuring, consuming, and digesting an abundance of food, and for storing a surplus for the pupa and the adult. The fact that some moths have found it unnecessary to eat at all in the adult stage would seem to attest the efficiency of the caterpillar as a provider for the whole life span of the individual. The only organs not particularly involved in the adaptive specialization of the caterpillar are the heart, the tracheal system, and the nervous system in its gross structure.

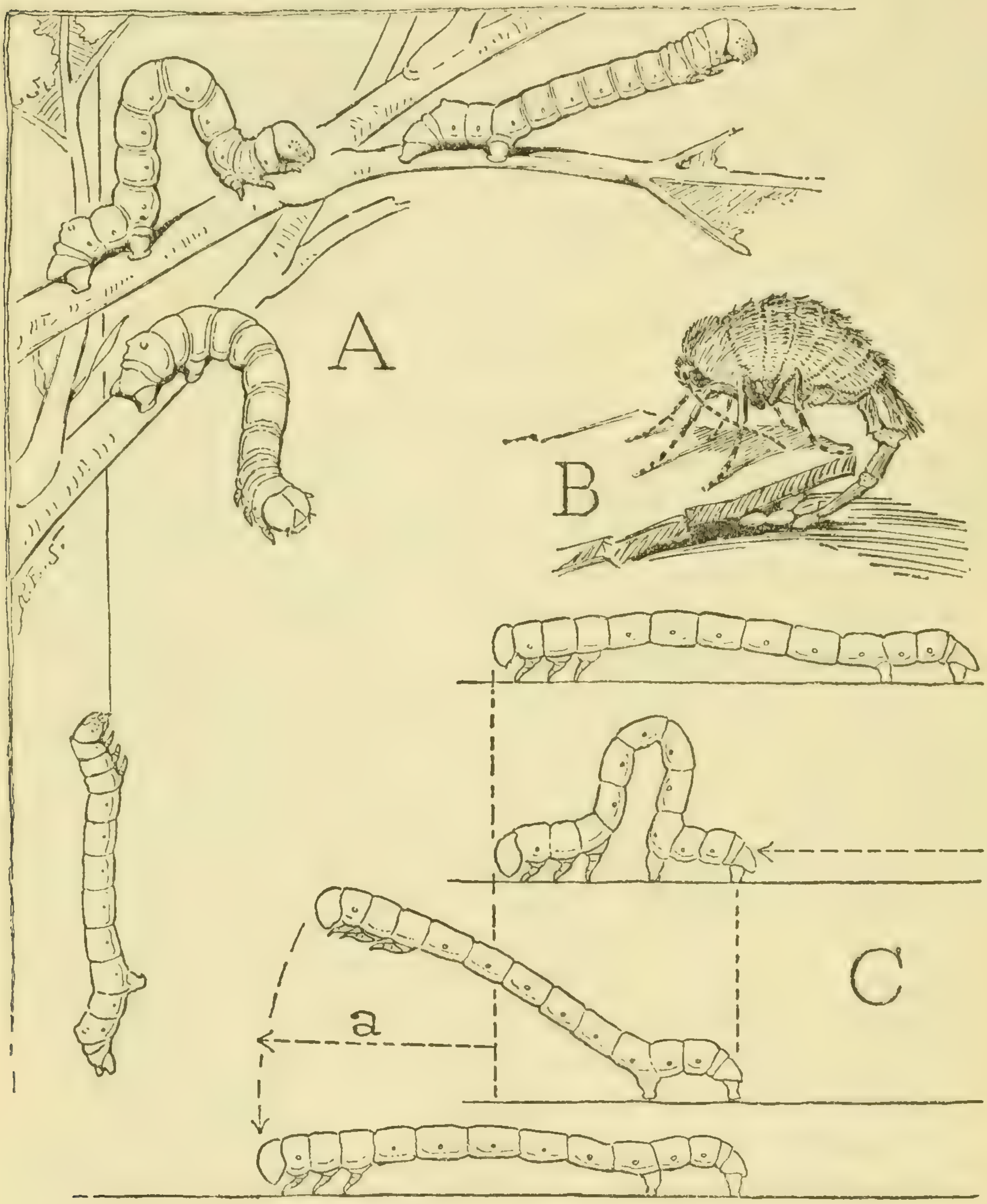

Fig. 12.—Geometridae.

A, Caterpillars of the spring cankerworms *Paleacrita vernata.* B, Female moth of spring cankerworm laying eggs. C, Successive locomotor phases of a geometrid caterpillar; *a,* distance advanced with each extension after looping.

The larval tracheal system is highly elaborate (fig. 13), but in no way specialized. The nervous system of a noctuid caterpillar is described by DuPorte (1914) and that of a hepialid by Swaine (1920-21). In the hepialid *Sthenopis thule* and an eriocraniid, according to Swaine, there are eight abdominal ganglia, but the connectives in both the thorax and the abdomen are fused into single interganglionic strands. The same is true of a species of *Hepialus* examined by the writer. The union of the nerve connections is thus a specialized feature in this otherwise relatively primitive group. On the other hand, in caterpillars of the higher Lepidoptera the last two ganglia are united in the seventh abdominal segment.

The theory that would explain the different forms of holometabolous larvae on the assumption that they have hatched at different stages of embryonic development assigns the caterpillar to the polypod stage of embryogeny. The polypod stage is that in which rudiments of the gnathal and thoracic appendages are well formed, and vestiges of limbs are present on the abdomen. This stage of the embryo presumably represents a disappearing "centipede" stage in the evolution of the insects.

The polypod theory as applied to the caterpillar encounters two principal objections. First, it assumes that the abdominal prolegs of the larva are serially homologous with the thoracic legs, an assumption that is highly improbable. Second, if we look at an embryo in the polypod stage of development, such as that shown by Eastham (1930) for *Pieris rapae* (fig. 14), it is seen that the head is still in a very primitive state. The gnathal segments are not yet added to the embryonic head (*emH*), and the prospective mouth parts (*Md, 1Mx, 2Mx*) are mere undifferentiated lobes. Yet, when the larva leaves the egg it is already a perfectly formed young caterpillar. The head is a syncephalon, the mouth parts are fully developed for feeding and silk spinning. All this is quite at variance with the idea that the caterpillar is an arrested polypod stage of the embryo.

While in most ways the caterpillar is structurally and functionally subservient to the adult, in one respect it has been self-centered. This is in its production and spinning of silk, which seems to have no primary relation to the welfare of the moth or butterfly. The silk is formed in the labial glands, which ordinarily in other insects secrete saliva. Since caterpillars use their silk in various ways, it is not clear what use it may have been to them in the first place.

True silk is formed only by arthropods, particularly the insects and spiders, but the silk-producing organs may be glands in quite different parts of the body having no homology with one another. Silk produc-

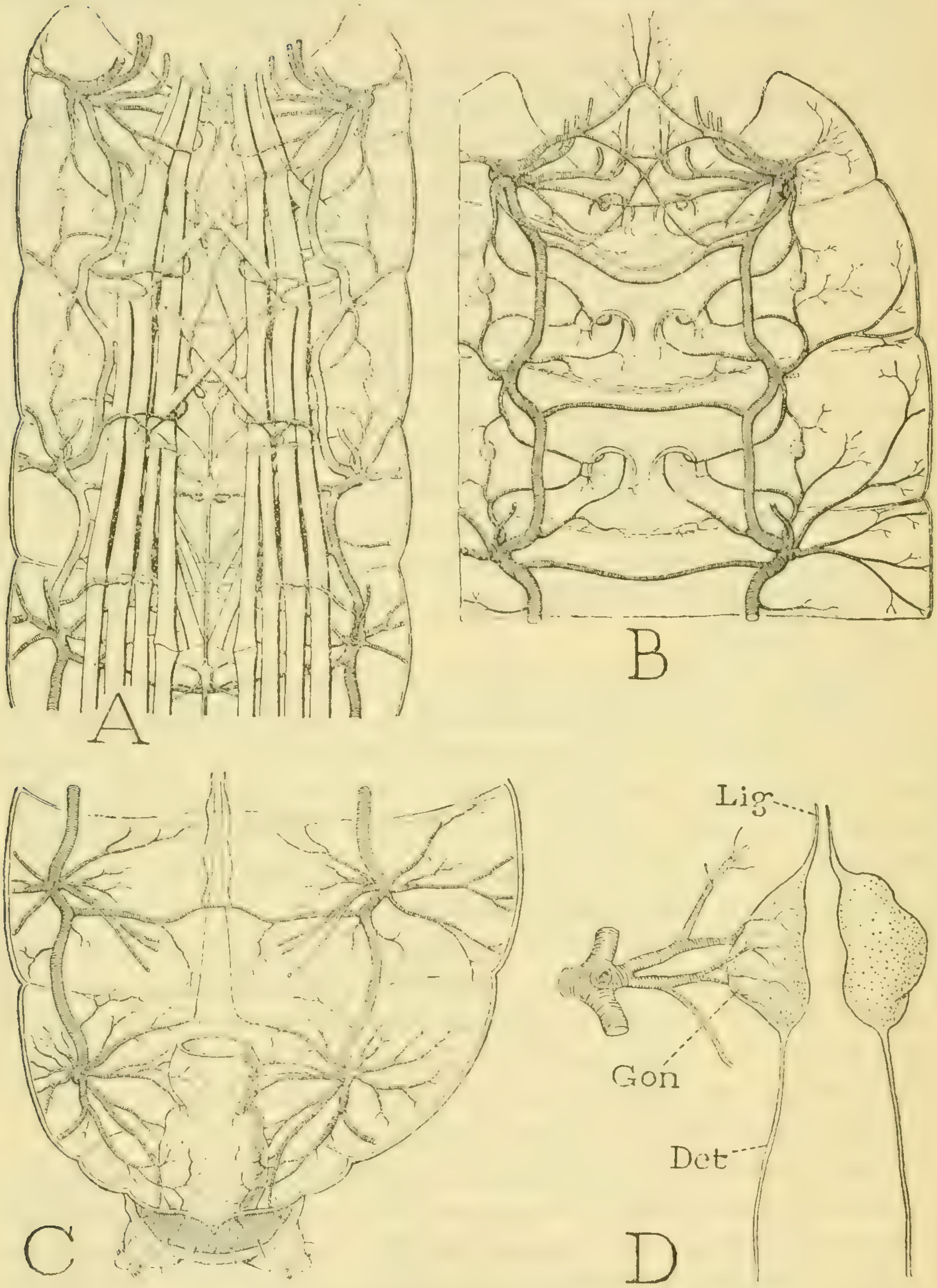

FIG. 13.—Examples of the tracheal system of a caterpillar.

A, Cutworm (noctuid), ventral half of thorax and first two abdominal segments. B, Same, thoracic segments with muscles removed. C, Same, ventral tracheation of end of abdomen. D, Corn ear worm, *Heliothis zea*, gonads and their tracheation in fifth abdominal segment; *Dct*, duct; *Gon*, gonad; *Lig*, suspensory ligament.

tion by the labial glands is common to the larvae of Trichoptera, Lepidoptera, and Hymenoptera, and it may be supposed that the functional change in the glands took place in the common ancestors of these three groups. Among the Neuroptera some species secrete silk in the Malpighian tubules and spin it from the anus. The female of the water beetle *Hydrophilus pistaceus,* described by Lesperon (1937), deposits her eggs on the lower surface of the leaves or stems of water plants enclosed in a cocoon of silk spun from glands opening into the oviducts at the bases of the ovaries. A luminous, silk-spinning mycetophilid fly larva, *Bolitophila luminosa,* as described by Ganguly (1960), produces silk in the labial glands and spins it as a snare for capturing insects attracted by light generated in its Malpighian tubules. The so-called balloon fly, *Hilara* of the Empididae, has been shown by Eltringham (1928) to spin its silk from glands in the enlarged basal tarsomeres of the fore legs. The Embioptera are well known to spin silk from glands in the fore tarsi. The art of silk spinning has been most highly cultivated by the spiders, whose silk glands are in the abdomen.

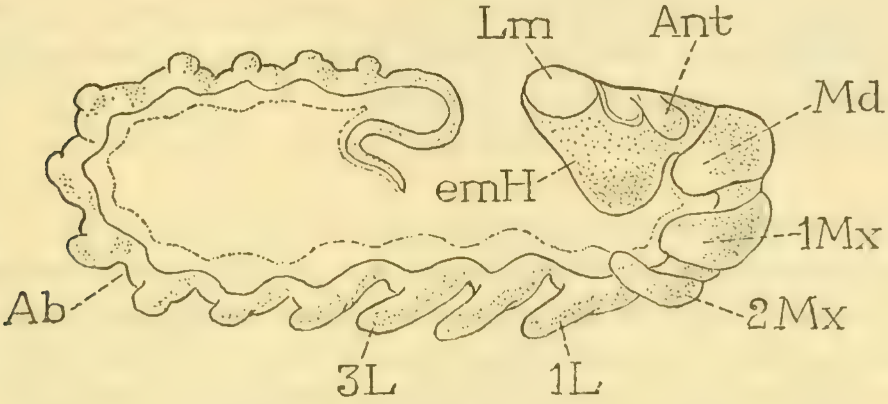

FIG. 14.—The polypod stage of the embryo of *Pieris rapae* (from Eastham, 1930).

Ab, abdomen; *Ant,* antenna; *emH,* embryonic head; *L,* thoracic leg; *Md,* mandible; *1Mx,* first maxilla; *2Mx,* second maxilla.

Lesperon (1937) has described the histology and physiology of the silk glands and the secretion of silk in the several groups of silk-spinning insects. Bradfield (1951) discusses the relation of phosphatases and nucleic acids in the silk glands of spiders and caterpillars, showing their function in the secretion and discharge of silk from the glands.

Of the various ways that caterpillars use their silk, we may note the following. Some species that live in trees but pupate on the ground let themselves down by dropping at the end of a thread drawn out from the spinneret. Others spin a web on the smooth surface of a leaf on which they are feeding to obtain a better foothold. Still others construct a shelter or retreat by drawing leaves together and securing them by strands of silk. Then there are the casemakers and bagworms that enclose themselves in a close-fitting jacket or a bag by weaving together bits of leaf. The webworms and tent caterpillars make those large silken domiciles in trees, in which a whole family hatched from one batch of eggs lives a communal life. As the tent caterpillars go out on the limbs to forage, they leave a trail of silk to guide them back to the nest where they spend the night. When ready to pupate, tent caterpillars simply jump off the tree. Caterpillars of butterflies spin a small web mat against a support from which they can hang awaiting pupation. Some secure themselves with a silken girdle around the thorax which remains as a suspensorium for the pupa.

The most important use of silk would seem to be that of many moth caterpillars of enclosing themselves in a closely woven cocoon, within which they shed the last larval cuticle and change to the pupa. Cocoon spinning evidently began among the Micropterygidae, since Tillyard (1922) describes the larva of *Sabatinca* as spinning a cocoon of rather coarse silk having a leathery appearance. However, he says that "no definite spinneret apparatus could be discovered," and he makes no mention of the silk-producing glands. On the other hand, in *Micropteryx calthella* Hannemann (1956) describes and figures a pair of oval glands in the thorax having a common duct that opens into a salivarial chamber between the hypopharynx and the labium, but these glands he says secrete saliva that is discharged on the food. The leaf-mining larva of the eriocraniid *Mnemonica auricyania* is described by Busck and Böving (1914) as having a spinneret from which it spins a cocoon in the ground. Of all the insects the caterpillar is the best-known silk-spinner, and the silkworm probably outranked the honey bee as an insect of commercial importance until the production of competing artificial fabrics. Artificial honey has not yet been invented.

Though the faculty of producing and spinning silk was evidently not acquired by the ancestral caterpillars for any specific purpose, yet the evolution of their modern spinning apparatus involved a very considerable reconstruction of their mouth parts, and the conversion of the salivary glands into silk-producing organs.

The ordinary salivary glands of insects lie in the thorax; their ducts unite in a common outlet duct that opens into the space between the hypopharynx and the labium, known as the salivarium. On the walls of the salivarium near the mouth of the duct are attached opposing muscles from the hypopharynx and the labium, which probably regulate the flow of the saliva.

The silk glands of the caterpillar are a pair of long tubes (figs. 7, 8 C, *skGld*) extending from the head far back into the abdomen. Each gland is thrown into loops and coils, and the slender ducts open into a small chamber called the *silk press* (fig. 15 A, *Pr*), which opens through the spinneret at the end of the labium. A small accessory racemose gland (*acgld*) opens into each duct near its termination.

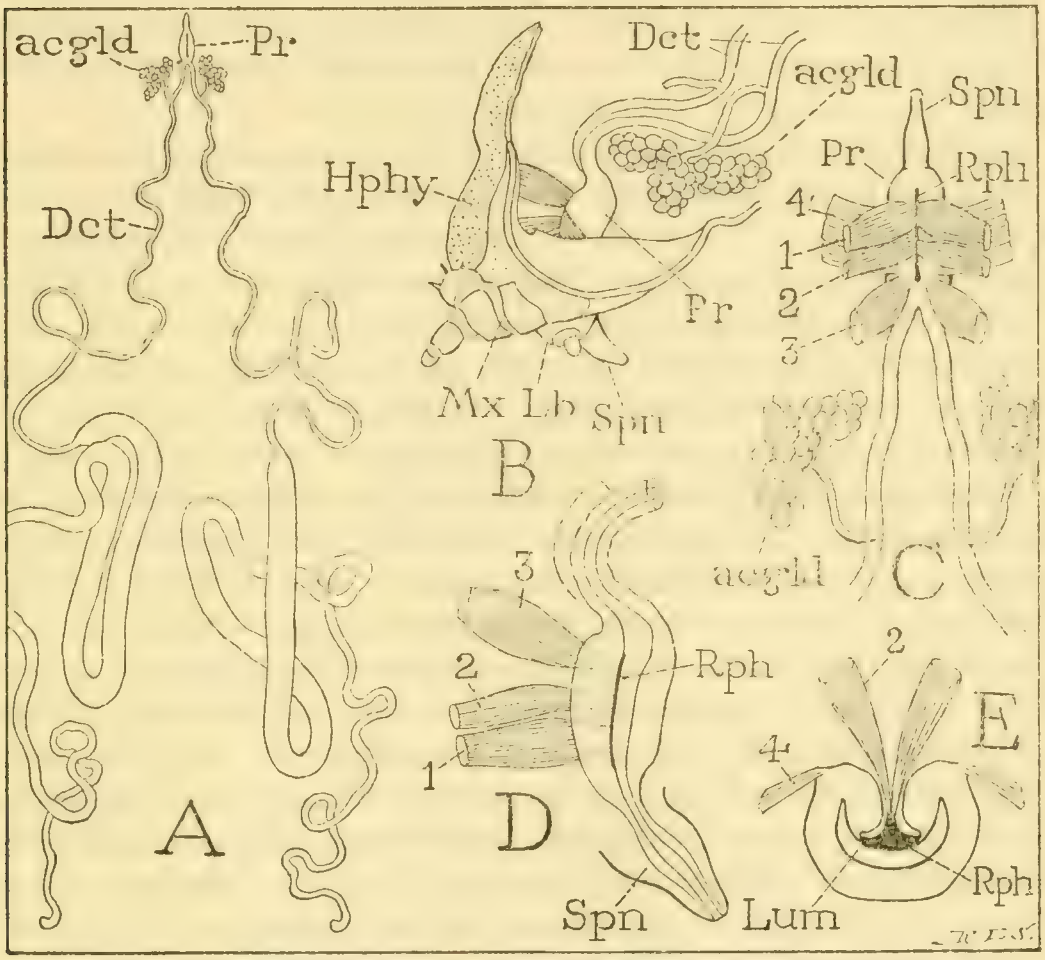

FIG. 15.—Silk glands and spinning apparatus of the tent caterpillar, *Malacosoma americanum*.

A, The silk glands. B, Section of head lobe formed of the labium, maxillae, and hypopharynx containing the silk press and bearing the spinneret. C, Silk press and ends of ducts, dorsal. D, Longitudinal section of silk press. E, Transverse section of silk press.

acgld, accessory gland; *Dct*, silk gland duct; *Hphy*, hypopharynx; *Lb*, labium; *Lum*, lumen of silk press; *Mx*, maxilla; *Pr*, silk press; *Rph*, raphe; *Spn*, spinneret. *1,2,3*, dorsal muscles of silk press; *4*, ventral muscle of press.

The silk press of the caterpillar is clearly the salivarium of other insects, which has been converted into a closed chamber by the union of the hypopharynx with the basal part of the labium (fig. 5 E, *Pr*). The salivary muscles are strongly developed (fig. 15 C), three pairs

(*1, 2, 3*) from the hypopharynx being inserted on a sclerotic bar, or *rhaphe* (*Rph*), in the dorsal wall of the press, and a single pair from the labium (*4*) attached laterally. The lumen of the press is continued into a narrow exit tube (D) that opens on the end of the spinneret (*Spn*). The hypopharyngeal wall of the press is deeply inflected (E) into the lumen (*Lum*), but evidently can be lifted by the muscles, and then by an elastic springback drive the liquid silk from the spinneret. The silk press is probably also a silk ejection pump.

As already noted, the maxillae are closely associated with the labium, forming a prominent lobe on the underside of the head bearing the spinneret (fig. 5 B,C), but the hypopharynx (*Hphy*) also is involved in this structure, since it is united with the inner wall of the labium (*Lb*). While these parts are movable by their own muscles, the characteristic figure-eight movements of the spinning caterpillar are made by the head and the freely swinging fore part of the body, activated by the elaborate head and body musculature (fig. 11 A,B).

When the caterpillar in its evolution had once become fully adapted structurally for the performance of its functions in relation to its future pupal and adult state, its successors were then free to vary in superficial ways, and to adopt habits suitable to their own interests. So, as the adults in their evolution were diversified into many species, their caterpillars likewise underwent evolutionary changes as they adopted different ways of living and feeding, until they became as distinctive of their species as the adults. Though most caterpillars have remained vegetarians, feeding in the open on the leaves of herbs or trees, some have penetrated the fruit, others have taken to mining the leaves, boring into stems or wood, or burrowing into the ground, while a few have become aquatic and have developed gills in the form of slender tracheated filaments growing from the back. All these are plant feeders.

There are species of caterpillars, however, that have renounced vegetarianism for other kinds of food. A good review of these aberrant feeders has been given by Brues (1936), and Clark (1926) has described the carnivorous caterpillars. The wax moth invades beehives and its larvae burrow destructively through the honeycomb, feeding on the wax and the bees' store of pollen. Larvae of the clothes moth eat fur, wool, and feathers. A number of species have become carnivorous, feeding as predators on live aphids, larval coccids, other young homopterons, pupae of moths, spider eggs, and eggs of the bagworm. A lycaenid caterpillar has imitated the aphids by excreting from glands on the end of its abdomen a liquid agreeable to ants.

For protection the ants take this caterpillar into their nest, and here the treacherous creature eats the ants' larvae.

Finally, there are species that have descended to parasitism. Members of the Epipyropidae live as external parasites on the back of fulgorids or other homopterons, and several pyralid species are ectoparasites on live sloths. Two species are known to be internal parasites of the coccid *Kermes*. Rau (1941) records the rearing of six species of moths from nests of the wasp *Polistes*. The larvae of these species are parasitic on the wasp larvae, and spin their cocoons in the host cell, where they pass the winter. Egg laying by the moths has not been observed, but the females are suspected of entering the wasps' nest at night when the inmates are asleep.

All this diversity of habits on the part of the caterpillars shows that the caterpillar structure, though highly specialized and standardized, is still adaptable to various ways of living. It is a presumed tenet of evolution that all perpetuated adaptations are beneficial to the species. However, since it would seem that there is enough vegetation in the world to support all the caterpillars there are, why have some species departed from the ways of their ancestors? Brues (1936) points out that the preference of insects for certain kinds of food is an instinct, not a matter of conscious taste, and that aberrant food habits are therefore due to basic hereditary changes in instinct. We are then left with the question of why do instincts change.

The caterpillar goes through several stages of increasing growth between moults, but it preserves its larval form and structure up to the end. Then at one final moult, after shedding its caterpillar skin, it appears to have suddenly changed into a pupa. That the change of form is not so sudden as it appears to be will be shown later.

The larval status and the pupal-adult development are regulated by two opposing hormones. A juvenile hormone, formed in the corpora allata of the head, maintains the larval form; a hormone discharged from glands in the prothorax, under stimulus by a hormonal secretion from the brain, controls moulting and permits further development. The prothoracic gland hormone is known as the moulting hormone because, as said by Van der Kloot (1961), it "acts on the tissues to promote all the changes characteristic of a molt," but it has no influence on the development that follows the moult. This hormone then might be likened to a green traffic light that allows traffic to cross the intersection, but has nothing to do with where it goes after crossing. The developmental course of the insect after the moult depends on its hereditary factors, it may become another larva, a pupa, or an adult. The prothoracic gland hormone has been named "ecdyson," unfortunately since it has no relation to ecdysis. The corpus allatum hormone has been supposed to operate entirely by inhibiting adult development, but more recent investigations indicate that it actively affects the larva. The immature insect grows between moults and may undergo slight or considerable changes at the moults. Hence, Wigglesworth (1959) has pointed out that "the hypothesis that this hormone merely inhibits differentiation toward the adult becomes untenable." Further, he says, "the corpus allatum hormone is clearly doing something active and positive in causing differential growth of larval type." A review of the structure and function of the endocrine glands of Lepidoptera has been given by Hinton (1951).

While most of the adult development either is somehow inhibited in the larva, or the thoracic-gland hormone is not always secreted in sufficient amount, some adult structures do develop from an early stage in the larva. A striking example is that described by Eassa (1953) of the growth of the adult antennae and mouth parts in the larval stages of *Pieris brassicae*. The adult antenna begins its development in the first larval instar as a thickening of the epidermis beneath the larval organ. As the antennal rudiment enlarges, the epidermis folds inward as a containing peripodal pocket. During the following instars the base of the antenna moves upward beneath the larval cuticle until it reaches the position of the adult organ on the face. The peripodal pocket likewise elongates, but as an open slit, and finally it opens out so as to free the antenna, still beneath the larval cuticle. The everted wall of the pocket becomes the imaginal epidermis of the head between the adult and the larval antennae.

Likewise, as shown by Eassa, the rudiments of the adult maxillae appear in the first larval instar as thickening of the epidermis beneath the larval maxillae. Through the following instars they develop within pockets of the epidermis. The galeae grow to such an extent that they become wrinkled, and when everted in the early pupal stage they are long and folded upon themselves. The larval mandibles shrink to the vestigial organs of the adult. The imaginal labium develops mostly during the fifth larval instar.

It is well known that the invaginated leg and wing buds of most holometabolous insects develop during the larval stage. In some of the nematocerous Diptera they are evaginated beneath the larval cuticle in the last larval instar, as the writer (1959) has noted in the mosquito.

The postembryonic development of the internal reproductive organs of the psychid lepidopteron *Solenobia triquetrella* is described by Ammann (1954) and by Brunold (1957). Rudiments of the testes and ovaries are present at hatching, and are in the process of dividing into compartments. No considerable change occurs during the first four larval instars, but further development proceeds during the rest of the larval life, including formation of the outlet ducts.

From these examples of imaginal development during the larval stage it is evident that an inhibitory influence does not equally affect all adult structures. Bodenstein (1957) has given some attention to this phase of the subject. He notes that in the larva of *Drosophila* the imaginal discs (i.e., rudiments of imaginal organs) grow at a rather constant rate, as shown by Eassa in *Pieris.* The growth of these rudiments during the intermoult periods indicates that the concentration of the thoracic-gland hormone is sufficient for the growth of these parts, but is not enough to induce moulting. "From all this," Bodenstein says, "one must conclude that the ability of different tissues to respond with growth to a given titer of prothoracic-gland hormone varies. Some tissues are able to grow in a low, others only in a higher titer."

The thoracic-gland hormone brings about moulting, but the development of the next larval instar and whatever differentiation it may make is controlled by the corpus-allatum hormone. It would seem, therefore, that the whole developmental process that takes place in the larva depends on the relative concentration of the two hormones in the blood. The way it works out seems to be that development is permitted in adult tissues and organs whose growth does not interfere with the functions of the larva, while the purely larval structures are maintained and larval growth is allowed to proceed.

The body wall, the alimentary canal, the muscular system, the nervous and circulatory systems, the tracheae are all preserved intact to the end of the active state of the caterpillar. With species that spin a cocoon and remain quiescent within it a varying length of time before pupation, metamorphic changes may begin during or shortly after spinning. In the silkworm, *Bombyx mori,* Verson (1905) says that degeneration of the mesenteron epithelium begins after the emptying of the alimentary canal at the time of spinning. As the larval cells are thrown off they are replaced by regenerative cells, so that the mesenteron wall remains continuous. It is observed likewise by Deegener (1908) that metamorphic changes in the alimentary canal of *Malacosoma castrensis* begin in the spinning larva. In *Vanessa,* according to Henson (1929), degenerative changes in the mesenteron take place in the fifth larval stage. In *Heterogenea limacodes* it is said by Samson (1908) that the larval epithelium of the mesenteron degenerates and is replaced by the imaginal epithelium even during the spinning by the caterpillar, which takes place in October, though pupation does not occur until the following May. Also histological changes in the Malpighian tubules begin just after the larva has spun its cocoon; reconstruction of the tubules is completed in the pupa. After a short rest the silk glands degenerate, and in the course of the winter a part of the larval musculature is lost.

Considering the growth of adult organs that may proceed in the active larva, and the metamorphic changes that take place in the quiescent larva after spinning its cocoon, it seems that there must be some mechanism that regulates the hormone secretions. Actually, the two hormone sources are in communication with the brain. The thoracic glands receive their stimulus for activity from the hormonal secretion of the brain by way of a pair of bodies in the back of the head of nerve-tissue origin, known as the corpora cardiaca. These bodies are directly connected by nerves with the secreting centers of the brain, and a nerve from each corpus cardiacum goes to the corpus allatum of the same side. It is possible, therefore, that the brain is the regulatory center of the entire endocrine system. In fact, it has been shown by Scharrer (1952) in the cockroach *Leucophaea* that the corpora allata are affected histologically and functionally by the amount of brain secretion in the corpora cardiaca. When the brain nerve to one corpus cardiacum is cut, preventing the brain secretion from entering the latter, the connected corpus allatum increases in size, its cells appear to contain more cytoplasm, the nuclei become more vesicular, and the nucleoli more distinct. Corpora allata in this condition, Scharrer says, are "functionally equal to, or perhaps even more competent than, normally innervated glands." This would seem to indicate that the more brain secretion there is in the corpora cardiaca the less active are the corpora allata, and vice versa. The brain, of course, does not act autocratically; it is itself activated by external or internal stimuli transmitted through the sensory nerves. When the brain activities cease, all growth and developmental processes stop, and the insect goes into diapause. This is shown by Van der Kloot (1955) to be true of the diapausing pupa of the *Cecropia* moth. After prolonged exposure to low temperatures, endocrine activity of the brain is restored, "diapause ends and the development of the adult moth begins."

Inasmuch as most animals grow from youth to maturity without the aid of a juvenile hormone, it is not clear why or how the early insects acquired glands for producing this hormone. However, it is reported by Schneiderman and Gilbert (1959) that substances having at least the effect of the corpus-allatum hormone when injected into insects have been extracted from Crustacea and other invertebrates, and even from the adrenal cortex of cattle. These writers suggest, therefore, that something of the nature of the insect juvenile hormone may be widely present in all animals, and that evolution has produced specific sensitivity to it in certain tissues, as in the insects. In any case, it seems certain that if the early insects did not have a juvenile hormone, they could never have developed their special kind of metamorphosis.

The corpora allata arise at an early age of the embryo from the ventral ectoderm of the head between the mandibular and maxillary segments, and migrate to their dorsal position in most insects behind the brain. Though the Thysanura do not have typical corpora allata, they do have a pair of apparently glandular bodies attached to the outer surfaces of certain muscles of the maxillae. These bodies are termed the *corps jugaux* by Chaudonneret (1949), who reasonably contended that they are the corpora allata in a primitive position between their ventral points of origin and their usual dorsal position in other insects. The function of these bodies in the Thysanura, however, is not determined, and, so far as known to the writer, thoracic endocrine glands have not been observed in these insects. Yet the thysanurans molt throughout their entire life. Perhaps the corps jugaux are really moulting glands that have remained in the head, where they take their origin.

METAMORPHOSIS

When at last the juvenile hormone that has maintained the caterpillar in its larval form gives way entirely to the thoracic-gland hormone, the caterpillar comes to the end of its life, provided it has not already been eaten by a bird or other predator, killed by some parasite, or poisoned by an insecticidal spray. If the caterpillar were a sentient being, knowing the ordeal it must now go through, it should be filled with apprehensions. However, the caterpillar is a creature of instincts, with no consciousness of self to be carried over into the butterfly. The butterfly is a new thing entirely, having its own instincts and outlook on life, and very probably no memory of ever having been a caterpillar. The transformation processes are purely biochemical, under the guidance of hormones and the factors of inheritance.

Yet the caterpillar seems to feel the approach of its time for pupation; it becomes restless and food no longer has any appeal. Tent caterpillars suddenly rush out from their tents to the ends of twigs on the tree and recklessly jump off to the ground, where they may travel long distances to find a suitable place for pupation. Others wander about in search of a secluded place, and some species pupate in the ground. The caterpillars of most moths enclose themselves in silken cocoons. The spinning of a cocoon is a complex piece of architectural work, but the caterpillar is endowed with a sensory-neuromuscular spinning mechanism that works automatically as a series of coordinated acts. If its cocoon is destroyed when partly spun, most caterpillars cannot begin over again, but must go on from where they left off. The stimulus for spinning has been shown by Van der Kloot and Williams (1953) to be of internal origin, in part hormonal, but largely the condition of the silk glands. The activating nerve center, however, according to these investigators (1954), is in the brain.

The caterpillars of butterflies do not enclose themselves in cocoons. In preparation for pupation they spin a mat or cone of silk on the underside of a twig or leaf or against some upright object, and then hang themselves from it head down by means of the claws of the anal prolegs and spines on the suranal plate. Some give themselves extra security by spinning a loop of silk from the support that forms a girdle around the thorax. When the pupa is formed it splits the larval skin over the back and down the face. Then by convulsive movements it pushes the larval skin up to its rear end and hangs freely from the attached skin. It is commonly said that the pupa holds on by pinching a fold of the skin between the movable segments of its abdomen. According to Riley (1879), however, there are small ridges and knobs on the end of the pupal abdomen that serve partly to grasp the suspended larval skin, but the principal suspensorium is the "rectal ligament," which evidently is the extracted cuticular lining of the intestine held by the anal sphincter of the pupa. This "ligament," Riley says, will support a weight 10 to 12 times that of the pupa. The tenth abdominal segment of the pupa is prolonged into a process known as the *cremaster* (or hanger) armed at the end with spines and hooks. The pupa now extracts itself from the larval skin by swinging the cremaster to one side and anchoring it into the silken support. Here the pupa hangs independently by the cremaster until the butterfly emerges. The shriveled larval skin may remain on the support until it drops off or is blown away by the wind.

When the caterpillar (fig. 16 A) sheds its last cuticular skin and reveals the pupa (D) that has taken its place, the change is indeed striking. The fully formed pupa, however, is the finished product of a transformation process. The caterpillar itself in its final stage (B)

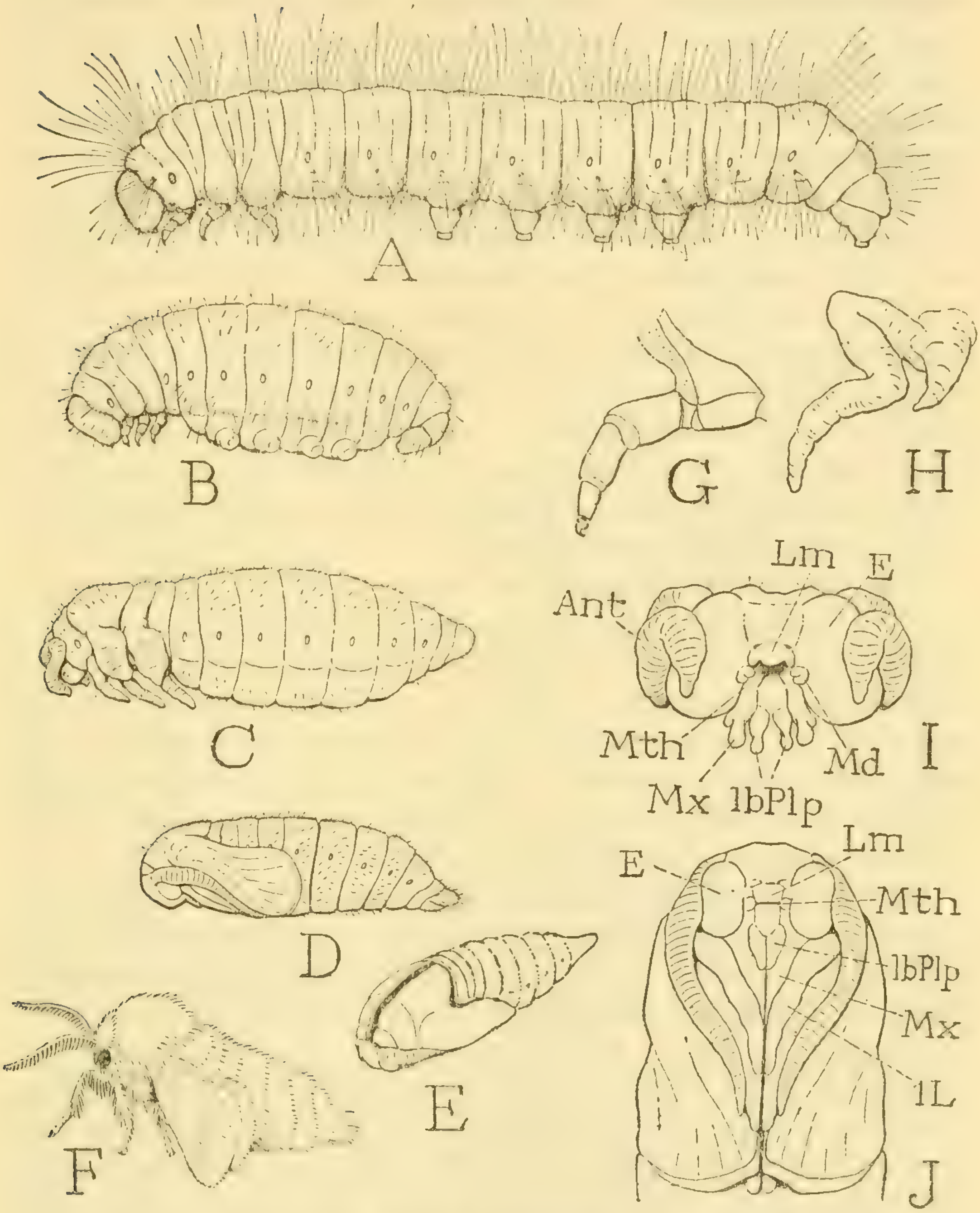

FIG. 16.—External changes during metamorphosis of the tent caterpillar, *Malacosoma americanum.*

A, The mature active caterpillar (length 3¾ inches). B, Final contracted stage of caterpillar in cocoon. C, The pharate pupa in last larval cuticle. D, The mature pupa. E, The split pupal shell after emergence of the moth (F). G, A larval leg. H, Leg of pharate pupa. I, Head of pharate pupa, anterior. J, Head and thorax of mature pupa, ventral.

Ant, antenna; *E,* compound eye; *1L,* first leg; *lbPlp,* labial palpus; *Lm,* labrum; *Md,* mandible; *Mth,* mouth; *Mx,* maxilla.

becomes immobile and greatly contracted. When it moults, the remodeled body still within the unshed larval cuticle appears as a preliminary stage of the pupa (C). An entirely new and different cuticle has been secreted by the epidermis, and the larval prolegs have been discarded with the larval skin. The wings are now everted, and the legs have taken on more of the adult structure (II). On the head (I) the large adult antennae (*Ant*) are conspicuous, and the mouth parts are undergoing development, except the mandibles (*Md*) which are reduced to small knobs. This concealed early period of the pupa has been called the "prepupa" or "propupa," but it is not a stage of the pupa equivalent to a larval instar, since it is not separated by a moult from the mature pupa (D). It is therefore better named by Hinton (1958) the cloaked, or *pharate,* pupa. By further development within the larval cuticle the pharate pupa becomes the mature pupa (D) in which the wings are enlarged, the legs and antennae are lengthened, and the mouth parts somewhat larger.

With the final shedding of the larval cuticle (the pupal ecdysis) the fully formed pupa (fig. 16 D) is liberated. The pupal mouth parts, antennae, wings, and legs lie flat against the body. In most Lepidoptera they become cemented to the body by an exuding, gluelike substance that soon hardens to a shell-like glaze over the entire surface. The pupa is then called a *chrysalis.* From now on the pupa does not change externally, but within it the special tissues of the larva go into dissolution, and adult development proceeds to the completion of the imago.

With most Lepidoptera the mouth parts continue their development within the pupal cuticle until they attain the typical adult structure (fig. 17 A). In the pupa of the tent caterpillar here described, however, the mouth parts actually regress from their state of development seen externally on the pupal cuticle (fig. 16 J) because the moth is one that does not feed. In the adult moth (fig. 17 B) the maxillae (*Mx*) have been reduced to small, entirely separate lobes at the sides of the mouth. The labium (*Lb*) also is much reduced, but its palpi have increased to long, three-segmented appendages. There is no trace of mandibles.

The degree of change that takes place within the pupa from larva to adult differs in different insects. In some, many of the larval tissues simply begin a new growth that forms directly the corresponding adult tissues. In others the special larval tissues break down, and their disintegration may be so nearly complete that little is left of the original larva. In extreme cases, therefore, the so-called metamorphosis of the insect is not literally a transmutation of the larva into the imago. The caterpillar, for example, does not actually become a moth or butterfly. The newly developing adult takes whatever parts of the larva can be utilized with adaptive modifications, such as the heart, the tracheae, and the nervous system. Otherwise it is a new creature built up from imaginal cells that have remained undifferentiated during the life of the larva, while the unused parts of the larva are cast off or go into dissolution within the pupa. As already noted, some adult organs may begin their development in an early instar of the larva.

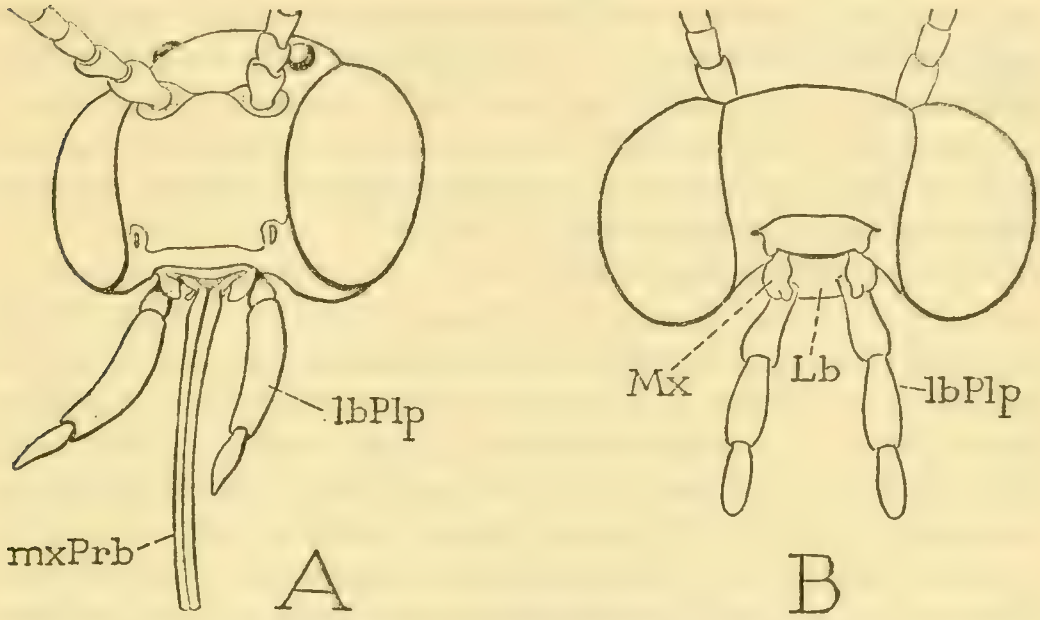

FIG. 17.—Examples of moths with and without a proboscis.

A, Head of peach borer moth, *Sanninoides exitiosa*, with fully developed maxillary proboscis. B, Tent caterpillar moth, *Malacosoma americanum*, with greatly reduced maxillae, no organs of feeding.

Lb, labium; *lbPlp*, labial palpus; *Mx*, maxilla; *mxPrb*, maxillary proboscis.

The interior of a lepidopterous pupa is filled with what appears to be a thick creamy substance. Under the microscope it is seen to consist of a clear, pale, amber-yellowish liquid containing a mass of minute bodies, some of which are blood cells and phagocytes, but most of them are disintegrating fat cells and liberated granules and fat droplets. The principal structural changes that take place within the pupa of a moth or butterfly affect the musculature, the fat tissue, and the alimentary canal.

The transformation of the muscular system differs in degree in different insects according to the difference in the musculature of the larva and the adult. Some larval muscles go over unchanged into the adult, others undergo a certain amount of reconstruction without losing their identity, and still others that are specifically larval muscles go into complete dissolution. Important muscles of the imago having no representatives in the larva are newly formed in the pupa.

In the Lepidoptera the dorsal and ventral bands of longitudinal larval muscles are preserved at least into the pupa. In the pharate pupa of *Malacosoma americanum* these muscles remain clean and intact with distinct striations, and are active through the pupal stage, enabling the pupa to move its abdomen. According to Finlayson (1956) the longitudinal muscles degenerate during the first two days of adult life. On the contrary, the fibers of the outer system of body wall muscles in the larva of *Malacosoma* are already in the pharate pupa distinctly in a state of disintegration. They have lost their healthy appearance, looking soft and flabby, and their striations are faint or gone. Associated with these muscles are always large numbers of phagocytic cells, and in the mature pupa this system of larval muscles completely disappears.

The adult musculature of the thorax of *Telea polyphemus* has been fully described and illustrated by Nüesch (1953). Both the thorax and its musculature are entirely reconstructed in the pupa. Blaustein (1953) gives a detailed account of the histogenesis of a longitudinal wing muscle in *Ephestia kühniella*. Small undifferentiated cells destined to become muscle cells, or myocytes, assemble where the new muscle is to be. By division these myoblasts form a syncytium of muscle cells during the first days after pupation. The cells then unite into long strands that become muscle fibers. The nuclei move to the periphery, a sarcolemma is formed, and fine thickenings in the myoplasm become fibrillae. Development of the muscle is completed by the twelfth day of the pupa, on the thirteenth the striations appear. Finally the completed muscle is attached to the body wall.

The vision of a muscle being independently formed in the midst of chaos within the pupa is a most mysterious thing in insect metamorphosis. In the first place, what directs the wandering myoblasts to assemble at the place where a specific muscle must be? Second, what compels the assembled myoblasts to go through the changes and complex associations that result in the formation of a contractile muscle?

The formation of most imaginal muscles, at least in some lepidopterous pupae, depends on their connection with nerves. Williams and Schneiderman (1952) and Williams (1958) describe experiments on diapausing pupae of *Cecropia* and *Polyphemus* from which the entire nervous system had been removed. When induced to develop, these pupae transformed into externally perfect moths, but on dissection they were found to be completely without muscles, except for the muscles of the alimentary canal and the heart. Others likewise have observed that the imaginal muscle rudiments must first be innervated to begin development. It seems, then, that myoblasts can assemble at the mechanically correct place for a specific new muscle, but here they must wait for a nerve connection before they can form the muscle. Finlayson (1956), in a further discussion of the relation of innervation to muscle development, says that sheets of fine muscle fibers lying under the epidermis of adult moths develop in the absence of innervation. (Possibly he refers to the heart muscles.)

The fat tissue, or so-called fat body, of older caterpillars still in an active condition consists of flat branched and lobulated cell masses having sharply distinct outlines. In the early pupa the fat masses break up into large granular cells, which later become ragged and frayed, and finally go into a state of disintegration, liberating their granular inclusions and droplets of oily fat. This material becomes food for the developing imaginal tissues, and in the lepidopteron much of it must be carried over to the adult to supplement the meager diet of the moth or butterfly.

The alimentary canal of the larva (fig. 7), as already shown, is entirely remodeled in the pupa in adaptation to the liquid diet of the adult (fig. 4). Verson (1905) gives a detailed description of the larval alimentary canal of the silkworm *Bombyx mori* and the metamorphic processes beginning at the time of cocoon spinning. The stomodaeum and proctodaeum are enlarged from circular growth centers, the so-called imaginal rings, at their inner ends. The degenerating larval epithelium of the mesenteron is thrown off into the lumen, and is replaced by an imaginal epithelium formed from groups of persisting regenerative cells. Essentially the same process of mesenteron reconstruction is described by Henson (1929) for *Vanessa,* and by Blaustein (1935) for *Ephestia kühniella.* The moth of *Ephestia* takes no food, and the stomodaeum is said by Blaustein to be reduced to a narrow tube closed from the mesenteron by a solid mass of cells. Some other moths that do not eat, such as the tent caterpillar moth, still retain an intact alimentary canal, suggestive that fasting in the adult stage is a recently acquired habit with them.

The fact that the organs of the pupa, external or internal, are those of the adult in a formative stage, and that the larval organs are cast off with the moult to the pupa, or go into dissolution within the pupa, supports the view that the pupa is a preliminary stage of the adult. For the attachment of the muscles on the adult cuticle, therefore, a secondary moult is necessary. This is the theory of Poyarkoff (1914), which is upheld by Hinton (1948), by Rockstein (1956), and by DuPorte (1958). An opposing theory, that of Jeschikov (1929), elaborated by Heslop-Harrison (1958), contends that the larva is a free-living stage of the embryo, and that the pupa represents the condensed nymphal instars of insects without metamorphosis. The idea of embryos climbing trees, eating leaves with fully developed mouth parts, and spinning cocoons, however, sounds like something from science fiction, and the condensation of several active instars into a single immobile stage having no resemblance to a nymph is biologically hard to visualize. Particularly it would seem strange that a flightless "nymphal" stage of a lepidopteron should have adult mouth parts, and the same might be said of other insects having specialized feeding organs in the adult stage, which appear first in the pupa.

There is nothing inherently improbable about the occurrence of an adult moult between the pupa and the imago; adult moulting occurs in other arthropods, in the apterygote insects, and the mayflies. Experimentally, moulting can be induced in the adult insect as well as in the nymph and larva (see Wigglesworth, 1954, p. 48). The corpus allatum hormone governs both nymphs and larvae alike, and at the end of the juvenile period it gives way to the prothoracic-gland hormone, which produces a moult followed by either an imago or a pupa according to whether the insect is hemimetabolous or holometabolous. These glands in insects without a pupal stage degenerate at the moult to the adult, but in holometabolous insects they persist into the pupal stage. Bodenstein (1953) has shown that even in the cockroach the prothoracic glands do not degenerate at the moult to the adult if the corpora allata are removed without injury to the corpora cardiaca. The young adult cockroach then moults again. In the holometabolous pupa, therefore, when the corpora allata have ceased to be functional, the moult to the imago can be an adult moult effected by the thoracic-gland secretion.

LIFE OF THE ADULT

The moth or butterfly is fully formed within the pupal shell and then emerges as a mature insect, except that the internal organs of reproduction may not yet be fully functional. The adult escapes through a slit along the back of the pupa (fig. 16 E). The butterflies have an easy time of getting out, since they are immediately free on emergence. Among the moths, however, many species on emergence from the pupa find themselves still enclosed in a cocoon. Some are fortunate in that the pupa itself has protruded its front end from the cocoon and thus allows the moth to escape. The pupae of Eriocraniidae have large active mandibles by which they tear open the cocoon and come to the surface of the ground where the adult can emerge into the air. In some cases the caterpillar is activated by an instinctive foresight and either leaves the head end of the cocoon very weakly woven, or makes a hinged door that the moth can open.

Those moths that on escape from the pupa find themselves still imprisoned in a closed cocoon are confronted with the problem of how to get out. Help comes from an unexpected source. In these species the shrunken silk glands of the larva now secrete a clear liquid, which issues from the mouth of the moth and softens the adhesive coating of the cocoon threads, thus enabling the moth to push its head through the end of the cocoon and escape. Trouvelot (1867) described the pre-emergence activities of *Telea polyphemus* as seen through a mica window inserted into the side of the cocoon. When the moth is fully formed within the pupa it becomes highly active and soon splits the pupal skin over the thorax. The head and legs are at once disengaged and the solvent liquid flows from the mouth. The insect now waits for the liquid to take effect on the cocoon. Then it makes strong contractions and extensions of the body, which force its head through the moistened silk. The strands separate, spread apart, and the moth issues without breaking a fiber.

Some of the moths and many of the butterflies are the most beautifully colored of living things, their only rivals being among the birds and the flowers. With the birds it is principally the males that are endowed with beauty, and for the utilitarian purpose of attracting the females. Of the flowers, it has been said that many are born to blush unseen and waste their sweetness on the desert air, but the poet did not know that the flowers too have a practical reason for both their perfume and their color, which is to attract the pollinating insects. The Lepidoptera, on the contrary, seem to make no use of their ornamentation. Though in many species the males are more brightly colored than the females, it is the males that are attracted to the females, and not by the charm of color in this case, but by odor. Kellogg (1907) has shown that the male of the silkworm moth finds a female entirely by her scent. The scent glands are eversible from the last abdominal segment of the female. When the glands are cut off, the male reacts as strongly to the glands themselves as to an intact female, and entirely ignores a female deprived of her glands. The silkworm moths cannot fly, but the males of some other moths are well known to be attracted to the females from long distances. The males themselves of many butterflies produce scents, some of which are attractive, others repellent.

If color plays no important part in the lives of moths and butterflies, except in the case of protective imitation and mimicry, it is difficult to understand why so many of them are endowed with such brilliant coloration and color patterns—surely not to appeal only to *our* esthetic sense and make attractive displays in the specimen cases of entomologists. It would seem, then, that we need a theory to explain their colors on a scientific basis of usefulness to the insects themselves. The same might apply to the colors and designs of seashells (or perhaps also to the beauty of a landscape).

Most butterflies live lives of unfettered freedom. They toil not, neither do they spin, nor make provision for the future, and yet no other insect is arrayed like some of them. Flitting from flower to flower, sipping nectar, courtship and marriage—this is the life of a butterfly. Only when the time comes for egg laying does the female moth or butterfly meet her one responsibility. Since many caterpillars are very particular about what plants or other material they feed on, the adult female must deposit her eggs where the young caterpillars on hatching will find their proper food. It seems as if the female retains a memory of her own caterpillar days, and the same maternal instinct is shared by various other insects. This "instinct," however, has been shown by Thorpe and Jones (1937) and by Thorpe (1938, 1939) to be due, in some insects at least, to the olfactory conditioning of the larva to its food, which is carried over to the adult female and induces her return to a source of the same odor. This is not exactly memory in the human sense, and it is probably more reliable, but it does not explain the possession by the female of a return instinct. A remarkable example of this instinct is shown by the monarch butterfly, the larvae of which feed on the milkweed. In the fall many adults in northern regions migrate in flocks to the south, where they spend the winter; in the spring the females return north and find milkweeds on which to deposit their eggs.

The conditioning factor of the return instinct is not always food; the female dragonfly or the female mosquito must deposit her eggs in an aquatic environment suitable to the larvae. The same is true of the moth *Nymphula,* the larvae of which are aquatic. The females of *N. maculalis* described by Welch (1916) lay their eggs on the undersurfaces of leaves of the yellow waterlily, using wherever available oviposition holes cut in the leaves by the beetle *Donacia.* The moth inserts her abdomen through one of these holes and attaches her eggs to the underside of the leaf in concentric circles around the beetle eggs. The moths are said to remain in the neighborhood of the water, but certainly no larval conditioning could account for their special ovipositing instinct. The larvae live submerged on the undersides of the leaves, where they enclose themselves in cases formed of cut-out pieces of leaves, but they do not swim.

Butterflies have many natural enemies, including entomologists with collecting nets, but those of northern and temperate regions that survive the summer may be still plentiful at the end of the season. In the fall or early winter when cold weather comes on most of them simply die a peaceful death. Hardy individuals of some species, such as the mourning-cloak butterfly *Nymphalis antiopa,* however, live through the winter under logs or stumps lying on the ground, and the monarch butterfly imitates the birds in flocking south for the winter.

For the others, both moths and butterflies, nature has made some provision for carrying their species through the winter in an immature stage. Perhaps most commonly it is the pupa that hibernates, but with some species the caterpillar lives through the winter, or the winter is passed in the egg stage. The overwintering caterpillar is usually within the protection of a cocoon, but the brown woolly bear hibernates in a covering of its own wool, and young tent caterpillars remain in the egg shells. The female moth of this species, *Malacosoma americanum,* lays her eggs in late spring attached to a twig of a favorite tree of the caterpillar, and covers them with an impervious coating of material from the accessory glands of her reproductive system. Within three weeks or a little longer the young caterpillars are fully formed in the eggs. Here they remain protected under the egg covering through the summer, fall, and winter to emerge early the following spring.

It is interesting to note how the lives of insects in northern regions have become adapted to the alternation of winter with summer. By contrast, tropical species can go on indefinitely as a succession of broods without interruption. The northern insects, therefore, have undergone a special evolution to meet the condition of survival imposed upon them. Even within a single order such as the Lepidoptera different species have solved the problem of survival in different ways.

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Birds often form groups that include individuals of several different species. Such heterogeneous groups may be called "mixed species flocks."

There are many different kinds of mixed species flocks. Some are composed of only two species, while others may include many more, probably over a dozen in extreme cases. Some mixed flocks are essentially transitory, while others are semipermanent, very long-sustained or dissolved and re-formed at more or less regular intervals. Some seem to be very loosely organized, while others are tightly integrated and have a complicated social structure.

Mixed species flocks are found almost everywhere, in almost all environments; but they seem to be most common and varied and probably attain the greatest structural complexity in certain regions of the humid Tropics. In such regions, most of the more complex flocks are largely or completely composed of passerines.

Mixed species flocks have been noted by almost all ornithologists and naturalists who have traveled in the Tropics since Bates (1863), Wallace (1869), and Belt (1874). Among the more recent or longer accounts of such flocks are descriptions in Chapin (1932), Davis (1946), Johnson (1954), Mitchell (1957), Moynihan (1960), Rand (1954), Slud (1960), Stanford (1947), Stresemann (1917), Swynnerton (1915), and Winterbottom (1943 and 1949). Many other, earlier, descriptions of mixed flocks are listed in Rand, 1954. Some aspects of mixed flocks have been discussed at considerable length in some or all of these publications; but the social reactions between individuals of different species within mixed flocks have not been analyzed in detail.

This paper is an attempt to provide more precise information about some of the behavior mechanisms responsible for the formation and maintenance of certain types of mixed species flocks. It also includes some suggestions about the probable course of evolution of such flocks.

Most of the observations were made in Panamá between September 1957 and November 1960. Special attention was paid to mixed flocks of finches, tanagers, honeycreepers, and warblers. Several different types of mixed flocks of these birds are common in different habitats in Panamá. The two that were studied most intensively may be called the "blue and green tanager and honeycreeper flocks" and the "montane bush flocks." These are terms of convenience. Flocks of the first type frequently include other species in addition to blue and green tanagers and honeycreepers. Flocks of the second type are not confined to bushy habitats.

Mixed blue and green tanager and honeycreeper flocks were observed, off and on, throughout the whole period of this study. Other types of mixed flocks were observed much more briefly (see below).

THE BLUE AND GREEN TANAGER AND HONEYCREEPER FLOCKS

DESCRIPTION OF THE MOST COMMON SPECIES

Before proceeding to discuss these flocks, it may be helpful to describe the appearance of some of the species involved and to say something of their behavior apart from mixed flocks in central Panamá. This will be partly a recapitulation of data included in other publications (e.g., Skutch, 1954; Sturgis, 1928; and Moynihan, op. cit.).

Plain-colored Tanager (*Tangara inornata*).[1]—A comparatively small tanager. Sexes nearly identical in plumage: largely dull gray, with black wings and tail and bright blue patches on the upper wing coverts.

Resident in Panamá. Most common along the edges of fairly mature forest but occurring also in young second-growth forest. Primarily a bird of the treetops.

Very gregarious apart from mixed species flocks. Very restless and active. Very noisy, frequently uttering loud and sharp *tsit* call notes, which may be accelerated to produce mechanical-sounding rattles.

Palm Tanager (*Thraupis palmarum*).—A moderately large tanager. Sexes nearly identical in plumage: dull olive-green, with black wings and tail.

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[1] The scientific names of all the Panamanian species cited in this paper follow Eisenmann, 1952 and 1955.

Resident in Panamá. Common both in young second-growth forest and along the edges of fairly mature forest. Primarily a bird of the treetops.

Moderately gregarious apart from mixed species flocks, several pairs or family groups sometimes occurring together. Somewhat less active and restless than the plain-colored tanager. Very noisy, frequently uttering rather plaintive-sounding *wheet* call notes. Adult males (at least) also utter twittering songs very frequently in some of the situations in which other species usually utter call notes (see Eisenmann, 1952, for a transcription of the typical song of this species in Panamá).

Blue Tanager (*Thraupis episcopus*).—Slightly smaller than the palm tanager. Sexes nearly identical in plumage; dull light blue, with brighter blue wings and tail (in the Panamanian subspecies *diaconus*).

Resident in Panamá. Most common in young, scattered, second-growth forest, but occurring also along the edges of fairly mature forest. Primarily a bird of the treetops but less markedly so than the plain-colored or palm tanagers.

Moderately gregarious apart from mixed species flocks, like the palm tanager, and similar to the palm tanager in notes and movements.

Golden-masked Tanager (*Tangara larvata*).—Similar to the plain-colored tanager in size. Sexes nearly identical in plumage; conspicuously marked with an intricate pattern of bright blue, yellow, black, and white.

Resident in Panamá. Most common in young, scattered, second-growth forest and in gardens, but occurring also along the edges of fairly mature forest. Common in bushes, near the ground, as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks, seldom or never congregating in groups larger than a single family. Otherwise similar to the plain-colored tanager in behavior.

Green Honeycreeper (*Chlorophanes spiza*).—Very tanagerlike in appearance. Like the species of the genus *Tangara* in size and shape, aside from the bill. Sexes very different in adult plumage. The adult male is bright blue-green with a black head. The adult female is bright grass-green all over. Juveniles of both sexes are grass-green like the adult female.

Resident in Panamá. Distribution similar to that of the plain-colored tanager; most common along the edges of fairly mature forest. Primarily a bird of the treetops.

Also very similar to the plain-colored tanager in voice and movements, but not usually very gregarious apart from mixed species flocks

Shining Honeycreeper (*Cyanerpes lucidus*).—Much smaller than the green honeycreeper, and much less tanagerlike in general appearance. Sexes very different in adult plumage. The adult male is blue, with black throat, wings, and tail. The adult female is green above, with a bluish head, and dirty white below, streaked with bluish. Juveniles of both sexes are similar to the adult female.

Resident in Panamá. Most common along, perhaps confined to, the edges of fairly mature forest. Primarily a bird of the treetops.

Very similar to the green honeycreeper in voice and movements. Only slightly gregarious apart from mixed species flocks.

Red-legged Blue Honeycreeper (*Cyanerpes cyaneus*).—Similar to the shining honeycreeper in size and shape. Sexes different in appearance in adult plumages. The adult male has two distinct plumages. In full nuptial plumage the adult male is a brilliant sapphire blue, with turquoise blue crown, black upper back and tail, and black wings with bright yellow edgings on the primaries and secondaries. In nonbreeding plumage the adult male is dull gray-green, with the same wings and tail as in the breeding plumage. The adult female is always dull gray-green all over. Juveniles of both sexes are similar to the adult female.

Resident in Panamá. Very common both in young, scattered, second-growth forest and along the edges of fairly mature forest. Primarily a bird of the treetops.

Very gregarious apart from mixed species flocks. Very restless and noisy, frequently uttering several different types of call notes and/or hostile notes, most of which are quite distinctive in sound.

Blue Dacnis (*Dacnis cayana*).—Rather similar to the green honeycreeper and the *Tangara* tanagers in shape, but slightly smaller. Sexes very different in appearance when adult. The adult male is bright blue (greenish in some lights) with black markings. The adult female and juveniles of both sexes are grass-green with bluish heads.

Resident in Panamá. Most common in young second-growth forest but occurring also along the edges of fairly mature forest. Primarily a bird of the treetops.

Only very slightly gregarious apart from mixed species flocks. Rather active and restless, but less noisy than the green honeycreeper or the red-legged blue honeycreeper.

Crimson-backed Tanager (*Ramphocelus dimidiatus*).—A rather large tanager (approximately the same size as the palm and blue tanagers). Very conspicuously and distinctively colored. The adult male is bright crimson and black. The adult female and juveniles of both sexes are similar but duller.

Resident in Panamá. Common both in young, scattered, second-growth forest and along the edges of fairly mature forest, both in moderately low bushes and in the treetops.

Moderately gregarious apart from mixed species flocks. Active and noisy, frequently uttering nasal *anh* notes which are quite unlike the notes of any other Panamanian tanagers or honeycreepers except the other species of *Ramphocelus*.

Summer Tanager (*Piranga rubra*).—Migratory. Absent from Panamá during the northern breeding season. Most individuals observed in Panamá seemed to be young; in more or less complete juvenal plumage, dull yellowish in color (males usually begin to assume the rosy-red adult plumage before leaving in the spring).

Fairly common in many different types of vegetation in many areas of Panamá.

Almost completely nongregarious apart from mixed species flocks in Panamá. Not very active. Moderately noisy, frequently uttering a rattling *pi-ti-ti-tuck* call.

White-lined Tanager (*Tachyphonus rufus*).—A rather large tanager. Sexes very different in appearance when adult. The adult male is black, with white underwing coverts. The adult female and juveniles of both sexes are rufous brown.

Resident in Panamá. Most common in young, scattered, second-growth forest, but common also in moderately low bushes as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks. Moderately active. Not very noisy.

Fulvous-vented, Thick-billed, and Yellow-crowned Euphonias (*Tanagra fulvicrissa, T. laniirostris,* and *T. luteicapilla*).—Small to very small tanagers. The adult males of all three species are largely black glossed with steel-blue above, with yellow foreheads and yellow underparts. The adult females and juveniles of all three species are largely olive.

All three species are resident in Panamá. The fulvous-vented euphonia is most common along the edges of fairly mature forest. The thick-billed and yellow-crowned euphonias are more characteristic of young second growth.

All three species seem to be only moderately gregarious apart from mixed species flocks. They are all very active and noisy, uttering a variety of call notes almost constantly when moving.

Bananaquit (*Coereba flaveola*).—Another honeycreeper type, but very different from the blue and green honeycreepers in many respects.

Very small. Sexes nearly identical: gray above, with a black cap, and white superciliary stripes, and largely yellow below.

Resident in Panamá. Common both in young second-growth forest and scrub, and along the edges of fairly mature forest, in low bushes as well as in the treetops.

Only very slightly gregarious apart from mixed species flocks. Active. Very noisy during the breeding season, when the males may utter shrill monotonous songs for hours on end.

Yellow Warbler (*Dendroica petechia*).—All the yellow warblers observed with mixed species flocks during this study appeared to be migrants belonging to the subspecies *aestiva* which breeds in North America. They were largely yellow with rufous on the crown (but not over the whole head, as in the resident race *erithachorides*). They were observed only during the Northern Hemisphere winter.

In Panamá these warblers are widely distributed and moderately common. They are active, but silent, and almost completely nongregarious apart from mixed species flocks.

Streaked and Buff-throated Saltators (*Saltator albicollis* and *S. maximus*).—Relatively large finches. In both species the sexes are nearly identical. The streaked saltator is grayish olive above, with white superciliary stripes, and whitish below, streaked with grayish olive. The buff-throated saltator is largely olive above and gray below, with white superciliary stripes and a buff throat bordered by black.

Both species are resident in Panamá and most common in young second-growth forest. They are primarily birds of the treetops and the upper levels of moderately high shrubbery.

They are not very active or noisy, and only slightly gregarious apart from mixed species flocks.

OTHER SPECIES

The species described above are the ones that occur most frequently in the blue and green tanager and honeycreeper flocks in central Panamá, in the Canal Zone and adjacent areas.

Many other species may also occur in such flocks, but much less frequently, either because they themselves are rare, or because they are not attracted to such flocks very strongly. Among these species are the scarlet-thighed dacnis (*Dacnis venusta*), the white-winged tanager (*Tachyphonus luctuosus*), the yellow-rumped tanager (*Ramphocelus icteronotus*), the resident yellow-tailed and yellow-backed orioles (*Icterus mesomelas* and *I. chrysater*), the migrant Baltimore oriole (*I. galbula*), the clay-colored thrush (*Turdus grayi*), a variety of flycatchers (especially the yellow-bellied elaenia, *Elaenia flavogaster,* the social flycatcher, *Myiozetetes similis,* and the rusty-margined flycatcher, *M. cayanensis*), and several different types of vireos and cotingas.

There are also some species, including the green-backed sparrow (*Arremonops conirostris*), the dusky-tailed ant-tanager (*Habia fuscicauda*), the blue-black grassquit (*Volatinia jacarina*), the variable seedeater (*Sporophila aurita*), and the yellow-bellied seedeater (*S. nigricollis*), that are associated with blue and green tanager and honeycreeper flocks in some circumstances, but are usually more or less distinctly separated by habitat preference (see below).

Finally, there are some species, such as hummingbirds, woodpeckers, and the Tovi parakeet (*Brotogeris jugularis*), that are not infrequently found in close physical proximity to blue and green tanager and honeycreeper flocks, but still appear to be essentially independent of such flocks, as their movements are seldom or never coordinated with those of the flocks.

DESCRIPTION OF THE FLOCKS

Mixed blue and green tanager and honeycreeper flocks are very widely distributed in central Panamá, but they are most characteristic of lowland areas. Some of the species of what may be called the "blue and green tanager and honeycreeper alliance" [2] seem to be absolutely confined to the lowlands. Other species of the alliance occur in both lowland and highland areas. I have seen some of them near the peaks of the highest mountains in central Panamá, around 3,200-3,400 feet above sea level, and even higher in western Panamá (see below); but all or most of them are more common in the lowlands than in the mountains. I have never seen large typical mixed blue and green tanager and honeycreeper flocks above 2,000 feet elevation in central Panamá.

Most of the species that occur in mixed blue and green tanager and honeycreeper flocks are essentially arboreal, and all the species that are regular members of such flocks are primarily "edge" birds. Most of them also prefer to remain as high above the ground as possible. Typical mixed blue and green tanager and honeycreeper flocks usually stay in or near the treetops, and never occur very far

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[2] The term "alliance" will be used throughout this paper to include all the species that are regular members (see below) of a particular type of mixed flock, plus any other species that occur in that particular type of mixed flock relatively frequently.

inside the forest below the canopy. They come nearest to the ground in certain areas where tall trees are scarce. In such areas they sometimes come down to the top of low scrub, no more than a few feet above the ground. They may then be joined by such species as the green-backed sparrow and the dusky-tailed ant-tanager, which usually occur inside low scrub. These low-scrub species usually drop out of mixed blue and green tanager and honeycreeper flocks as soon as the other members of the flocks return to the trees.

All or most of the members of any given mixed blue and green tanager and honeycreeper flock are usually in approximately the same level of vegetation at any given time. This is one of the more distinctive features of such flocks (see below).

Mixed blue and green tanager and honeycreeper flocks are formed most frequently and are most often large during the nonbreeding season. Birds of many species of the blue and green tanager and honeycreeper alliance tend to associate with individuals of other species of the alliance relatively infrequently during the breeding season, as they adopt territories or (if they already own territories) they spend more and more time in the immediate vicinity of their nests; but they seldom or never stop associating completely. Every once in a while during the breeding season a mixed blue and green tanager and honeycreeper flock will be formed which is quite as large and complex as any formed during the nonbreeding season.

Mixed blue and green tanager and honeycreeper flocks are not very stable in any circumstances. Associations between individuals of different species of the blue and green tanager and honeycreeper alliance tend to be brief and are very seldom or never sustained continuously over a whole day. The composition of mixed blue and green tanager and honeycreeper flocks is also extremely variable, almost from minute to minute. Birds of different species are constantly coming together, staying together for a brief period, and then becoming separated again as some move on (perhaps going a considerable distance away) and others do not.

In spite of this short-term variability, it is quite obvious that the same birds of the same species tend to come together again and again. In favorable habitats (see below) the same birds of the same species may rejoin one another a dozen times a day and will certainly rejoin one another day after day for periods of at least several months.

None of the species of the blue and green tanager and honeycreeper alliance seems to have any special behavior patterns whose main function is to attract individuals of other species. In many or most cases, individuals of different species just tend to stick together whenever they happen to run across one another in the course of their ordinary activities.

Mixed blue and green tanager and honeycreeper flocks can be formed at any time of the day between sunrise and sunset; but they are probably more common and larger, on the average, during early morning, when all the species of the alliance are most active, than during later periods of the day.

The social spacing of individual birds in mixed blue and green tanager and honeycreeper flocks is quite as variable as the composition of such flocks. Sometimes some or all of the members of a flock are very close together, within a few inches of one another. Oftener they are more scattered, most of them being separated from their nearest neighbors by distances of several feet or yards. Sometimes they are so widely scattered that their membership in the same flock is revealed only by their tendency to move in the same direction at approximately the same time.

The more highly integrated mixed blue and green tanager and honeycreeper flocks (which are not necessarily the flocks in which the members are nearest to one another in space) seem to be confined within certain definite ranges. In some cases, at least, the borders of these ranges seem to be directly determined by features of the vegetation or topography, rather than social contacts between adjacent flocks.

Individual birds, pairs, and larger family groups of some species may defend territories while they are part of mixed flocks (see below) ; but there is no joint defense of the flock range as a whole.

Most of the species of the blue and green tanager and honeycreeper alliance seem to have rather generalized feeding habits. Most of the tanagers, and probably the saltators, eat a great deal of fruit; the honeycreepers eat fruit and nectar; and all the species of the alliance eat many insects. The feeding habits of all these species seem to overlap widely. It is very common to see at least three or four species feeding on the same food at the same time in the same place. This occurs most frequently when some favored fruit or flower is particularly abundant, and when swarms of insects emerge after hatching.

It might be supposed, therefore, that the association of many of these species in mixed flocks is purely coincidental. It is conceivable that such flocks might be formed and maintained simply because many species are attracted to, and remain near, the same food sources.

There are various indications, however, that at least some (and perhaps the majority) of the associations between species of the blue and green tanager and honeycreeper alliance are produced by some social factors, in addition to (or instead of) the direct and immediate stimulus of food.

The effects of such special social factors are obvious in the case of some associations. Birds of some species definitely do tend to join and follow birds of certain other species in places (e.g., the top branches of tall, dead, bare trees) where there is little or no food available and/or when they are obviously not in the mood to feed (as shown by the fact that they do not begin to feed immediately after joining or following).

The factors controlling the behavior of other species are more obscure. It is evident, nevertheless, that the birds of the blue and green tanager and honeycreeper alliance inhabiting any given area are relatively seldom scattered randomly among the particular parts of that area where food is most abundant at any given time. They tend to occur in "clumps," first in one part and then in another.

The minor movements of many mixed flocks are also extremely suggestive. The behavior of birds feeding in *Cecropia* trees on Barro Colorado Island may be cited as an example. These trees are common along the edges of clearings, and many or most of the trees in any particular area seem to bear fruit at almost exactly the same time. Large mixed flocks of the frugivorous members of the blue and green tanager and honeycreeper alliance frequently feed on the ripe *Cecropia* fruits. Such flocks are usually very restless. All the birds of a mixed flock may be feeding on the fruits of one particular tree, when one bird or part of the flock may suddenly fly over to an adjacent tree and begin to feed there. In such cases, the remaining members of the flock, left in the first tree, frequently (perhaps usually) fly over to the second tree sooner or later. A mixed flock may visit a dozen different *Cecropia* trees in fairly rapid succession in this way. It is also quite common for a flock to fly back and forth, visiting and feeding in these same trees again and again. In view of the frequency of such back-and-forth alternation, and the fact that the fruits of almost all the trees usually seem to be in essentially identical condition, it is difficult to believe that all the members of such a mixed flock are really looking for a different food when they move. It seems more likely that most of the members of the flock are simply reacting to the movements of the first birds to fly; and the first birds may have flown, or started to fly, for any one of several different reasons, including pure "restlessness," slight alarm, or a brief outburst of aggressiveness within the flock. Such reactions would at least suggest that some positive social relationships are widespread among most of the species of the blue and green tanager and honeycreeper alliance.

It is difficult to believe, in any case, that birds of different species could occur together as frequently as many members of the blue and green tanager and honeycreeper alliance without forming social bonds among themselves.

Many or most of the birds in mixed blue and green tanager and honeycreeper flocks may be attracted to one another as a result of some conditioning process, having "learned" that the presence of other species is usually an indication of food in the neighborhood. Birds of the blue and green tanager and honeycreeper alliance may also tend to secure more food more easily, in the long run (although not always), when in mixed flocks than when not in mixed flocks. It is even possible that facilitation of feeding is the principal adaptive advantage of the habit of forming mixed flocks, i.e., the principal reason why such habits were selected during the evolution of many species of the blue and green tanager and honeycreeper alliance (but see comments below). Even if all these possibilities should be established as proven facts, however, they would not be evidence that the attraction of food is the sole cause of the formation and maintenance of many or most of the associations between individuals of different species in most of the mixed blue and green tanager and honeycreeper flocks observed at the present time.

There are even some indications that some slight social attraction between individuals of different species is very widespread among passerine birds in general, even species that are seldom or never found in mixed flocks. Observation of many different species of passerine birds in Panamá would suggest that an individual of almost any species may approach, or at least perform intention movements of approaching, individuals of almost any other species, especially upon first hearing or seeing the other individuals. This may be nothing more than "curiosity"; but it does tend to bring birds together, and it may be one of the sources from which more strongly gregarious tendencies have been developed in the course of evolution (see below).

All other factors being equal, the chances of one bird's approaching another bird of another species seem to be dependent upon the degree of resemblance between the two birds. Birds of different species are more likely to approach one another if they resemble one another in certain conspicuous features, such as color or voice, than if they are very different from one another in all features.

Although food may not be the only, or the principal, attraction bringing birds of the blue and green tanager and honeycreeper alliance together, the mixed flocks of this alliance may still be considered primarily feeding groups in one sense. Almost all the birds in such flocks spend most of their time feeding, or (apparently) looking for food, as long as they remain in the flocks. (They also spend most of their time feeding and looking for food when they are not in mixed flocks.) This does not mean that birds never perform other activities in mixed flocks. Any individual or group of any species in a mixed flock may preen or perform other comfort activities, or engage in hostile disputes, or start courtship, or even just pause to rest while in the flock; but the performance of such nonfeeding patterns usually tends to reduce the cohesion of the flock. The birds performing such nonfeeding patterns tend to drop out of the flock if they continue such activities for any appreciable length of time. The flock just moves off and leaves them behind.

The only nonfeeding activities that may greatly increase the cohesion of mixed flocks are escape and mobbing reactions. Escaping and mobbing birds tend to bunch together particularly closely. Mobbing also attracts other birds in the neighborhood, and the sight of one bird escaping may induce other birds to fly in the same direction.

In the course of the present study, mixed flocks of the blue and green tanager and honeycreeper association were observed most thoroughly in three different areas:

(1) On Barro Colorado Island, in and around the large clearing of the biological station. This clearing is roughly rectangular, approximately a quarter of a mile long and 300-500 yards wide in most places, and stretches up a steep hill (approximately 275 feet high) from the shores of Gatún Lake. It is surrounded by fairly mature second-growth forest on three sides. There are also some trees and patches of shrubbery (mostly fruit trees and introduced ornamental bushes) scattered irregularly within the clearing. Mixed blue and green tanager and honeycreeper flocks are common in the trees around the edge of the clearing, and sometimes visit the trees and shrubs within the clearing, especially when the birds are crossing from one side of the clearing to the other.

(2) On the mainland, about 2 miles away, near the little town of Frijoles. In this area observations were made along approximately a half mile of railroad track and along several narrow paths leading off the track. The vegetation in this area is second growth, obviously younger than most of the forest on Barro Colorado Island. It is also extremely diverse, ranging from low scrub and gardens around houses

to moderately thick forest. There are a few cultivated fields (most of which were bare or planted with low crops at the times of observation) scattered in the midst of the forest and scrub, and a few yards of grass along both sides of the railroad track. The ground beside the railroad track is level, but the rest of the area is quite hilly. Mixed blue and green tanager and honeycreeper flocks occur in almost all the scrubby and forested parts of this area. (A peculiar feature of this area is a series of steel pylons, carrying electric cables, at regular intervals along the railroad track. Most of these pylons are separated from the nearest trees by an appreciable distance. The distribution of some birds is sometimes greatly affected by the presence of these pylons.)

(3) About 10 miles from the other two, near the town of Gamboa. The vegetation in this area is much the same as in the Frijoles area. Most of the observations in this area were made along approximately a mile of concrete road. Mixed species flocks are common along the edges of the forest and high scrub on both sides of the road.

The nature of the mixed flocks in these areas may be illustrated in more detail by the accompanying tables.

(It should be emphasized that the data in these tables are merely examples. The analyses of flocks and the behavior of individual species in the following pages are based upon many other types of counts and other observations, in addition to the data summarized in these particular tables.)

The data summarized in the first group of tables (1 to 19) were obtained by observation of birds in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959. This time of the year is the nonbreeding season for the members of the blue and green tanager and honeycreeper alliance.

Table 1 is an attempt to indicate the frequencies with which various species may occur in mixed flocks in this area at this time of the year. It is a count of the number of times individuals of the 12 most frequently observed species of tanagers, honeycreepers, and warblers were seen in mixed flocks and not in mixed flocks during the whole period of observations. This count was made as follows:

An observer walked around the clearing and counted every finch, tanager, honeycreeper, and warbler seen. Any of these birds seen in a tree or bush in which there were also one or more other birds of some other species (any other species, including nonpasserines) at the same time were counted as being in a mixed flock. The only exceptions were some birds in very large trees. In such trees a bird was counted as being in a mixed flock only if there were one or more birds of some other species within approximately 50 feet. Any finch, tanager, honeycreeper, or warbler flying in a group with one or more birds of some other species was also counted as being in a mixed flock. Each bird was counted individually. Thus, for instance, when two tanagers of the same species were seen together they were counted as two in the table.

TABLE 1.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	106 (10)	478 (46)	569	1047
Palm tanagers	27 (9)	145 (48)	156	301
Blue tanagers	18 (7)	121 (45)	148	269
Golden-masked tanagers ...	9 (18)	25 (41)	36	61
Green honeycreepers	9 (8)	50 (44)	63	113
Red-legged blue honeycreepers	4 (3)	84 (73)	31	115
Blue dacnises	0	33 (50)	33	66
Crimson-backed tanagers ...	1	40 (25)	121	161
Summer tanagers	0	23 (43)	30	53
Fulvous-vented euphonias ..	1 (4)	14	11	25
Bananaquits	3 (2)	52 (39)	82	134
Yellow warblers	0	17 (18)	75	92

Birds other than finches, tanagers, honeycreepers, and warblers were counted only when they occurred in association with the latter but were counted in the same way.

The observer made no attempt to follow any single birds or flocks.

As soon as any single bird or flock was counted, he resumed walking around the clearing. As most periods of observation lasted for several hours, the observer repeatedly retraced his steps and made counts in the same places. Many individual birds and some flocks were undoubtedly counted several times during any single period of observation. Individual birds and flocks that did not move about very much were counted repeatedly in the same places. (It should be noted, however, that the composition of mixed flocks usually changed, to a greater or lesser extent, between successive counts.) Individual birds and flocks that did move about appreciably (as most did) were often counted several times in different places, although a definite attempt was made not to count the same individuals or flocks twice within 15 minutes. Most individual birds around the clearing were also counted repeatedly on successive days.

Thus the figures shown in table 1 under the headings "Number of times individuals seen in mixed flocks" and "Number of times individuals seen not in mixed flocks" are certainly very much larger than the real numbers of individual birds seen in mixed flocks and apart from mixed flocks.

It is difficult to estimate the actual numbers of individual birds of different species in and around the clearing during the periods in which these counts were made, as few of the birds were distinctively marked or banded, and there were certainly some changes in the populations of some or all species between October and December. As a very rough estimate, I would guess that there were at least 10 plain-colored tanagers (quite possibly 16), 4 palm tanagers, 4 blue tanagers, 2 golden-masked tanagers, 5 green honeycreepers, 6 red-legged blue honeycreepers, 4 crimson-backed tanagers, 2 summer tanagers, 2 fulvous-vented euphonias, 4 bananaquits, and 2 yellow warblers in and around the clearing more or less regularly during all or most of the period between October and December. Additional individuals of all or most of these species turned up from time to time, but usually did not stay long.

(It will be noted that no finches are included in table 1. Most of the finches in and around the clearing seldom or never joined the mixed flocks of the blue and green tanager and honeycreeper alliance or went very high in the trees. The only exceptions were variable seedeaters, some of which, especially males, did go high in the trees and were frequently associated with mixed blue and green tanager and honeycreeper flocks. They are not counted in table 1 simply because they spent most of their time on the ground or in low grass in the clearing when they were not in the trees, and it was felt that to count only the variable seedeaters in trees would provide a very inadequate sample of the population of the area and convey a misleading impression of the behavior of the species.)

The method used in compiling table 1 (which was used in order to obtain the largest possible count of associations between species) has certain inevitable defects. It is probable, for instance, that some birds that were really associated with mixed flocks were not counted as members of such flocks simply because they did not happen to be in the same trees as the other members of their flocks when they were counted. It is also probable that some of the groups of birds that were classified as mixed flocks during this count were essentially chance aggregations of individuals that were not really reacting to one another in any significant way. Many or most of the birds in most of the groups, however, did show some tendencies to keep together, at least intermittently or for brief periods of time. Many of the groups seemed to be very well organized, composed of individuals that tended to join or follow one another in a very regular manner.

Perhaps the most conspicuous examples of groups held together by relatively strong social bonds were flocks that moved about as units, all the individuals of the group flying close together at the same time and in the same direction. The number of times individuals of different species were seen flying in such groups is also indicated in table 1 under the heading "Number of times individuals seen in obviously integrated mixed flocks."

The figures in parentheses in table 1 are percentages of the total number of times individuals of any given species were seen, both in mixed flocks and not in mixed flocks. Thus, for instance, the 106 times individual plain-colored tanagers were seen in tightly integrated mixed flocks are approximately 10 percent of the total number of times (1,047) individual plain-colored tanagers were seen, both in mixed flocks and not in mixed flocks.

Table 2 may be considered a supplement to table 1. It is a record of the same observations as those recorded in table 1, summarized in a different way.

The number of times the different species (not the individual birds) were seen in mixed flocks and not in mixed flocks is indicated in the first two columns of table 2. In order to get these figures, individual birds were not counted separately unless they were seen without any other individuals of the same species nearby. Thus, for instance, when two or more tanagers of the same species were seen together in the same small tree at the same time they were counted as one in these columns.

The total number of times each species was seen is also indicated in table 2, in the third column. The percentage of times each species was seen in mixed flocks is shown in the fourth column. These percentage figures were calculated by using the figures in the first and third columns.

TABLE 2.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	172	202	374	46	2.78	2.82
Palm tanagers	126	108	234	54	1.15	1.44
Blue tanagers	96	111	207	46	1.26	1.33
Golden-masked tanagers	25	36	61	41	1.00	1.00
Green honeycreepers	50	58	108	46	1.00	1.09
Red-legged blue honeycreepers ..	47	22	69	68	1.79	1.40
Blue dacnises	26	32	58	45	1.27	1.03
Crimson-backed tanagers	19	65	84	23	2.11	1.86
Summer tanagers..	20	27	47	43	1.15	1.11
Fulvous-vented euphonias	13	11	24	54	1.08	1.00
Bananaquits	44	68	112	39	1.18	1.21
Yellow warblers ..	17	75	92	18	1.00	1.00

Finally, the average number of individuals of the different species per mixed flock and per nonmixed flock is indicated in the last two columns of table 2. For this purpose every solitary individual that was seen by itself alone, without any other birds of the same or any other species nearby, was considered to form a separate nonmixed flock of its own.

Tables 3 to 6 are counts of special reactions within the mixed flocks in and around the clearing on Barro Colorado Island.

Table 3 is a partial list of interspecific following reactions observed between October 26 and December 20. For the purposes of this table, only flying reactions were counted, when a bird of one species flew after a bird of another species. In some cases, the two birds flew from one tree to another; in other cases, from one branch to another within the same tree. Only rapid reactions were counted, when one bird flew after another within 30 seconds after the first bird flew. Only those reactions are shown in which the following bird was a tanager, honeycreeper, or warbler (of any species—not only the ones included in tables 1 and 2).

TABLE 3.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Unambiguous interspecific following reactions by tanagers, honeycreepers, and warblers. (Interspecific following reactions by finches are omitted from this table because all such reactions observed during this period were ambiguous in one way or another.)

No. of cases seen	Species following	Species being followed
15	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
4	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
2	Golden-masked tanager	Plain-colored tanager
1	do.	Blue tanager
3	Green honeycreeper	Plain-colored tanager
1	Summer tanager	Plain-colored tanager
1	do.	Palm tanager
2	Fulvous-vented euphonia	Plain-colored tanager
1	Bananaquit	Green honeycreeper
1	Chestnut-sided warbler	Golden-masked tanager
34		

Table 3 is also a partial list because it includes only the following reactions which were seen quite clearly and could not be misinterpreted, i.e., when it was possible to identify both the followed bird and the follower with absolute certainty. Many following reactions are omitted from this table because they were ambiguous in one way or another. Thus, for instance, none of the cases in which a bird of one species followed a group of two or more species is included in the table, as it was impossible to determine exactly which particular species was being followed in such cases. Similarly, cases in which two or more birds of one species followed a bird of another species were counted as single cases of interspecific following, as all but one of the following birds may have been following the first follower. Thus, the actual number of interspecific following reactions in the mixed blue and green tanager and honeycreeper flocks on Barro Colorado Island was certainly larger, and probably very much larger, than the number of such reactions shown in the table.

TABLE 4.—*Data from observations in and around the clearing on Barro Colorado Island between November 10 and December 20, 1959*

Unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and warblers. (Interspecific joining as well as interspecific following reactions by finches are omitted from this table because all such reactions observed were ambiguous.)

No. of cases seen	Species following and/or joining	Species being followed and/or joined
3	Plain-colored tanager	Palm tanager
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
19	Palm tanager	Plain-colored tanager
3	do.	Blue tanager
1	do.	Green honeycreeper
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
5	Blue tanager	Plain-colored tanager
2	do.	Palm tanager
1	do.	Chestnut-sided warbler
4	Golden-masked tanager	Plain-colored tanager
1	do.	Blue tanager
3	Green honeycreeper	Plain-colored tanager
1	do.	Bananaquit
1	Red-legged blue honeycreeper	Green honeycreeper
1	Summer tanager	Plain-colored tanager
1	do.	Palm tanager
2	Fulvous-vented euphonia	Plain-colored tanager
1	Bananaquit	Green honeycreeper
1	Chestnut-sided warbler	Golden-masked tanager
54		

This table is set up with the following species shown on the left and the species they followed shown (separately for each following species) on the right.

Table 4 is a partial list of both interspecific following and interspecific joining reactions observed on Barro Colorado Island. For the purposes of this table, a bird was considered to have joined another when it flew (or hopped, in a few cases) within 10 feet of the other (the other bird being perched at the time) without obviously forcing the other bird to leave. Only those interspecific joining reactions are shown in which the joining bird was a tanager or honeycreeper of any species. As in the case of the following reactions, only those joining reactions are shown which were completely clear and unambiguous. Thus, interspecific joining reactions were also actually much more common than indicated in the table.

This table was compiled by adding together all the suitable cases of interspecific following and interspecific joining seen during the period between November 10 and December 20,[3] and it is set up in the same way as table 3.

TABLE 5.—*Data from observations in and around the clearing on Barro Colorado Island between November 10 and December 20, 1959*

Unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and warblers. This is a different summary of the data shown in table 4. (Interspecific following and joining reactions by birds other than tanagers, honeycreepers, and warblers are not included among the cases of being followed and/or joined.)

Species	No. of times seen following and/or joining	No. of times seen being followed and/or joined
Plain-colored tanager	5	33
Palm tanager	25	6
Blue tanager	8	4
Golden-masked tanager	5	1
Green honeycreeper	4	3
Red-legged blue honeycreeper	1	3
Crimson-backed tanager	0	2
Summer tanager	2	0
Fulvous-vented euphonia	2	0
Bananaquit	1	1
Chestnut-sided warbler	1	1

Table 5 is a different type of partial summary of the same interspecific following and joining reactions shown in table 4. In table 5, the number of times each species was seen to follow or join and the number of times it was seen to be followed or joined are summarized separately, without indicating the other species involved in each case.

None of the interspecific following or joining reactions included in the preceding tables were accompanied by overt indications of

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[3] Recording of interspecific joining reactions was not begun until November 10. This is the reason why earlier cases of interspecific following have been omitted from the summaries in tables 4 and 5.

hostility;[4] but overt interspecific hostility was not really rare in the mixed blue and green tanager and honeycreeper flocks on Barro Colorado. No interspecific contact fights, actual bill-to-bill or body-to-body struggles, were seen during the periods the flocks were studied intensively; but so-called supplanting attacks (see Hinde, 1952) were quite frequent. A supplanting attack may be said to occur when one bird flies to the spot where another bird is perched, and the other bird moves away immediately. Supplanting attacks may intergrade with joining attempts, but the difference between the two types of reactions is usually clear. Some of the supplanting attacks in the mixed flocks on Barro Colorado Island were accompanied by forward pecking or jabbing movements, obviously aggressive, by the attacking birds.

TABLE 6.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Interspecific supplanting attacks by tanagers and honeycreepers. (No finches or warblers were seen to perform interspecific supplanting attacks in this area during this period of observation.)

No. of cases seen	Species supplanting	Species being supplanted
1	Plain-colored tanager	Golden-masked tanager
1	do.	Green honeycreeper
1	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
1	do.	Bananaquit
25	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
11	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	do.	Fulvous-vented euphonia
1	Green honeycreeper	Plain-colored tanager
1	do.	Shining honeycreeper
2	Crimson-backed tanager	Blue tanager
49		

Table 6 is a partial list of the interspecific supplanting attacks observed on Barro Colorado Island between October 26 and December 20. This table is organized according to the same principles as the tables immediately preceding. Only those reactions are shown in

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[4] The term "hostility" will be used throughout this paper to include all overt attack and escape behavior, as well as all reactions that seem to be produced by the interaction of attack and escape tendencies.

which a tanager or a honeycreeper was the active agent—in this case the attacker—and the specific identities of both the supplanting and supplanted birds were clear.

Table 7 is a very partial indication of the frequency with which some species failed to induce interspecific reactions when such reactions might have been expected. It is a list of the number of times species of finches, tanagers, and honeycreepers were seen to fly away from mixed flocks in a very conspicuous manner (giving loud flight calls or call notes and performing exaggerated intention movements of flight before leaving) without being followed by any other species of the flocks. These incidents were also observed between October 26 and December 20.

TABLE 7.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	40
Palm tanager	9
Blue tanager	13
Red-legged blue honeycreeper	3
Bananaquit	1

Tables 8 to 19 are designed to show the frequencies with which the 12 most commonly observed species of tanagers, honeycreepers, and warblers (the same species shown in tables 1 and 2) were associated with one another in mixed flocks on Barro Colorado Island during the whole period between October 26 and December 20. Each species is treated in a separate table, showing the number of times it was seen with every other species in flocks composed of two species and in flocks composed of three or more species. Every association between two species, even in flocks of three or more species, is counted separately. Thus, for instance, if plain-colored tanagers, palm tanagers, and blue tanagers were seen together in the same flock, their group was recorded as one association between plain-colored tanagers and palm tanagers, one association between plain-colored tanagers and blue tanagers, and one association between palm tanagers and blue tanagers. The figures in these tables are counts of associations between species, not individuals. When several individuals of each of two species were seen together in the same flock, their group was counted as a single association between the two species.

TABLE 8.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between plain-colored tanagers and certain other species in mixed flocks.

Species	No. of times seen with plain-colored tanagers in 2-species flocks	No. of times seen with plain-colored tanagers in flocks of 3 or more species
Palm tanager	39	37
Blue tanager	19	31
Golden-masked tanager	5	7
Green honeycreeper	11	11
Red-legged blue honeycreeper	3	8
Blue dacnis	2	2
Crimson-backed tanager	1	7
Summer tanager	2	3
Fulvous-vented euphonia	1	4
Bananaquit	3	2
Yellow warbler	1	5

TABLE 9.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between palm tanagers and certain other species in mixed flocks.

Species	No. of times seen with palm tanagers in 2-species flocks	No. of times seen with palm tanagers in flocks of 3 or more species
Plain-colored tanager	39	37
Blue tanager	9	25
Golden-masked tanager	0	5
Green honeycreeper	0	12
Red-legged blue honeycreeper	1	12
Blue dacnis	0	2
Crimson-backed tanager	1	5
Summer tanager	2	4
Fulvous-vented euphonia	1	3
Bananaquit	3	5
Yellow warbler	0	3

TABLE 10.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between blue tanagers and certain other species in mixed flocks.

Species	No. of times seen with blue tanagers in 2-species flocks	No. of times seen with blue tanagers in flocks of 3 or more species
Plain-colored tanager	19	31
Palm tanager	9	25
Golden-masked tanager	1	5
Green honeycreeper	2	7
Red-legged blue honeycreeper	1	9
Blue dacnis	1	2
Crimson-backed tanager	2	4
Summer tanager	1	3
Fulvous-vented euphonia	2	3
Bananaquit	0	3
Yellow warbler	0	3

TABLE 11.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between golden-masked tanagers and certain other species in mixed flocks.

Species	No. of times seen with golden-masked tanagers in 2-species flocks	No. of times seen with golden-masked tanagers in flocks of 3 or more species
Plain-colored tanager	5	7
Palm tanager	0	5
Blue tanager	1	5
Green honeycreeper	0	1
Red-legged blue honeycreeper	0	2
Blue dacnis	0	0
Crimson-backed tanager	0	0
Summer tanager	0	4
Fulvous-vented euphonia	0	1
Bananaquit	0	2
Yellow warbler	0	3

TABLE 12.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between green honeycreepers and certain other species in mixed flocks.

Species	No. of times seen with green honeycreepers in 2-species flocks	No. of times seen with green honeycreepers in flocks of 3 or more species
Plain-colored tanager	11	11
Palm tanager	0	12
Blue tanager	2	7
Golden-masked tanager	0	1
Red-legged blue honeycreeper	2	7
Blue dacnis	1	1
Crimson-backed tanager	0	2
Summer tanager	0	4
Fulvous-vented euphonia	0	0
Bananaquit	9	4
Yellow warbler	0	2

TABLE 13.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between red-legged blue honeycreepers and certain other species in mixed flocks.

Species	No. of times seen with red-legged blue honeycreepers in 2-species flocks	No. of times seen with red-legged blue honeycreepers in flocks of 3 or more species
Plain-colored tanager	3	8
Palm tanager	1	12
Blue tanager	1	9
Golden-masked tanager	0	2
Green honeycreeper	2	7
Blue dacnis	2	3
Crimson-backed tanager	0	0
Summer tanager	1	2
Fulvous-vented euphonia	0	1
Bananaquit	3	6
Yellow warbler	0	5

Table 14.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between blue dacnises and certain other species in mixed flocks.

Species	No. of times seen with blue dacnises in 2-species flocks	No. of times seen with blue dacnises in flocks of 3 or more species
Plain-colored tanager	2	2
Palm tanager	0	2
Blue tanager	1	2
Golden-masked tanager	0	0
Green honeycreeper	1	1
Red-legged blue honeycreeper	2	3
Crimson-backed tanager	0	0
Summer tanager	1	1
Fulvous-vented euphonia	0	0
Bananaquit	0	2
Yellow warbler	2	0

Table 15.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between crimson-backed tanagers and certain other species in mixed flocks.

Species	No. of times seen with crimson-backed tanagers in 2-species flocks	No. of times seen with crimson-backed tanagers in flocks of 3 or more species
Plain-colored tanager	1	7
Palm tanager	1	5
Blue tanager	2	4
Golden-masked tanager	0	0
Green honeycreeper	0	2
Red-legged blue honeycreeper	0	0
Blue dacnis	0	0
Summer tanager	0	1
Fulvous-vented euphonia	0	0
Bananaquit	0	1
Yellow warbler	1	1

Table 16.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between summer tanagers and certain other species in mixed flocks.

Species	No. of times seen with summer tanagers in 2-species flocks	No. of times seen with summer tanagers in flocks of 3 or more species
Plain-colored tanager	2	3
Palm tanager	2	4
Blue tanager	1	3
Golden-masked tanager	0	4
Green honeycreeper	0	4
Red-legged blue honeycreeper	1	2
Blue dacnis	1	1
Crimson-backed tanager	0	1
Fulvous-vented euphonia	0	0
Bananaquit	2	3
Yellow warbler	0	2

TABLE 17.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between fulvous-vented euphonias and certain other species in mixed flocks.

Species	No. of times seen with fulvous-vented euphonias in 2-species flocks	No. of times seen with fulvous-vented euphonias in flocks of 3 or more species
Plain-colored tanager	1	4
Palm tanager	1	3
Blue tanager	2	3
Golden-masked tanager	0	1
Green honeycreeper	0	0
Red-legged blue honeycreeper	0	1
Blue dacnis	0	0
Crimson-backed tanager	0	0
Summer tanager	0	0
Bananaquit	0	0
Yellow warbler	0	0

TABLE 18.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between bananaquits and certain other species in mixed flocks.

Species	No. of times seen with bananaquits in 2-species flocks	No. of times seen with bananaquits in flocks of 3 or more species
Plain-colored tanager	3	2
Palm tanager	3	5
Blue tanager	0	3
Golden-masked tanager	0	2
Green honeycreeper	9	4
Red-legged blue honeycreeper	3	6
Blue dacnis	0	2
Crimson-backed tanager	0	1
Summer tanager	2	3
Fulvous-vented euphonia	0	0
Yellow warbler	0	3

TABLE 19.—*Data from observations in and around the clearing on Barro Colorado Island between October 26 and December 20, 1959*

Associations between yellow warblers and certain other species in mixed flocks.

Species	No. of times seen with yellow warblers in 2-species flocks	No. of times seen with yellow warblers in flocks of 3 or more species
Plain-colored tanager	1	5
Palm tanager	0	3
Blue tanager	0	3
Golden-masked tanager	0	3
Green honeycreeper	0	2
Red-legged blue honeycreeper	0	5
Blue dacnis	2	0
Crimson-backed tanager	1	1
Summer tanager	0	2
Fulvous-vented euphonia	0	0
Bananaquit	0	3

Tables 20 to 27 are based upon observations in the area near Gamboa between July 12 and August 15, 1960. Many of the birds of the blue and green tanager and honeycreeper alliance appeared to have just finished breeding at this time. All the data in these tables were obtained by the same methods as the data from Barro Colorado Island.

TABLE 20.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	0	96 (54)	82	178
Palm tanagers	3 (1)	167 (68)	78	245
Blue tanagers	2	293 (55)	241	534
Red-legged blue honeycreepers	0	31 (48)	33	64
Blue dacnises	0	11 (69)	5	16
Crimson-backed tanagers ...	2 (1)	93 (53)	81	174
White-lined tanagers	0	1 (20)	4	5
Yellow-crowned euphonias ..	0	26 (47)	29	55
Thick-billed euphonias	0	14 (78)	4	18
Streaked saltators	0	48 (44)	62	110
Buff-throated saltators	0	36 (51)	35	71

Tables 20 and 21 show how frequently the 11 most commonly observed species of finches, tanagers, and honeycreepers (of the blue and green tanager and honeycreeper alliance) were seen in mixed flocks and not in mixed flocks, and the average number of individuals of these species per mixed flock and per nonmixed flock. Very few warblers were seen with blue and green tanager and honeycreeper

TABLE 21.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	46	35	81	57	2.09	2.34
Palm tanagers	85	47	132	64	1.96	1.66
Blue tanagers	147	138	285	52	1.99	1.75
Red-legged blue honeycreepers	20	19	39	51	1.55	1.74
Blue dacnises	7	3	10	70	1.57	1.67
Crimson-backed tanagers	62	51	113	55	1.50	1.59
White-lined tanagers	1	4	5	20	1.00	1.00
Yellow-crowned euphonias	18	17	35	51	1.44	1.71
Thick-billed euphonias	9	2	11	82	1.55	2.00
Streaked saltators	40	58	98	41	1.20	1.07
Buff-throated saltators	29	29	58	50	1.24	1.21

TABLE 22.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Unambiguous interspecific following reactions by tanagers and finches. (No honeycreepers or warblers were seen to perform unambiguous interspecific following reactions in this area during this period of observation.)

No. of cases seen	Species following	Species being followed
1	Palm tanager	Blue tanager
1	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	do.	Crimson-backed tanager
1	Variable seedeater	Plain-colored tanager

TABLE 23.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Unambiguous interspecific joining reactions by tanagers, honeycreepers, and finches. (No warblers were seen to perform unambiguous interspecific joining reactions in this area during this period of observation.)

No. of cases seen	Species joining	Species being joined
2	Palm tanager	Plain-colored tanager
2	do.	Blue tanager
3	Blue tanager	Plain-colored tanager
3	do.	Palm tanager
1	Blue dacnis	Palm tanager
1	Crimson-backed tanager	Blue tanager
1	Buff-throated saltator	Plain-colored tanager
1	do.	Blue tanager

TABLE 24.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Interspecific supplanting attacks by tanagers and finches. (No honeycreepers or warblers were seen to perform interspecific supplanting attacks in this area during this period of observation.)

No. of cases seen	Species supplanting	Species being supplanted
1	Plain-colored tanager	Yellow-crowned euphonia
1	do.	Seedeater *
2	Palm tanager	Blue tanager
1	do.	Plain-colored tanager
1	do.	Yellow-bellied elaenia
1	Blue tanager	Plain-colored tanager
1	do.	Palm tanager
1	Crimson-backed tanager	Blue tanager
1	Buff-throated saltator	Blue tanager

* This bird was almost certainly a female or juvenile male variable seedeater.

TABLE 25.—*Data from observations near Gamboa between July 12 and August 15, 1960*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	7
Palm tanager	5
Blue tanager	10
Red-legged blue honeycreeper	1
Crimson-backed tanager	6
Thick-billed euphonia	1
Buff-throated saltator	1
Green-backed sparrow	1
Yellow-bellied seedeater	1

TABLE 26.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Yellow-crowned euphonia	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		2	5	0	0	1	0	1	0	0	3
Palm tanager			19	1	0	4	0	0	0	1	1
Blue tanager				1	0	12	0	1	1	3	4
Red-legged blue honeycreeper...					1	2	0	0	0	1	0
Blue dacnis						0	0	0	0	0	0
Crimson-backed tanager							0	1	0	1	1
White-lined tanager								0	0	0	0
Yellow-crowned euphonia									0	0	0
Thick-billed euphonia										0	0
Streaked saltator											0
Buff-throated saltator											

TABLE 27.—*Data from observations near Gamboa between July 12 and August 15, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Yellow-crowned euphonia	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		14	17	5	3	8	0	4	1	7	1
Palm tanager			31	1	3	9	0	7	4	12	1
Blue tanager				10	2	19	1	10	6	17	8
Red-legged blue honeycreeper...					1	3	0	1	2	2	3
Blue dacnis						3	0	1	1	1	0
Crimson-backed tanager							1	3	1	11	7
White-lined tanager								0	0	0	1
Yellow-crowned euphonia									1	2	1
Thick-billed euphonia										0	0
Streaked saltator											3
Buff-throated saltator											

flocks at Gamboa during the period of observations. The data in these tables are arranged in exactly the same way as the corresponding data in tables 1 and 2.

Tables 22, 23, and 24 are counts of interspecific following, joining, and supplanting reactions. The following and joining reactions are not added together. Otherwise the data in these tables are arranged in exactly the same way as the corresponding information about Barro Colorado birds.

Table 25 is a count of nonfollowing reactions, as in table 7.

Tables 26 and 27 show the frequency of associations between the most commonly observed species of the blue and green tanager and honeycreeper alliance at Gamboa. The data in these tables are the same type as in tables 8 to 19, but they are arranged in a different way. All the associations between species in flocks of two species are summarized in one table, while all the associations between species in flocks of three or more species are summarized in the other table.

Tables 28 to 34 are based upon observations in the area near Frijoles between November 30, 1959, and January 19, 1960. Most of the birds of the blue and green tanager and honeycreeper alliance were not breeding throughout this period; but some of them may have begun to show a little breeding behavior toward the end of the period. These tables include the same kind of data obtained and arranged in the same way as the data on the birds at Gamboa.

Tables 35 to 39 include similar data obtained during observations near Frijoles between July 7 and August 16, 1960, just after the breeding season. Interspecific following, joining, and supplanting reactions were so rare during this period that they are all summarized in the same table. Good examples of leaving mixed groups in a conspicuous manner without being followed were so very rare that they are not shown at all.

Tables 40 to 43 are summaries of observations made in several areas. Tables 40 and 41 are summaries of all the unambiguous interspecific following and joining attempts by finches, tanagers, and honeycreepers at both Gamboa and Frijoles during all periods of observation. Table 42 is a summary of all the interspecific contact fights (in which actual blows were delivered) between finches, tanagers, and honeycreepers observed at Gamboa and at Frijoles between July 7 and August 16. No interspecific contact fights were seen at Frijoles between November and January. Table 43 is a summary of all the intraspecific contact fights (among members of the blue and

TABLE 28.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	2	14	50	64
	(3)	(22)		
Palm tanagers	0	15	38	53
		(28)		
Blue tanagers	3	34	56	90
	(3)	(38)		
Red-legged blue honeycreepers	6	23	45	68
	(9)	(34)		
Blue dacnises	3	9	16	25
	(12)	(36)		
Crimson-backed tanagers ...	3	23	88	111
	(3)	(21)		
White-lined tanagers	0	12	19	31
		(39)		
Streaked saltators	0	7	22	29
		(24)		
Buff-throated saltators	1	6	6	12
	(8)	(50)		

TABLE 29.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per unmixed flock.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	12	21	33	36	1.17	2.38
Palm tanagers	10	32	42	24	1.50	1.19
Blue tanagers	24	37	61	39	1.41	1.51
Red-legged blue honeycreepers ..	11	26	37	30	1.64	1.54
Blue dacnises	5	9	14	36	1.80	1.67
Crimson-backed tanagers	20	54	74	27	1.15	1.63
White-lined tanagers	11	13	24	46	1.09	1.46
Streaked saltators	5	16	21	24	1.40	1.37
Buff-throated saltators	6	6	12	50	1.00	1.00

TABLE 30.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Unambiguous interspecific following reactions by tanagers, and joining reactions by tanagers and honeycreepers. (No honeycreepers, warblers, or finches were seen to perform unambiguous interspecific following reactions, and no warblers or finches were seen to perform unambiguous interspecific joining reactions in this area during this period of observations.)

No. of cases seen	Species following	Species being followed
1	Palm tanager	Plain-colored tanager
1	Blue tanager	Plain-colored tanager
1	Crimson-backed tanager	Dusky-tailed ant-tanager
	Species joining	Species being joined
1	Palm tanager	Blue tanager
2	Blue tanager	Red-legged blue honeycreeper
1	do.	Plain-colored tanager
1	Red-legged blue honeycreeper	Plain-colored tanager
1	Crimson-backed tanager	Blue tanager
1	do.	Blue dacnis
1	White-lined tanager	Blue tanager
1	do.	Blue dacnis

TABLE 31.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Interspecific supplanting attacks by tanagers and finches. (No honeycreepers or warblers were seen to perform interspecific supplanting attacks in this area during this period of observations.)

No. of cases seen	Species supplanting	Species being supplanted
3	Plain-colored tanager	Blue dacnis
2	Palm tanager	Plain-colored tanager
1	Blue tanager	Plain-colored tanager
3	do.	Red-legged blue honeycreeper
1	do.	Crimson-backed tanager
1	do.	Summer tanager
1	Streaked saltator	White-lined tanager

TABLE 32.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

The number of times species of the blue and green tanager and honeycreeper alliance were seen to leave mixed flocks in a very conspicuous manner without being followed by individuals of other species.

Species	No. of times seen
Plain-colored tanager	3
Palm tanager	1
Blue tanager	7
Red-legged blue honeycreeper	1
Crimson-backed tanager	2
White-lined tanager	4
Black-capped saltator	1
Blue-black grassquit	1

TABLE 33.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Streaked saltator	Buff-throated saltator
Plain-colored tanager		2	0	1	0	0	0	0	0
Palm tanager			1	0	0	0	0	0	0
Blue tanager				2	0	2	2	1	0
Red-legged blue honeycreeper....					1	0	0	0	0
Blue dacnis						2	1	0	0
Crimson-backed tanager							2	0	1
White-lined tanager								1	0
Streaked saltator									0
Buff-throated saltator									

TABLE 34.—*Data from observations near Frijoles between November 30, 1959, and January 19, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Streaked saltator	Buff-throated saltator
Plain-colored tanager		1	5	2	1	2	1	2	2
Palm tanager			0	0	0	2	2	2	0
Blue tanager				3	1	4	3	1	3
Red-legged blue honeycreeper....					1	3	0	0	2
Blue dacnis						1	0	0	1
Crimson-backed tanager							1	1	2
White-lined tanager								1	1
Streaked saltator									0
Buff-throated saltator									

green tanager and honeycreeper alliance) seen at Barro Colorado, Gamboa, and Frijoles during all periods of observations.

(It was even more difficult to estimate the numbers of individuals of different species in the Gamboa and Frijoles areas than on Barro Colorado.)

TABLE 35.—*Data from observations near Frijoles between July 7 and August 16, 1960*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks.

Species	No. of times individuals seen in obviously integrated mixed flocks	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	0	28 (68)	13	41
Palm tanagers	0	30 (28)	79	109
Blue tanagers	0	117 (49)	120	237
Red-legged blue honeycreepers	0	26 (68)	12	38
Blue dacnises	0	20 (71)	8	28
Crimson-backed tanagers	0	84 (48)	89	173
White-lined tanagers	0	16 (70)	7	23
Thick-billed euphonias	0	15 (100)	0	15
Streaked saltators	0	32 (38)	53	85
Buff-throated saltators	0	24 (59)	17	41

There may have been something like 16 plain-colored tanagers, 28 palm tanagers, 50 blue tanagers, 17 red-legged blue honeycreepers, 5 blue dacnises, 24 crimson-backed tanagers, 2 white-lined tanagers, 16 yellow-crowned euphonias, 8 thick-billed euphonias, 18 streaked saltators, and 13 buff-throated saltators in the Gamboa area during the periods of observation, and approximately 12 plain-colored tanagers, 14 palm tanagers, 30 blue tanagers, 12 red-legged blue honeycreepers, 7 blue dacnises, 23 crimson-backed tanagers, 8 white-lined

TABLE 36.—*Data from observations near Frijoles between July 7 and August 16, 1960*

The number of times certain species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks and apart from mixed flocks, and the average number of individuals of each of these species per mixed flock and per nonmixed flocks.

Species	No. of times species seen in mixed flocks	No. of times species seen not in mixed flocks	Total No. times species seen	Percentage of times species seen mixed	Average No. individuals per mixed flock	Average No. individuals per nonmixed flock
Plain-colored tanagers	18	7	25	72	1.56	1.86
Palm tanagers	25	47	72	35	1.20	1.68
Blue tanagers	67	76	143	47	1.75	1.58
Red-legged blue honeycreepers ..	21	7	28	75	1.24	1.71
Blue dacnises	11	4	15	73	1.82	2.00
Crimson-backed tanagers	56	55	111	50	1.50	1.62
White-lined tanagers	15	6	21	71	1.07	1.17
Thick-billed euphonias	9	0	9	100	1.67	—
Streaked saltators	28	46	74	38	1.14	1.15
Buff-throated saltators	21	13	34	62	1.14	1.31

TABLE 37.—*Data from observations near Frijoles between July 7 and August 16, 1960*

A complete list of all the unambiguous interspecific following, joining, and supplanting reactions by tanagers and finches observed. (No honeycreepers or warblers were seen to perform unambiguous interspecific reactions in this area during this period of observations.)

1 case of a blue tanager following a plain-colored tanager
1 case of a crimson-backed tanager following a blue tanager
1 case of a plain-colored tanager joining a white-lined tanager
1 case of a blue tanager joining a palm tanager
1 case of a blue tanager joining a crimson-backed tanager
1 case of a streaked saltator joining a palm tanager
1 case of a streaked saltator joining a seedeater *
1 case of a plain-colored tanager supplanting a blue dacnis
1 case of a plain-colored tanager supplanting a lesser elaenia
1 case of a streaked saltator supplanting a blue tanager

* This bird was almost certainly a female or juvenile male variable seedeater.

TABLE 38.—*Data from observations near Frijoles between July 7 and August 16, 1960*

Associations between some species in mixed flocks composed of only two species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		0	4	0	0	0	1	0	0	1
Palm tanager			3	0	0	2	0	1	1	0
Blue tanager				1	0	7	1	0	1	1
Red-legged blue honeycreeper					1	0	0	0	1	0
Blue dacnis						0	0	0	0	0
Crimson-backed tanager							1	1	1	2
White-lined tanager								0	0	0
Thick-billed euphonia									0	0
Streaked saltator										0
Buff-throated saltator										

TABLE 39.—*Data from observations near Frijoles between July 7 and August 16, 1960*

Associations between some species in mixed flocks composed of three or more species.

	Plain-colored tanager	Palm tanager	Blue tanager	Red-legged blue honeycreeper	Blue dacnis	Crimson-backed tanager	White-lined tanager	Thick-billed euphonia	Streaked saltator	Buff-throated saltator
Plain-colored tanager		1	3	1	2	3	0	1	0	0
Palm tanager			6	1	2	4	2	1	4	3
Blue tanager				3	1	14	3	4	3	5
Red-legged blue honeycreeper					2	4	1	1	2	1
Blue dacnis						4	0	1	2	0
Crimson-backed tanager							1	1	5	5
White-lined tanager								0	2	1
Thick-billed euphonia									1	0
Streaked saltator										3
Buff-throated saltator										

TABLE 40.—*Summary of all the unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

This is a summary of the data shown in tables 22, 23, 30, and 37.

No. of cases seen	Species following and/or joining	Species being followed and/or joined
1	Plain-colored tanager	White-lined tanager
4	Palm tanager	Blue tanager
3	do.	Plain-colored tanager
7	Blue tanager	Plain-colored tanager
5	do.	Palm tanager
2	do.	Red-legged blue honeycreeper
2	do.	Crimson-backed tanager
1	Red-legged blue honeycreeper	Plain-colored tanager
1	Blue dacnis	Palm tanager
3	Crimson-backed tanager	Blue tanager
1	do.	Blue dacnis
1	do.	Dusky-tailed ant-tanager
1	White-lined tanager	Palm tanager
1	do.	Blue dacnis
1	Streaked saltator	Palm tanager
1	do.	Seedeater
1	Buff-throated saltator	Plain-colored tanager
1	do.	Blue tanager
1	Variable seedeater	Plain-colored tanager
38		

TABLE 41.—*Summary of all the unambiguous interspecific following and joining reactions by tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

The same data as given in table 40, arranged in a different way. (Interspecific following and joining reactions by birds other than tanagers, honeycreepers, and finches are not included among the cases of being followed and/or joined.)

Species	No. of times seen following and/or joining	No. of times seen being followed and/or joined
Plain-colored tanager	1	13
Palm tanager	7	8
Blue tanager	16	8
Red-legged blue honeycreeper	1	2
Blue dacnis	1	2
Crimson-backed tanager	5	2
White-lined tanager	2	1
Streaked saltator	2	0
Buff-throated saltator	2	0

tanagers, 8 thick-billed euphonias, 16 streaked saltators, and 11 buff-throated saltators in the Frijoles area during observations between July 7 and August 16.

Most of these species were probably almost equally abundant during both series of observations at Frijoles. The only obvious exceptions were blue tanagers and thick-billed euphonias. They were appreciably less abundant during the earlier periods of observation, between November 30 and January 19, than during the later periods.

TABLE 42.—*Interspecific contact fights among tanagers, honeycreepers, and finches observed near Gamboa and Frijoles*

(No warblers were seen to be involved in interspecific contact fights in either area.)

No. of cases seen	More aggressive species	Less aggressive species
1	Plain-colored tanager	Variable seedeater
1	Palm tanager	Social flycatcher
3	Blue tanager	Palm tanager
1	do.	White-lined tanager
1	White-lined tanager	Crimson-backed tanager
1	Blue-black grassquit	Crimson-backed tanager
1	Clay-colored thrush	Crimson-backed tanager
1	Rusty-margined flycatcher	Yellow-crowned euphonia

TABLE 43.—*Intraspecific contact fights observed on Barro Colorado Island and near Gamboa and Frijoles*

Only fights within species of the blue and green tanager and honeycreeper alliance are shown.

Species	No.
Plain-colored tanager	9
Palm tanager	6
Blue tanager	10
Green honeycreeper	1
Red-legged blue honeycreeper	1
Blue dacnis	1
Crimson-backed tanager	1
Bananaquit	15
Buff-throated saltator	2

These estimates may be too high; but there were certainly many more birds in the areas at Gamboa and Frijoles where observations were made than in the clearing on Barro Colorado Island. This was partly a reflection of the fact that the Gamboa and Frijoles areas were much larger than the clearing on Barro Colorado.

THE ROLES OF DIFFERENT SPECIES WITHIN MIXED FLOCKS

PLAIN-COLORED TANAGER

Plain-colored tanagers occur in mixed blue and green tanager and honeycreeper flocks very frequently and usually play a very significant role in such flocks. The presence of these birds in any given area tends to stimulate the formation of mixed flocks in the area; and their presence in any mixed flock tends to increase the cohesion of the flock. These effects are usually produced by the reactions of individuals of other species to plain-colored tanagers, not the reactions of plain-colored tanagers to individuals of other species. Some of the reactions of individuals of other species of plain-colored tanagers seem to be indirect results of the extreme intraspecific gregariousness of plain-colored tanagers.

Intraspecific gregariousness may be contrasted to interspecific gregariousness. Throughout this paper, the former term will be used to include all the tendencies of individuals of any given species to associate with one another. The latter term will be used to include all the tendencies of individuals of one species to associate with individuals of other species.

Flocks of 10 to 16 plain-colored tanagers are common in suitable environments, especially along the edges of fairly mature forest, during the nonbreeding season. Such flocks tend to break up during the breeding season, when individual males and pairs adopt territories; but it is still not uncommon to see groups of 4 to 6 moving about together and/or feeding together for more or less brief periods of time even during the height of the breeding season.[5] The frequency with which

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[5] The territories of many tropical lowland tanagers (and many other tropical species of other groups) are more difficult to recognize and study than the territories of most related Temperate Zone species.

The conventional definition of territory is "any defended area"; but territorial defense is comparatively rare among tropical tanagers. Individual birds and/or pairs of the same species in the same general area may keep apart from one another for long periods of time, each individual or pair remaining in its own particular part of the area, without showing any overt hostility to one another. It is probable, however, that such behavior is often or usually the result of previous territorial disputes which do occur occasionally between members of the same species. A few disputes may be sufficient to fix territorial boundaries for many months, or even years. Neighboring birds may learn the boundaries of their territories after a few disputes, and may retain this learning for long periods of time without further reinforcement. The territories of many tropical birds may become "traditional" more easily than those of many migratory Temperate Zone birds simply because the tropical birds are almost completely plain-colored tanagers associate with one another does not seem to be affected by the presence or absence of individuals of other species. None of the other species of tanagers that frequently occur in mixed flocks with plain-colored tanagers are as gregarious apart from mixed flocks as plain-colored tanagers.

Some of the social behavior patterns of plain-colored tanagers seem to be very specialized. Among these specializations are increased frequency and exaggeration of wing-flicking and tail-flicking movements (stereotyped "intention movements" of flight), extreme restlessness (plain-colored tanagers are more nearly constantly active than most other tanagers), increased frequency of call notes, loss of song (which seems to have been replaced by a variation of the call-note patterns), and various modifications and/or reductions of hostile behavior.

As a result of their frequent call notes and vigorous movements, plain-colored tanagers are usually very conspicuous—probably more so, on the average, than individuals of many other species of the blue and green tanager and honeycreeper alliance.

All or most of the specialized social behavior patterns of plain-colored tanagers seem to be adaptations to promote gregariousness (see the discussion in Moynihan, 1960) and were probably evolved originally to promote intraspecific gregariousness. Many other species of birds that are gregarious among themselves, but not usually associated with mixed species flocks, have evolved similar characters, which may promote associations between individuals of the same species in several different ways. If nothing else, a bird that is very conspicuous is more often noticed and more easily recognized by other individuals of the same species than it would be if it were less conspicuous.

Some of these specialized social behavior patterns of plain-colored tanagers also seem to affect the behavior of individuals of many other

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sedentary. There is evidence that the same pairs of some species of tropical tanagers retain, or revert to, the same territories year after year.

In the case of the more highly gregarious species, the situation is further complicated by the fact that territorial birds frequently abandon their territories at more or less regular intervals in order to join and/or follow flocks of the same or other species. Thus, the territories of many tropical tanagers may be both very stable over long periods of time, and very unstable, i.e., held only intermittently, over short periods of time.

The groups of plain-colored tanagers that are formed during the breeding season may be composed of birds that have abandoned their territories completely for the time being, and/or birds that have met in a neutral area between their territories, which they are still prepared to defend. In some cases, at least, these groups are not composed of an adult pair plus their still juvenile young of the previous breeding season.

species, to which the tanagers are undoubtedly very attractive. They are joined and followed[6] by individuals of other species very frequently, relatively much more frequently than are any other birds of the blue and green tanager and honeycreeper alliance. During the course of the present investigation the attractiveness of plain-colored tanagers was most obvious in the study area on Barro Colorado Island; but it was also quite evident at Frijoles and Gamboa, where these birds were relatively much less abundant (see table 41).

The attractiveness of the plain-colored tanager is often clearly independent of its food-finding or food-providing ability. Of all the species of the blue and green tanager and honeycreeper alliance, it is the species most often joined by birds of other species in places where there is little or no food available, and most often joined and followed by other birds that are obviously not in the mood to feed at the time. (I saw nothing to suggest that plain-colored tanagers are more efficient than individuals of many other species in finding the fruits and insects on which many members of the blue and green tanager and honeycreeper flocks feed.)

These facts would indicate that birds of other species are usually or always attracted to plain-colored tanagers by some aspect of the latter, probably behavior, as the plumage of plain-colored tanagers is particularly dull and probably does not provide many strong stimuli. The plumage may facilitate associations with other species; but it is probably not directly attractive in itself (see discussion below). The behavior patterns of plain-colored tanagers that attract individuals of other species are almost certainly the patterns that also promote intraspecific gregariousness, as plain-colored tanagers do not perform any other patterns much more frequently or conspicuously than individuals of many other species.

It has already been mentioned that many or most passerine birds show some tendency to approach birds of almost any other species. This tendency may be called "generalized" gregariousness (one type of interspecific gregariousness, as defined above), and observation of many species would suggest that it is usually more strongly stimulated by the sight and sound of conspicuously active and noisy birds than

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[6] Unless specifically stated otherwise, the terms "joined" and "followed" (or "join" and "follow") are used in a rather restricted sense in this and subsequent discussions. They are applied only to reactions in which the active bird, the joiner or follower, does not appear to be hostile (or, at least, no more strongly hostile than during all social reactions).

by the sight and sound of quiet and placid birds. Thus, any species that has become conspicuously active and noisy in order to promote intraspecific gregariousness will almost inevitably tend to attract birds of other species particularly strongly. This seems to be what has happened in the case of the plain-colored tanager.

There are also some indications that generalized gregariousness is usually more strongly stimulated by the sight and sound of a group of birds than by the sight and sound of a single bird of the same species. Thus, birds of a species that has developed a high degree of intraspecific gregariousness may tend to attract individuals of other species comparatively frequently even when they are not particularly conspicuous.

A few species of the blue and green tanager and honeycreeper alliance seem to be attracted to plain-colored tanagers more strongly than would be expected on the basis of generalized gregariousness alone. Such species seem to have developed "special interspecific preferences" for plain-colored tanagers (see below). This may help to explain why plain-colored tanagers are joined and followed so very much more frequently than are individuals of any other species of the blue and green tanager and honeycreeper alliance, and by individuals of some species so much more frequently than by individuals of other species; but it is obvious that plain-colored tanagers are also very attractive to many other passerine birds that have not developed any friendly interspecific social reactions stronger than generalized gregariousness.

The relationships between plain-colored tanagers and other species in mixed blue and green tanager and honeycreeper flocks are usually essentially one way. Plain-colored tanagers join and follow individuals of other species very much less frequently than they are joined and followed by individuals of other species.

There is some evidence, in fact, that plain-colored tanagers may actually dislike being joined or followed by individuals of other species. They sometimes attack or perform intention movements of attacking some other birds with which they are associated in mixed flocks, especially such relatively small birds as variable seedeaters and blue dacnises. They do not, however, show much overt aggressiveness toward the species that join and follow them most frequently and persistently. This lack of aggressiveness is probably due to several causes. It has already been mentioned that the hostile behavior of plain-colored tanagers seems to have become modified and/or reduced in several ways, presumably as an adaptation to promote intraspecific gregariousness.[7] More important, perhaps, is the fact that the three species that join and follow plain-colored tanagers most frequently and persistently, i.e., the palm tanager, blue tanager, and green honeycreeper, are much larger and/or much more aggressive and able fighters than plain-colored tanagers. They may intimidate plain-colored tanagers sufficiently strongly to suppress any overt expressions of aggressiveness by the latter, even when the latter are irritated by their presence.

It might be supposed, therefore, that the other species in mixed blue and green tanager and honeycreeper flocks were essentially parasitic on the plain-colored tanagers. Whatever the advantages of forming mixed flocks may be (see below), all or most of these advantages might be obtained by the other species and not the plain-colored tanagers.

This may be true in some cases, but not in all. Two types of evidence would suggest that plain-colored tanagers must also derive some advantage, at least sometimes, from their associations with individuals of other species.

The most convincing evidence in this connection is the plumage of the plain-colored tanager. It is very much duller than that of any other species of the genus *Tangara*. This dullness may be considered a type of neutral coloration, and seems to be an adaptation to facilitate associations between plain-colored tanagers and individuals of other species. The neutral coloration of the plain-colored tanager has already been discussed in an earlier paper (Moynihan, op. cit.). Part of this discussion may be quoted here:

> The dull coloration of the Plain-colored Tanager would seem to be a specific adaptation to help the species play its role in . . . mixed flocks. It seems to be effective just because of its dullness, its neutral quality. If the Plain-colored Tanager were more conspicuously colored, it might be less attractive to, or exert less influence upon, its associates of other species . . . The drab appearance of the Plain-colored Tanager probably makes it look less different to its brightly colored associates than it would if it had a distinctive bright pattern of its own. Of course, the Plain-colored Tanager might be even more effective in attracting other species if it could develop the same conspicuous colors and patterns as theirs; but most of the species with which it associates are so different from one another that it would be very difficult or impossible to mimic them all. The Plain-colored Tanager seems to have evolved a "compromise" type of coloration

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[7] Observation of captive plain-colored tanagers and golden-masked tanagers under identical conditions would suggest that both the attack and escape drives of the very gregarious plain-colored tanagers are weaker, or less easily aroused, than the corresponding drives of the closely related but less gregarious golden-masked tanagers.

instead, one that is moderately different from those of almost all its associates, without being too conspicuously different from any. The fact that the compromise, neutral, coloration is drab may also have another advantage. It may make the other signal patterns of the species, the restlessness, calling, flash patterns of wings and tail, and flicking movements, relatively more effective than they would be otherwise. The drabness may allow the other characters to attract and hold a greater share of the attention of observers.

In other words, the attractiveness of plain-colored tanagers is partly a direct result of their behavior; but their behavior can only produce its full effect because their plumage is neutral, and their neutral plumage has probably been evolved as a special adaptation to permit their behavior to produce its full effect.

It may also be significant that plain-colored tanagers do sometimes join and follow individuals of other species. Such reactions are relatively very rare, but actually not too uncommon. Solitary individuals and pairs of plain-colored tanagers may also approach individuals of other species without performing clear-cut joining or following reactions of the type recorded in the accompanying tables. This may be the reason why the average number of plain-colored tanagers per mixed flock is less than the average number per nonmixed flock (see tables 2, 21, 29, and 36). It is perhaps unlikely that plain-colored tanagers would approach, join, or follow individuals of other species as frequently as they do if associations with other species were always disadvantageous, especially as any approach to individuals of other species will tend to induce these other individuals to join or follow the plain-colored tanagers in return.

PALM TANAGER

The usual social role of palm tanagers in mixed blue and green tanager and honeycreeper flocks is at least as important as that of plain-colored tanagers. In most circumstances, individual palm tanagers seem to become associated with mixed flocks approximately as frequently as do individual plain-colored tanagers, when allowances are made for the fact that the two species are seldom equally abundant in any given area. Like the plain-colored tanagers, palm tanagers also tend to stimulate the formation and increase the cohesion of mixed flocks; but the two species produce their effects in very different ways. Palm tanagers are very active joiners and followers. In most circumstances they join and follow other species relatively much more frequently than do any other tanagers of the blue and green tanager and honeycreeper alliance.

Palm tanagers also tend to perform more supplanting attacks upon individuals of other species than do any other tanagers of the blue and green tanager and honeycreeper alliance. These supplanting attacks do not, however, disturb the mixed flocks very greatly, as the supplanted individuals seldom fly very far away.

The relationships between palm tanagers and the other species of the blue and green tanager and honeycreeper alliance can be divided into two main types.

The reactions of palm tanagers to individuals of most other species seem to be nothing more than expressions of generalized gregariousness (or equally nonspecific hostility, in some cases). They do not seem to react to most other species unusually frequently or strongly.

The reactions of palm tanagers to plain-colored tanagers and blue tanagers seem to be much more specialized. Palm tanagers join, follow, and supplant plain-colored tanagers and blue tanagers [8] much more frequently than they join, follow, and supplant individuals of any other species in apparently similar social circumstances, i.e., when they are equally close to plain-colored tanagers, blue tanagers, and individuals of other species, and when these species seem to be approximately equally noisy and conspicuous. Palm tanagers also join, follow, and supplant plain-colored tanagers and blue tanagers much more frequently than do individuals of other species in similar social circumstances. These reactions would seem to be too frequent to be expressions of generalized gregariousness alone: they seem to be expressions of stronger social bonds, which might be called "special interspecific preferences."

As a rough generalization, it can be said that palm tanagers usually show a strong special interspecific preference for plain-colored tanagers, and a weaker special interspecific preference for blue tanagers; but both these preferences are rather variable, and tend to be much more obvious during some types of social reactions than during others.

In most circumstances, palm tanagers seem to join and follow plain-colored tanagers almost as frequently as they join and follow all or most other members of their own species (perhaps more frequently in many cases). They may also supplant plain-colored tanagers more frequently than they do other palm tanagers.

The relatively great frequency of supplanting attacks by palm tanagers upon plain-colored tanagers is not an indication that the former

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[8] It should be stressed, again, that this discussion is an analysis of the behavior of species in central Panamá. The reactions of palm tanagers to blue tanagers may be different in parts of South America (see below).

are usually more aggressive toward the latter than toward most other members of their own species—quite the opposite in fact. It is simply because they tend to encounter plain-colored tanagers more frequently, in many environments, than any other members of their own species, except their own mates and other members of their own family groups. The comparative rarity of encounters between palm tanagers is probably an indication that they are usually more aggressive toward one another than toward individuals of any other species.

(The aggressiveness of palm tanagers toward one another is obviously variable, and often quite different, on the average, in different situations; but they do appear to be more aggressive toward one another in most circumstances than are plain-colored tanagers in the same or similar circumstances.

I have seen fairly large groups of 8 to 10 palm tanagers, with and without associated individuals of other species, in both the breeding and the nonbreeding seasons; but such groups are relatively rare. Most pairs and family groups of palm tanagers usually maintain territories during both the breeding and nonbreeding seasons—or, at least, keep well apart from one another. Such territorial birds frequently join and follow individuals of other species; but they usually stop following individuals of other species when the latter move into the territories of other palm tanagers.)

The characteristic variety of reactions by palm tanagers to plain-colored tanagers may be explained as differential responses to different stimuli presented by plain-colored tanagers.

All, or almost all, reactions between any two birds are probably at least slightly ambivalent. Thus, for instance, whenever a bird of one species sees or hears a bird of another species it is quite likely to perform some hostile patterns, at least uttering a hostile note or performing an intention movement of some hostile pattern, in addition to, or instead of, approaching or showing indications of a desire to approach the other bird in a nonhostile ("friendly") manner. Any bird presumably presents a complex of partly contradictory stimuli to any other bird that sees or hears it. Some of these stimuli are attractive, others are irritating (i.e., tend to release attack by the perceiving bird), and still others are intimidating (i.e., tend to release escape by the perceiving bird).

Palm tanagers seem to react to plain-colored tanagers as if they found them slightly less attractive, much less irritating, and very much less intimidating than other palm tanagers. This is perhaps what would be expected in view of the fact that plain-colored tanagers are much smaller than palm tanagers but rather similar in plumage and even more active and noisy. Size is always an important factor in determining the nature of the hostile reactions between any two birds of any species; but its direct effect upon positively "friendly" reactions is usually considerably weaker.

As indicated or implied by the figures in the accompanying tables, palm tanagers tend to join, follow, and supplant blue tanagers less frequently than plain-colored tanagers when the two latter species are even approximately equally abundant. In such environments as the clearing on Barro Colorado Island, palm tanagers also tend to follow blue tanagers less closely than plain-colored tanagers and are relatively less frequently associated with blue tanagers in mixed flocks of only two species. All these facts would suggest that the social relationships between palm tanagers and blue tanagers are usually weaker than those between palm tanagers and plain-colored tanagers.

This is particularly interesting because palm tanagers and blue tanagers are strikingly similar to one another in voice, movements, and shape, as well as being very closely related. The fact that palm tanagers usually react less strongly to blue tanagers than to plain-colored tanagers is an indication that the palm tanager tends to react more strongly to the plumage patterns of the other species it encounters than to their behavior, size, or shape, and/or that the behavior patterns of the plain-colored tanager which are adapted to promote gregariousness are really remarkably effective.

Although less strong and frequent, the reactions of palm tanagers to blue tanagers are similar to their reactions to plain-colored tanagers in one important respect. Palm tanagers seem to find blue tanagers more like other palm tanagers in attractiveness than in irritating or intimidating qualities, and they usually supplant, threaten, and escape from blue tanagers relatively much less frequently than they join and follow them.

Thus, both the special interspecific preferences of palm tanagers may be said to be expressed primarily by "friendly" reactions and only secondarily by hostility. This is not true of all the special interspecific preferences of some other species (see below).

Palm tanagers join both plain-colored tanagers and blue tanagers rather frequently without starting to feed immediately afterward.

Being rather noisy and moderately restless, palm tanagers sometimes attract individuals of many other species; but this effect is seldom conspicuous. They induce overt, complete joining and following responses by individuals of other species comparatively rarely.

There may be several reasons for this. Palm tanagers are among the largest birds of the blue and green tanager and honeycreeper alliance and are probably more intimidating than such smaller species as the plain-colored tanager and the red-legged blue honeycreeper (see below). In many cases, moreover, individuals of other species are not able to join or follow palm tanagers before the palm tanagers have joined or followed them.

The dull plumage of palm tanagers may be neutral in more or less the same way as the similar plumage of plain-colored tanagers. It may be an adaptation to increase the frequency with which palm tanagers are approached by individuals of many other species probably permitting them to be approached more frequently than they would be if they were more brightly colored (unless the bright coloration were of a very special type—see below). The plumage of palm tanagers is probably not an adaptation to facilitate their associations with plain-colored tanagers alone. Palm tanagers are much more widely distributed than plain-colored tanagers (see below).

The social tendencies of palm tanagers are probably essentially the same in all environments; but they may fail to be expressed by overt behavior under certain conditions.

As their name would imply, palm tanagers show a definite preference for palm trees, nesting in the tree crowns or, less frequently, in other tall trees of similar shape, with dense crowns and bare trunks. They may also show a preference for manmade structures that have some of the same characteristics as palm trees. Near Frijoles, for instance, they were greatly attracted to the pylons along the railroad track, and some may have nested in the tops of these. Even when they nested in adjacent trees, many of the palm tanagers at Frijoles spent much of their time resting in the pylons.

Palm tanagers that have selected palm trees or similar trees or similar manmade structures as nesting sites are often reluctant to leave the vicinity of such sites during the whole period immediately before, during, and immediately after the breeding season. Other members of the blue and green tanager and honeycreeper alliance are equally reluctant to visit such trees or structures if they are far from other trees.

Thus, palm tanagers that select isolated trees or structures as nesting sites also tend to be isolated socially. They do not encounter other members of the blue and green tanager and honeycreeper alliance very frequently and usually do not follow other birds very far even when they do meet them. Such palm tanagers cannot play their usual role in mixed flocks. They are reduced to the role of occasional and very temporary associates of the mixed flocks as long as they remain very closely attached to their nest sites.

It has already been mentioned that individuals of many species tend to associate with mixed flocks less frequently during the breeding season than during the nonbreeding season; but the palm tanagers observed in central Panamá tended to sever their connections with mixed flocks more nearly completely than all or most individuals of all or most other species. This may have been partly due to the fact that their nesting sites were more often isolated. The favorite nesting sites of palm tanagers in central Panamá are in coconut palms; and many or most of the coconut palms in this region are quite isolated from other tall trees.

In any case, the differences between the interspecific social reactions of palm tanagers during the breeding and nonbreeding seasons seem to be greater, on the average, than the differences between the corresponding reactions of any other species of the blue and green tanager and honeycreeper alliance.

The behavior of the palm tanagers at Frijoles in July and August 1960, when they were associated with mixed flocks much less frequently than individuals of many other species, was a good example of social isolation persisting immediately after the breeding season. All or almost all the palm tanagers in the Frijoles area seemed to have finished breeding before observations were begun in July 1960; but many of them were still in family groups and still more or less strongly attached to nest sites in isolated coconut palms or pylons.

BLUE TANAGER

The role of blue tanagers in mixed blue and green tanager and honeycreeper flocks is very similar to that of palm tanagers, but less unbalanced and probably less important, in most circumstances, and more nearly uniform throughout the year.

Blue tanagers tend to join, follow, and supplant individuals of many other species; but they do so relatively less frequently and less rapidly than palm tanagers in most environments. As they are also attractive to individuals of other species in much the same way as palm tanagers, they are more often joined and followed by individuals of other species than are palm tanagers in most environments. They still, however, tend to join and follow individuals of other species more often than they are joined and followed by individuals of other species.

The only species that tends to join and follow blue tanagers very frequently is the palm tanager. In many areas blue tanagers continue to associate with mixed flocks more frequently than do palm tanagers during the breeding season, as the nesting sites of blue tanagers are usually less isolated than those of many palm tanagers. In such areas, during the breeding season, blue tanagers tend to join and follow individuals of other species *much* more frequently than they are joined and followed by individuals of other species. The role of blue tanagers in mixed flocks is much more consistently "active" in such circumstances than when palm tanagers are also frequently associated with mixed flocks.

In an earlier paper (Moynihan, 1960) it was stated that there are usually more palm tanagers than blue tanagers in mixed flocks. Subsequent observations would indicate that this is not generally true (see accompanying tables).

Blue tanagers appear to have a definite interspecific preference for plain-colored tanagers. This is probably similar to the corresponding preference of palm tanagers in quality, but averaging somewhat weaker. Blue tanagers also seem to have a special interspecific preference for palm tanagers themselves. This may be almost or quite as strong as the reciprocal preference of palm tanagers for blue tanagers, and equally similar in quality; but it is usually weaker than the preference of blue tanagers for plain-colored tanagers.

GOLDEN-MASKED TANAGER

Golden-masked tanagers were not observed very often during the present study. When they were seen with mixed flocks they showed a definite tendency to join and follow plain-colored tanagers. They may also have shown a very slight special interspecific preference for blue tanagers. (It may be significant that both golden-masked and blue tanagers have considerable amounts of bright blue in their plumages. The golden-masked tanager, the Panamanian form of the blue tanager, and the plain-colored tanager all have bright blue flash patches on the wings, which are revealed very conspicuously in flight.)

GREEN HONEYCREEPER

The behavior of green honeycreepers in mixed flocks is reminiscent of palm tanagers and blue tanagers; but by no means absolutely identical. Some aspects of the social role of green honeycreepers in mixed flocks are very distinctive. Like the palm and blue tanagers, green honeycreepers occur in mixed flocks quite frequently and tend to approach (or try to approach) individuals of other species more often than they are approached by individuals of other species. In one way the social role of green honeycreepers is even more unbalanced than that of palm tanagers; they do not seem to be as attractive to any other species as palm and blue tanagers are to one another. In another way the social role of green honeycreepers in mixed flocks is more obviously ambivalent than that of any other common species of the blue and green tanager and honeycreeper alliance. Green honeycreepers frequently try to approach individuals of other species in an apparently nonhostile or "friendly" manner; but they also tend to be very aggressive toward individuals of other species. They are probably more often openly aggressive toward individuals of other species than are any other regular members of the mixed blue and green tanager and honeycreeper flocks.

This ambivalent behavior of green honeycreepers in mixed flocks seems to be a reflection of their behavior to one another (see Moynihan, 1960). There are indications that they are strongly attracted to one another by some sort of gregarious or general social impulse; but they seldom or never occur in stable unmixed flocks of their own species alone. This is largely owing to the fact that whenever two unrelated green honeycreepers (i.e., birds that are not members of the same pair or family group) come together, they almost always start to dispute vigorously with one another. Sooner or later (usually sooner) one bird will attack the other and drive it away.

It is quite possible that the reactions of green honeycreepers to individuals of many other species are produced by the same tendencies or internal drives as their reactions to one another; but the two types of reactions seldom take exactly the same form, i.e., they seldom include exactly the same movements, postures, or calls, in exactly the same sequence. Such differences may be due to several factors. It is obvious, for instance, that green honeycreepers seldom respond as strongly to individuals of other species as to other members of their own species, even when the quality of the response is the same in both cases. It is also evident that the social reactions of green honeycreepers are greatly affected by several aspects of the social environments in which they occur. Green honeycreepers may perform different acts, or (at least) the same acts with different frequencies, in different social environments, even when their internal motivation is the same in the different environments. This is also characteristic of the behavior of birds of all species; but it is often particularly conspicuous in the case of green honeycreepers in mixed flocks.

It is possible to recognize certain relatively minor subdivisions or subgroups, special associations of a few species, within the larger group of the blue and green tanager and honeycreeper alliance as a whole. These subgroups are not very distinct and never exclusive; but some species, including the green honeycreeper, behave slightly differently in different subgroups.

Different types of subgroups may be recognized by the use of different criteria. Perhaps the most easily distinguished are two subgroups that may be called predominantly tanager flocks and predominantly honeycreeper flocks. The former are largely composed of tanagers, especially plain-colored, palm, and blue tanagers, and include relatively few honeycreepers; while the latter are largely composed of honeycreepers, sometimes accompanied by many warblers (see below), and include relatively few tanagers.

Green honeycreepers differ from the other common honeycreepers of central Panamá in being associated with predominantly tanager flocks almost as frequently as with predominantly honeycreeper flocks.

In predominantly tanager flocks, their most conspicuous social reactions are attempts to join and follow individuals of other species. They seem to be much more strongly attracted to plain-colored tanagers than to any other species of tanager. They join and follow plain-colored tanagers relatively more frequently than they do individuals of any other common species of the blue and green tanager and honeycreeper alliance; and they occur with plain-colored tanagers in mixed flocks of only two species relatively much more frequently than with individuals of any other species of tanager. Their responsiveness to plain-colored tanagers seems to be a special interspecific preference, essentially similar to the corresponding preferences of such species as the palm tanager and the blue tanager.

The vocal patterns of the green honeycreepers may be significant in this connection. They frequently utter sharp call notes and rattling calls that are distinctly different in sound from any of the common vocal patterns of the red-legged blue honeycreeper and the blue dacnis, but very similar to the most common vocal patterns of the plain-colored tanager and the golden-masked tanager. Observation of captive birds would suggest that green honeycreepers are strongly attracted by the sound of the calls and notes of plain-colored tanagers and golden-masked tanagers that are most like their own calls and notes. There is also some evidence that the vocal repertory of the green honeycreeper is rather specialized, more so than the corresponding repertories of the red-legged blue honeycreeper and the blue dacnis.

It is conceivable, therefore, that the vocal repertory of the green honeycreeper has become increasingly similar to those of some *Tangara* tanagers, by convergent evolution, because this similarity facilitates associations with these tanagers, and such associations are usually advantageous to green honeycreepers. If so, this similarity may be considered a form of "social mimicry" (Moynihan, 1960).

(It is possible that green honeycreepers have a slight special interspecific preference for golden-masked tanagers. If so, this preference would be similar to their preference for plain-colored tanagers in quality, but probably much weaker. Under natural conditions green honeycreepers seem to join and follow golden-masked tanagers relatively much less frequently than they join and follow plain-colored tanagers.)

Green honeycreepers perform relatively few aggressive movements, but sometimes utter many aggressive calls in predominantly tanager flocks. This would suggest that they are sometimes motivated by strong aggressive tendencies in such flocks, but that these tendencies are often partly inhibited. It is probable that they find many of their companions in predominantly tanager flocks quite irritating (although presumably less irritating than other members of their own species) and also very intimidating. Most tanagers are as large as, or even larger than, green honeycreepers, and would be expected to be intimidating to the latter.

The reactions of green honeycreepers to other honeycreepers are rather more varied than their reactions to tanagers. They tend to perform many supplanting attacks upon red-legged blue honeycreepers. They may also attempt to join and follow the latter in a "friendly" manner; but such attempts are relatively very rare, and are probably nothing more than expressions of generalized gregariousness.

Green honeycreepers do not usually attack red-legged blue honeycreepers as frequently as they attack other members of their own species; but I have seen them do so in certain special circumstances, when several green honeycreepers and red-legged blue honeycreepers were feeding in the same small tree. The green honeycreepers became particularly aggressive in such circumstances. Their aggressiveness may have been released originally by their proximity to one another; but they seemed to vent this aggressiveness upon one another and upon the red-legged blue honeycreepers quite indiscriminately.

The hostility of green honeycreepers toward red-legged blue honeycreepers might be considered a peculiar form of special interspecific preference, much more limited in scope than the special interspecific preferences of some species for plain-colored tanagers, but equally strong in its way.

As red-legged blue honeycreepers are the most common birds in predominantly honeycreeper flocks (see below), green honeycreepers tend to perform many more supplanting attacks in such flocks than in predominantly tanager flocks.

We were not able to study the social relations between green honeycreepers and blue dacnises in detail, as the latter were rather rare on Barro Colorado Island, the only area where green honeycreepers were observed with appreciable frequency during the course of the present investigation; but our observations suggest that green honeycreepers react to blue dacnises in a way that is more like their reaction to plain-colored tanagers than their reaction to red-legged blue honeycreepers. We saw green honeycreepers join and follow, or attempt to approach, blue dacnises relatively frequently, but we did not see them supplant them. This latter fact may be particularly significant because blue dacnises are appreciably smaller than green honeycreepers.

The social relations between green honeycreepers and bananaquits are essentially intermittent. Sometimes the former seem to ignore the latter almost completely, but at other times they may attempt to join, follow, and/or supplant them very frequently and persistently. (The probable explanation of this peculiar relationship is discussed below in connection with the social role of bananaquits.)

Green honeycreepers join such birds as plain-colored tanagers and bananaquits quite frequently without beginning to feed immediately afterward, even when they are not obviously very aggressive.

Female green honeycreepers are usually more aggressive than males; and there are some indications that they are associated with mixed flocks slightly less frequently than are males.

It will be noticed that relatively few cases of joining, following, and supplanting by green honeycreepers are included in the accompanying tables. This might convey a somewhat misleading impression, as green honeycreepers do attempt to join, follow, and supplant individuals more frequently than the figures in these tables would suggest. The apparent discrepancy may be explained in several ways. Most of the flocks observed when these counts were made were predominantly tanager flocks, in which green honeycreepers perform fewer overt reactions to individuals of other species than in other types of mixed flocks. Individuals of other species also tend to react to green honeycreepers by attempts at evasion. They often fly away, or at least hop to another branch, when they see a green honeycreeper approaching, even before the green honeycreeper gets very close. They may have learned that green honeycreepers are often aggressive. In many cases, when an individual of another species retreated before a green honeycreeper in this way, the incident could not be classed as a clear-cut case of either joining or supplanting, according to the criteria used in compiling the accompanying tables.

As a general conclusion, green honeycreepers may be said to have two contradictory effects upon mixed flocks. They may tend to increase the cohesiveness and attractiveness of a mixed flock and/or tend to disrupt the flock. They may produce these effects successively or simultaneously. The disruptive effect of green honeycreepers is not, however, always as strong as might be expected. The increased calling and rapid movements provoked by, or accompanying, supplanted attacks and other aggressive patterns by green honeycreepers may tend to attract other birds in much the same way as do mobbing reactions.

SHINING HONEYCREEPER

Shining honeycreepers were not observed very frequently during the present study. They are common on Barro Colorado Island, but seldom conspicuous around the laboratory clearing. When they were seen, their behavior was more or less reminiscent of green honeycreepers.

Their social behavior apart from mixed species flocks in central Panamá seems to be quite remarkably similar to that of green honeycreepers. Shining honeycreepers have much the same range and types of display patterns [9] as green honeycreepers, and also tend to be very aggressive, and therefore only very slightly gregarious among themselves.[10]

In mixed flocks, however, the social role of shining honeycreepers seems to be less important than that of green honeycreepers. Shining honeycreepers do tend to join and follow individuals of other species, at least occasionally, but they do so relatively much less frequently than do green honeycreepers. All or most of their interspecific joining and following reactions seem to be expressions of generalized gregariousness. As far as I could tell, they do not have the special inter-

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[9] The term "display" will be used throughout this paper to include all vocal patterns and all movements and postures that appear to have become specialized to subserve a signal function.

[10] Slud (1960) says that shining honeycreepers are rather strongly gregarious among themselves in part of Costa Rica; but this is definitely not true of the shining honeycreepers of central Panamá.

specific preference for plain-colored tanagers which is such a conspicuous feature of the behavior of such species as the palm tanager and the green honeycreeper. Shining honeycreepers join predominantly honeycreeper flocks much more frequently than predominantly tanager flocks.

The only birds of other species that tend to provoke unusually strong reactions from shining honeycreepers are red-legged blue honeycreepers, which they tend to supplant quite frequently, much more frequently than they supplant individuals of any other species and almost as frequently as they supplant one another. I have also seen captive female shining honeycreepers (which were in cages with males of their own species) react to wild male red-legged blue honeycreepers outside their cages in almost exactly the same way that they would react to strange males of their own species at comparable distances, i.e., they performed several displays that were largely hostile but also contained nonhostile (presumably sexual) components. It is possible, therefore, that shining honeycreepers tend to regard red-legged blue honeycreepers as nothing more than slightly subnormal or suboptimal members of their own species.

Individuals of other species seldom react very strongly to shining honeycreepers, but when they do it is almost or exactly the same way that they react to red-legged blue honeycreepers (see below). Unfortunately, I saw very few encounters between shining honeycreepers and green honeycreepers. Green honeycreepers may tend to be as aggressive toward shining honeycreepers as they are toward red-legged blue honeycreepers, but this needs to be confirmed by further observations.

RED-LEGGED BLUE HONEYCREEPER

Red-legged blue honeycreepers are highly gregarious among themselves, in much the same way as plain-colored tanagers. They also resemble plain-colored tanagers in being very restless and noisy. It might be expected, therefore, that their role in mixed flocks would be equally similar to that of plain-colored tanagers. This is not quite the case, however. Red-legged blue honeycreepers behave very much like plain-colored tanagers in mixed flocks, but their behavior does not usually produce results that are very similar to the results of the behavior of plain-colored tanagers.

Red-legged blue honeycreepers occur in mixed flocks very frequently. They occur in all types of mixed blue and green tanager and honeycreeper flocks. They are usually much more numerous than individuals of any other species in predominantly honeycreeper flocks.

This may be illustrated by the figures in table 44, which is based upon observations of birds in two large flowering trees in the clearing on Barro Colorado Island between December 19 and December 23, 1959. During this period these trees were visited by individuals of many species of the blue and green tanager and honeycreeper alliance, separately and/or in mixed flocks. Almost all the mixed flocks seen during this particular series of observations were predominantly honeycreeper flocks. The figures in the table indicate the number of times individuals of the species most commonly seen during these observations were seen in mixed flocks and not in mixed flocks. These figures were compiled and are arranged in the same way as the corresponding figures in tables 1, 20, 28, and 35.

TABLE 44.—*Data from observations on Barro Colorado Island between December 19 and 23, 1959*

The number of times individuals of some species of the blue and green tanager and honeycreeper alliance were seen in mixed flocks (predominantly honeycreeper flocks) and apart from mixed flocks.

Species	No. of times individuals seen in mixed flocks	No. of times individuals seen not in mixed flocks	Totals
Plain-colored tanagers	44 (92)	4	48
Palm tanagers	19 (70)	8	27
Blue tanagers	17 (65)	9	26
Green honeycreepers	20 (59)	14	34
Red-legged blue honeycreepers	175 (68)	82	257
Blue dacnises	42 (74)	15	57
Summer tanagers	59 (71)	24	83
Bananaquits	18 (32)	39	57

(The results of this series of observations are not included with the results of the other observations on Barro Colorado Island summarized in tables 1-19.)

Red-legged blue honeycreepers usually tend to ignore all or most of their associates in mixed flocks. They join, follow, and supplant individuals of other species comparatively rarely. They are joined, followed, and supplanted by individuals of other species more frequently than they themselves join, follow, and supplant; but they are joined and followed relatively much less frequently than are plain-colored tanagers, and are also relatively much less common than plain-colored tanagers in obviously tightly integrated mixed flocks and in flocks composed of only two species. They do not seem to be particularly attractive to any species of tanager. With the possible exception of blue dacnises (see below), no other honeycreepers seem to behave as if they had a strong "friendly" interspecific preference for red-legged blue honeycreepers under natural conditions. I have never seen a female shining honeycreeper react to a male red-legged blue honeycreeper as a potential mate under natural conditions.

It is obvious, nevertheless, that the noisiness and rapid movements of red-legged blue honeycreepers greatly increase the conspicuousness of the mixed flocks in which they occur and probably, therefore, increase the attractiveness of such flocks to many birds of many species. It is my impression that mixed flocks that include red-legged blue honeycreepers tend to attract more birds of other species than otherwise identical flocks that do not include red-legged blue honeycreepers. In particular, migrant warblers of many species seem to be more likely to join mixed flocks that include red-legged blue honeycreepers than all or most other mixed flocks in the same environments. I am not sure of the precise social relationships between most of these warblers and red-legged blue honeycreepers. It seems unlikely that any of these warblers have any special interspecific preference for red-legged blue honeycreepers.

Red-legged blue honeycreepers may attract individuals of many other species as frequently as is possible by stimulating generalized gregariousness alone. Their social role in many mixed flocks is probably very similar to what the social role of plain-colored tanagers would be if plain-colored tanagers did not stimulate the "friendly" special interspecific preferences of some other species so strongly.

The fact that red-legged blue honeycreepers do not evoke as many nonhostile interspecific preferences as plain-colored tanagers may be due largely to the distinctive nature of some of their most common vocal patterns, which are quite different from the corresponding patterns of any other species of the blue and green tanager and honeycreeper alliance in central Panamá, and the bright and intricately patterned nuptial plumage of the males. Such characters are presumably advantageous because they help to maintain the reproductive isolation of the species. They may also tend to promote other types of social isolation as well.

It is possible that red-legged blue honeycreepers have begun to evolve certain characters to increase their attractiveness to other species. This might be one of the functions of the dull "eclipse" plumage of the males during the nonbreeding season. The males of other species of honeycreepers do not have eclipse plumages, and that of male red-legged blue honeycreepers is really quite remarkably similar to the year-round plumages of both male and female plain-colored tanagers and palm tanagers (and the eclipse plumage of male scarlet tanagers, *Piranga olivacea*).[11]

Male red-legged blue honeycreepers show more intraspecific gregariousness than do females; and they also seem to occur in mixed flocks relatively more frequently than do females.

BLUE DACNIS

Blue dacnises were not very common in any of the areas where mixed blue and green tanager and honeycreeper flocks were studied; but they appeared to contribute appreciably to the cohesion of mixed flocks, at least predominantly honeycreeper flocks, whenever they occurred in such flocks. They seemed to join and follow individuals of other species (especially red-legged blue honeycreepers) relatively frequently; and they were also joined and followed by individuals of other species (especially green honeycreepers) relatively frequently.

CRIMSON-BACKED TANAGER

All the species discussed above (with the possible or probable exception of the shining honeycreeper) may be considered regular members of mixed blue and green tanager and honeycreeper flocks. They are regular in the sense that they tend to associate with one another whenever a suitable opportunity to do so occurs, at least during the nonbreeding season. Each of these species usually approaches, or is approached by, at least one of the other species whenever they encounter one another during the nonbreeding season. Individuals of these species usually prefer to associate with individuals of other species of the group even when they have a wide choice of alternatives, i.e., when it would be just as easy for them to associate with individuals of species of other groups that have more or less similar insectivorous and/or frugivorous habits.

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[11] The scarlet tanager is also the only species of its genus that has a complete eclipse plumage. It would be interesting to know if scarlet tanagers associate with mixed flocks in their winter quarters in the Tropics, and, if so, in what capacity.

The crimson-backed tanager is not quite a regular member of the mixed blue and green tanager and honeycreeper flocks in this sense.

Crimson-backed tanagers do occur in mixed flocks with blue and green tanagers and honeycreepers—so frequently, in fact, that they may be considered members of the blue and green tanager and honeycreeper alliance (see definition above). They also join, follow, and/or supplant regular members of the blue and green tanager and honeycreeper flocks occasionally, and are occasionally joined, followed, and/or supplanted by regular members of these flocks. Such clear-cut reactions are relatively rare, however. Crimson-backed tanagers are usually joined and followed by other members of the blue and green tanager and honeycreeper alliance even less frequently than are red-legged blue honeycreepers in similar social situations. Crimson-backed tanagers often appear to be purely casual associates of mixed blue and green tanager and honeycreeper flocks, keeping some distance away from all or most of the other members of such flocks, and frequently moving in different directions from the other members of the flocks. Even more significantly, crimson-backed tanagers also prefer to associate with some other species that are not members of the blue and green tanager and honeycreeper alliance (see below).

The fact that both the plumage and the most common notes of crimson-backed tanagers (see above) are very conspicuously different from the corresponding characters of any regular member of the blue and green tanager and honeycreeper flocks is probably a definite hindrance to more frequent and closer associations between crimson-backed tanagers and most other members of the blue and green tanager and honeycreeper alliance. Crimson-backed tanagers must stimulate the generalized gregariousness of many or all the other members of this alliance; but they probably do so less strongly than they would if their appearance and notes were less distinctive.

It is also possible, since crimson-backed tanagers are comparatively large birds, that they tend to alarm the smaller blue and green tanagers and honeycreepers rather strongly.

There is no evidence, however, that any of the other members of the blue and green tanager and honeycreeper alliance have developed a definite aversion to crimson-backed tanagers, as they seem to have to some related species (see below).

Blue tanagers tend to associate with crimson-backed tanagers somewhat more frequently and/or more closely than do all or most of the other members of the blue and green tanager and honeycreeper alliance. This may be due to the fact that blue tanagers and crimson-backed tanagers have rather similar habitat preferences. Both species occur in young second-growth forest and scrub relatively more frequently than do such species as the plain-colored tanager, the palm tanager, the green honeycreeper, and the *Cyanerpes* honeycreepers.

Crimson-backed tanagers are usually very noisy and often travel in family groups or small flocks of several family groups. Mixed flocks that include crimson-backed tanagers are particularly conspicuous and tend to attract a wide variety of birds of other species not usually associated with such flocks. The other species attracted by crimson-backed tanagers are not usually the same as those attracted by red-legged blue honeycreepers. Crimson-backed tanagers seem to be especially attractive to several orioles and flycatchers.

SUMMER TANAGER

The social role of summer tanagers in mixed blue and green tanager and honeycreeper flocks is very different from the corresponding roles of any other tanagers or honeycreepers. In Panamá summer tanagers seldom associate with one another. It is relatively rare to see more than a single summer tanager in any given area at any given time.

These single summer tanagers become associated with mixed species flocks relatively frequently. They are probably associated with all types of blue and green tanager and honeycreeper flocks and with several other types of mixed flocks almost equally frequently (see below). They seem to discriminate between different types of mixed species flocks only insofar as they prefer flocks that inhabit the edges of forest or scrub and include some insectivorous or partly insectivorous species. They are largely insectivorous themselves in lowland Panamá, and are most common along the edges of forest and scrub.

Summer tanagers are seldom very conspicuous in mixed flocks. They are usually silent as long as they are associated with individuals of other species, and tend to remain on the outskirts of mixed flocks. While they are associated with mixed blue and green tanager and honeycreeper flocks, they are sometimes joined and followed by individuals of other species, especially such species as the green honeycreeper and the palm tanager which have particularly strong joining and following tendencies; but it is my impression that they usually become associated with such flocks in the first place because they themselves join the flocks.

The usual role of summer tanagers in mixed blue and green tanager and honeycreeper flocks is reminiscent of the roles of many furnariids (or dendrocolaptids) in other types of mixed flocks (see below).

Summer tanagers seem to be more nearly parasitic on their companions in mixed blue and green tanager and honeycreeper flocks than are any other birds commonly associated with such flocks.

BANANAQUIT

Bananaquits may play a rather important role in mixed flocks—but only occasionally. They are often rather silent and inconspicuous. At such times, they may occur in mixed blue and green tanager and honeycreeper flocks without having much effect upon their companions in the flocks. They may join and follow individuals of other species, or be joined, followed, and supplanted by individuals of other species; but such reactions are not usually very common.

During the breeding season, however, male bananaquits sing very frequently, and territorial bananaquits (apparently of both sexes) often engage in prolonged and noisy disputes. When bananaquits are noisy, they are joined, followed, and supplanted by individuals of other species much more frequently than when they are silent. They are particularly likely to be joined, followed, and supplanted by green honeycreepers.

It is not very clear why green honeycreepers should react so vigorously to bananaquits at times, as bananaquits do not resemble green honeycreepers in appearance or voice. The explanation may be simply that green honeycreepers react strongly to individuals of any other species that are conspicuous, and feel free to approach bananaquits because the latter are so much smaller than they are. Interestingly enough, bananaquits do not seem to have evolved any special characters for the primary purpose of either encouraging or discouraging green honeycreepers. It is possible that most bananaquits do not encounter green honeycreepers very frequently. Individuals of the two species encounter one another fairly frequently in such environments as the clearing on Barro Colorado Island; but bananaquits are also very common in certain types of second-growth vegetation in which green honeycreepers are rare or absent. Or perhaps the two species have come into contact with one another only relatively recently.

Associations between bananaquits and green honeycreepers are very seldom long sustained. This may be largely due to the fact that noisy bananaquits tend to stop vocalizing when approached by green honeycreepers.

There were some indications that some or all of the bananaquits on Barro Colorado Island tended to join and follow green honeycreepers more frequently than they joined and followed individuals of any other species of the blue and green tanager and honeycreeper alliance. This may have been the result of conditioning. These particular bananaquits may have become used to green honeycreepers simply because they were approached by the latter so frequently.

OTHER SPECIES

There is comparatively little to be said about the other species sometimes associated with mixed blue and green tanager and honeycreeper flocks. Some of them were rather rare in the areas where these flocks were studied. None of them appears to play a very significant role in any appreciable number of blue and green tanager and honeycreeper flocks, although some of them are very important in other types of mixed flocks (see below).

The streaked saltator and the yellow warbler may be cited as examples of rather common species that have very weak generalized gregarious tendencies and/or whose generalized gregarious tendencies are usually very weakly stimulated by members of the blue and green tanager and honeycreeper alliance. The differences between the frequencies of interspecific social reactions by streaked saltators and yellow warblers and by the other species cited in the accompanying tables may be taken as a rough measure of the extent to which the latter species have become important social factors in the blue and green tanager and honeycreeper alliance.

PARTIAL SUMMARY

Many mixed blue and green tanager and honeycreeper flocks are rather complex societies. Each of the more common species of the alliance tends to play a characteristic social role, more or less distinctly different from that of every other species in the mixed flocks of the alliance. These roles are the results of complex interactions between each species and at least one (usually several) other species. Several of the species tend to react differently to each of several other species. Most of the more common species have also evolved special adaptations, of plumage and/or behavior, to facilitate the performance of their characteristic roles in mixed flocks.

The most remarkable and apparently specialized social bonds between different species in mixed blue and green tanager and honeycreeper flocks are the special interspecific preferences.

Diagrams 1 and 2 are tentative summaries of the interspecific pref-

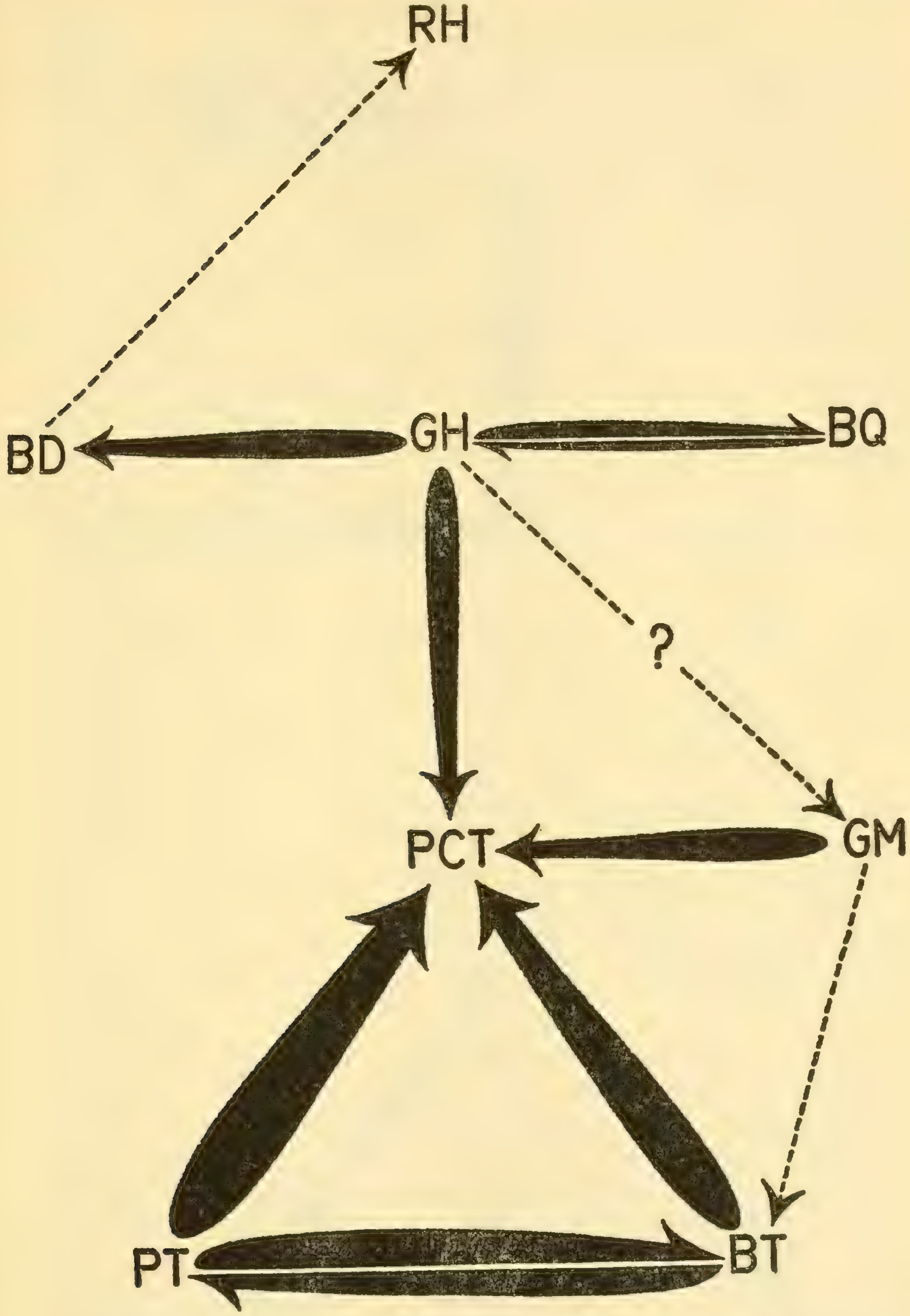

DIAGRAM 1.—The special interspecific preferences of the most commonly observed species of the blue and green tanager and honeycreeper alliance revealed by predominantly "friendly" joining and following reactions.

The species are identified by initials. RH = red-legged blue honeycreeper. BD = blue dacnis. GH = green honeycreeper. BQ = bananaquit. PCT = plain-colored tanager. GM = golden-masked tanager. PT = palm tanager. BT = blue tanager.

The arrows point from the species exhibiting a special interspecific preference to the species that is the object of this preference. The width of the arrows is roughly proportional to the apparent strength of the preferences.

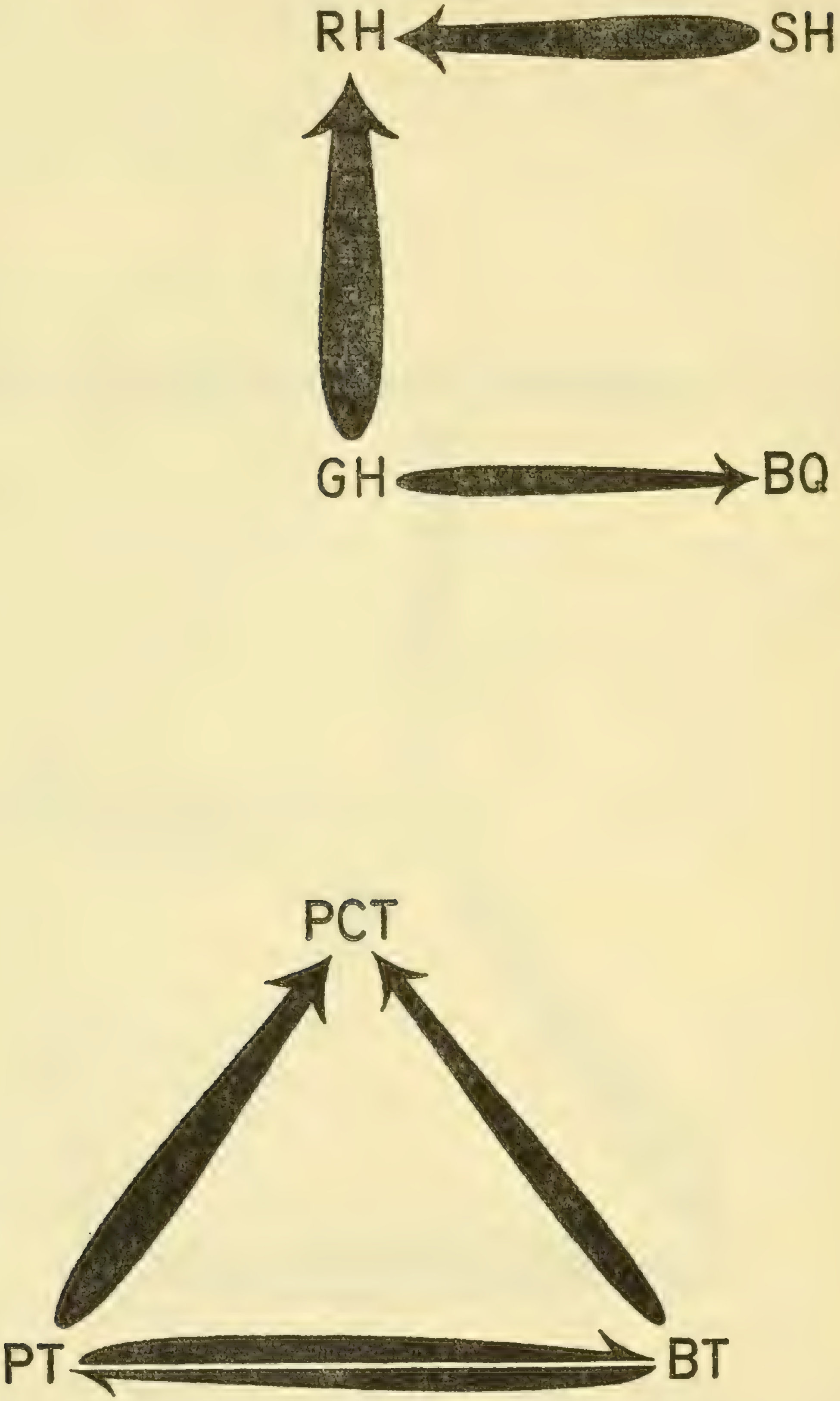

Diagram 2.—The special interspecific preferences of the most commonly observed species of the blue and green tanager and honeycreeper alliance revealed by supplanting attacks and other predominantly aggressive reactions. Organized in the same way as diagram 1.

The species are identified by the same initials as in diagram 1, with one addition: SH = shining honeycreeper.

erences of the most commonly observed species of the blue and green tanager and honeycreeper alliance. Diagram 1 shows the special interspecific preferences revealed by predominantly friendly joining and following reactions. Diagram 2 shows the special interspecific preferences revealed by supplanting attacks and other predominantly aggressive reactions. Both diagrams may be incomplete; but they probably include all or almost all of the strongest and most significant special interspecific preferences of the regular members of typical mixed blue and green tanager and honeycreeper flocks in central Panamá.

In spite of their distinctness, the roles of the various species occurring in mixed blue and green tanager and honeycreeper flocks may be classified into a small number of rather broad categories. Such a classification may be useful for comparative purposes.

There have been several previous attempts to classify the social roles of species occurring in different types of mixed flocks in different areas of the Tropics.

In his first paper on mixed flocks of Rhodesian birds, Winterbottom (1943), divided the species of such flocks into two categories: "nucleus" species and "circumference" species. Individuals of the nucleus species always occurred in groups, by themselves alone, or in association with individuals of other species. Individuals of the circumference species were not highly gregarious among themselves, but did join mixed flocks. Winterbottom suggested that most mixed flocks were formed by circumference species joining nucleus species. The terms themselves would suggest that individuals of the nucleus species usually occurred at the front and/or the center of mixed flocks and the circumference species at the sides and/or toward the rear of the flocks.

Davis (1946) classified the species of mixed flocks in some Brazilian forests according to several criteria. His main categories were "regular" species and "accidental" species. These were defined as follows: "The regular species stay with the flock for long periods of time, are seldom seen away from the flock, and have the calls and behavior patterns of a flocking species. . . . The accidentals associate merely temporarily with the group as it moves along. These species do not have the calls and behavior of flocking birds." Davis also recognized categories of "migrants," species that "are present for either the breeding or the nonbreeding period," and "nomads," species that "are irregular in occurrence and vary greatly in numbers."

In a later paper, Winterbottom (1949) attempted to combine Davis's classification with his own earlier classification, and suggested the following four main categories: (1) "nucleus" species, (2) other "regular" species, (3) "regular accidental" species, and (4) "accidental" species. He also suggested that a fifth category might be recognized: "accidental nucleus" species.

This last scheme can be used as the basis for a classification of the roles of different species in mixed blue and green tanager and honeycreeper flocks; but it needs to be revised in several ways for this purpose. The criteria for distinguishing the various categories may also be defined in more strictly behavioral terms in order to eliminate the factors that are essentially extrinsic to the mixed flocks.

An initial distinction may be made between "nuclear" and "attendant" species. Nuclear species can be defined as species whose behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of mixed flocks. Individuals of such species approach individuals of other species relatively frequently and/or behave in such a way that they are particularly attractive to individuals of other species. In any case, they contribute something more than their mere presence. Nuclear species, in this sense, may or may not be regular members of the mixed flocks in which they are sometimes nuclear. They may also occur at any place in mixed flocks. Some nuclear species usually occur at the front and/or center of mixed flocks but others do not. Attendant species do much less to stimulate the formation and/or maintain the cohesion of mixed flocks. They contribute little or nothing except their presence.

Nuclear species can be divided into two main types, which may be called "active" and "passive." These may be defined as follows. Individuals of active nuclear species usually join and/or follow individuals of other species much more often than they are joined and/or followed by individuals of other species. (Many or most of the species called "other regular species" by Winterbottom would probably be classified as active nuclear species according to this definition.) Individuals of passive nuclear species are usually joined and/or followed by individuals of other species much more often than they join and/or follow individuals of other species. (All or most of Winterbottom's "nucleus" species would probably be classified as passive nuclear species according to this definition.)

It may also be convenient to divide the species occurring in any particular type of mixed flock into "regular" and "occasional" members of such flocks. The characteristics of regular members have already been mentioned. Regular members of a particular type of mixed flock usually or always approach and/or are approached by one or more of the other species commonly occurring in that type of mixed flock whenever a suitable opportunity occurs (at least during the nonbreeding season). Occasional members of a particular type of mixed flock frequently, perhaps usually, do not approach and/or are not approached by the other species commonly occurring in that type of mixed flock when opportunities to do so occur (even during the nonbreeding season). Thus, a rare species that is a regular member of a certain type of mixed flock may actually occur in flocks of that type less frequently than a common species that is an occasional member, if the common species has many more opportunities to become associated with mixed flocks of that particular type. The term "occasional," in this sense, is probably largely synonymous with the term "accidental," as used by Davis and Winterbottom. The latter term is not used in this paper because it might convey a misleading impression. The associations between occasional members of mixed flocks and their companions in such flocks are not really fortuitous, or accidental, in the ordinary sense of the word.

The characters used to define the categories listed above are essentially relative. It is perfectly conceivable that some species might play intermediate roles in certain types of mixed flocks. This may be true of some of the species of montane bush flocks (see below). The roles of most species in mixed blue and green tanager and honeycreeper flocks, however, are so clear-cut and one-sided that they can be assigned to particular categories without any difficulty. It is possible, therefore, to summarize the roles of the various species in mixed blue and green tanager and honeycreeper flocks as follows:

The plain-colored tanager is always a regular and passive nuclear species. The red-legged blue honeycreeper is always regular and nuclear and probably always passive.

The blue tanager and the green honeycreeper are always regular and active nuclear species. The golden-masked tanager is probably similar. The shining honeycreeper may be a regular or an occasional active nuclear species.

The palm tanager is always an active nuclear species and always regular except in some environments in the breeding season.

The bananaquit is always regular. Sometimes it is a passive nuclear species. At other times it is an attendant species.

The summer tanager is always an attendant, and usually or always occasional.

The role of the crimson-backed tanager is more obviously complicated than those of all or most of the other species. It is a very common occasional member of mixed blue and green tanager and honeycreeper flocks, and attendant in relation to the regular members of such flocks. While it is associated with mixed blue and green tanager and honeycreeper flocks, however, it sometimes functions as a passive nuclear species for other occasional members of the flocks.

The blue dacnis is apparently always nuclear and regular. It has not been observed frequently enough to determine if it is a passive nuclear and/or an active nuclear species.

Most of the remaining species are probably occasional attendant species in mixed blue and green tanager and honeycreeper flocks. Some of them are nuclear, or regular attendants, in other types of mixed flocks; but their roles in such flocks do not seem to affect their roles in the blue and green tanager and honeycreeper flocks.

DIFFERENT TYPES OF MIXED FLOCKS

The frequencies with which blue and green tanager and honeycreeper flocks are formed, and the degree of integration within such flocks, are obviously different in different environments and in the same environment at different times. This may be due partly to the fact that different species are dominant in different environments and/or in the same environment at different times. It was not possible to study this aspect of flock behavior in detail; but some of the figures in the accompanying tables may help to illustrate some of the variations that can occur.

Individuals of most species were seen in mixed flocks most frequently near Gamboa and near Frijoles in July and August of 1960, when blue tanagers were the most common of the tanagers and honeycreepers. Individuals of most species were seen in mixed flocks least frequently near Frijoles between November 1959 and January 1960, when crimson-backed tanagers were the most common of the tanagers and honeycreepers. Relatively more birds were seen in tightly integrated flocks around the clearing on Barro Colorado Island, where plain-colored tanagers were dominant, than in any of the other areas.

It seems likely that most of the birds of the blue and green tanager and honeycreeper alliance around the clearing on Barro Colorado Island were very much habituated to one another. They were confined to a relatively small area, separated from the nearest similar areas by large expanses of heavy forest and/or the waters of Gatún Lake, and tended to encounter one another again and again.

Environments like the clearing on Barro Colorado Island are rare in central Panamá now, as most of the heavy forests of this region have been cut down; but they must have been relatively much more common before the region acquired a dense human population. It is possible that isolated clearings in heavy forest were the most important habitat of mixed blue and green tanager and honeycreeper flocks before human interference became appreciable. Many of the social behavior patterns of many species of the blue and green tanager and honeycreeper alliance may have been evolved originally as adaptations to life in mixed flocks that were more like the flocks observed on Barro Colorado Island than any of the other flocks observed in the course of the present study.

THE MONTANE BUSH FLOCKS

Montane bush flocks are much less widely distributed in Panamá than mixed blue and green tanager and honeycreeper flocks. The montane bush flocks that were studied most intensively during the present investigation are characteristic of the hills and mountains of western Panamá and seldom or never occur below 3,000 feet above sea level.

These flocks were studied on the western slopes of the Volcán de Chiriquí (El Baru), between approximately 4,500 feet and 7,500 feet above sea level (from the town of El Volcán to elevations well above the town of Cerro Punta), during four short periods of observation: between September 17 and September 21, 1958; between March 2 and March 9, 1959; between March 19 and March 30, 1960; and between October 3 and October 10, 1960. Special attention was paid to the flocks at higher altitudes, above 6,000 feet.

All or most of the upper slopes of the Volcán de Chiriquí must have been covered by heavy montane forest at one time. Much of the forest of the western slopes has been cut down within fairly recent years, but large patches remain, especially above 6,000 feet. Second-growth forest and scrub are also found in many areas. Most of the observations of mixed flocks were made along the edges of forest and scrub.

Many of the birds commonly occurring in mixed bush flocks in this region were performing reproductive behavior patterns in March; but all or most of them appeared to be in the middle of the nonbreeding season in September and October.

THE MOST COMMON SPECIES

It may be useful to describe the appearance of the most common species of the montane bush alliances in western Panamá and summarize the most distinctive features of their social behavior apart from mixed flocks, in much the same way as was done for the most common species of the blue and green tanager and honeycreeper alliance.

Brown-capped Bush-tanager (*Chlorospingus ophthalmicus*).—A comparatively small tanager. Sexes nearly identical in plumage: largely olive above and yellow below, with brown head, conspicuous triangular white patches behind eyes, white under wings (very conspicuous in flight), and grayish-buffy throat.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes, both in the treetops and in very low vegetation.

Very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering loud and sharp *tsit* call notes and mechanical-sounding rattles.

Sooty-capped Bush-tanager (*Chlorospingus pileatus*).—Very similar to the brown-capped bush-tanager in general appearance, but head largely blackish, with white postocular stripes and whitish throat.

Resident in Panamá. Usually at slightly higher altitudes than the brown-capped bush-tanager. Common along the edges of forest and scrub.

Not very gregarious apart from mixed species flocks. Similar to the brown-capped bush-tanager in voice, and almost equally active and restless.

Black-cheeked Warbler (*Basileuterus melanogenys*).—A very tanagerlike warbler. Reminiscent of *Chlorospingus* in shape. Sexes nearly identical in appearance: generally olive above and whitish below, with black cheeks, white superciliary stripes, black stripes above white superciliaries, and chestnut crown.

Resident in Panamá. Common along the edges of forest and scrub, at fairly high altitudes. Usually rather low in vegetation.

Not very gregarious apart from mixed species flocks. Very active and restless. Sometimes, but not always, very noisy.

Yellow-thighed Finch (*Pselliophorus tibialis*).—A rather large finch. Sexes nearly identical in plumage: largely blackish, with bright yellow thighs.

Resident in Panamá. Common along the edges of forest and scrub over a rather wide range of altitudes. Usually occurring relatively low in vegetation.

Not very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering twittering phrases.

Yellow-throated Bush-finch (*Atlapetes gutturalis*).—A rather large finch. Sexes nearly identical in plumage: largely black above and white below, with yellow throat and white crown stripe.

Resident in Panamá. Common along the edges of forest and scrub over a very wide range of altitudes. Usually occurring relatively low in vegetation.

Not very gregarious apart from mixed species flocks. Moderately active. Usually very quiet.

Miscellaneous Furnariidae.—Various species of furnariids, e.g., the ruddy tree-runner (*Margarornis rubiginosus*), the buff-fronted foliage-gleaner (*Philydor rufus*), and the red-faced spinetail (*Cranioleuca erythrops*) are more or less frequently associated with montane bush flocks.

All these species are somewhat similar in appearance, insofar as they all have rufous wings and tails. They are all resident in Panamá, and only very slightly gregarious apart from mixed species flocks.

Silver-throated Tanager (*Tangara icterocephala*).—A comparatively small tanager. Sexes nearly identical in plumage: largely golden yellow, with a whitish throat and black and green stripes on the back.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes. Frequently occurring in treetops.

Not very gregarious apart from mixed species flocks. Very restless and active. Very noisy; frequently uttering very distinctive buzzy call notes.

Wilson's Warbler (*Wilsonia pusilla*).—A small, chunky warbler. Sexes slightly different in appearance. Male generally yellowish, with conspicuous black crown. Female without black crown.

Migrant. In Panamá from September to March (approximately). Widely distributed over a wide range of altitudes in Panamá. Common both in the treetops and in low scrub.

Almost completely nongregarious apart from mixed species flocks in Panamá. Active and noisy, frequently uttering loud "Tsit" call notes.

Slate-throated Redstart (*Myioborus miniatus*).—A flycatcherlike warbler. Sexes nearly identical in appearance: largely black above and yellow below, cheeks and throat blackish, chestnut on crown, and white tips on tail feathers.

Resident in Panamá. Common along the edges of forest and scrub over a wide range of altitudes. Occurs in almost all levels of vegetation.

Not very gregarious apart from mixed species flocks. Very active and restless. Not very noisy.

Collared Redstart (*Myioborus torquatus*).—Similar to the slate-throated redstart in appearance, but with yellow cheeks and chin and a black breast band.

Resident in Panamá. Common along the edges of forest and scrub. Most common at slightly higher altitude than those at which the slate-throated redstart is most common. Occurs in all levels of vegetation.

Moderately gregarious apart from mixed species flocks. Very active and restless. Not very noisy.

Several other species are certainly associated with montane bush flocks at least moderately frequently. Among these are the summer tanager, the speckled tanager (*Tangara chrysophrys*), the golden-crowned warbler (*Basileuterus culicivorus*), the flame-throated warbler (*Vermivora gutturalis*), the brown-capped vireo (*Vireo leucophrys*), the blue-throated toucanet (*Aulacorhynchus caeruleogularis*), the pale-vented thrush (*Turdus obsoletus*), and various tyrannid flycatchers. Some of these species may play important roles in some montane bush flocks (see below); but they were either relatively rare in the areas where mixed montane bush flocks were studied most intensively and/or are associated with mixed montane bush flocks much less regularly or less closely than such species as the *Chlorospingus* tanagers and the yellow-thighed finch.

DESCRIPTION OF THE FLOCKS

The general social organization of most mixed montane bush flocks is similar to that of most blue and green tanager and honeycreeper flocks in the lowlands, but by no means absolutely identical.

Mixed montane bush flocks are more varied than blue and green tanager and honeycreeper flocks. They include different species at different altitudes. Some species of the montane bush alliances seem to be confined to a rather narrow range of altitudes. Other species occur over a wider range of altitudes but are not equally common throughout their ranges.

At relatively low altitudes, i.e., around 4,500-5,200 feet on the western slopes of the Volcán de Chiriquí, the montane bush flocks tend to include more species than the corresponding flocks at higher altitudes, and are rather distinctive in some other ways. These comparatively low-altitude flocks will be discussed below, after the discussion of the higher-altitude flocks.

The brown-capped bush-tanager, the yellow-thighed finch, the slate-throated redstart, various furnariids, and (sometimes) Wilson's warbler are usually the most conspicuous species in mixed bush flocks from approximately 5,200 to 6,800 feet on the western slopes of the

Volcán de Chiriquí. Above approximately 6,800 feet the brown-capped bush-tanager is more or less abruptly replaced by the sooty-capped bush-tanager, and the collared redstart becomes more common than the slate-throated redstart. In spite of their different compositions, most of the higher-altitude flocks, both above and below 6,800 feet, are essentially very similar in structure.

They are usually comparatively stable, more so than most mixed blue and green tanager and honeycreeper flocks. Individuals of all the species occurring in these montane bush flocks do tend to join and leave one another frequently, or are joined and left by one another frequently; but there are indications that individuals of some of these species tend to remain together with individuals of other species continuously for longer periods of time, on the average, than do individuals of any of the species of the blue and green tanager and honeycreeper alliance. Some of the higher-altitude mixed montane bush flocks are also long sustained as groups in spite of the fact that the individual birds in such flocks may change from time to time. This may be clarified by an example. A pair of birds of a strongly territorial species may remain associated with a mixed montane bush flock as long as the flock remains within the pair's territory and then drop out of the flock when the flock moves on; but this pair's place in the flock may be taken, immediately, by another pair of the same species, so that the specific composition of the flock is not changed by the change of individual birds.

The comparative stability of the higher-altitude mixed montane bush flocks seems to be correlated with certain other distinctive features of social behavior within such flocks. Interspecific joining and following reactions are comparatively common, more so than in all or most mixed blue and green tanager and honeycreeper flocks, while interspecific supplanting attacks are comparatively rare, much less common than in all or most mixed blue and green tanager and honeycreeper flocks.

The frequencies of some interspecific reactions in some higher-altitude montane bush flocks may be illustrated by the figures in table 45. These figures are counts of the number of times individuals of certain species were seen to be involved in interspecific joining, following, and supplanting reactions in higher-altitude montane bush flocks during approximately 25 hours of intermittent observations between October 4 and October 10, 1960, on the Volcán de Chiriquí. The method of observation used was the same as in the counts of reactions in mixed blue and green tanager and honeycreeper flocks, except that each individual montane bush flock was usually watched continuously for a considerable length of time (usually 15 minutes to 1 hour). In compiling table 45, a bird was considered to have joined another (or several others) when it approached within 10 feet of another, or others, without continuing to move after the others, and without forcing the others to move away. The joined birds were usually more or less stationary before being joined. A bird was considered to be following another (or others) when it hopped or flew steadily after the others, while the others were moving themselves.[12] Supplanting attacks were recognized by the same criteria as in the counts of similar reactions in mixed blue and green tanager and honeycreeper flocks.

Table 45.—*Interspecific following, joining, and supplanting reactions involving some species of the montane bush alliances in some higher-altitude mixed flocks observed between October 4 and 10, 1960*

	No. of times individuals seen in mixed flocks	No. of flocks in which seen	No. of times seen following other species	No. of times seen joining other species	No. of times seen being followed by other species	No. of times seen being joined by other species	No. of times seen supplanting other species	No. of times seen being supplanted by other species
Brown-capped bush-tanager	37	11	3	2	18	19	0	1
Yellow-thighed finch	33	16	22	7	10	6	0	0
Red-faced spinetail	4	2	10	12	1	0	0	0
Silver-throated tanager	15	7	0	2	0	0	1	3
Wilson's warbler	31	31	15	7	3	0	0	1
Collared redstart	16	10	3	9	6	0	0	0

Table 45 is a list of all the interspecific joining, following, and supplanting reactions observed, including ambiguous cases when one bird joined or followed a group composed of individuals of several other species. The figures in this table are not strictly comparable with the counts of interspecific reactions in mixed blue and green tanager and honeycreeper flocks shown in the preceding tables. The reactions of each species are listed separately in the table, without attempting to identify the other species involved in any given reaction.

Many of the higher-altitude mixed montane bush flocks seem to be formed in much the same way as all or most mixed blue and green tanager and honeycreeper flocks (but see also comments below). Like

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[12] All the joining and following reactions cited in the subsequent discussion of the usual social roles of different species in mixed montane bush flocks were distinguished by the same criteria as in this count.

the mixed blue and green tanager and honeycreeper flocks, they seem to be formed more frequently and include more birds of more species, on the average, during the nonbreeding season than during the breeding season. They are also more common and tend to be larger in the early morning than at other times of the day.

Many of the higher-altitude mixed montane bush flocks seem to have definite ranges, and tend to move through their ranges along definite and rather stereotyped pathways. They tend to visit the same sites in more or less the same sequence again and again on the same day and on successive days.

Some of the members of the higher-altitude montane bush alliances seem to be purely insectivorous, but others eat fruits and seeds as well as insects. All spend most of their time feeding while they remain in the flocks. As in the case of the members of the blue and green tanager and honeycreeper alliance, however, it is obvious that individuals of different species of the higher-altitude montane bush alliances are sometimes attracted to one another by some social factor or factors in addition to, or instead of, the direct stimulus of food (see below). It was my impression, in fact, that members of the higher-altitude montane bush alliances are attracted to one another by purely social factors, apart from food, more frequently than are members of the blue and green tanager and honeycreeper alliance.

Unlike the members of most blue and green tanager and honeycreeper flocks, the members of most higher-altitude mixed montane bush flocks are frequently scattered through many different levels of vegetation. It is very common to see higher-altitude mixed montane bush flocks that include some birds feeding and moving on or near the ground, other birds feeding and moving in moderately low shrubbery, and still others feeding and moving in the treetops, all at the same time.

(Some of the mixed montane bush flocks above 6,000 feet on the Volcán de Chiriquí appeared to be accompanied by one, two, or three squirrels (probably *Sciurus granatensis*).[13] The associations between these squirrels and the mixed bird flocks were not very close, as the squirrels were always, or almost always, several feet away from the nearest birds; but the squirrels occurred in the general vicinity of mixed flocks more frequently than would seem likely by chance alone.

It may be significant, in this connection, that these squirrels are noisy animals, frequently uttering sharp chattering calls that are

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[13] I am indebted to Dr. Charles O. Handley, Jr. (in litt.), for the probable identification of these squirrels.

reminiscent of the calls of some thicket-inhabiting finches (but not the finches usually occurring in mixed montane bush flocks on the Volcán de Chiriquí). The squirrels may tend to enchance the conspicuousness and the attractiveness of the mixed bird flocks with which they are associated.)

Brief observations of the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí would suggest that they are usually more loosely organized than the higher-altitude mixed montane bush flocks. It has already been mentioned that the lower-altitude mixed montane bush flocks frequently include more species than the higher-altitude flocks; but they usually include relatively few individuals of the species that play the most important nuclear roles in the higher-altitude flocks. The structure of the lower-altitude mixed flocks is similar to that of the higher-altitude mixed flocks insofar as the members of the lower-altitude flocks may also occur at many different levels of vegetation; but the associations between most of the common species of the lower-altitude flocks seem to be briefer, on the average, than the associations between most of the common species of the higher-altitude flocks. Interspecific joining and following reactions seem to be comparatively rare in the lower-altitude mixed montane bush flocks; but interspecific supplanting attacks are comparatively common, much more so than in the higher-altitude mixed montane bush flocks, and perhaps as common as in mixed blue and green tanager and honeycreeper flocks.

THE ROLES OF DIFFERENT SPECIES WITHIN MIXED FLOCKS

BROWN-CAPPED BUSH-TANAGER

The usual social role of brown-capped bush-tanagers in mixed species flocks, especially at moderately high altitudes, is very similar to that of plain-colored tanagers in blue and green tanager and honeycreeper flocks.

Brown-capped bush-tanagers are frequently joined and followed by individuals of many other species, much more frequently than they themselves join and follow individuals of other species.

As in the case of the plain-colored tanagers, the usual social role of brown-capped bush-tanagers in mixed flocks seems to be largely or completely a consequence of their social behavior apart from mixed flocks. Some of the intraspecific social behavior patterns of the two species are even more strikingly similar than their interspecific relations.

Brown-capped bush-tanagers are highly gregarious among themselves in almost exactly the same way as plain-colored tanagers. During the nonbreeding season most brown-capped bush-tanagers tend to associate with one another in rather stable groups of 4 to 8 or 10 individuals. Many or most of these groups appear to be composed of more than one family (i.e., parents and one brood of young). Individual birds, pairs, and family groups are seldom territorial during the nonbreeding season, or, at least, seldom defend territories for any appreciable continuous length of time. Some individuals, apparently adult males, may show indications of territorial defense for a few minutes, especially very early in the morning and late in the afternoon during the nonbreeding season, but such behavior is apparently always very brief at this season. During the breeding season, the larger groups of brown-capped bush-tanagers tend to break up. Pairs and apparently unmated single birds separate comparatively frequently and remain on individual territories for comparatively long periods of time. They usually spend most of the mornings, at least, on their own territories, but large groups are still re-formed occasionally, especially in the afternoons. I have seen flocks of brown-capped bush-tanagers during the later part of the courtship phase of the breeding season that were quite as large as any flocks of the same species observed during the nonbreeding season.

This high degree of intraspecific gregariousness is correlated with the usual types of movements and calls. Brown-capped bush-tanagers are very restless, almost constantly active, moving from bush to bush and tree to tree with very great rapidity. They are also very noisy (see comments below, in the discussion of the sooty-capped bush-tanager). They frequently perform exaggerated wing-flicking and tail-flicking movements, very much like the corresponding movements of plain-colored tanagers. They also utter many loud and hard call notes and rattling calls which are almost equally reminiscent of the most common calls of plain-colored tanagers. Some of these similarities between the two species are probably due to convergence, as there are indications that the genera *Chlorospingus* and *Tangara* are not very closely related to one another. *Chlorospingus* is probably more closely related to some of the bush-finches and/or the *Ramphocelus* tanagers, while *Tangara* is probably more closely related to some of the tanagers usually included in the genus *Thraupis;* and neither

Chlorospingus nor *Tangara* seems to be particularly primitive among tanagers.[14]

It seems likely, therefore, that much of the attractiveness of brown-capped bush-tanagers to individuals of other species is due to their possession of special characters that were originally evolved to promote intraspecific gregariousness. Individuals of other species are probably usually or frequently attracted to them by the same characters that attract brown-capped bush-tanagers to one another; but there are certain obvious exceptions to this general rule.

Brown-capped bush-tanagers frequently dispute among themselves, even during the nonbreeding season when they associate with one another in relatively large groups. During such disputes they usually utter many hostile vocalizations. All or most of these vocalizations seem to function as a threat during intraspecific encounters. When uttered by one brown-capped bush-tanager they usually induce other brown-capped bush-tanagers to retreat, at least temporarily.

There is some evidence that brown-capped bush-tanagers tend to utter relatively more vocal threat patterns and perform relatively fewer overt attack movements during intraspecific disputes than do many related species in similar circumstances. This may be an adaptation to promote intraspecific gregariousness, as vocal threats are probably less disruptive within a flock than overt attack movements.

Interestingly enough, the vocal threat patterns of brown-capped bush-tanagers may have an effect upon individuals of other species, which is just the reverse of their usual effect upon other brown-capped bush-tanagers. The sound of all or most of their threat calls seems to be definitely attractive to individuals of some other species. This may be illustrated by the behavior of some birds observed at approximately 5,700 feet elevation on the Volcán de Chiriquí between October 3 and October 10, 1960. There were two or three pairs of family groups of brown-capped bush-tanagers in this particular area at this time. They roosted separately at night and began to move around and feed separately at dawn. They were usually rather quiet when they first began to move around and feed, and were not usually accompanied by individuals of other species. Sooner or later, in the course of their wanderings, two of the pairs or family groups would come face to face, apparently by accident. Such encounters would induce an outburst of threat calls by some or all of the brown-capped bush-

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[14] The phylogenetic relationships between different genera of tanagers and finches will be discussed in a series of separate papers (in preparation) after more detailed descriptions of their most significant behavior patterns.

tanagers involved. As soon as this outburst occurred, the brown-capped bush-tanagers were usually joined by individuals of other species, such as yellow-thighed finches or red-faced spinetails, who had been ignoring them until they became very noisy. The disputes between the brown-capped bush-tanagers usually subsided after a few minutes. The disputing birds either separated or joined up with one another to form a more or less amicable flock. In either case, some or all of the brown-capped bush-tanagers were usually followed for long periods of time after the end of the dispute by some or all of the individuals of other species that had been attracted by the sound of the dispute.

(Occasionally, but relatively very rarely, a brown-capped bush-tanager is also attracted by the sound of other brown-capped bush-tanagers uttering threat calls during a dispute. It may then fly to join the disputing birds and utter threat calls itself and/or actually begin to fight with the other birds. This would suggest that the sound of threat calls by one brown-capped bush-tanager usually or always stimulates both the attack and escape drives of other brown-capped bush-tanagers that hear the calls. The escape drives of the birds that hear such calls are probably usually or always stimulated more strongly than their attack drives; but their attack drives are apparently stimulated strongly enough to be expressed by overt activity in some cases.

There are indications that the reactions of individuals of other species that are attracted by the sounds of the threat calls of brown-capped bush-tanagers are seldom or never produced by the same motivation as the similar reactions of other brown-capped bush-tanagers. Individuals of other species that are attracted by the sounds of the threat calls of brown-capped bush-tanagers seldom or never perform hostile patterns themselves after joining the brown-capped bush-tanagers. Their reactions seem to be usually or always essentially "friendly." They apparently recognize the threat calls of brown-capped bush-tanagers as calls of a species with which they are accustomed to associate; but they seldom or never react as if they understood the hostile significance of such calls.)

The reactions of individuals of other species to the threat calls of brown-capped bush-tanagers might suggest that the usual social role of the latter in mixed flocks is largely determined by their vocal patterns rather than their movements or their physical appearance; but the effect of their vocal patterns is probably reinforced by some or all of their other characteristics. It is possible, for instance, that the role of brown-capped bush-tanagers in mixed flocks is facilitated by their tendency to range through many different levels of vegetation. They are most often found moderately high (approximately 10 to 40 feet above the ground) in medium-sized trees and tall shrubbery; but they also occur in the tops of very tall trees and in very low shrubbery only a few inches above the ground. They probably occur at both extreme levels of vegetation more often than individuals of most other species of the montane bush alliances; and they frequently move from one extreme to the other or alternate between the two extremes very rapidly. Thus they tend to encounter a wide diversity of individuals of many different species, including species that are rather strictly confined to comparatively narrow levels of vegetation.

It is my impression that brown-capped bush-tanagers tend to play a less important role in lower-altitude mixed montane bush flocks, below approximately 5,200 feet, than in higher-altitude mixed montane bush flocks. They seem to be joined and followed by individuals of other species relatively less frequently in the lower-altitude flocks than in the higher-altitude flocks. Part or all of this difference seems to be due to the fact that brown-capped bush-tanagers are usually relatively less conspicuous in the lower-altitude flocks. They tend to be relatively rare at lower altitudes. The lower-altitude flocks also tend to include individuals of more species than the higher-altitude flocks; and some of the species that occur in lower-altitude flocks but not in higher-altitude flocks are very noisy and/or very restless. Thus the attention of the other members of the lower-altitude mixed flocks is more often distracted, i.e., diverted from the brown-capped bush-tanagers, than is that of the other members of the higher-altitude mixed flocks.

The brown-capped bush-tanager must be classified as a passive nuclear species. Its social role in mixed flocks is not, however, quite as one sided as that of the plain-colored tanager. It seems to join and follow individuals of other species slightly more frequently than do plain-colored tanagers.

The range of the brown-capped bush-tanager on the Volcán de Chiriquí overlaps that of the sooty-capped bush-tanager to some extent. Brown-capped bush-tanagers may react to sooty-capped bush-tanagers more strongly than they do to individuals of many other species. At least I have heard them begin to utter hostile calls when they heard sooty-capped bush-tanagers utter hostile calls in the distance. But such reactions are relatively very rare and very brief. I have never heard brown-capped bush-tanagers utter more than a few hostile calls in response to sooty-capped bush-tanagers. They react to sooty-capped bush-tanagers much less frequently and less strongly than might be expected in view of the fact that the two species may occupy the same habitats, are rather similar in physical appearance, and have very similar repertories of calls, display movements, and postures. The few definite social reactions of brown-capped bush-tanagers to sooty-capped bush-tanagers probably occur when the former mistake the latter for suboptimal members of their own species.

Brown-capped bush-tanagers are more responsive to yellow-thighed finches, which are very different from brown-capped bush-tanagers in appearance and have some rather different habits, but are common throughout the range of brown-capped bush-tanagers on the western slopes of the Volcán de Chiriquí.

Brown-capped bush-tanagers react to the hostile calls of yellow-thighed finches more frequently and more vigorously than they do to those of sooty-capped bush-tanagers. I have seen single brown-capped bush-tanagers fly considerable distances to join groups of yellow-thighed finches that were disputing among themselves and uttering many hostile calls. These brown-capped bush-tanagers usually uttered many hostile calls of their own after joining the yellow-thighed finches, sometimes continuing to utter these calls as long as the yellow-thighed finches continued disputing among themselves. These incidents occurred near the upper border of the range of brown-capped bush-tanagers on the western slopes of the Volcán de Chiriquí, in which area these birds are relatively rare. It is possible, therefore, that the single brown-capped bush-tanagers that reacted so vigorously to the hostile calls of yellow-thighed finches did so because they were unable to associate with and perform their usual hostile behavior with other individuals of their own species. Their hostile motivation may have "accumulated" because it could not be vented in its usual way, and then "overflowed" upon suboptimal objects that would not have released hostility in other circumstances. The reactions of these single brown-capped bush-tanagers were particularly interesting, nevertheless, because the hostile calls of yellow-thighed finches are very different from any calls of brown-capped bush-tanagers and because the same brown-capped bush-tanagers that reacted to the hostile calls of yellow-thighed finches usually ignored all the calls of sooty-capped bush-tanagers in the same neighborhood.

I once heard a single territorial brown-capped bush-tanager near the upper border of the range of the species utter many hostile calls which were obviously provoked by and directed toward a silent yellow-thighed finch some yards away. This reaction was presumably an even more extreme case of "overflow."

Brown-capped bush-tanagers also seem to join and follow yellow-thighed finches slightly more frequently than they do individuals of any other species; but this may be due to the fact that they are more often in closer proximity to yellow-thighed finches than to individuals of other species, as a result of the behavior of yellow-thighed finches (see below).

THE SOOTY-CAPPED BUSH-TANAGER

The sooty-capped bush-tanager is very similar to the brown-capped bush-tanager in general activity and methods of feeding as well as display patterns. It was seen in low shrubbery relatively more frequently than brown-capped bush-tanagers on the Volcán de Chiriquí; but this may have been largely or completely due to the fact that there were fewer tall trees in most of the areas where sooty-capped bush-tanagers were studied than in most of the areas where brown-capped bush-tanagers were studied.

It is perhaps remarkable, therefore, that sooty-capped bush-tanagers are much less gregarious among themselves than are brown-capped bush-tanagers. They seldom or never form flocks larger than a single family group of a pair of adults plus their most recent brood of young. Each pair or family group seems to defend its own particular territory throughout the year, including the breeding season.

Sooty-capped bush-tanagers also seem to play a less important role in mixed flocks than brown-capped bush-tanagers. They are joined and followed by individuals of other species more often then they themselves join and follow individuals of other species, and the actual frequency with which they are joined and followed is usually quite high; but they are certainly joined and followed by individuals of other species relatively less frequently than are brown-capped bush-tanagers. There are also some indications that sooty-capped bush-tanagers may join and follow individuals of other species relatively (but probably not actually) more frequently than do brown-capped bush-tanagers.

As in the case of the brown-capped bush-tanagers, the vocalizations of sooty-capped bush-tanagers seem to be more attractive than their movements to individuals of other species. They probably do not utter calls as frequently, on the average, as do brown-capped bush-tanagers, and they are sometimes almost completely silent for several minutes at a time. (This is presumably correlated with the lesser degree of intraspecific gregariousness shown by sooty-capped bush-tanagers.) It is very obvious that they are joined and followed by individuals of other species much less frequently when they are silent, even when they are very active, than when they are vocal, even when they are not very active. The hostile calls of sooty-capped bush-tanagers, a sound very much like the corresponding calls of brown-capped bush-tanagers, also seem to be considerably more attractive to individuals of other species than many or all of their nonhostile calls (see below).

Sooty-capped bush-tanagers are sometimes attracted by the hostile calls of yellow-thighed finches in very much the same way as are brown-capped bush-tanagers. (I have not seen sooty-capped bush-tanagers react to the hostile calls of brown-capped bush-tanagers, perhaps because brown-capped bush-tanagers were relatively rare in the areas where I saw the two species together.)

The sooty-capped bush-tanager may thus be considered a passive nuclear species; but it is less effective as such than the brown-capped bush-tanager.

THE BASILEUTERUS WARBLERS

Black-cheeked warblers were not as common as bush-tanagers in the areas where mixed montane bush flocks were studied most intensively; but they were observed frequently enough to discover their usual social role in at least some types of mixed flocks.

Black-cheeked warblers seem to be approximately as gregarious among themselves as are sooty-capped bush-tanagers, which they resemble in several ways, but are more strictly confined to moderately low shrubbery. They are very much like sooty-capped bush-tanagers in physical appearance. The two species are similar in shape, and their plumage looks very much the same at a distance in the field. Both species appear to be big headed and plump bodied, generally olive in color, with blackish heads marked by light chins and whitish lines above and behind the eyes. Black-cheeked warblers are less frequently vocal than sooty-capped bush-tanagers; but their most common vocal patterns, including sharp call notes and rattles, are reminiscent of both the bush-tanagers. These similarities are not likely to be coincidental. They may be some form of mimicry.

In one area on the Volcán de Chiriquí, just below 7,000 feet, where sooty-capped bush-tanagers were quite common, black-cheeked warblers joined and followed individuals of other species, and were also joined and followed by individuals of other species moderately frequently. They joined and followed individuals of other species relatively more frequently than did the sooty-capped bush-tanagers in the same area (in the same patches of shrubbery), and were joined and followed by individuals of other species relatively less frequently than were the sooty-capped bush-tanagers. The role of the black-cheeked warblers in the mixed flocks of this area appeared to be only slightly nuclear, and almost exactly intermediate between passive and active.

In another area, slightly above 7,000 feet, sooty-capped bush-tanagers were comparatively rare, and black-cheeked warblers appeared to be joined and followed by individuals of other species relatively more frequently than in the area below 7,000 feet. All the species which joined and/or followed the black-cheeked warblers above 7,000 feet also occurred in the same area as the black-cheeked warblers below 7,000 feet. This would suggest that black-cheeked warblers may take the place of sooty-capped bush-tanagers in mixed flocks in areas where the latter are rare or absent (and brown-capped bush-tanagers are absent).

There was no evidence that black-cheeked warblers have a special interspecific preference for sooty-capped bush-tanagers, or that the latter have a special interspecific preference for the former in either of the areas where the two species were seen together. It is conceivable, therefore, that one of these species has become more like the other, or that they are convergent, in voice and appearance, in order to facilitate associations with other species. It may be advantageous for the black-cheeked warbler and/or the sooty-capped bush-tanager to be joined and/or followed by individuals of other species. If associations with other species are advantageous to the black-cheeked warbler, then it may be advantageous for it to resemble the sooty-capped bush-tanager because individuals of other species tend to join and follow sooty-capped bush-tanagers. If associations with other species are advantageous to the sooty-capped bush-tanager, it may be advantageous for it to resemble the black-cheeked warbler because individuals of other species tend to join and follow black-cheeked warblers. If associations with other species are advantageous to both the black-cheeked warbler and the sooty-capped bush-tanager, the similarities between them may tend to increase the frequency and/or speed with which individuals of other species join and follow both of them, as individuals of other species may become conditioned more rapidly and easily to the essentially single set of stimuli actually presented by both the black-cheeked warbler and the sooty-capped bush-tanager than they would to the two sets of stimuli which would be presented by the two species if they were not so similar to one another.

Black-cheeked warblers join and follow yellow-thighed finches more frequently than they do individuals of any other species and relatively more frequently than do brown-capped bush-tanagers. They may have a definite special interspecific preference for yellow-thighed finches.

Golden-crowned warblers were seen in the lower-altitude mixed montane bush flocks slightly above 5,000 feet on the western slopes of the Volcán de Chiriquí. They appeared to be rather strongly gregarious among themselves (see also Eisenmann, 1957) and to play an important nuclear role in some of the lower-altitude mixed flocks. Their usual social role in such flocks may be similar to that of brown-capped bush-tanagers in many higher-altitude mixed montane bush flocks.

YELLOW-THIGHED FINCH

Social relationships between yellow-thighed finches and individuals of many other species are extremely significant factors in the organization of most higher-altitude mixed montane bush flocks on the Volcán de Chiriquí. Yellow-thighed finches can play two different roles in such flocks, and may play either one or both of these roles simultaneously and/or successively. They probably occur in the higher-altitude mixed montane bush flocks of the Volcán de Chiriquí more frequently than individuals of any other species, and they range farther up the mountain than do brown-capped bush-tanagers.

They tend to react actively to individuals of almost all the other species they encounter. They usually join and follow individuals of most other species much more frequently than they are joined and followed by individuals of most other species. They do not, however, perform joining and following reactions equally frequently. They tend to follow individuals of most other species much more frequently than they join individuals of the same other species. The actual number of joining reactions performed by yellow-thighed finches in most higher-altitude mixed montane bush flocks is usually quite large, but always, or almost always, much smaller than the number of following reactions performed at more or less the same time. They certainly follow individuals of other species without actually joining them much more frequently than do any other members of any of the montane bush alliances.

Some other species of the montane bush alliances tend to perform many more interspecific joining reactions than interspecific following reactions (see below). The marked contrast between certain species that are primarily followers and others that are primarily joiners is one of the most characteristic features of mixed montane bush flocks, which are quite different from mixed blue and green tanager and honeycreeper flocks in this respect. All or most of the active nuclear and attendant species in mixed blue and green tanager and honeycreeper flocks cannot be classified as either followers or joiners in the same way as some species of the mixed montane bush flocks.

All other factors being equal, individuals of all or most species would probably usually prefer to follow rather than join individuals of other species. By following, a bird can associate with another bird without coming too close, which might provoke a dispute. In some circumstances, however, following tends to be more difficult than joining. The ease or difficulty of following or joining is often largely dependent upon the nature of the vegetation in which such reactions occur.

Yellow-thighed finches may be able to follow so much more frequently than to join because they are essentially birds of thickets and low shrubbery. They sometimes go fairly high into trees, 20 or 30 feet above the ground, but only in certain exceptional situations. They seldom or never do so except when there is a thick curtain of shrubberylike vegetation extending continuously or nearly continuously from the ground up to a higher level, e.g., when there are thick tangles of vines extending from just above the ground to the higher branches of trees.

Individuals of other species that also occur in thickets and low shrubbery on the Volcán de Chiriquí also tend to perform more interspecific following reactions than interspecific joining reactions as long as they remain in thickets and low shrubbery. This is true of the bush-tanagers and black-cheeked warblers, as well as individuals of several less passive species (see below). On the other hand, individuals of at least some active species of the montane bush alliances tend to perform more interspecific joining reactions than interspecific following reactions when they are in high shrubbery and trees (see below). They may also perform relatively more interspecific joining reactions when they are in high shrubbery and trees than when they are in low shrubbery and thickets.

The explanation of all or most of these differences is fairly obvious. Low shrubbery and thickets tend to be denser than high shrubbery and trees, and twigs and branches that birds can use as perches tend to be much closer together in thickets and low shrubbery than in high shrubbery and trees. Birds moving through thickets and low shrubbery can usually regulate their distances from one another more or less at will, because they can move by very short stages, hopping or flying between perches that are only a few inches apart. Such birds can usually follow one another without joining whenever they want to. Birds moving through trees do not always have the same freedom of choice. They may have to move from tree to tree by comparatively long flights because the trees are not very close together, and may not be able to regulate their distances from one another as precisely as can birds in thickets and low shrubbery. They may have to bunch up in certain particular trees, i.e., perform joining reactions, if they are to keep in touch with one another at all.[15]

In the case of yellow-thighed finches there is also another factor involved. These birds in thickets and low shrubbery are often attracted to individuals of other species that are moving through higher vegetation more or less distinctly separated by a layer of open space from the underlying low vegetation. In such circumstances the yellow-thighed finches are usually prevented from trying to join the individuals of other species by their reluctance to move through the open space.

Although yellow-thighed finches will follow and join individuals of almost any other species, they seem to prefer to follow brown-capped bush-tanagers when the latter are common, sooty-capped bush-tanagers when brown-capped bush-tanagers are rare or absent, and black-cheeked warblers at high altitudes where brown-capped bush-tanagers are absent and sooty-capped bush-tanagers are rare or absent.

The marked special interspecific preference of yellow-thighed finches for brown-capped bush-tanagers is also shown in several other ways. Yellow-thighed finches are often attracted by the hostile as well as the nonhostile vocal patterns of brown-capped bush-tanagers. They do not seem to react as positively to the hostile calls of any other species as they sometimes do to those of brown-capped bush-tanagers.

Yellow-thighed finches also tend to follow brown-capped bush-

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[15] The frequencies of interspecific reactions by members of the blue and green tanager and honeycreeper alliance are also affected by density of vegetation. Individuals of most species of this alliance tend to perform relatively more interspecific following reactions in environments such as the clearing on Barro Colorado Island, where the treetops form a continuous band of vegetation around the edge of the clearing, than in environments such as the areas near Gamboa and Frijoles, where trees are more scattered.

tanagers for longer periods of time than they do individuals of other species, and sometimes follow them at greater distances than they do individuals of other species. I have seen a pair of yellow-thighed finches in low shrubbery follow a flock of brown-capped bush-tanagers moving through trees above the shrubbery for several hours at a time, and repeatedly follow the same flock on several successive days, in spite of the fact that the brown-capped bush-tanagers were usually 30 to 50 feet above and approximately 20 feet ahead of them.

It is often particularly clear that yellow-thighed finches and brown-capped bush-tanagers are not obtaining extra food by associating with one another. In the case of the association cited immediately above, for instance, the brown-capped bush-tanagers were usually feeding on insects while the yellow-thighed finches following far below and behind them were usually feeding on fruit and other vegetable matter.

Yellow-thighed finches usually do not react to brown-capped bush-tanagers that are more than 50 feet above them, or to individuals of most other species that are as much as 30 feet above them. Thus they have almost no contact with individuals of those species of the montane bush alliances that usually remain in or near the tops of tall trees.

As a general rule yellow-thighed finches tend to follow and join individuals of all other species more frequently when the latter are being vocal than when they are silent.

Yellow-thighed finches are gregarious among themselves in much the same way and to approximately the same extent as sooty-capped bush-tanagers and black-cheeked warblers. Individual pairs and family groups seem to defend individual territories throughout the year (see below). Rather surprisingly, however, yellow-thighed finches have many characters that are strongly reminiscent of characters of other species that are more highly gregarious among themselves.

Yellow-thighed finches are remarkably conspicuous. Their generally black plumage is usually easy to see against a background of shrubbery. Their yellow thighs seem to be flash patterns, which function in the same way as the bright wing and/or tail patches of many other gregarious species. They hop very frequently, and their yellow thighs are revealed very conspicuously when they hop. They are not very shy, and are much less skulking than the other bush finches, e.g., the species of the genus *Atlapetes,* which may be their nearest relatives. They usually move in a peculiar floppy, clumsy-looking way, which tends to attract the eye of any observer. They are also noisy. They usually utter one or more types of call notes almost constantly as they move through the shrubbery. Whenever one bird of a pair or family group comes very close to another, as happens very frequently, one (or more) of the birds usually utters a moderately loud, twittering, greeting call. During obviously hostile territorial disputes between neighboring yellow-thighed finches, the disputing birds usually utter harsher, louder versions of the same twittering call. These hostile calls sometimes appear to be attractive to individuals of several other species, in addition to the bush-tanagers cited above.

None of the other members of the montane bush alliances is as generally and consistently conspicuous as yellow-thighed finches. The conspicuous characters of yellow-thighed finches contribute greatly to the general conspicuousness of the mixed flocks with which they are associated, and sometimes seem to attract individuals of other species to themselves. It is possible that the production of either one or both of these effects is the primary function of these characters, i.e., the principal adaptive advantage they were originally evolved to secure. If so, this would be a rather unusual specialization. None of the other Panamanian finches, tanagers, or honeycreepers seems to have developed as extreme a group of conspicuous characters as an adaptation to stimulate the formation and maintain the cohesion of mixed flocks but not unmixed flocks.

It should be noted that the geographical distribution of yellow-thighed finches is not very wide (see below). It seems unlikely that they are more gregarious among themselves in other areas than they are on the Volcán de Chiriquí, where they are very abundant.

Yellow-thighed finiches are sometimes joined and/or followed by individuals of other species with some appreciable frequency; but it is probably only in certain flocks composed of yellow-thighed finches and yellow-throated bush-finches alone that they are ever consistently joined and followed by individuals of another species more frequently than they join and follow individuals of other species.

THE EFFECTS OF THE TERRITORIAL BEHAVIOR OF CERTAIN SPECIES UPON CERTAIN MIXED FLOCKS

It has already been mentioned several times that individuals of several different species are attracted by the hostile calls of yellow-thighed finches and/or sooty-capped bush-tanagers, and that mated pairs and family groups of many territorial species associate with mixed flocks. These factors interact in a rather interesting way in mixed montane bush flocks just below 7,000 feet on the western slopes of the Volcán de Chiriquí, where both sooty-capped bush-tanagers and yellow-thighed finches are common.

In this area the members of a pair or family group of sooty-capped bush-tanagers will sometimes try to follow a mixed flock, with which they have been associating while the flock was in their territory, when the flock leaves their territory. Such attempts are seldom or never successful. As soon as the members of a pair or family group of sooty-capped bush-tanagers overstep the boundary of their territory, they find themselves within the territory of another pair or family group of sooty-capped bush-tanagers. The owners of this latter territory always, or almost always, rush to defend their territory, and always, or almost always, manage to repel the intruders after a more or less prolonged dispute. Such disputes are usually accompanied by a great variety of hostile patterns by both the intruders and the defenders, including overt attack and escape movements and many hostile calls and notes. Similar incidents are common among the yellow-thighed finches in the same area. Yellow-thighed finches also try to follow mixed flocks into the territories of neighbors of their own species, and provoke similar disputes as a result.

The overt attack and escape movements performed during such disputes among sooty-capped bush-tanagers and yellow-thighed finches tend to have a disruptive effect upon any mixed flock in which, or in the immediate vicinity of which, they occur. The other members of the flock tend to scatter to get out of the way of the disputing birds, which usually fly back and forth in a very energetic manner. At the same time the hostile calls and notes of the disputing birds are so attractive to birds of other species that the other members of the flock do not usually scatter very far, and other birds that were not associated with the flock before the dispute began may come to join it. As a general rule it may be said that most of the mixed montane bush flocks of this area are never more attractive than when disputes among sooty-capped bush-tanagers and/or yellow-thighed finches are going on inside them. Thus they are most attractive just at the time when they are in greatest danger of disruption. This may tend to prolong the existence of many of these mixed flocks.

Such actions and reactions are particularly important in the flocks slightly below 7,000 feet because the territories of sooty-capped bush-tanagers and yellow-thighed finches tend to coincide in this area. The territories of both species are partly determined by the same aspects of terrain and vegetation, and boundaries are usually established where there are gaps in the shrubbery. Both species tend to react to these gaps in the same way. Every patch of shrubbery in this area that is the territory of a single pair or family group of sooty-capped bush-tanagers is usually also the territory of a single pair or family group of yellow-thighed finches. Thus whenever a mixed flock moves over a gap in the shrubbery in this area it tends to provoke a dispute among both sooty-capped bush-tanagers and yellow-thighed finches. Similar reactions probably occur among individuals of the same and other species associated with mixed montane bush flocks in other areas on the Volcán de Chiriquí; but they are usually or always less conspicuous.

YELLOW-THROATED BUSH-FINCH

Yellow-throated bush-finches seem to occur in mixed montane bush flocks much less frequently than either of the bush-tanagers, the black-cheeked warblers, or yellow-thighed finches, in spite of the fact that they are common over a wider range of altitudes than any of these latter species. They do, however, follow and join individuals of other species occasionally. They are most likely to follow and join yellow-thighed finches, probably at least twice as often as they follow and join individuals of any other species frequently associated with mixed montane bush flocks.

As yellow-throated bush-finches live in thickets and low shrubbery, it might be supposed that their occasional associations with yellow-thighed finches were purely coincidental; but there is some evidence that a slight but definite special interspecific preference is also involved. Yellow-throated bush-finches follow and join yellow-thighed finches relatively more frequently than do chestnut-capped bush-finches (*Atlapetes brunnei-nucha*) or large-footed finches (*Pezopetes capitalis*), which also occur in thickets in some of the same areas on the Volcán de Chiriquí.

Yellow-throated bush-finches are conspicuously colored, but shy, skulking, and quiet. They seem to be followed and joined by individuals of other species less frequently than they follow and join individuals of other species.

FURNARIIDS

A very large proportion of the species of the family Furnariidae (*sensu lato,* including the tree-creepers or dendrocolaptids) are frequently associated with mixed flocks of one type or another; but the red-faced spinetail was the only species of furnariid studied in detail during the present investigation.

Red-faced spinetails usually occur moderately high in trees, although they may come down to low shrubbery from time to time. They are very inconspicuous birds, not very brightly colored, usually very quiet, and not very gregarious among themselves. Single birds, pairs, and family groups of this species are usually found widely separated from one another, and are probably territorial.

Red-faced spinetails are joined and followed by individuals of other species very rarely, but they join and follow individuals of other species very frequently. They seem to be particularly strongly attracted to brown-capped bush-tanagers, and tend to join them (at least when the latter are in trees) much more frequently than they follow them (using the terms "join" and "follow" as defined above). I have seen the same pair of red-faced spinetails join the same flock of brown-capped bush-tanagers repeatedly over a period of several hours every morning for seven successive days.

Brief observations of other furnariids on the Volcán de Chiriquí would suggest that all or most of them are similar to red-faced spinetails insofar as they tend to join and follow individuals of other species more frequently than they themselves are joined and followed. All or most of them probably also tend to join more frequently than follow.

All these species are primarily or exclusively insectivorous. Some of them, such as the tree-creepers and the ruddy tree-runners, usually or always feed on insects they find in or on the bark of trees. Such species do not seem to derive much benefit in the way of food from their associations with mixed flocks. They do not usually feed on insects stirred up by other members of the flocks.

SILVER-THROATED TANAGER

On the western slopes of the Volcán de Chiriquí, silver-throated tanagers are rather common slightly above 5,000 feet, and extend in decreasing numbers up to at least 6,000 feet. In this area they are sometimes associated with mixed montane bush flocks, but they do not seem to be regular members of such flocks, and sometimes deliberately refrain from joining them. When they do associate with mixed flocks they are seldom or never closely integrated with the other members of the flocks. They are essentially birds of the treetops, although they do come down to low shrubbery, almost to the ground, occasionally; and they seem to be more strongly attracted to the very heterogeneous lower-altitude mixed flocks, which usually include many other arboreal species, than to the less heterogeneous higher-altitude flocks, which usually include a large proportion of thicket-inhabiting birds. They seem to join and follow individuals of all or most other species more often than they themselves are joined and followed; and they join and follow brown-capped bush-tanagers more often than they do any other common species of the montane bush alliances.

Although silver-throated tanagers are not very important members of the mixed flocks on the Volcán de Chiriquí, they seem to be associated with such flocks there more closely and more frequently, on the average, than with mixed flocks on Cerro Campana (see below).

(A few brief glimpses of a few speckled tanagers in the very heterogeneous lower-altitude mixed montane bush flocks on the Volcán de Chiriquí would suggest that their role in such flocks is probably not very different from that of silver-throated tanagers.)

WILSON'S WARBLER

This is another species that plays a very distinctive role in mixed montane bush flocks. Wilson's warblers follow and join individuals of other species much more frequently than they are followed and joined. They also tend to follow individuals of other species more frequently than they join individuals of other species. The relative frequencies of interspecific following and joining reactions performed by Wilson's warblers (at least when they are in shrubbery or low trees) are very similar to the relative frequencies of interspecific following and joining reactions performed by yellow-thighed finches; but the actual numbers of both types of reactions by Wilson's warblers are usually much less than the actual numbers of the same reactions by yellow-thighed finches in similar situations. Wilson's warblers also come close to individuals of other species much less frequently than do yellow-thighed finches.

They tend to hang about the outskirts of a remarkably wide variety of groups of other species in all the montane forest and scrub habitats above 4,500 feet on the Volcán de Chiriquí (they may also occur at lower altitudes, but I have not observed the birds of lower altitudes). During the part of the year when Wilson's warblers are in Panamá, almost every large and medium-sized mixed montane bush flock (i.e., almost every flock composed of more than two species) is accompanied by a single Wilson's warbler. Single Wilson's warblers also attach themselves moderately frequently to smaller mixed flocks and to single birds, pairs, family groups, and larger unmixed flocks of almost every other species of all the montane bush alliances, as well as some species that usually remain apart from the montane bush alliances.

It would thus appear that Wilson's warblers are almost completely undiscriminating in their choice of associates—less discriminating than any other species frequently associated with mixed montane bush flocks, with the possible exception of summer tanagers (see below). They seem to be equally satisfied to become associated with almost any other montane passerine birds. This lack of discrimination is really quite remarkable.

It is relatively very rare to see two or more Wilson's warblers close together, or associated with the same mixed flock at the same time, because they usually fight among themselves whenever they come within 10 or 15 yards of one another. They seem to be very strongly territorial in Panamá. The fights between Wilson's warblers are almost always brief and decisive. One bird attacks and the other usually flees immediately. Such fights are seldom accompanied by any unusually loud burst of calling or other displays such as are common during disputes among bush-tanagers or yellow-thighed finches. The inconspicuous nature of such fights may be advantageous, in the case of Wilson's warblers, because it may help to prevent others of this species from being attracted to, and attempting to join in, the fights when the disputing birds might be unable to repel additional intruders very promptly. (Disputes among individuals of many other species of birds are sometimes attractive to other individuals of the same species as well as other species.) Anything that helps to prevent or reduce intraspecific gregariousness is presumably advantageous in the case of Wilson's warblers in Panamá.

Wilson's warblers are quite conspicuous in other ways, however. They are brightly colored, and utter very loud call notes almost constantly (if not usually very rapidly). As neither their colors nor their notes are very different from those of many other species of the montane bush alliances, it is perhaps surprising that they are not joined and/or followed more frequently by individuals of other species. Their comparatively slight attractiveness may be due to their very slight degree of gregariousness among themselves in Panamá. As noted above, single birds are probably always less attractive than pairs or larger groups of the same species, all other factors being equal.

Wilson's warblers certainly tend to enhance the conspicuousness of the mixed flocks with which they are associated and probably, therefore, increase the attractiveness of such flocks to other birds; but they seem to contribute relatively little, directly, to increase the cohesion of the flocks.

SLATE-THROATED REDSTART

The social relations of slate-throated redstarts with individuals of other species on the Volcán de Chiriquí are somewhat reminiscent of the corresponding relations of silver-throated tanagers.

Slate-throated redstarts are very brilliantly colored and very active. They are probably more conspicuous visually than individuals of any other species of the montane bush alliances, except the closely related collared redstarts (see below). They do not, however, play a very important role in most mixed montane bush flocks.

On the western slopes of the Volcán de Chiriquí, slate-throated redstarts are common below 6,000 feet, and also occur in smaller numbers up to at least 7,000 feet. They occur in many different levels of vegetation, from just above the ground to high in tall trees. Throughout this wide range they join and follow, and are joined and followed by, individuals of many other species; but none of these reactions seems to be common enough to suggest that slate-throated redstarts have a special interspecific preference for any other species, or are the object of any special interspecific preference of any other species. Slate-throated redstarts are certainly joined and followed by individuals of other species relatively much less frequently than are bush-tanagers or black-cheeked warblers, and join and follow individuals of other species relatively much less frequently than do yellow-thighed finches, many furnariids, or Wilson's warblers. They are joined by the undiscriminating Wilson's warblers relatively more frequently than by yellow-thighed finches or furnariids.

Associations between slate-throated redstarts and individuals of other species also tend to be relatively brief and not very close, and would thus appear to be essentially "casual." In the course of their normal activities slate-throated redstarts and individuals of many other species tend to encounter one another very frequently, and they may stay more or less together for some time; but the slate-throated redstarts eventually become separated from the others without any obvious signs of reluctance on either side. They probably do associate with other species of the montane bush alliances relatively more frequently than do silver-throated tanagers; but they probably should not be classified as regular members of the mixed montane bush flocks.

Slate-throated redstarts are not very gregarious among themselves, and it is relatively very rare to see more than one or two of them associated with the same mixed flock at the same time. When they are associated with mixed flocks, they probably produce an effect that is not very different from that produced by Wilson's warblers. Slate-throated redstarts probably also tend to enhance the conspicuousness of mixed flocks, without contributing very much, directly, to enhance the cohesion of the flocks.

COLLARED REDSTART

Collared redstarts are most common above 6,000 feet on the western slopes of the Volcán de Chiriquí; but their behavior apart from mixed flocks is very similar to that of slate-throated redstarts. It is interesting, therefore, that their usual social role in mixed flocks is much more important than that of slate-throated redstarts.

Collared redstarts tend to join individuals of other species relatively much more frequently than do slate-throated redstarts. Their usual method of joining is very distinctive. They seldom fly directly to join other birds, but make short flights to catch insects, and then tend to land beside individuals of other species when they return from their insect-catching flights. Slate-throated redstarts also make short flights to catch insects; but they do not show nearly as strong a tendency to land beside individuals of other species on their return. This peculiar type of interspecific joining behavior would be explained if collared redstarts were much more strongly attracted to individuals of other species when they themselves are flying than when they are not.

Collared redstarts may land beside individuals of almost any other species, but they seem to prefer sooty-capped bush-tanagers. Such reactions may be expressions of a definite special interspecific preference. (Collared redstarts are rare in areas where brown-capped bush-tanagers are common. It is possible that they are as strongly attracted to brown-capped bush-tanagers, when they meet them, as they are to sooty-capped bush-tanagers; but I did not see enough encounters between collared redstarts and brown-capped bush-tanagers to be able to analyze the relations between the two species.)

There are indications that the relative frequency of interspecific joining reactions (compared with interspecific following reactions) by collared redstarts is approximately the same as the corresponding frequency of similar reactions by red-faced spinetails, and much greater than the corresponding frequency of similar reactions by yellow-thighed finches or Wilson's warblers. Collared redstarts may follow individuals of other species slightly more frequently than do slate-throated redstarts; but they certainly follow individuals of other species much less frequently than they join individuals of other species. They are also followed by individuals of other species relatively much more frequently than are slate-throated redstarts. It is difficult to see exactly why this should be so, as they are not very much more conspicuous or active than slate-throated redstarts. Perhaps collared redstarts are followed more frequently because they fly away from the close proximity of individuals of other species more frequently. (They are close to individuals of other species more frequently simply because they join individuals of other species more frequently.) All other factors being equal, the sight of a bird taking flight a few inches away is much more likely to induce another bird to follow than the sight of a bird taking flight a few feet or yards away.

Like slate-throated redstarts, collared redstarts are followed by Wilson's warblers much more frequently than by individuals of any other species; but they are also followed, not infrequently, by such birds as yellow-thighed finches and sooty-capped bush-tanagers, birds that seldom or never follow slate-throated redstarts. Collared redstarts may be followed by individuals of other species relatively as frequently as are sooty-capped bush-tanagers.

Collared redstarts sometimes appear to be the leaders of mixed flocks. Sometimes a whole mixed flock will move in the direction in which a collared redstart is making most of its insect-catching flights. This sort of movement is undoubtedly significant, at least in some cases; but the appearance of leadership by collared redstarts is probably often slightly deceptive. In many large flocks composed of many species, collared redstarts may lead some but not all the other members of the flocks. One or two collared redstarts, for instance, may be followed by one or two yellow-thighed finches and/or sooty-capped bush-tanagers, which are followed, in turn, by individuals of other species. In such cases, the individuals of other species do not usually continue to move after the collared redstarts if the yellow-thighed finches and/or the sooty-capped bush-tanagers go in a different direction.

(There is at least one area on the Volcán de Chiriquí, near 6,000 feet, where the birds of the local montane bush alliance are often divided into two types of flocks that are rather comparable to the "predominantly tanager" and "predominantly honeycreeper" flocks of the blue and green tanager and honeycreeper alliance. In this area there is a great deal of low scrub plus a few scattered very tall trees. The foliage of the tall trees is usually separated from the underlying scrub by a wide open space.

Most of the members of the montane bush alliance in this area tend to stay in the low shrubbery; but a few species spend considerable time in the tall trees. The birds high in trees may form mixed flocks that are independent of mixed flocks in the shrubbery at the same time. The higher and lower flocks may move in different directions. The high flocks are usually composed of one or two collared redstarts and one Wilson's warbler, plus a few birds of other species, such as flame-throated warblers, furnariids, and slate-throated redstarts (if present in the area). These high flocks apparently never include yellow-thighed finches or black-cheeked warblers, and seldom include sooty-capped bush-tanagers. The collared redstarts are usually the real leaders of the high flocks, as all, or almost all, the other members of the high flocks usually tend to follow the collared redstarts directly.

It should be stressed, however, that such high flocks are relatively rare and more or less atypical. All, or almost all, the birds in the high flocks in this area also go down to the shrubbery more or less frequently, where they tend to associate with more typical mixed montane bush flocks that include yellow-thighed finches and black-cheeked warblers. In other areas at the same elevation where the same species of birds occur but the vegetation is not divided into two distinctly separated strata, the birds are seldom or never divided among higher and lower flocks moving independently of one another.)

OTHER SPECIES

Flame-throated Warbler.—I did not see flame-throated warblers very frequently on the Volcán de Chiriquí and was not able to analyze their usual social role in mixed flocks. All I can say about them is that they are very conspicuous (both brightly colored and noisy), found around 6,000 feet and above, apparently usually or always territorial, more common in trees than in low shrubbery, and probably join and follow individuals of other species (at least collared redstarts) more frequently than they are joined and followed by individuals of other species.

Brown-capped Vireo.—Brown-capped Vireos were observed only at 6,000 feet and above on the Volcán de Chiriquí. In this area they are frequently associated with mixed montane bush flocks, especially flocks in trees of moderate height. They seem to join individuals of other species more frequently than they follow or are followed or joined by individuals of other species. They do not seem to exhibit any special interspecific preferences. They are very inconspicuous and not very gregarious among themselves, and so probably do not contribute very much to enhance the conspicuousness of the mixed flocks with which they are associated.

Summer Tanager.—The usual social role of summer tanagers in mixed montane bush flocks on the Volcán de Chiriquí seems to be the same as in the mixed blue and green tanager and honeycreeper flocks of the lowlands of central Panamá.

Pale-vented Thrush.—This large, dull-colored, high montane species tends to have a disruptive effect on mixed montane bush flocks. Pale-vented thrushes seem to be attracted by individuals of many species of the higher-altitude montane bush alliances and/or are attracted to many of the same foods as these latter species; but they also tend to perform many supplanting attacks upon any and all other passerine birds in their immediate vicinity. Such behavior may be typical of thrushes of the genus *Turdus*. The few times that clay-colored thrushes were seen associated with mixed blue and green tanager and honeycreeper flocks they also tended to have a disruptive effect on the flocks.

PARTIAL SUMMARY

It may be useful to recapitulate briefly and summarize the usual social roles of different species in mixed montane bush flocks in the same terms as in the discussion of the species of mixed blue and green tanager and honeycreeper flocks.

Both bush-tanagers are regular members of mixed montane bush flocks and essentially passive nuclear species. They are not completely passive, however, and the sooty-capped bush-tanager is less passive than the brown-capped bush-tanager.

The collared redstart is a regular member of mixed montane bush flocks and apparently always a nuclear species. In some flocks (the "high" flocks) it is a passive nuclear species. In most flocks it is not definitely either passive or active.

The black-cheeked warbler is rather similar to the collared redstart. It is apparently always a regular nuclear species. It seems to be a passive nuclear species in some flocks and not definitely either passive or active in other flocks.

Wilson's warbler is a regular active nuclear species.

The yellow-thighed finch is a regular nuclear species. It may be an active nuclear species or a passive nuclear species, or both, depending upon the identity of the other species associated with it.

The silver-throated tanager may be an occasional active nuclear species on the Volcán de Chiriquí. The slate-throated redstart may be an occasional nuclear species, but not definitely either passive or active.

The brown-capped vireo and some or all of the furnariids associated with mixed montane bush flocks seem to be regular attendant species. The yellow-throated bush-finch is probably a regular attendant in flocks that include yellow-thighed finches, but an occasional attendant (at best) in other mixed flocks. The summer tanager seems to be an occasional attendant species in all types of mixed montane bush flocks.

It will be noted that many of the species of the montane bush alliances are more difficult to assign to discrete categories, according to their social roles in mixed flocks, than are the species of the mixed blue and green tanager and honeycreeper alliance. The significance of this difficulty will be discussed below.

Diagram 3 is a tentative summary of the special interspecific preferences of the most common species of the higher-altitude montane bush alliances revealed by predominantly "friendly" following and/or joining reactions. It should be compared with the summary of the corresponding preferences of species of the blue and green tanager and honeycreeper alliances shown in diagram 1.

THE COLORS OF SPECIES IN MIXED MONTANE BUSH FLOCKS

There is only a restricted range of colors in the plumages of almost all the species commonly occurring in the higher-altitude mixed montane bush flocks and the majority of the species commonly occurring in the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí. The plumages of these species are largely black and/or yellow (including yellow-olive), sometimes variegated with patches of brown and/or white. Bright greens, blues, and reds are lacking in the plumages of most of these species, and confined to small patches in the plumages of the others.

This general similarity of coloring may be adaptive in any one or all of several different ways. In any case, it probably tends to facilitate associations between individuals of different species. The birds of these species must become conditioned fairly early in their lives to the presence of companions that are predominantly black and/or yellow, with or without patches of brown and/or white. Some or all of these species may even be born with an innate recognition or preference for one or more of these colors. Thus an individual of any species exhibiting one or more of these colors is probably more attractive or, at least, less irritating and/or frightening to individuals of most of the species of the montane bush alliances than an otherwise similar bird of different colors.

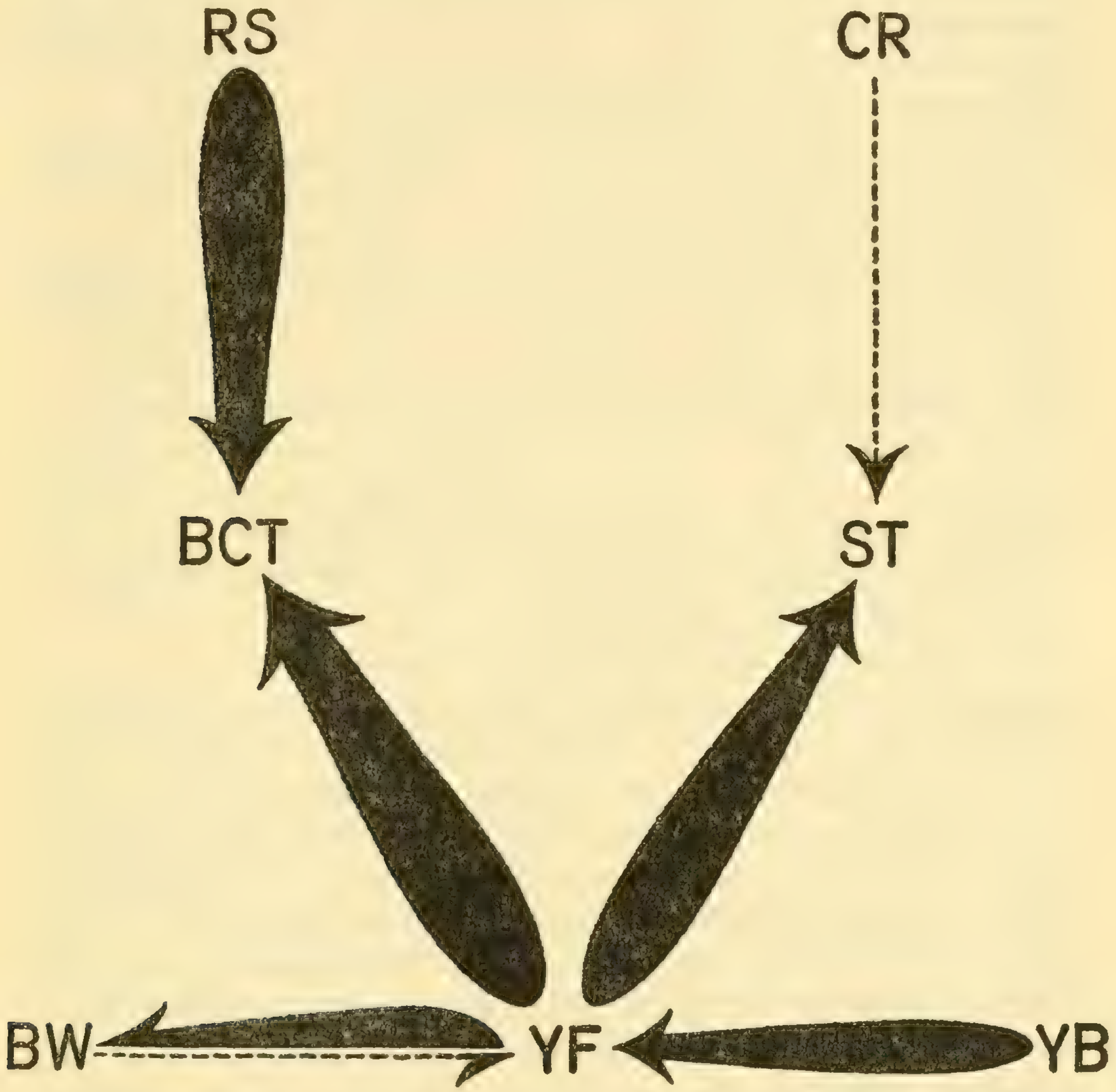

DIAGRAM 3.—The special interspecific preferences of the most common species of the higher-altitude montane bush alliances revealed by predominantly "friendly" following and/or joining reactions. Organized in the same way as diagrams 1 and 2.

The species are identified by initials. RS = red-faced spinetail. CR = collared redstart. BCT = brown-capped bush-tanager. ST = sooty-capped bush-tanager. BW = black-cheeked warbler. YF = yellow-thighed finch. YB = yellow-throated bush-finch.

Perhaps the best evidence that the similar coloring of most of the species in mixed montane bush flocks is a significant factor tending to stimulate the formation and maintain the cohesion of such flocks is provided by the behavior and social relations of certain other species that occur in the same areas but are colored very differently.

Blue tanagers occur up to 6,000 feet on the western slopes of the Volcán de Chiriquí. They may not have occurred at such high altitudes before much of the original montane forest was cut; but they seem to be well established along roads and around the town of Cerro Punta now. These blue tanagers frequently occur in the same general areas, even in the same trees, as species that are regular members of the mixed montane bush flocks, and they seem to feed on many of the same insects and fruits as some of the species that are regular members of the mixed montane bush flocks; but they do not usually associate with mixed montane bush flocks. They join the very heterogeneous lower-altitude mixed montane bush flocks occasionally, but they almost always keep strictly apart from the more closely integrated higher-altitude mixed flocks. This seems to be the result of definite choice. I have seen blue tanagers watch higher-altitude mixed montane bush flocks only a few yards away without showing the slightest indication of a desire to approach the flocks more closely or to follow individuals of any species in the flocks. Similarly, none of the birds in these higher-altitude mixed flocks showed any tendency to join and/or follow the blue tanagers.

The blue tanagers of the Volcán de Chiriquí belong to the same subspecies as the blue tanagers of the lowlands of central Panamá and behave in the same way apart from mixed species flocks. There is no reason to suppose that they do not have the same internal gregarious tendencies as the blue tanagers of the lowlands, which join and follow individuals of other species so frequently (see also below). It seems likely, therefore, that the usual lack of response by the blue tanagers of the Volcán de Chiriquí to the mixed flocks they encounter is largely or completely due to the characteristic coloration of all or most of the individuals in the flocks, a coloration that either fails to attract or actually repels (see below) the blue tanager. Many of the species in mixed montane bush flocks are not more different from blue tanagers in shape or behavior than many of the species that blue tanagers join and follow relatively frequently in the lowlands.

A few brief observations would suggest that the blue tanagers of the Volcán de Chiriquí are more strongly attracted to bay-headed tanagers (*Tangara gyrola*), which occur in small numbers slightly above 5,000 feet, than to any of the other species discussed above. It is surely not coincidental, in this connection, that bay-headed tanagers are largely bright blue and green and also tend to join mixed montane bush flocks relatively rarely. (The reactions of the blue tanagers of the Volcán de Chiriquí to bay-headed tanagers is positive evidence that these blue tanagers really do have the same gregarious tendencies as lowland blue tanagers in central Panamá.)

Similar factors may help to explain the social isolation of two resident species of the genus *Piranga* on the Volcán de Chiriquí, the white-winged tanager (*P. leucoptera*) and the flame-colored tanager (*P. bidentata*). Individuals of both species occur in some of the same areas as many regular members of the mixed montane bush flocks; but they seem to be associated with such flocks even less frequently than are blue tanagers. They obviously do not have the special joining reactions of summer tanagers. They also seem to be definitely unattractive (at least) to all or most of the species commonly occurring in mixed montane bush flocks. This may be partly due to the fact that adult male white-winged tanagers and flame-colored tanagers are largely bright red or orange (and immature males of both species frequently show traces of the same colors).

SIGNIFICANCE OF SOME OF THE PRINCIPAL DIFFERENCES BETWEEN MIXED BLUE AND GREEN TANAGER AND HONEYCREEPER FLOCKS AND THE HIGHER-ALTITUDE MIXED MONTANE BUSH FLOCKS

Among the more obvious differences between the higher-altitude mixed montane bush flocks (which seem to be the most highly, or most thoroughly, organized type of mixed montane bush flock) and the mixed blue and green tanager and honeycreeper flocks are the following:

1. All or most of the members of a mixed blue and green tanager and honeycreeper flock are usually confined to a rather narrow level of vegetation (usually the treetops) at any given time, while the members of higher-altitude mixed montane bush flocks are frequently scattered among many different levels of vegetation at the same time.

2. Supplanting attacks by individuals of one species upon individuals of other species are relatively common in mixed blue and green tanager and honeycreeper flocks, but relatively very rare in higher-altitude mixed montane bush flocks.

3. The nuclear members of mixed blue and green tanager and honeycreeper flocks are usually completely passive or completely active, while most of the nuclear species of higher-altitude mixed montane bush flocks can be either passive or active or may play an intermediate role.

4. Mixed blue and green tanager and honeycreeper flocks usually include species that have developed an apparently highly specialized

type of dull plumage to facilitate interspecific gregariousness; but none of the species of the higher-altitude mixed montane bush alliances seems to have evolved a specialized plumage to subserve similar functions.

These differences between the two types of flocks are presumably adaptive. They may also be causally related to one another.

It has already been mentioned that mixed blue and green tanager and honeycreeper flocks are usually restricted to one rather narrow level of vegetation because most of the species occurring in such flocks are usually restricted to one and the same rather narrow level of vegetation. Higher-altitude mixed montane bush flocks often extend through several different levels of vegetation because they frequently include species that prefer different levels of vegetation and/or frequently move back and forth between several different levels. (The usual restriction of most of the species of the blue and green tanager and honeycreeper alliance to one rather narrow level of vegetation may be an indication that most of these species are more narrowly specialized, restricted to narrower ecological niches, than many or most of the species of the higher-altitude montane bush alliances; but this would be extremely difficult, if not impossible, to prove.)

The members of mixed blue and green tanager and honeycreeper flocks are not only usually restricted to one rather narrow level of vegetation, but also frequently feed on the same foods. Thus they tend to compete with one another in a very direct way. This may help to explain why interspecific supplanting attacks are so relatively frequent in mixed blue and green tanager and honeycreeper flocks.

The performance of supplanting attacks within a flock is probably often disadvantageous because such attacks tend to reduce the cohesion of the flocks in which they occur; but this disadvantage must be outweighed, in the case of many or all of the members of the blue and green tanager and honeycreeper alliances by compensatory advantages. One of these is probably increased success in competition for food. Individuals of many species of the blue and green tanager and honeycreeper alliance probably obtain more food by performing supplanting attacks than they would if they did not do so. A bird that performs a supplanting attack upon another bird of the same or a different species, when the other bird is approaching food or actually eating, will usually force the other bird to retreat, at least temporarily, and may then be able to appropriate the food itself. It seems likely, therefore, that there have been strong selection pressures, during the evolution of many species of the blue and green tanager and honeycreeper alliance, in favor of retaining the habit of performing supplanting attacks. The frequent performance of both interspecific and intraspecific supplanting attacks is probably a primitive character, as such attacks are often performed by individuals of many species that are not very gregarious.

Andrewartha and Birch (1954) have suggested that competition between animals of different species is seldom very significant. Their discussion of this subject is not, perhaps, very convincing (see Lack, 1954, and comments by Brown and Wilson, 1956, and Hutchinson, 1959). In any case, it should be emphasized that the relations between many members of mixed blue and green tanager and honeycreeper flocks are particularly clear examples of competition. The competition between such birds is often as overt as possible.

Members of higher-altitude mixed montane bush flocks compete directly with one another less frequently than do members of mixed blue and green tanager and honeycreeper flocks. Individuals of different species in higher-altitude mixed montane bush flocks try to feed on the same foods at the same times less frequently than do individuals of different species in mixed blue and green tanager and honeycreeper flocks. Individuals of the higher-altitude montane bush alliances would probably obtain extra food less frequently by the performance of supplanting attacks than do individuals of the blue and green tanager and honeycreeper alliance. This may be the reason why the advantages of performing many interspecific supplanting attacks seem to be outweighed by the disadvantages of such behavior in higher-altitude mixed montane bush flocks (the disadvantages presumably being the same as in mixed blue and green tanager and honeycreeper flocks).

(It is possible that the total amount of competition, both direct and indirect, between species of the higher-altitude montane bush alliances is less than the total amount of competition between species of the blue and green tanager and honeycreeper alliance; but this would also be very difficult, if not impossible, to prove.)

The differences between the interspecific hostile reactions of the species of the higher-altitude montane bush alliances and those of the species of the blue and green tanager and honeycreeper alliance seem to be intrinsic at the present time. They seem to be due to internal differences between the birds themselves, not their different environments. Birds of the higher-altitude montane bush alliances may occur in social situations that seem to be essentially similar to those in which birds of the blue and green tanager and honeycreeper alliance perform many interspecific supplanting attacks. They may even become involved in such situations rather frequently (but less frequently, on the average, than birds of the blue and green tanager and honeycreeper alliance). But they still do not usually perform interspecific supplanting attacks in such situations. This would indicate that the reduced frequency of interspecific supplanting attacks by members of the higher-altitude montane bush alliances is a result of basic changes in their internal hostile drives (and/or their "innate" responsiveness to hostile stimuli) in the course of evolution. Interestingly enough, the intraspecific hostile reactions of all or most species of the higher-altitude montane bush alliances do not seem to have become reduced to the same extent in the course of evolution. Individuals of all or most of these species become engaged in disputes with other birds of the same species approximately as frequently as do members of the blue and green tanager and honeycreeper alliance which show a comparable degree of intraspecific gregariousness.

The frequency of interspecific supplanting attacks in mixed blue and green tanager and honeycreeper flocks may help to explain why the social roles of most of the nuclear species of these flocks are so clear cut and one sided, and why some species have developed unusually dull plumage. Because interspecific supplanting attacks tend to reduce the cohesion of mixed flocks, the species of the blue and green tanager and honeycreeper alliance have probably been subjected to particularly strong selection pressures in favor of developing mechanisms to minimize some of the effects of interspecific supplanting attacks and/or restore the cohesion of flocks as rapidly as possible after interspecific supplanting attacks. Both the dull plumage and/or the very one-sided nature of the social roles of some species may help to accomplish these objectives. They may both permit or facilitate particularly rapid "friendly" reactions within the mixed blue and green tanager and honeycreeper flocks.

The species of the higher-altitude mixed montane bush flocks may not have been subjected to strong selection pressures in favor of the development of similar characters simply because the cohesion of their flocks is seldom subjected to the sudden shocks of interspecific supplanting attacks.

SIMPLER MIXED FLOCKS

Three other types of mixed flocks that have been studied much less intensively than blue and green tanager and honeycreeper flocks or the mixed montane bush flocks may be described very briefly, as they are comparatively simple and their organization may reveal something of the probable course of evolution of mixed flocks in general.

MIXED FLOCKS OF SMALL FINCHES

Several species of small finches tend to associate with one another more or less frequently in various lowland areas in Panamá. Among these species are the variable seedeater, the yellow-bellied seedeater, the thick-billed seed-finch (*Oryzoborus funereus*), the blue-black grassquit (*Volatinia jacarina*), and the dark-backed goldfinch (*Spinus psaltria*).

The mixed flocks of small finches in Panamá never include as many species as the larger mixed blue and green tanager and honeycreeper flocks or mixed montane bush flocks; but they do seem to be specialized societies, not merely casual aggregations. Some aspects of the social relationships between some of these finches have already been discussed elsewhere (Moynihan, 1960). The most interesting feature of many mixed flocks of small finches is the physical resemblance between some of the species included in the flocks. The adult males of several of these species of finches, including species that do not seem to be very closely related to one another, have largely or completely black plumage. This may be "social mimicry." It is possible that one or more of these species have evolved such plumage simply to facilitate associations with other species having similar plumage.

A few additional features of the mixed flocks of small finches would suggest that their organization is most nearly similar to that of the mixed blue and green tanager and honeycreeper flocks. The finches that occur together most frequently in the lowlands of central Panamá near the Canal Zone are the variable seedeater and the blue-black grassquit. Relatively brief observations of mixed flocks composed of these two species alone would suggest that the usual social roles of both species in such flocks are very clear cut and one sided. Blue-black grassquits join variable seedeaters very frequently, but variable seedeaters seldom or never join blue-black grassquits in such flocks. (The usual social role of variable seedeaters in mixed flocks that include individuals of some other species, such as yellow-bellied seedeaters, may be rather different, at least in some respects; but I have not been able to measure the extent of this difference.) The contrasting reactions of variable seedeaters and blue-black grassquits in mixed flocks that do not include other species seem to be correlated with their social reactions apart from mixed flocks in much the same way as the corresponding reactions of most of the nuclear species of blue and green tanager and honeycreeper flocks and some of the nuclear species of mixed montane bush flocks. Variable seedeaters resemble such passive nuclear birds as plain-colored tanagers and brown-capped bush-tanagers in showing a high degree of intraspecific gregariousness; while blue-black grassquits resemble such active nuclear birds as palm tanagers and green honeycreepers in being only slightly gregarious among themselves apart from mixed flocks.

The members of all the mixed flocks of small finches in central Panamá usually feed on the same or similar food and tend to remain at approximately the same level (on or near the ground) most of the time they are together. It is probably significant, therefore, that interspecific supplanting attacks are common in such flocks. In flocks composed of variable seedeaters and blue-black grassquits alone, the variable seedeaters frequently supplant blue-black grassquits, but blue-black grassquits seldom or never supplant variable seedeaters.

MIXED FLOCKS ON CERRO CAMPANA

Cerro Campana is an isolated mountain, west of the Canal Zone in central Panamá, which reaches an altitude of approximately 3,300 feet above sea level. Part of the upper slopes of this mountain are covered by heavy montane forest, most of which seems to be mature. The bird fauna of the montane forest on Cerro Campana above approximately 2,000 feet includes a number of species that appear to be relicts in central Panamá. Several montane species that occur on both Cerro Campana and the Volcán de Chiriquí are found at much lower altitudes on the former mountain than on the latter. Such species may have been marooned on Cerro Campana at the end of the last cold period of the Pleistocene, and have become adapted to a warmer climate.

Many tanagers and related species occur on the upper slopes of Cerro Campana. Some of these species associate with one another to form mixed flocks, the most conspicuous of which occur in the treetops and along the edges of the montane forests, usually quite high above the ground. These flocks are usually composed of silver-throated tanagers, bay-headed tanagers, and/or tawny-capped euphonias (*Tanagra anneae*). Birds of other species also occur in such flocks, but seemingly relatively less frequently. Among the other birds I have seen associated with the mixed flocks of the montane forests of Cerro Campana are blue tanagers, green honeycreepers, black-and-yellow tanagers (*Chrysothlypis chrysomelas*) hepatic tanagers (*Piranga flava*), and various small flycatchers and (wintering) warblers. Such flocks seldom or never include more than a single individual, pair, or family group of any given species at any given time.

Unlike the other mixed flocks discussed above, these mixed flocks on Cerro Campana do not seem to be specialized societies. They appear to be essentially casual aggregations of birds that happen to be feeding more or less together in the same area but are not very strongly attracted to one another. Clear-cut interspecific following and joining reactions are relatively rare in such aggregations. Even the blue tanagers and the green honeycreepers do not join and/or follow individuals of other species very frequently on Cerro Campana. (They might join and/or follow one another very frequently if they had more chances to do so; but both species are rare in these montane forests.) None of the primarily montane species commonly occurring in these aggregations seems to have any definite special interspecific preference for any other species, and most of the associations between these species seem to be relatively brief. The species of the mixed flocks on Cerro Campana are also very diversely colored and do not seem to have developed any special type of plumage to facilitate their roles in the mixed flocks of this area.

In general, the mixed flocks of the montane forests on Cerro Campana are most reminiscent of the lower-altitude mixed montane bush flocks on the Volcán de Chiriquí, without the nuclear species which usually or frequently occur in the Chiriquí flocks.

RAMPHOCELUS FLOCKS

Different species of *Ramphocelus,* which usually do not form very close associations with birds of most other genera, do tend to associate with one another rather closely in some areas and habitats where their ranges overlap. I have seen associations between two different pairs of *Ramphocelus* species.

Mixed flocks of crimson-backed tanagers and yellow-rumped tanagers occur in many areas in central and eastern Panamá. I have observed them at rather long intervals between March 1958 and November 1960 in the Canal Zone, near María Chiquita on the Atlantic coast of central Panamá, and in Darién.

Mixed flocks of silver-billed tanagers (*R. carbo*) and black-throated tanagers (*R. nigrogularis*) were observed for a few days between December 17 and December 24, 1958, near Iquitos in the Amazonian region of eastern Perú.

CRIMSON-BACKED TANAGERS AND YELLOW-RUMPED TANAGERS

Adult male yellow-rumped tanagers are largely pure velvety black, with whitish bills and bright lemon yellow on the lower back and rump. Adult females and young of both sexes are generally brownish, with yellow lower back, rump, breast, and belly.

Yellow-rumped tanagers show a much higher degree of intraspecific gregariousness than crimson-backed tanagers. They tend to form flocks of 8 to 12 individuals (i.e., definitely larger than a single family group of parents and one brood of young). Such flocks seem to be maintained rather steadily throughout the nonbreeding season, and also occur, at least occasionally, in the breeding season.

Like most other highly gregarious birds, yellow-rumped tanagers are very restless and noisy. Some of their more complex calls are quite distinctive, very different from any calls of any other tanager or related species occurring in the lowlands of central and eastern Panamá; but their most common notes are very similar to those of crimson-backed tanagers in sound. Both yellow-rumped tanagers and crimson-backed tanagers utter thin *tseeet* notes and nasal *anh* notes very frequently.

The habitat preferences of yellow-rumped tanagers and crimson-backed tanagers are similar in some ways and different in others. Both species prefer scrub, but yellow-rumped tanagers prefer scrub along the banks of rivers and streams, and crimson-backed tanagers prefer scrub in slightly higher and drier areas some distance away from the banks of rivers. Yellow-rumped tanagers sometimes stray away from their usual habitats, and move into typical crimson-backed tanager habitats; but such occurrences seem to be relatively rare. Crimson-backed tanagers seem to occur in typical yellow-rumped tanager habitats somewhat more frequently.

All my observations of yellow-rumped tanagers and crimson-backed tanagers in the same flocks were made in typical yellow-rumped tanager habitats. In such habitats, yellow-rumped tanagers are always much more abundant than crimson-backed tanagers.

It is usually apparent in such habitats that crimson-backed tanagers tend to stay closer to yellow-rumped tanagers than to any other tanagers, honeycreepers, or finches in the same area at the same time. They may also follow and join yellow-rumped tanagers in a clear-cut and conspicuous manner more frequently than they follow and join all or most of the regular members of the blue and green tanager and honeycreeper flocks in the same (see below) and other habitats; but the actual frequency of such reactions is usually not very high. Crimson-backed tanagers certainly follow and join yellow-rumped tanagers much less frequently, on the average, than palm tanagers join and follow several other species of the blue and green tanager and honeycreeper alliance in central Panamá during the nonbreeding season. What the crimson-backed tanagers usually manage to do is stay in the vicinity of yellow-rumped tanagers without appearing to follow them in any regular manner or coming very close to any particular individual.

The responsiveness of crimson-backed tanagers to yellow-rumped tanagers is probably not strong enough to be considered a special interspecific preference. It is not a more frequent occurrence than would be expected as a result of generalized gregariousness, in view of the similar notes and preference for scrub of the two species.

Yellow-rumped tanagers also tend to follow and join crimson-backed tanagers relatively more frequently than they are followed and joined by the latter; but their reactions to crimson-backed tanagers are even more obviously not the results of a special interspecific preference. Yellow-rumped tanagers tend to follow and join almost all other tanagers and finches that occur in or near the scrub along river banks. Their responsiveness to individuals of so many other species seems to be a reflection of their extreme gregariousness among themselves. Their tendency to join and follow one another seems to be so strong that it frequently "overflows," to be vented upon suboptimal stimuli.

It has already been mentioned that special signal patterns and some related characters that seem to be adaptations to promote intraspecific gregariousness will usually or always tend to attract individuals of other species also, but that this attraction may be weakened by other factors. Most species are usually more strongly attracted to other species that are more or less similar to themselves than to other species that are very different. The relations between crimson-backed tanagers and most other species of the blue and green tanager and honeycreeper alliance were cited as an example. Most species of this alliance are probably attracted by the restlessness and general conspicuousness of crimson-backed tanagers, but not as strongly as they would be if the latter were not so distinctive in color and voice.

The relations between yellow-rumped tanagers and the species of the blue and green tanager and honeycreeper alliance may be an even more striking example of the same phenomenon or, perhaps more probably, an example of definite interspecific "aversion."

The characters of yellow-rumped tanagers that seem to be adapted to promote intraspecific gregariousness are somewhat more extreme or exaggerated than the corresponding characters of crimson-backed tanagers (the "flash" patterns of yellow-rumped tanagers are even more conspicuous than those of crimson-backed tanagers, and yellow-rumped tanagers are probably even noisier, on the average, than crimson-backed tanagers) ; but yellow-rumped tanagers seem to attract individuals of most species of the blue and green tanager and honeycreeper alliance much less frequently than do crimson-backed tanagers, even in the most favorable circumstances. Individuals of several species that are regular members of the blue and green tanager and honeycreeper flocks (including plain-colored tanagers, palm tanagers, blue tanagers, and golden-masked tanagers) sometimes come down to the shrubbery along the edges of rivers, if there are no trees nearby. At such times they usually ignore the yellow-rumped tanagers almost completely. Even palm tanagers seem to join and follow yellow-rumped tanagers relatively very rarely.

It is conceivable that most members of the blue and green tanager and honeycreeper alliance tend to ignore yellow-rumped tanagers simply because the latter are so distinctive in voice and appearance. To the human eye and ear, however, yellow-rumped tanagers are not more different from most of the members of the blue and green tanager and honeycreeper alliance than are crimson-backed tanagers. It is perhaps more likely, therefore, that most of the members of the blue and green tanager and honeycreeper alliance have developed a specialized aversion to yellow-rumped tanagers, a special power of resistance to the attraction of their restlessness and conspicuousness. This aversion may have been developed in order to avoid being sucked down into low shrubbery too frequently. There are indications that associations with any species that is largely confined to low scrub and thickets may be disadvantageous for most members of the blue and green tanager and honeycreeper alliance.

Two other scrub-inhabiting species, the dusky-tailed ant-tanager and the dusky-faced tanager (*Mitrospingus cassinii*), are common in parts of central and eastern Panamá. Both are noisy, restless, rather gregarious among themselves, and less distinctively colored than either yellow-rumped tanagers or crimson-backed tanagers. It has already been mentioned that dusky-tailed ant-tanagers sometimes encounter many members of the blue and green tanager and honeycreeper alliance in certain special circumstances. The same is true of dusky-faced tanagers. When such encounters occur, most of the members of the blue and green tanager and honeycreeper alliance, except crimson-backed tanagers (see below), tend to ignore the dusky-tailed ant-tanagers and dusky-faced tanagers in much the same way that they do yellow-rumped tanagers. (Slud, 1960, has already noted that dusky-faced tanagers are usually ignored by birds of other species in Costa Rica.) It seems likely that many or most members of the blue and green tanager and honeycreeper alliance have developed special aversions to dusky-tailed ant-tanagers and dusky-faced tanagers as well as yellow-rumped tanagers.

Such aversions are quite different from hostile interspecific preferences, such as those of green honeycreepers and shining honeycreepers for red-legged blue honeycreepers. The aversions are revealed by a conspicuous lack of overt responses, while the hostile interspecific preferences are expressed by supplanting attacks and/or other overt aggressive acts.

The habitat preference of yellow-rumped tanagers may also impede associations with other species in another way. Most members of the blue and green tanager and honeycreeper alliance (again with the exception of crimson-backed tanagers) are reluctant to remain in the scrub along the edges of rivers for any considerable length of time. They seldom remain in this environment for more than a few seconds or minutes before flying to trees or other scrub. This behavior effectively neutralizes the joining and following tendencies of yellow-rumped tanagers, simply because the latter are usually very reluctant to leave the river-bank scrub.

Although yellow-rumped tanagers do not play a significant social role in any highly integrated or very complex mixed flocks in central and eastern Panamá at the present time, they may be partly or completely preadapted to do so. It is easy to imagine how a relatively slight change in the habitat preference of yellow-rumped tanagers, or the appearance in the region of a new species that did not have a special aversion to them, or the loss of the special aversion by one of the species that already occurs in the region, would allow the yellow-rumped tanagers to play a more important nuclear role in mixed flocks (which might appear to be highly integrated from the very beginning).

(Crimson-backed tanagers occasionally associate quite closely with dusky-tailed ant-tanagers in certain scrub areas. Young crimson-backed tanagers just out of the nest seem to be more likely to form such associations than older birds. Such young birds may well be deceived by the appearance of dusky-tailed ant-tanagers, which are similar to crimson-backed tanagers in shape and many of their actions, and the males of which are brownish with some red on the throat and crown. The young crimson-backed tanagers may be reacting to dusky-tailed ant-tanagers as they would to other members of their own species.)

SILVER-BILLED TANAGERS AND BLACK-THROATED TANAGERS

The silver-billed tanagers and black-throated tanagers that were observed associating with one another were relatively few in number, one family group (parents with two or three young) of each species. These two families roosted separately at night, but usually came together shortly after dawn and spent an appreciable part of every day together for at least seven consecutive days (as long as my observations continued). These birds are very similar in shape and, to a lesser extent, color (red and black). Individuals of both species utter *tseeet* notes very frequently.

The social roles of the two species in this mixed flock were not very well differentiated. Sometimes the silver-billed tanagers joined and followed the black-throated tanagers; and sometimes the black-throated tanagers joined and followed the silver-billed tanagers. Both types of reactions were quite common, in both directions. Presumably further observations would have shown that one species joined and followed the other species at least slightly more frequently than the reverse, on the average, over a long period of time; but my observations were too brief to permit a quantitative analysis of the reactions between the two species. Interspecific supplanting attacks and other hostile patterns were quite common in this mixed flock. Sometimes one species was the aggressor, and sometimes the other.

Competition for food between the two species was certainly increased when they associated with one another. When they were not together the silver-billed tanagers usually stayed in moderately to very low scrub, while the black-throated tanagers usually stayed at a somewhat higher level in low trees. When they were together, however, the individuals of both species usually moved and fed at the same level, apparently eating the same foods. This change was usually due to a change in the behavior of the black-throated tanagers, which when they were associated with the silver-billed tanagers, frequently came down into scrub that was lower than anything they visited when they were alone.

It may be significant, in this connection, that black-throated tanagers were relatively rare in the area near Iquitos (the birds that associated with the silver-billed tanagers were the only black-throated tanagers I saw in this area), while the silver-billed tanagers were comparatively common. It is possible that this area is not a very favorable environment for black-throated tanagers, or that the ones I saw had just moved into the area and may have been partly dependent upon the silver-billed tanagers' ability to discover food sources (see below).

DISCUSSION

THE ADVANTAGES OBTAINED BY MEMBERSHIP IN MIXED FLOCKS

All or almost all the authors who have discussed the functions of mixed flocks have suggested that birds become associated in such flocks in order to get food, to get protection from enemies, and/or to satisfy some gregarious motivation or instinct (see the summary in Rand, 1954). All three suggestions may be correct. It should be noted, however, that the three functions are not strictly commensurable.

The habit of associating in mixed flocks may be an adaptation to get food and/or protection, but it can hardly be described as an adaptation, in the same sense of the term, to satisfy a gregarious instinct. From an evolutionary point of view the development of a gregarious instinct that can be satisfied by association in mixed flocks is probably a means to an end, not an end in itself.[16] A bird may join individuals of other species, or allow itself to be joined by individuals of other species, because such associations satisfy its gregarious instincts; but such instincts probably have been evolved, in all or most cases, because interspecific gregariousness provides certain concrete advantages. Gregariousness seems to be a type or method of adaptation,

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[16] In ethological terms, association with individuals of other species may be considered a "consummatory situation" for any bird that derives a definite satisfaction from such an association. Searching for individuals of other species to become associated with may be considered a form of "appetitive behavior." (See discussions of these terms in Tinbergen, 1951; Hinde, 1953; and Bastock, Morris, and Moynihan, 1953.) Unfortunately, there have been almost no analytical studies of the motivations impelling an individual of one species to become associated with individuals of other species. It is possible that individuals of some species have some sort of interspecific gregarious drive, which can be satisfied only by associations with individuals of other species, quite apart from any intraspecific gregarious drive or gregarious aspects of other instincts; but this has certainly not yet been proved to exist.

while food and protection are advantages that may be obtained by the adaptation.

It seems likely that many or most members of many or most mixed flocks obtain both extra food and added protection, more or less simultaneously, by their associations with one another; but the relative importance of the two advantages is probably very different for different species and for individuals of the same species at different times. This certainly seems to be true in the case of most members of the mixed flocks studied in Panamá.

Some observers of tropical mixed flocks (e.g., Chapin, 1932; Rand, 1954; Slud, 1960; and Swynnerton, 1915) have suggested that they are primarily feeding associations, that all or most birds become associated with such flocks primarily or exclusively because they tend to get more food when they are in mixed flocks than when they are not. This generalization seems to have been derived from observation of mixed flocks of birds that are primarily or exclusively insectivorous and live inside tropical forests (these were the first tropical mixed flocks to be studied).

Some of the primarily or exclusively insectivorous birds in mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks, e.g., summer tanagers, Wilson's warblers, red-faced spinetails, and the redstarts, probably obtain feeding advantages by associating with mixed flocks, and maintain such advantages nearly continuously as long as they remain within the flocks, in much the same way as do insectivorous birds inside tropical forests. The other members of mixed flocks must at least frequently serve as beaters for some of the insectivorous birds.

There are many indications, however, that the food factor is less important in the case of many other members of many mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks. The primarily frugivorous and/or nectarivorous birds probably do not obtain feeding advantages from their associations with mixed flocks as frequently or as consistently as do the insectivorous birds. It is often obvious that they are not helping one another to get food. It is difficult, in fact, to imagine how frugivorous and/or nectarivorous birds that are territorial or confined to definite home ranges could derive any considerable feeding advantages by associating with mixed flocks as long as they remain in or near their usual territories or ranges. Such birds are usually thoroughly familiar with the actual and potential sources of fruit and nectar in and near their territories or ranges.[17] They probably encounter more competition when they associate with individuals of other species of more or less similar feeding habits than they would if they always fed by themselves alone. It seems likely, therefore, that protection from enemies is the most important advantage obtained by many members of the blue and green tanager and honeycreeper alliance and the montane bush alliances by most of their associations in mixed flocks in ordinary circumstances.

The importance of the protection factor has been doubted by some observers of mixed flocks, largely because mixed flocks are so conspicuous that predators probably notice the members of such flocks more frequently than they would notice the same birds apart from mixed flocks. This does not, however, mean that birds in mixed flocks are actually preyed upon more frequently than birds of the same species apart from mixed flocks. (As far as I am aware, there have been no quantitative studies comparing the amount of predation upon birds in mixed flocks with the amount of predation upon birds of the same species in the same environment but not in mixed flocks.) There is, in fact, some actual evidence that birds in mixed flocks are particularly efficient at discovering and/or discouraging potential predators; and various theoretical considerations would suggest that the habit of forming mixed flocks may help to protect birds from predators in several other ways.

Birds in mixed flocks are usually particularly efficient at mobbing predators. Because they usually stay rather close together, the members of a flock usually respond relatively rapidly when one member of the flock begins mobbing.

Birds in mixed flocks probably notice predators more frequently and sooner, on the average, than they would if they were not in flocks. As soon as one member notices a predator, it will usually warn all the others. (Winterbottom, 1943, did not think that such warnings produced much effect in the mixed flocks he observed in Northern Rho-

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[17] In an earlier paper (Moynihan, 1960) it was mentioned that gregariousness may be particularly advantageous to birds that feed on fruits that occur in irregularly scattered masses, e.g., on scattered fruit trees far apart from one another. It may be necessary for such birds to make extensive searches over wide areas for their food, and they may tend to get more food, on the average, if they go searching in groups. The situation of most of the frugivorous members of the blue and green tanager and honeycreeper alliance and the montane bush alliances is usually quite different. They tend to feed on fruits and other vegetable materials that are fairly evenly distributed and common in the environments in which they live; and their searching for food is usually intensive rather than extensive.

desia. They do, however, seem to be very effective in the mixed flocks in Panamá. Alarm notes by one bird will at least put the other members of a flock in a state of alert.)

Birds that are not very shy by themselves will often retreat from a potential predator sooner when they are associated with shyer species in a mixed flock than when they are not in a mixed flock. Thus, for instance, the comparatively tame and unsuspicious plain-colored tanagers usually flee from an approaching human being sooner when they are in mixed flocks than when they are in similar flocks (of similar size) of their own species alone.

Predators attempting to attack a member of a flock may be distracted by the other members of the flock and hesitate for a moment, thus allowing all the members of the flock to escape. It is even possible that predators are more reluctant to try to attack a bird in a group than a solitary bird, because a group is slightly more intimidating.

Although protection may be the most important advantage obtained by many members of the blue and green tanager and honeycreeper alliance and the montane bush alliances in mixed flocks in ordinary circumstances, this does not necessarily mean that it is always the most important advantage. Even in the case of the frugivorous and/or nectarivorous birds, the discovery of food may be the most important advantage obtained by association with mixed flocks in certain special circumstances. Thus, for instance, a bird moving into a new and unfamiliar area may associate with individuals of other species in order to find the sources of food in this new area; but it may then continue to associate with the other individuals after it has discovered the food sources, and may then derive other advantages, such as added protection from predators, or no advantages at all.

It will be noted from the above account that the advantages that may be obtained by membership in mixed flocks, including both the discovery of food and protection from predators, could also be obtained by membership in flocks of a single species. This raises an interesting question. Granted that gregariousness is often advantageous in one way or another (as it obviously is), why do more species occur in mixed flocks than in unmixed flocks of their own species alone (apart from family groups)? Unmixed flocks might be easier to form and maintain, and might provide certain other social advantages that are lacking in mixed flocks. The answer to this question is probably that the members of an unmixed flock often compete with one another too strongly. Birds of the same species tend to compete with one another more strongly than birds of different species. Association with individuals of other species in mixed flocks may provide most of the advantages that could be obtained by association with other individuals of the same species in an unmixed flock, without the disadvantages of membership in an unmixed flock.

THE ORIGIN OF HIGHLY INTEGRATED MIXED FLOCKS

On logical grounds, one might expect that highly integrated mixed flocks could develop by extension and "regularizing" of occasional associations between species that are closely related to one another phylogenetically,[18] such as the crimson-backed and yellow-rumped tanagers, and/or by strengthening and specialization of the social bonds between less closely related species that may occur together in larger but essentially casual aggregations, such as the montane forest groups on Cerro Campana. There is some evidence that the latter process may have been more important than the former in the evolution of most highly integrated mixed flocks of passerine birds.

Occasional and loose associations between species that are closely related to one another phylogenetically are common in many areas. The reasons for this are obvious. Closely related species often have similar habits and often occur in the same general habitats when they occur in the same areas. Closely related species are also often similar in appearance, at least in shape or some details of their plumage patterns. Unless inhibited or counteracted by other factors, such similarities will inevitably tend to promote or facilitate associations between closely related species whenever they come into social contact with one another. Regular and close associations between closely related species seem to be much less common among passerine birds. Closely related (i.e., congeneric) species of passerine birds seem to be linked by specialized social bonds less frequently than are less closely related species. This may also be a result of competition.

As a general rule, different species of birds that occupy the same areas and habitats can only compete with one another to a certain limited extent if they are to continue to live side by side. One species will usually or always replace another (or others) in any given area and habitat unless there is some sort of (at least partial) ecological isolation between the species. The principle of "competitive exclusion," i.e., the principle that "complete competitors cannot coexist"

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[18] It will be necessary in some parts of the following discussion to use the terms "related" and "relationships" in two different senses, to refer to both phylogenetic and social relationships. The type of relationship discussed in any given passage will be specified, or should be clear from the context.

(Hardin, 1960), has been questioned or denied (see, for instance, Cole, 1960) ; but it does seem to be a valid generalization in the case of many species of birds (see, for instance, Lack, 1944 and 1947, and Moreau, 1948). All other factors being equal, species that are closely related to one another phylogenetically probably tend to compete with one another more strongly, in most cases, than species that are distantly related to one another, simply because the habits of closely related species (including their feeding habits) are usually more similar than the habits of distantly related species.

Although closely related species that occur in the same areas and habitats must almost certainly differ from one another in some aspects of their ecology, the ecological isolation between them can only be partial. For this reason, and because such species are usually or always similar to one another in many other characters, the ecological differences between such species probably tend to disappear in certain circumstances. Unless strongly reinforced by other factors, the partial ecological isolation between such species is almost certain to break down or become increasingly ineffective if the species should begin to associate with one another increasingly frequently and closely—as they are bound to do if they become incorporated in the same highly integrated type of mixed flock. There will thus be strong selection pressure, in many or most cases, to prevent closely related species from associating with one another very frequently and closely and/or to increase and strengthen the ecological differences between closely related species when they do associate with one another. Thus, highly integrated flocks that regularly include two or more closely related species are relatively rare (among passerines) ; and when they do occur, the closely related species tend to have very distinctly different feeding habits (e.g., the *Parus* species in mixed flocks in European woodlands—see Hartley, 1953; Gibb, 1954; and Snow, 1954).

Among the tanagers, honeycreepers, and finches of mixed flocks in Panamá, the most conspicuous examples of two closely related species frequently occurring in the same mixed flocks is provided by the palm tanager and the blue tanager. These two species coexist over a large part of tropical America; but they have slightly different habitat preferences, and the blue tanager seems to be slightly more insectivorous than the palm tanager (at least around the clearing on Barro Colorado Island). It is probably also significant that the palm tanager and the blue tanager are more often separated by their different habitat preferences during the breeding season, when competition between them might otherwise be most intense, than during the nonbreeding season.

(One aspect of the social relationships between these two species in Panamá may possibly be typical of the social relationships between many other overlapping species of equally similar habits. Palm tanagers and blue tanagers associate with one another very frequently in Panamá; but this is probably more often due to the fact that they both tend to join and follow plain-colored tanagers than to their tendencies to join and follow one another. Their associations, in other words, are more often indirect than direct.)

It seems likely, therefore, that the first highly specialized bonds to develop during the evolution of most highly integrated mixed flocks of passerine birds were bonds between species that were not very closely related, phylogenetically (i.e., species of different genera, or even, in many cases, different families).

All or almost all highly integrated flocks of passerine birds usually or always include individuals of certain particular species that show a high degree of intraspecific gregariousness and play a nuclear role in the mixed flocks. Numerous examples may be cited. Among the flocks of tanagers, honeycreepers, and finches in Panamá, there are the plain-colored tanagers in mixed blue and green tanager and honeycreeper flocks, the brown-capped bush-tanagers in mixed montane bush flocks, the variable seedeaters in mixed flocks of small finches, and the yellow-rumped tanagers in *Ramphocelus* flocks. Among other types of flocks there are white-flanked ant-wrens (*Myrmotherula axillaris*) in mixed flocks of insectivorous birds in the lowland forests of central Panamá (Johnson, 1954, and R. H. Barth Jr., in litt.); green-headed tanagers (*Tangara seledon*) in mixed flocks of tanagers and honeycreepers in southern Brazil (Mitchell, 1957); various species of *Acanthiza*, gray fantails (*Rhipidura flabellifera*), orange-winged sittellas (*Neositta chrysoptera*), and probably some other species, in mixed flocks of insectivorous birds in Australia (Gannon, 1934, and Hindwood, 1937); white-headed vangas (*Artamella viridis*) in some mixed flocks of forest birds in Madagascar (Rand, 1936); and black-capped chickadees (*Parus atricapillus*) in mixed flocks in North American woods in winter (Odum, 1942).

More often than not there is only one species that shows a high degree of intraspecific gregariousness included in any given type of mixed flock in any given area. This would suggest that the usual course of evolution of many highly integrated mixed flocks of passerine birds may be as follows. The first stage is probably usually the formation of specialized social bonds between a species that shows a high degree of intraspecific gregariousness and one or a few other species that do not show a high degree of intraspecific gregariousness. The former species is almost certain to become a passive nuclear species in the evolving flock. The subsequent history of the flock is probably largely dependent upon the nature of the other species that first become attached to the passive nuclear species. If these species become attendant species, the flock may not develop much further. If one or more of them should become an active nuclear species, however, this may provide a strong impetus to further elaboration of the flock. Active nuclear species will greatly increase the conspicuousness of the flock and contribute a variety of new stimuli, new sounds, colors, visual patterns, and/or movements, to broaden and strengthen the general effect which the flock produced upon other species in its vicinity. These additions may increase the attractiveness of the mixed flock to other species and induce the other species to become regular members of the flock in turn. If one or more of these new regular members should also become active nuclear species, this may provide another strong impetus to further elaboration of the flock. Thus, the flock may grow by a snow-balling process until all the suitable species in the area and environment have become incorporated in it in one way or another.

One of the later stages in the development of many large and complex types of mixed flocks may be the fusion of smaller types of mixed flocks, each of which grew up around a different passive nuclear species. It is possible, for instance, that the typical large blue and green tanager and honeycreeper flocks in Panamá were developed by an incomplete fusion of predominantly tanager flocks and predominantly honeycreeper flocks.

The evolution of very specialized morphological and behavioral characters, such as neutral coloration, social mimicry, and the reduction or loss of interspecific aggressiveness, by some or all of the regular members of the flock, may also be typical of the later stages in the development of many mixed flocks. Neutral coloration and the reduction of interspecific aggressiveness probably facilitate the incorporation of more new members in the flock; but social mimicry may have just the opposite effect. As social mimicry will tend to make the members of a flock more and more homogeneous in appearance and/or voice, it will probably make it more and more difficult for other species of dissimilar appearance or voice to join the flock. Social mimicry, in other words, will tend to make a flock a closed society. It is probably significant that the largest mixed flocks of small finches in Panamá, in which social mimicry seems to be most highly developed, include fewer species than many mixed blue and green tanager and honeycreeper flocks and mixed montane bush flocks.

THE DISTRIBUTION OF MIXED FLOCKS AND THE SPECIES INCORPORATED IN SUCH FLOCKS

There seems to be a general correlation between the social roles and the geographical distribution of many tanagers and finches and some other birds that are regular members of mixed flocks in tropical America. This correlation is clear in the case of the species of the mixed blue and green tanager and honeycreeper flocks. The plain-colored tanager, which is much the most important passive nuclear species in fully-developed blue and green tanager and honeycreeper flocks, has by far the most restricted distribution of any of the regular members of such flocks. It is confined to the lowlands of Colombia, Panamá, and Costa Rica.[19] This is appreciably smaller than the range of the golden-masked tanager, which is probably closely related to the plain-colored tanager (the two species share a number of characters that are not found in other Panamanian species of *Tangara*), and occurs in many of the same habitats in Panamá, but is apparently an active nuclear species in mixed blue and green tanager and honeycreeper flocks. Various subspecies of the golden-masked tanager extend from western Ecuador to southeastern México. (Hellmayr, 1936, includes the form *nigro-cincta* in the same species; but this has been questioned by Eisenmann, 1957. If *larvata* and *nigro-cincta* are really conspecific, then the range of the species also extends over most of tropical eastern South America.) All the other, more important, active nuclear species among the more common regular members of the mixed blue and green tanager and honeycreeper flocks, i.e., the palm tanager, the blue tanager, and the green honeycreeper, are at least as widely distributed as the golden-masked tanager, extending over all or most of the lowlands of tropical Central and South America.

Similar mixed flocks of tanagers and honeycreepers occur in the

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[19] Unless stated otherwise, these and the following summaries of the ranges of different species are based upon Hellmayr, 1925 (furnariids), 1935 (vireos, warblers, and honeycreepers), 1936 (tanagers), and 1938 (finches).

Hellmayr states that the plain-colored tanager is confined to Colombia and Panamá; but it has been found in northeastern Costa Rica by Slud (1960).

lowlands of southern Brazil, and have been described by Mitchell (1957). The most common birds in some of these flocks are green-headed tanagers. Mitchell suggests that they play a nuclear role in these flocks. Her description would imply that they show a high degree of intraspecific gregariousness and are usually or always passive nuclear in mixed flocks.[20] The distribution of green-headed tanagers is comparatively restricted. They are confined to the wooded regions

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[20] As the social behavior and social relationships of the green-headed tanager seem to be at least roughly similar to those of the plain-colored tanager, it may be of interest to compare some of the other characters of the two species.

Like the plain-colored tanager, the green-headed tanager seems to have lost the warbling song patterns that are conspicuous in the signal repertories of many less gregarious species of *Tangara* (Butler, 1894).

Mitchell noted that most of the plumage of many of the green-headed tanagers in the flocks she watched was "mottled and nondescript." The birds with such plumage may have been young. Mitchell also cites Descourtilz (1856) who thought that green-headed tanagers take three years to attain fully adult plumage. None of the Central American species of *Tangara* seems to take as long to attain fully adult plumage (Skutch, 1954). It is conceivable, therefore, that green-headed tanagers retain their dull juvenile plumage for a relatively long period of time as an adaptation to facilitate their role in mixed flocks. Their relatively dull juvenile plumage may subserve the same function, in the same way, as the dull neutral plumage of both adult and young plain-colored tanagers.

The fully adult plumage of green-headed tanagers is even more interesting in this connection. In an earlier discussion of the plain-colored tanager, quoted above, it was suggested that the dull neutral coloration of this species is partly a compromise. Such coloration may have been evolved because plain-colored tanagers could not evolve plumage colors and patterns more like those of their most common associates in mixed flocks, simply because the colors and patterns of these associates are themselves very diverse. It is possible, however, that green-headed tanagers have been able to achieve this difficult feat. The species that associate with green-headed tanagers are also very diverse in color and pattern; but the coloration of adult green-headed tanagers is far from dull. It includes areas of orange, yellow, two or three shades of green, bright blue, violet, and black, arranged in such a way as to provide the maximum amount of "flash." Many of the other species that encounter green-headed tanagers may find some or all of the colors of their own plumages matched or nearly matched in the colors of the plumage of adult green-headed tanagers. This would be expected to render adult green-headed tanagers particularly attractive to a wide variety of other species.

The plumage of adult red-necked tanagers (*Tangara cyanocephala*), which occur in some of the same flocks as green-headed tanagers, is equally brilliant and varied, including areas of bright red, bright green, blue, and black.

It might be convenient to call plumages such as those of adult green-headed tanagers and red-necked tanagers "bright neutral" plumages, in contrast to the "dull neutral" plumages of plain-colored tanagers and young green-headed tanagers.

of southeastern Brazil, Misiones, and eastern Paraguay. Mitchell also cites a number of other species as more or less frequent associates of the green-headed tanager in mixed flocks, including the red-necked tanager, Spix's scarlet-crested tanager (*Tachyphonus cristatus*), the rufous-headed tanager (*Hemithraupis ruficapilla*), the yellow-headed tanager (*H. flavicollis*),[21] the bananaquit, and the blue dacnis. Mitchell's description would imply that all or most of these species are usually or always active nuclear or attendant species in these flocks. They are all much more widely distributed than the green-headed tanager.

Slud (1960) has described certain aspects of some mixed flocks that occur in lowland forest and scrub in northeastern Costa Rica, in an area that is more humid, or more consistently humid, than most of central Panamá. Some of these Costa Rican flocks are largely or completely composed of tanagers, honeycreepers, and/or finches. Slud cites three species of tanagers and one species of finch that are rare or absent in central Panamá but are common and tend to play nuclear roles in mixed flocks in Costa Rica. These species are the black-faced grosbeak (*Caryothraustes poliogaster*), the olive tanager (*Chlorothraupis carmioli*), the tawny-crested tanager (*Tachyphonus delatrii*), and the great shrike-tanager (*Lanio aurantius*).[22] The first three species show a high degree of intraspecific gregariousness and seem to play passive nuclear roles in all or most of the mixed flocks with which they are associated. Their social behavior would thus appear to be essentially identical with that of plain-colored tanagers in central Panamá. Great shrike-tanagers are not highly gregarious among themselves, but also seem to play a passive nuclear role in mixed flocks. All four of these passive nuclear species have comparatively restricted ranges. The black-faced grosbeak extends from southeastern México to central Panamá. The olive tanager extends from eastern Nicaragua to eastern Panamá, and has an isolated population in part of tropical Perú. The tawny-crested tanager extends from eastern Nicaragua to western Ecuador. The great shrike-tanager extends from southeastern México to western Panamá. It will be noticed that none of these species is widely distributed in the Amazonian region of South America. The ranges of these species cannot, unfortunately, be compared with those

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[21] The Latin names of these purely South American species follow Pinto (1944). The English vernacular names are those used by Mitchell.

[22] Both the scientific and vernacular names of these species follow Eisenmann, 1955.

of their most important associates, as Slud does not mention which species played active nuclear roles in the flocks he observed. He does, however, state that the green honeycreeper, which is an active nuclear species in central Panamá, also occurs in mixed flocks in Costa Rica. Three of the four passive nuclear species cited by Slud are the only species of their genera in Costa Rica (and most of Central America); but there are two other species of *Tachyphonus* in Costa Rica, the white-shouldered tanager and the white-lined tanager, that do not seem to play nuclear roles in the Costa Rican mixed flocks, any more than they do in mixed blue and green tanager and honeycreeper flocks in central Panamá (see above). It may be significant, therefore, that both the white-shouldered tanager and the whilte-lined tanager are very widely distributed, much more so than the closely related but passive nuclear tawny-crested tanager. The white-shouldered tanager and the white-lined tanager extend over all or most of Amazonian South America.

(Both sexes or the adult males of the four passive nuclear species cited by Slud are largely black and/or yellow or yellow-olive. Several other tanagers and some migrant warblers that Slud observed associating with mixed flocks are also prominently marked with black and/or yellow. Such similarities are presumably not coincidental and may facilitate the formation of mixed flocks in much the same way as the similar colors of many members of the montane bush alliances.)

Finally, variable seedeaters, which are very gregarious among themselves, are much less widely distributed than blue-black grassquits, which are much less gregarious among themselves but tend to join and follow variable seedeaters in mixed flocks of small finches.

These facts would suggest that there may be a very general rule, among many different types of lowland tanagers and finches in tropical America, that species that play passive nuclear roles in mixed flocks have comparatively narrow ranges, while species that play active nuclear roles have very broad ranges.

Within the lowlands of the American Tropics, the occupation of new areas may be easier for individuals of active nuclear species adapted to lowland tropical habitats than for individuals of passive nuclear species that are otherwise equally well adapted to such habitats. Individuals of the two types of species may reach new areas equally frequently, on the average, and may be almost equally likely to secure mates in new areas (see below); but individuals of active nuclear species moving into a new area are probably much more likely to form strong social bonds with other species already established in the area than are individuals of passive nuclear species. Individuals of active nuclear species moving into a new area probably tend to join and follow individuals of many already-established species, including passive nuclear species, other active nuclear species, and less specialized species. Individuals of passive nuclear species moving into a new area are probably not joined and followed by individuals of as many already established species. They may attract active nuclear species and less specialized species, but probably not other passive nuclear species. Individuals of active nuclear species may also tend to react to individuals of already-established species more frequently and more rapidly than individuals of already-established species react to individuals of passive nuclear species. By associating more closely with the already-established species, individuals of active nuclear species probably discover the food sources and/or potential danger spots of an area with which they are unfamiliar more rapidly than do individuals of passive nuclear species in similar circumstances.

There may also be a general, but indirect and much less consistent, correlation between the ranges and social roles of the species of the montane bush alliances of Panamá. Interestingly enough, this correlation seems to be almost the reverse of the correlation noted in the case of the tanagers and finches of the lowland flocks.

The brown-capped bush-tanager, the most important passive nuclear species of the higher-altitude montane bush flocks, and a species that shows a high degree of intraspecific gregariousness, is very widely distributed in montane and hill regions from southern México to northern Argentina. The golden-crowned warbler, which also shows a high degree of intraspecific gregariousness and may play an equally important passive nuclear role in the lower-altitude montane bush flocks, is also very widely distributed from northeastern México to eastern and southern Brazil.

None of the species of the montane bush alliances that usually or always tend to join and/or follow other species very frequently are as widely distributed as the brown-capped bush-tanager or the golden-crowned warbler. Some of them, including species that are usually active nuclear species and those that are usually attendants in mixed montane bush flocks, have comparatively very restricted ranges. The yellow-thighed finch, the ruddy tree-runner, the black-cheeked warbler, and the collared redstart, are restricted to the mountains of Panamá and Costa Rica; and several others do not extend very much farther into the mountains of northern Central America and/or northwestern South America. It will be noted that none of these species shows a very high degree of intraspecific gregariousness.

The sooty-capped bush-tanager, which is an important passive nuclear species but which does not show a high degree of intraspecific gregariousness like the brown-capped bush-tanager and the golden-crowned warbler, is also confined to the mountains of Panamá and Costa Rica.

It is possible, therefore, that the brown-capped bush-tanager and the golden-crowned warbler are more widely distributed than most of their associates, not so much because they are passive nuclear species in mixed flocks as because they are both highly gregarious among themselves. All other factors being equal, a high degree of intraspecific gregariousness probably is (or was until recently) relatively much more advantageous to most montane species than to most lowland species in most regions of tropical America.

The forest and scrub areas inhabited by most lowland tanagers and finches were probably nearly continuous, or interrupted by only relatively small areas of other habitats, over the larger part of tropical America before human settlement became very dense (see also comments below). Most of the lowland tanagers and finches of the American Tropics probably occupied all or a large part of their ranges more or less gradually. Individuals of many of these species must have been able, in many cases, to move into new areas previously uninhabited by their species without going very far from the areas in which they themselves were raised. Thus, even a single individual of a species that did not show a high degree of intraspecific gregariousness was probably often able to obtain a mate, when it moved into a new area, by attracting one from an adjacent area previously occupied by the species, or because other individuals of the same species would tend to stray into the new area on their own initiative. In such circumstances, many lowland species that did not show a high degree of intraspecific gregariousness were probably able to spread as easily as, or more easily than, many lowland species that did show a high degree of intraspecific gregariousness.

The original situation of the montane species in tropical America must have been very different. Areas of montane forest and scrub have probably always been rather scattered in much of Central and South America, and many of these cannot have been occupied by a process of gradual diffusion. In order to reach such areas, individuals of montane species must have had to make long jumps over wide expanses of unsuitable habitats. Individuals of montane species that show a high degree of intraspecific gregariousness can probably cross such wide gaps and occupy new areas successfully more frequently than individuals of montane species that do not show a high degree of intraspecific gregariousness because they will often arrive in a new area on the other side of a wide gap in a group, from which mates can be obtained, while individuals of other species will usually arrive singly and be unable to obtain mates, as they will seldom or never be able to attract other individuals of their own species from adjacent areas, and other individuals of their own species will not be likely to stray into the new area of their own accord.[23]

The migrant species, which occur in mixed flocks in the Tropics only part of the year, have not been mentioned in the preceding discussion because they are a very special case. It might be noted, however, that most of them are quite widely distributed when in the Tropics, and tend to occur in a relatively wide variety of habitats. They all seem to be primarily joiners and/or followers when they associate with mixed flocks in the Tropics, either attendant species or not very important active nuclear species. They also tend to choose a relatively wide variety of companions of other species.

Published accounts of mixed flocks of tanagers, honeycreepers, and/or finches (with or without warblers) would suggest that such flocks are not evenly distributed throughout tropical America. More different types of mixed flocks of these birds have been noted in the lowlands of Central America and southern Brazil than in the lowlands of the Amazon basin, in spite of the fact that there are probably more genera and species of lowland tanagers and honeycreepers in the Amazon basin than anywhere else in the American Tropics. Similarly, more different types of mixed flocks of these birds have been noted in the mountains of Central America than in the central Andean region, in spite of the fact that there are more genera and species of montane tanagers, honeycreepers, and finches in the central Andes than anywhere else in the mountains of the American Tropics.

The greater number of records of mixed flocks in Central America and southern Brazil may be partly an artifact, as there have been more observers interested in avian behavior and ecology in these re-

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[23] The distribution of montane species in much of tropical America is essentially insular. It has often been remarked that species of land birds that show a high degree of intraspecific gregariousness are more likely to cross water gaps and establish themselves successfully on islands than are species of otherwise similar birds that do not show a high degree of intraspecific gregariousness (see, for instance, Mayr, 1931, and Amadon, 1950).

gions than in the Amazon basin and the central Andes; but it may also reflect a real difference in the abundance of mixed flocks in these regions. Some observations of my own may be of interest in this connection.

Both palm tanagers and blue tanagers were observed very frequently near Iquitos, in Amazonian Perú, in December of 1958. According to Hellmayr (1936), both of these species in this region are subspecifically distinct from the representatives of the same species in Panamá; but most of their habits seemed to be identical with those of the Panamanian forms. The only very distinctive feature of the behavior of the Iquitos palm tanagers and blue tanagers was their very slight degree of interspecific gregariousness. Individuals of both species frequently occurred in small flocks of their own species alone near Iquitos; but they very seldom occurred in mixed flocks and never in highly integrated mixed flocks during my observations in this area. It was particularly surprising that the palm tanagers and blue tanagers near Iquitos did not associate with one another very frequently because they often fed on the same or similar foods in the same trees.

(The rarity of associations between palm tanagers and blue tanagers near Iquitos may have been partly due to the fact that there were no species of *Tangara* comparable to the plain-colored tanager in this area. Thus the palm tanagers and blue tanagers near Iquitos did not tend, or did not have the chance, to associate with one another indirectly in the same way as the same species in central Panamá. But they also joined and followed one another directly much less frequently than palm tanagers and blue tanagers in Panamá.)

As noted above, silver-billed tanagers were also very common near Iquitos. Aside from the one family that occurred in association with the family of black-throated tanagers, the silver-billed tanagers of this area seldom or never occurred in mixed flocks. They were very similar to crimson-backed tanagers in appearance and actions; but they did not seem to be nearly as attractive to individuals of other species as crimson-backed tanagers in central Panamá.

Two small finches, *Sporophila castaneiventris* and *Oryzoborus angolensis,* were observed in open scrub and grasslands near Iquitos. Neither species occurred in mixed flocks as frequently as some of the Central American species of the same genera.

Montane birds of the central Andes were studied during two brief visits to Ecuador between August 4 and August 9, 1959, and between May 19 and June 2, 1960, on the slopes of Pichincha and Atacazo above Quito, near Quito itself, and near the town of San Antonio below Quito. There is a good deal of bush and scrub in this area, especially on Pichincha and Atacazo; and much of it is reminiscent of the montane bush on the Volcán de Chiriquí. It is inhabited by a great variety of tanagers, honeycreepers, and finches, many of which have many of the same habits as the members of the montane bush alliances on the Volcán de Chiriquí. Some of these birds are supposed to be closely related to species that associate in mixed flocks in Panamá. Among them are two species of *Thraupis, bonariensis* and *cyanocephala,* and two conspicuous and brightly colored species of *Atlapetes, leucoptera* and *rufinucha,* which feed and move through shrubbery in very much the same way as bush-tanagers on the Volcán de Chiriquí. In spite of these resemblances, the tanagers, honeycreepers, and finches of the montane bush near Quito do not seem to form mixed flocks like the mixed flocks of the montane bush alliances on the Volcán de Chiriquí. Individuals of several species frequently occur together when they feed in the same trees or shrubbery in the montane bush near Quito; but all or most of these associations seem to be purely casual aggregations. Such associations seem to be usually or always brief, and do not appear to be organized in any very regular or definite way.

These observations would suggest that mixed flocks of tanagers, honeycreepers, and/or finches may really be more common (and may even tend to be more highly organized, on the average) in Central America and southern Brazil than in the Amazonian region or the central Andes.

The tanagers and honeycreepers are certainly primarily tropical South American groups, at least at the present time. Most of the finches that occur in mixed flocks in Central America also belong to primarily tropical South American groups. Both Central America and southern Brazil seem to be marginal, partly isolated, and relatively unfavorable areas for such groups. The southern Brazilian region verges on the Temperate Zone. The forests of southern Brazil, where the mixed flocks of tanagers, honeycreepers, and finches have been noted, are partly separated from the main body of Amazonian forests at the present time by wide intervening areas of savanna and comparatively dry scrub (see, for instance, Cruz Lima, 1945, and Darlington, 1957). Central America also verges on the Temperate Zone. The tropical forests of Central America are probably less complex, providing fewer habitats, than the forests of the Amazon basin (Holdridge, quoted in Slud, 1960). Many birds of primarily North American groups have penetrated into Central America, to a greater or lesser extent, where they provide competition for birds of South American origin. The forest and scrub areas of lowland Central America are partly separated from the forests of the Amazonian region at the present time by the Andes of northwestern South America and some other physiographic barriers, while the montane forest and scrub of Central America are separated from the Andes by intervening lowland areas such as the Atrato River valley and central Panamá. Some or all of the barriers partly separating Central American faunas from South American faunas may have been less important, or may not have existed at all, during some of the climatic fluctuations of the Pleistocene; but they have certainly been intermittently effective, at least slowing the spread of many species of birds, for a considerable length of time (see Chapman, 1917 and 1926).

It is possible, therefore, that species of tanagers, honeycreepers, and neotropical finches that have developed the habit of associating in mixed flocks in any capacity or social role may tend to survive better in relatively unfavorable or partly isolated habitats and/or invade relatively unfavorable or partly isolated habitats more successfully than related and otherwise similar species that have not developed such habits.

SUMMARY

Several different types of mixed species flocks, composed of finches, tanagers, honeycreepers, and/or warblers (and sometimes species of other groups as well) are common in Panamá. Two types of these flocks were studied in some detail: mixed blue and green tanager and honeycreeper flocks in the lowlands of central Panamá, and mixed montane bush flocks on the Volcán de Chiriquí in western Panamá.

Mixed blue and green tanager and honeycreeper flocks are complex societies. Each of the species commonly occurring in such flocks tends to play a characteristic and rather consistent social role, which is more or less distinctly different from that of every other species commonly occurring in the flocks. Such roles are the results of complex interactions between each species and at least one (usually several) other species. Several of the species tend to react differently to each of several other species. Some species seem to have developed "special interspecific preferences" for certain other species. Special interspecific preferences may be expressed by apparently "friendly" joining and following reactions and/or by largely or completely hostile supplanting attacks. Some of the species commonly occurring in mixed blue and green tanager and honeycreeper flocks have also developed other special characters, such as dull "neutral" plumage, to facilitate the performance of their characteristic social roles within mixed flocks.

The species that occur in mixed blue and green tanager and honeycreeper flocks can be divided into "regular" and "occasional" members of the flocks. They can also be divided into "nuclear" and "attendant" species. A species may be considered nuclear in any given type of mixed flock if its behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of that particular type of mixed flock. Some species are nuclear in one type of mixed flock but not in others. The nuclear species of mixed blue and green tanager and honeycreeper flocks can be divided into "passive" nuclear species and "active" nuclear species. Passive nuclear species are usually joined and followed by other species much more frequently than they join and follow other species. Active nuclear species usually join and follow other species much more frequently than they are joined and followed by other species.

The mixed montane bush flocks that occur at higher altitudes on the Volcán de Chiriquí seem to be approximately as complex and as highly organized as mixed blue and green tanager and honeycreeper flocks; but their social structure is not identical with that of the latter in all details. Interspecific supplanting attacks are much less common in the higher-altitude mixed montane bush flocks than in mixed blue and green tanager and honeycreeper flocks. Some of the nuclear species of higher-altitude mixed montane bush flocks are not consistently passive or consistently active. Most of the differences between the social organization of the higher-altitude mixed montane bush flocks and the social organization of mixed blue and green tanager and honeycreeper flocks may be due to the fact that the members of higher-altitude mixed montane bush flocks compete directly with one another for food less frequently than do members of mixed blue and green tanager and honeycreeper flocks.

Several other types of mixed flocks, including flocks of small finches, forest birds on an isolated mountain in central Panamá, and species of the genus *Ramphocelus* were studied in less detail. These flocks appeared to be simpler and/or less highly organized than mixed blue and green tanager and honeycreeper flocks or the higher-altitude mixed montane bush flocks on the Volcán de Chiriquí.

It seems likely that most species of neotropical finches, tanagers, honeycreepers, and/or warblers obtain several advantages, including extra food and protection from predators, by associating in mixed flocks. The additional protection from predators may be the most important advantage obtained by most of these species when they associate in mixed flocks in most circumstances.

The initial step in the evolution of most highly organized mixed flocks of passerine birds was probably the formation of special social bonds between a species that showed a high degree of intraspecific gregariousness and one or more species that did not show a high degree of intraspecific gregariousness. The former probably became a passive nuclear species in most cases. The subsequent history of such flocks was probably largely dependent upon the appearance and behavior of the other species that became attached to the passive nuclear species. Some of the characters of some species that seem to be adaptations to promote the formation and/or maintain the cohesion of a particular type of mixed flock may facilitate the incorporation of additional species as new regular members in mixed flocks of that particular type; but other characters that seem to be adaptations to subserve the same functions may tend to prevent the incorporation of additional species.

The finches and tanagers that are known to play passive nuclear roles in mixed flocks in the lowlands of central Panamá or other lowland areas of the American Tropics are less widely distributed than species that are known to play active nuclear roles in the same mixed flocks (and some closely related species that do not play any sort of nuclear role in mixed flocks). Active nuclear species of finches and tanagers that are adapted to the lowland Tropics may be able to invade new areas within the American lowland Tropics more successfully, in most cases, than otherwise similar but passive nuclear species.

Two largely passive nuclear species of the mixed montane bush flocks on the Volcán de Chiriquí are much more widely distributed than most of the other species commonly occurring in such flocks. The comparatively wide distribution of these passive nuclear species may be due to the fact that they both show a high degree of intraspecific gregariousness. On logical grounds, it might be expected that montane species that show a high degree of intraspecific gregariousness would be able to invade new montane areas in the American Tropics more successfully, on the average, than otherwise similar species that do not show a high degree of intraspecific gregariousness.

Various observations during this study, and published records, would suggest that mixed flocks of tanagers, honeycreepers, and/or finches are not evenly distributed throughout tropical America. It is possible that species of tanagers, honeycreepers, and neotropical finches that have developed the habit of associating in mixed flocks, in any capacity or social role, may tend to survive better in relatively unfavorable or partly isolated habitats within the Tropics and/or invade such habitats more successfully than related and otherwise similar species that have not developed such habits.

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