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THE COMPARATIVE BIOLOGY OF TWO SPECIES
OF SWIFTS IN TRINIDAD, WEST INDIES

Charles T. Collins

THE COMPARATIVE BIOLOGY

OF TWO SPECIES OF SWIFTS

IN TRINIDAD, WEST INDIES.

CHARLES T. COLLINS[1]

SYNOPSIS: The comparative biology of the short-tailed swift, *Chaetura brachyura*, and the chestnut-collared swift, *Cypseloides rutilus*, was studied in Trinidad during parts of 1962-66. In many aspects both species proved similar to congeners for which information exists. Both breed during the rainy season when insect food is abundant, but their breeding activities are triggered by different proximate factors.

Ch. brachyura lays a clutch averaging 3.8 eggs in nests of twigs cemented to the walls of manholes. *Cyp. rutilus* lays a clutch of 2 eggs in nests of mosses, lycopsids, and ferns built on rocky outcrops over rivers and mountain streams, and occasionally in sea caves. The environmental temperature of nest sites of *rutilus* is lower than for those of *brachyura*, and the nestlings of *rutilus* are brooded longer and more continuously than nestlings of *brachyura*. *Cyp. rutilus* has a lower mortality of eggs and young than *brachyura*, its nest sites being presumably less accessible to predators.

The young of *brachyura* grow more rapidly than those of *rutilus*, but both species perfect their capacity for thermoregulation at about the same rate. In *rutilus*, a down-like semiplume portion of its first teleoptile plumage emerges at an early age and aids in thermoregulation. The young of *brachyura* leave the nest when about 3 weeks old and hang on the walls of the nest cavity until they fledge at the age of 4-5 weeks; *rutilus* young remain in the nest until they fledge at 5-6 weeks.

These two swifts appear to feed on the same types and sizes of aerial food, but their foraging ranges only partially overlap; *rutilus* feeds at higher elevations than *brachyura* and to some extent at higher altitudes. The differences in foraging ranges may enable them to avoid interspecific competition for food. Similar adaptations seem to be present in other species of swifts.

Most of the differences in the biology of these two species of swifts are associated with reproduction and reflect adaptations by *rutilus* to the cool, damp environment of the nest site.

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INTRODUCTION

Swifts of the family Apodidae form a well-defined group of stream-lined, fast-flying birds which spend most of the daylight hours on the wing in pursuit of their insect prey. They occur throughout the world but are most plentiful in tropical regions. Although the biology of swifts has been studied in Africa (Moreau, 1941, 1942a, 1942b), South America (Sick, 1948a, 1948b, 1959) and Malaysia (Medway, 1962a, 1962b), the family as a whole is still poorly known. The nests of several species have only recently been discovered (Rowley and Orr, 1962; Collins, 1968) and others are undescribed. A new species remained undetected in a well studied part of northwestern South

America as late as 1962 (Eisenmann and Lehmann, 1962). The difficulty of locating swift nests, which are usually solitary and often in inaccessible cliff crevices or in hollow trees, has clearly hindered the study of many species, particularly in the tropics. Currently detailed life history data are limited for the most part to a few species of the temperate zone (Arn-Willi, 1960; Lack and Lack, 1951, 1952; Weitnauer, 1947; Fischer, 1958).

The island of Trinidad, with one of the largest swift faunas for an area its size in the world, offers abundant opportunities for ecological studies. The preliminary work by Snow (1962) indicated the practicality of a detailed comparison of two of the nine species of Trinidadian swifts. These two species, the Short-tailed Swift, *Chaetura brachyura* (Jardine), and the Chestnut-collared Swift, *Cypseloides rutilus* (Vieillot), are approximately the same size but have striking differences in nesting ecology, clutch size, and the development of the young. The present study was undertaken to analyze these differences and, where possible, to point out their adaptive significance.

Differences in nest type have been shown to be useful in differentiating species of swiftlets of the genus *Collocalia* (Sims, 1961; Medway, 1961, 1966; Brandt, 1966), while differences in ecology and clutch size appear to be significant indicators of higher intrafamilial relationships (Lack, 1956). Thus the study of the comparative ecology of additional species, in conjunction with studies of the anatomy, osteology, and paleontology of swifts, should provide knowledge useful in understanding the evolution of the Apodidae.

STUDY AREA

The William Beebe Tropical Research Station of the New York Zoological Society in Arima Valley, Trinidad, formed the base of operations for this study. The Station, located at an elevation of 800 feet four miles north of the town of Arima, provides an excellent vantage point from which to observe feeding swifts, as well as being close to nesting concentrations of both species. The present study included approximately twelve months of field work in Trinidad during part or all of the breeding seasons of 1962-1964, exact dates being 26 June - 1 September 1962; 25 April - 11 July 1963; 8 May - 11 November 1964; 19 October - 6 November, and 24 November - 1 December 1966.

The ecology of Arima Valley has been described in some detail by Beebe (1952), and the best description of the vegetation types in Trinidad is that by Beard (1946).

Field observations were concentrated in the eastern half of St. George County and included areas of low country savanna, upper montane rain forest at elevations of 2500 to 3000 feet, and the rocky coastline of the north shore of the island. The principal nesting area for *Ch. brachyura* was Waller Field, a United States Air Force base deserted for more than ten years and heavily overgrown with grasses, brush, and low second-growth forest (Fig. 1.) except for the roads and a few cement structures. Most nests of *Cyp. rutilus* were located in the northern half of Arima Valley, but a few were in sea caves on the north coast, particularly near the town of Blanchisseuse.

METHODS AND MATERIALS

Individual nests were checked regularly during the nesting season, usually not more often than once a day in order to avoid excessive disturbance and possible desertion.

In 1962 adults and nestlings were banded with numbered bands of colored plastic and, starting in 1963, also with U. S. Fish and Wildlife Service numbered metal bands. Nestlings less than 8-10 days old could not be banded and were marked with spots of color applied with a felt marking pen to the skin of the back or belly. Color marking of nestlings and adults was only used to a limited extent. An attempt to color mark a prebreeding flock of *Ch. brachyura* by painting the primaries of one wing yellow proved unsuccessful, as the birds could not be readily distinguished in the field. Adults and nestlings were weighed with a spring balance of the type obtainable from the British Trust for Ornithology. This balance was calibrated in half-gram intervals, and weights were estimated to the nearest quarter gram.

Environmental temperatures were taken with Six's type maximum-minimum recording thermometers. Body temperatures were measured with a small bulb mercury thermometer made by the Schultheis Corporation. Readings were taken with the bulb inserted about 10 mm into the cloaca.

Cold stress experiments were a part of the investigation of nestling

Figure 1.—Savanna area near manhole nest sites of *Chaetura brachyura*, Waller Field, Trinidad.
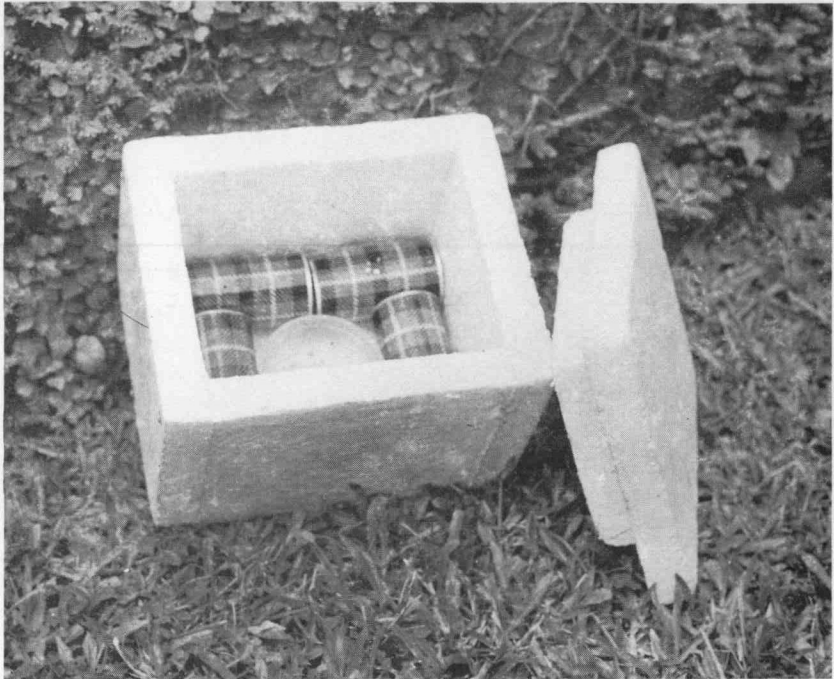
Figure 2.—Cold chamber used in tests of thermoregulatory capacity of nestling swifts.

thermoregulation. These required a 6x8x5-inch cold chamber made of foam plastic insulation material 1⅛" thick (Fig. 2.), which four 6-oz. cans of "Skotch Ice" (refreezable liquid) kept at a temperature of approximately 5°C for several hours. Nestlings were placed individually in the chamber in the field for a period of 5 minutes, and their temperatures were recorded before and after cold exposure. Even though sharp body temperature drops were recorded for very young nestlings, the tests caused no apparent ill effects.

Swifts of both species were captured at night roosting places for weight and molt studies. Flocks of *Ch. brachyura* were generally confined in a roost site and examined the following morning. A hand net was used to capture *Cyp. rutilus* adults roosting at night in a river gorge in Arima Valley; they were held in captivity over night and released the following morning. Although mist nets were successfully employed in Trinidad in catching large numbers of swifts of several other species (Collins, 1967a) only a few individuals of *brachyura* and none of *rutilus* were mist-netted in this study.

GENERAL DESCRIPTION

Chaetura brachyura[1] is one of four similar-appearing congeneric species that occur in Trinidad. It is a small bird about 115 mm long with a short stubby tail (28-33 mm) and long narrow wings (117-127 mm). In fresh plumage it is dark black-brown, except for the rump and under tail coverts which are pale ashy brown; the throat is slightly paler than the breast; the feathers of the darker areas, particularly the remiges, have a noticeable greenish gloss or iridescence. In worn plumage the gloss is purple or completely bleached out to a lusterless dark brown, and the bird appears paler, particularly on the throat, and is more brownish than black. Occasional individuals collected in late summer have extremely light brown underparts, the cause of which is not understood. Birds in juvenal plumage have less gloss on the body than adults and show a more grayish tinge on the paler rump and under tail areas.

Cypseloides rutilus[1] appears to be a larger swift (135 mm) owing to its longer tail (38-42 mm), but its wings are about the same length (119-128 mm) as those of *Chaetura brachyura* and, as shown later, the body weights of the two species are similar. In over all color *rutilus* is dark sooty black-brown, darker on the wings and tail than on the body. The males have a complete collar of rufous feathers covering the nape, auricular, loral, and malar regions, and the throat and upper portion of the breast, but not the interramal area. The females are generally uniform dark brown. A few birds have a partial rufous collar on the nape and extending laterally to the edges of the throat, with sometimes additional flecks on the throat and breast. Two such birds collected in Trinidad both proved to be females. Despite numerous statements to the contrary, juveniles do not completely lack the collar, but invariably have some rufous present as a partial collar. The edges of the collar are not so sharply delimited as in the adults, and the crown feathers also have narrow reddish edges. The extent of the rufous coloring in the juvenal plumage varies, but it is never so extensive as in adult males nor is it completely lacking as in most adult females.

Albinistic feathers were observed in the adult plumages of both *brachyura* and *rutilus*. In *brachyura* albinism was confined to just a

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[1] In Trinidad, *Ch. brachyura* is represented by the race *brachyura* and *Cyp. rutilus* by the race *rutilus* (Peters, 1940). Although Peters (1940) places *rutilus* in the genus *Chaetura*, I concur with the presently accepted views of Zimmer (1953) and Lack (1956) that the species is more properly included in the genus *Cypseloides*.

few feathers on the upper breast or head, while in *rutilus* it sometimes involved numerous feathers on several parts of the body (Collins, 1967b).

RANGE

   Chaetura brachyura inhabits the southernmost Lesser Antilles and northern South America. It occurs on the islands of St. Vincent, Trinidad, and Tobago and on the mainland from Venezuela and Colombia south to Peru and the Matto Grosso of Brazil.

   Cypseloides rutilus ranges from southern Mexico to Peru and Bolivia and east through northern Venezuela and Trinidad. A separate population also occupies the highlands of southeastern Venezuela and neighboring Guyana.

NESTS AND NEST SITES

NESTS OF THE GENUS *Chaetura*

   Relatively few records for nests in natural settings exist for most species of *Chaetura,* and for those of some species we have no knowledge at all. The available information suggests that all tend to utilize hollow trees or stumps and may occasionally affix their bracket-shaped nests to vertical rocky ledges or the walls of caves (Lack, 1956a). Most species in the genus have been quick to accept various artificial equivalents of these natural hollows, and as early as the 1870's accounts began to appear in journals of their nesting in such man-made structures as chimneys, wells, cisterns, and a variety of buildings (Lack, 1956a; Fischer, 1958). The species most clearly illustrating this habit is the North American Chimney Swift, *Chaetura pelagica* (Linnaeus), which "now breeds much more often in chimneys than in trees" (Lack, 1956a). Other New World species of *Chaetura* known to use man-made structures are *vauxi vauxi* (Townsend) in temperate areas (Baldwin and Hunter, 1963; Baldwin and Zaczkowski, 1963) and *vauxi aphanes* Wetmore and Phelps, Jr. (Sutton, 1948), *andrei* Berlepsch and Hartert (Sick, 1959), and *brachyura* (Haverschmidt, 1958) in tropical South America. In Trinidad *brachyura* has previously been reported to nest in chimneys and sea-caves (Belcher and Smooker, 1936), as well as in subterranean manholes and a nest box erected for swifts (Snow, 1962).

   Chaetura brachyura—The nest sites of *brachyura* followed in this study were in vertical manholes that were part of the underground drainage system of Waller Field (Fig. 3). Snow (1962) discovered

11 of these sites and kept them under observation from May 1957 until September 1961. I found an additional 10 holes used as nest or roosting sites during this study between 1962 and 1964. Most of the manholes were cylindrical concrete tubes 4 to 20 feet deep and connected with smaller lateral drainage pipes at the bottom. Their inside diameter was about 4½ feet, and their concrete tops were usually pierced by a circular access hole 2 feet in diameter, which was at one time closed by a metal manhole cover. One hole, slightly narrower and made of bricks, had a more uneven surface than the smooth walls of those made of concrete. The only site not in one of these holes was located in a subterranean, concrete-walled room about 20 feet long, 10 feet wide, and 10 feet high. The swifts entered and left this room through a 12-inch square opening in the ceiling, which was nearly flush with the ground level (Collins, 1967c). The tops of several of the manholes were flush with the ground; others protruded as much as 4 feet above it. One of the manholes used predominantly as a roosting site was nearly roofed over with a metal sheet covered by cement, with only a very small hole, 5½ by 10 inches, for the swifts to enter. Fourteen of the 21 sites were partly filled with water or had water flowing through the bottom drainage pipe during the nesting season. Water rising in the hole destroyed the nests in three sites and trapped one adult. Although the nest sites were usually brightly illuminated they had very little air circulation, and the relative humidity was always above 95 per cent. The temperature in these manholes during the nesting season ranged from 25.0 to 33.3°C. A characteristic daily range was from a low of 26.0° to a high of 30.5°C.

Although nest building was not observed for this species, the finished nest of *brachyura* is so similar to all those reported for other New World species in the genus that the building process must be quite similar. The best studied species, *Chaetura pelagica*, collects nesting material by grasping treetop twigs in its feet and breaking them off while in flight (Fischer, 1958). The nest is made entirely of such twigs glued together and affixed to a vertical surface by means of a secretion of the sublingual salivary glands. *Ch. brachyura* shows a pronounced enlargement of these glands during the breeding season, as has been reported for *pelagica* (Johnston, 1958) and several species of *Collocalia* (Marshall and Folley, 1956; Medway, 1962c).

The nest of *brachyura* is a shallow half-saucer made of twigs 20-75 mm long and usually only 1-2 mm in diameter (Fig. 4). It is slightly

Figure 3.—Manhole nest sites of *Chaetura brachyura*, Waller Field, Trinidad.

smaller than the nests described for some other species of *Chaetura* (Table 1). The nests were glued to the walls of the manholes at varying heights, some being near the top under the overhang where they were in deep shadow and others as much as 10 feet down where they often received direct sunlight for part of the day. Nests were occasionally re-used in successive years but most of them fell off the wall soon after the nesting season. Before re-use additional twigs appeared to be added to the nest, as has been recorded for *Ch. pelagica* (Amadon, 1936; Fischer, 1958). In only a few cases did *brachyura* build up the semicircular arch of saliva on the wall above the nest so

TABLE 1. NEST DIMENSIONS OF SWIFTS OF THE GENUS *Chaetura*. (W)—width of nest at greatest point along rim, (FB)—greatest distance from back to front rim, (D)—greatest depth from rim to bottom of nest. Measurements in centimeters.

	Number of nests	Average	Range
C. brachyura			
W		6.18	5.4 - 6.9
FB	8	5.33	4.0 - 6.5
D		2.52	1.8 - 3.3
C. pelagica[1]			
W		— —	7.5 - 11.3
FB	?	— —	5.0 - 7.5
D		— —	2.5 - 3.1
C. vauxi[2]			
W		10.0	— —
FB	1	6.0	— —
D		4.0	— —
C. andrei[3]			
W		8.5	7.5 - 9.5
FB	3	4.3	3.5 - 5.0
D		3.7	2.5 - 3.0
C. chapmani[4]			
W		6.9	— —
FB	1	5.9	— —
D		2.4	— —

[1]Fischer, 1958; Bendire, 1895
[2]Dickinson, 1951
[3]Sick, 1959
[4]Collins, M.S.

Figure 4.—Nests of *Chaetura brachyura*.

characteristic of *pelagica* nests (Fischer, 1958: Fig. 8), and the absence of this additional support may account for their more rapid destruction. Egg laying starts about 10 days after the beginning of construction and before the nest is completed. The nests are unlined, but in two cases a feather was glued in among the sticks, and one nest containing recently hatched young had a large white feather in the bottom.

A variety of other organisms also occupied the manhole nest sites. Those that were partly filled with water usually contained the tree frog *Hyla rubra*. An unidentified snake and a lizard, *Ameiva ameiva,* were each seen once at the bottom of dry holes, presumably having entered through the connecting drainage pipe. Wet and dry holes alike often contained one or more nests of the "Jack Spaniard" or paper wasp (*Polistes canadensis*) under the overhanging edge of the top and the globular mud nest of the potter wasp (*Eumenes canaliculatus*) on the walls. Spiders of several types frequented the manholes, and Snow (1962) once saw a large spider (*Mygale* sp.) pounce on and kill a nestling that fell out of the nest.

NESTS OF THE GENUS *Cypseloides*

The nests of 4 of the 10 species presently included in the genus *Cypseloides*[1] are still unknown. Those that have been described, however, show a good deal of similarity in both site and material. Lack, in his review of the nesting habits of swifts (1956a), states that "all the species of *Cypseloides* for which the nest is reliably known agree in building on steep cliffs, usually in association with water, making a cone-shaped nest of mud and moss lined with fern-tips or twigs." For *Cypseloides niger* (Gmelin), Knorr (1961) postulates five "ecological requirements" for nest sites: "the presence of water, high relief . . . , inaccessibility to terrestrial marauders, darkness, and the lack of flyway obstructions in the vicinity of the nest." This type of nesting situation is so characteristic that many nests of *niger* have been found by searching for these "ecological requirements" rather than for birds showing signs of possible breeding (Michael, 1927; Knorr, 1961, 1962). I used the same procedure to find additional *rutilus* nest sites in Trinidad, and I venture it might be applied with equal success in locating the yet undescribed nests of *Cypseloides biscutatus* (Sclater), *cherriei* Ridgway, *cryptus* Zimmer, and *lemosi* Eisenmann and Leh-

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[1] Until more detailed information is available I feel it is best to include the species of *Aerornis, Nephoecetes,* and *Streptoprocne* in the genus *Cypseloides* as proposed by Lack (1956a).

mann. Certain nests attributed to *Cypseloides* do not conform to this general pattern or the descriptions of other nests of the same species. One attributed to *fumagatus* (Streubel) by Holt, (1927-1928) and one to *zonaris* (Shaw) by Todd and Carriker (1922) were both described as being made of twigs glued together with salvia. The nest attributed to *fumigatus* contained five young and was located inside a house gable, an improbable site and brood size for a *Cypseloides* species. Both nests were probably made by some species of *Chaetura*.

Also *Cypseloides semicollaris* lays its eggs on sandy ledges in caves (Rowley and Orr, 1962) and *zonaris* was once suspected of nesting in burrows in a cliff in Guatemala (Anthony, in Griscom, 1932:194), certainly an atypical site for any New World swift. In Africa, however, *Apus horus* (Heuglin) characteristically nests in the deserted burrows of bee-eaters and swallows (Harwin, 1960; Steyn, 1966).

Figure 5a.—Cone-shaped nest of *Cypseloides rutilus*.

Cypseloides rutilus.—In the first description of a *rutilus* nest, Orton (1871) states ones in Colombia were "chiefly of moss, very compact and shallow and located in dark culverts about two feet above the water." Belcher and Smooker (1936) characterize nests in Trinidad as "half cups stuck to a perpendicular wall of rock . . . over a swiftly running stream." Snow (1962) describes the nest as "a substantial bracket, semicircular in horizontal section with a wide depression for the eggs . . . made of various plant fibers, usually including some moss."

My observations show some variation in the shape of *rutilus* nests. Some nests built on smooth vertical surfaces resembled truncated cones (Fig. 5a) similar to those reported for *rutilus* in Mexico by Rowley (1966) and for *fumigatus* and *zonaris* in Argentina by Dabbene (1918) [cited by Lack (1956a) as Reborati, 1918]. Others, located on small rock ledges, were little more than pads of nest ma-

Figure 5b.—Disc-shaped nest of *Cypseloides rutilus.*

terial, somewhat thicker along the outer rim, with a wide but shallow cup for the eggs (Fig. 5b). This type of nest closely resembles the "disk-shaped" ones reported for *zonaris* and *niger* when similarly located on damp rocky ledges (Rowley and Orr, 1965; Michael, 1927). The shape of the nest thus seems somewhat dependent on whether it is affixed to a smooth rocky surface or perched on a narrow ledge. Larger species such as *zonaris* require greater support for their nests and consequently would be expected to build on ledges. The smaller and lighter weight species such as *rutilus* and *fumigatus* can also build cone-shaped nests fixed to vertical surfaces. Presumably owing to its extreme weight (170-180g[1], the largest New World swift, *Cypseloides semicollaris* (Saussure), builds no nest at all and lays its eggs on sandy ledges in caves (Rowley and Orr, 1962).

Regardless of the shape, *rutilus* nests in Trinidad appeared to be primarily of soft plant material with some mud intermixed. This mud presumably helps hold the nest material together and affix it to the rock as no salivary glue appeared to be used. The universal us of saliva in swift nest construction has already been questioned (Marshall and Folley, 1956; Johnston, 1961), and its use should not be assumed for *rutilus* until further information is available. The plant materials used in Trinidadian *rutilus* nests included a liverwort of the genus *Plagiochilax*, the lycopsids *Selaginella cladorrhizans* and S. cf. *arthritica*, and the filmy fern *Trichomanes membranaceum*. All of these plants grow in damp shady places, particularly on rocky outcrops along streams (Fig. 6) and thus in proximity to the nest sites of these swifts.

No information is available on the collection of the nest material or nest construction by any species of *Cypseloides*. Nests are used several successive years; a new lining of fresh green material is added annually, and the annual additions show as distinct layers. Sea cave nests of *rutilus* appeared to be constructed of slightly different materials and contained seaweed as reported for a similarly located nest of *niger* (Legg, 1956).

In Trinidad *rutilus* nests have been found on rocky outcrops overhanging pools in mountain streams (Fig. 7), on the rocky walls of a river gorge, in sea caves, in man-made culverts (Fig. 5a) and in one case on the under side of a bridge (Belcher and Smooker, 1936; Snow, 1962). Of the 15 nest sites observed during this study, 2 were along mountain streams, 6 were in a river gorge, 4 in sea

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[1] Weight data obtained from two specimens in the U. S. National Museum.

Figure 6.—Nesting material of *Cypseloides rutilus* growing on stream-side rock ledge.

caves, and 3 were in man-made culverts under a road or under a bridge; 9 of these sites were ones found earlier by Snow (1962).

All the sites were similar to those for other *Cypseloides* species in being in deep shadow, inaccessible to terrestrial animals, and

closely associated with water. They did not agree with all the "requirements" outlined for *niger* in that they were rarely associated with high relief. All were in forested areas at relatively low elevations from sea level to 1100 feet. Most nests were in deep shadow and none received direct sunlight. Streamside nests were only 2-4

Figure 7.—Stream nesting habitat of *Cypseloides rutilus*, Arima Valley, Trinidad.

feet above the water, but nests in a gorge were as much as 25 feet above the river where the walls were still damp from seepage water. The sea-cave nests were about 6-8 feet above either permanent water or tidal wash. In Mexico, Rowley (1966) found nests of *rutilus* in caves in a rocky escarpment along a stream and also on the vertical walls of a river gorge from 18 inches to about 15 feet above the water level; in both situations the nest sites were in deep shadow.

In contrast to the nests of the larger species, *zonaris* and *niger*, which nest near and sometimes behind waterfalls, only one Trinidadian *rutilus* nest was near falling water. This nest, on a smooth wall about 8 feet above a pool into which a small waterfall poured, was just outside the spray zone of the fall. However Rowley (1966) noted a stream of water "cascading partially over the entrance" of a nesting cave of *rutilus* in Oaxaca, Mexico, and Lowery and Dalquest (1951) collected adults roosting in a cave behind a waterfall elsewhere in Mexico.

The largest concentration of nests was in the rock-walled Guacharo Gorge cut into limestone by the Arima River near the head of Arima Valley. This gorge on the Spring Hill Estate has been a nesting place for these swifts for at least 40 years, Belcher and Smooker (1936) having reported a nest there in 1926. Occupied nests were situated along the gorge at varying intervals, the shortest being about 35 feet. Elsewhere the least distance I have recorded between active *rutilus* nests was about 7 feet, which was all that separated two nests on the walls of a cave-like rock archway 8 feet above a channel cutting through Saut D'Eau Island, an islet off the north coast of Trinidad. It is worth noting that these swifts had to cross about a quarter mile of ocean to reach their nearest feeding ground. The swifts inhabiting sea caves on Huevos Island also probably cross stretches of water to reach mainland feeding areas.

In Oaxaca Rowley (1966) found four *rutilus* nests at varying intervals along a mile-long river gorge and clusters of nests in two small shallow caves. One cave, approximately 25 feet deep, 10 feet wide, and 15 feet high, contained 5 old nests, while the second cave, about the same size but with a higher ceiling, contained 6 occupied nests.

The most prominent organisms sharing these nest sites were bats (mostly of the family Phyllostomidae) that used the shady areas as daytime roosts, several species of small frogs, and a cave cricket.

I once caught a small snake, *Leptodeira annulata,* on a ledge only a few feet from an active swift nest. As its name implies, the Guacharo Gorge also contained a small colony of the "guacharo" or oilbird (*Steatornis caripensis*) as did two of the sea caves mentioned earlier in which *rutilus* was thought to nest (Snow, 1962).

Environmental temperatures at typical *rutilus* nest sites ranged from 18.8 to 26.2° C, but had a usual daily range of 21.5 to 25.0° C. Seacave nest sites tended to be a bit warmer, with maximum temperatures reaching 27.2° C. The range in temperature recorded over 13 months at one nest site in the river gorge was 18.8 to 23.8° C. Relative humidity at the nest sites was always above 95 per cent.

BREEDING SEASON

Most land birds in Trinidad have a well defined breeding season. In contrast to the annual period of molt, which shows little yearly variation, the breeding season varies considerably from species to species and from year to year (Snow and Snow, 1964) The breeding seasons for the two swifts *Ch. brachyura* and *Cyp. rutilus* extend from April until August or early September, but varying within this period considerably from year to year. The season coincides with the height of the annual rainy season when insects are presumably most plentiful. This probably represents an adaptive synchronization that assures both an adequate supply of food when females are forming eggs and when young are to be fed (Thompson, 1950; Lack, 1954, 1966). A similar adaptive relationship seems to exist in Trinidad with the swallows, which also depend upon flying insets for their food (Snow and Snow, 1964).

Although the ultimate factor regulating the breeding season seems to be an abundant food supply to support egg production and nestling growth, the proximal, or triggering environmental factors are more obscure. The role of the photoperiod in controlling breeding in tropical and equatorial birds is still subject to debate. Experimental work has shown that the gonads of several low-latitude birds will respond to increasing photoperiod (Marshall and Disney, 1956; Miller, 1959), as has been demonstrated for many temperate latitude species. However, the small annual change in photoperiod at the lower latitudes make it more reasonable to assume that these swifts, and possibly other tropical birds, respond to a combination in photoperiod and some more variable environmental

stimulus as Tordoff and Dawson (1965) showed for the erratic breeding of the Red Crossbill, *(Loxia curvirostra)*. This crossbill shows only a partial response to increasing or constant long photoperiods; the completion of gonadal development and the triggering of breeding depends on some proximate environmental factor, such as an increased availability of suitable food.

The most obvious environmental factor regulating the breeding of these Trinidadian swifts is the onset of the annual rainy season. Yet the responses of the two species differ somewhat. *Ch. brachyura* usually begins nesting before *Cyp. rutilus*, and very soon after the first heavy rains of the season. The first sign of breeding activity is the appearance of new nests or, in some cases, the addition of new material to old nests. These activities coincide with the start of the summer rainy season and, in years when brief heavy rains preceed the period of intense summer rainfall, *brachyura* may start nesting even earlier. In 1959 heavy rains early in April were followed by a dry spell that lasted until the onset of the true summer rains in mid-May. This false start triggered breeding by *brachyura* in April, followed by a lull during the dry spell, and a renewal of nesting activity in late May (Snow, 1962). During the extremely wet winter and spring of 1964 *brachyura* began breeding very early, although the main rainy season did not start until late May. A summary of the number of *brachyura* nests begun in the years 1957 to 1964 in half-month intervals is presented in Table 2. Several

TABLE 2. BREEDING SEASON OF *Chaetura brachyura*. Figures show number of nests started during half-month intervals.

Period	1957*	1958*	1959*	1960*	1961*	1962	1963	1964	All Years
1-15 April			1					1	2
16-30 April		1			1		3	2	7
1-15 May	5	4	1	3	1	2	4	4	24
16-31 May	4	3	2	3	2	1	2	4	21
1-15 June	1		4	3	4		2		14
16-30 June	1	1	5	1	2	4		1	15
1-15 July	3	2		1	3	3	1		13
16-31 July	1	4	2	1	1	1	**	1	11
1-15 Aug.	3		1	2	3	1	**	1	11
16-31 Aug.					3	1	**		4
1-15 Sept.	1	1			1		**		3
TOTAL	19	16	16	14	21	13	12	14	125

*Data from Snow (1962)
**No observations.

other Trinidadian birds appeared to be influenced directly by the return of rainy weather. In several cases the first strong rains of the season triggered reproductive activity. Almost immediately nest building and the gathering of nest material was conspicuous, and a peak in the number of eggs laid soon followed (Snow and Snow, 1964). Temporary dry spells also sharply reduced breeding activites in several species. Similar dramatic shifts in breeding activity associated with rainfall levels have been noticed also in nearby Venezuela (Gilliard, 1959).

Cyp. rutilus started its breeding activities later than *Ch. brachyura* and in most years showed a greater population synchrony (Table 3). The first sign of renewed nesting was always the appearance of a fresh lining of greenery in the old nests in preparation for their re-use. Before the rains start this material is in short supply, for it dies away during the dry season and only regains its lushness when the rains return. *Cyp. rutilus* apparently awaits the reappearance of suitable nest material to begin its breeding cycle. Such plant material is in turn dependent on the return of the full summer rains and, in some cases, on the rising of water levels in the streams.

This sequence of events was particularly noticeable when eastern Trinidad experienced a very wet winter and spring in 1964. As mentioned earlier, this unseasonable wet weather stimulated very early breeding by *Ch. brachyura*. At the same time Arima Valley experienced a fairly normal dry season, which did not end until

TABLE 3. BREEDING SEASON OF *Cypseloides rutilus*. Figures show number of nests started during half-month intervals.

Period	1957*	1958*	1959*	1960*	1961*	1962	1963	1964	All Years
1-15 April									
16-30 April				1					1
1-15 May		1	1	1					3
16-31 May	1	1		2		1	5	6	16
1-15 June		1	1		2	3	5	1	13
16-30 June		1	2		1	2			6
1-15 July		2			1				3
16-31 July		2	1	2	1	2	**		8
1-15 Aug.	1	1	1	2	1	1	**	4	11
16-31 Aug.			1		3	2	**	2	8
TOTAL	2	9	7	8	9	11	10	13	69

*Data from Snow (1962)

**No observations

nearly continuous heavy rains fell on 22-23 May. Prior to this time no indication of breeding was apparent at any known *Cyp. rutilus* nest site in the valley; the stream water levels were low, and no suitable nest material was available. A few days after these first heavy rains the mossy stream-side plant life recovered a great measure of its former lushness. On checking six *rutilus* nest sites on 29 May I found all six nests relined with fresh greenery. On 3 June three of these contained one or more eggs. By 6 June four of the six nests had full clutches while a fifth contained a partial clutch. The sixth nest, though relined, was not used that year.

CLUTCH SIZE

Chaetura brachyura

Like other species of *Chaetura* swifts, *brachyura* lays compara- tively large clutches. The 26 complete clutches observed from 1962 to 1964 ranged from 2 to 7 eggs, with a mean clutch size of 3.8 (Table 4). This is slightly less than in the other *Chaetura* species for which data are available (Table 5). In the earlier observations on this same population from 1957 to 1961, 41 clutches ranged in size from 1-6 and had a mean of 3.6 eggs per clutch (Snow, 1962; Table 2). Unusual clutches of 8 and 9 have been recorded for both *pelagica* and *brachyura*, but each case appeared to result from two females laying in the same nest (Fischer, 1958; Snow, 1962). The 7-egg clutches recorded for *vauxi* (Baldwin and Zaczkowski, 1963) and *brachyura* (this study) both seemed to be the product of but

TABLE 4. DISTRIBUTION OF CLUTCH SIZES OF *Chaetura brachyura* BY HALF- MONTH INTERVALS FOR YEARS 1962 TO 1964.

Period	\<- Clutch Size							
	1	2	3	4	5	6	7	Totals
16-30 April				1			1	2
1 -15 May			1	2	2			5
16-31 May		1	1	3	1			6
1 -15 June			1					1
16-30 June		3		1	1			4
1 -15 July			2	1		1		4
16-31 July			1		1			2
1 -15 Aug.			1					1
16-31 Aug.			1					1
All months	0	3	8	8	5	1	1	26

TABLE 5. CLUTCH SIZE OF SWIFT SPECIES IN THE GENUS *Chaetura*.

Species	Number of clutches	Range	clutch Average size	Reference
C. pelagica	25	2 - 5	4.2	Fischer, 1958
"	27	3 - 7	4.0	Dexter (in Fischer, 1958)
"	19	4 - 6	5.3	Sherman, 1952
C. brachyura	41	1 - 6	3.6	Snow, 1962
"	26	2 - 7	3.8	this study
C. andrei	3	4 - 5	4.6	Sick, 1959
C. vauxi	?	3 - 7	?	Baldwin & Zaczkowski, 1963; Bent, 1940.

a single female and in both cases the eggs were laid or hatched within a short time of each other.

An additional example of two females laying in a single nest was noted for *brachyura* in 1963. In this case a clutch of 4 eggs was laid in a newly constructed nest between 7-13 May, and the clutch still consisted of only 4 eggs on 17 May. On 21 May a fifth egg was noticed and when the nest was checked on 23 May a sixth had been added. Four 2-day-old young and two eggs were in the nest on 2 June, after an incubation period of approximately 17 days. The remaining two eggs hatched on 6 and 7 June and both of the newly hatched young birds were found later on the same day dead or nearly dead on the floor of the nest cavity. Presumably they were inadvertently shoved out of the nest by the movements of the older and stronger nestlings. An evening check of this nest showed three adults roosting together near the nest; one of them was known to be a yearling bird raised in that nest cavity the preceding year.

Two females trying to lay in the same nest may have caused disruption of egg laying and ejection of eggs in two other cases. Adult birds were frequently observed roosting in nest cavities with a nesting pair, though not in close approximation. At three other nests extra-parental cooperation was observed in the feeding of the young.

In *Ch. pelagica* extra-parental cooperation occurs regularly and may involve birds of all ages and both sexes, including young of the previous year. These helpers share in the incubation and brooding duties as well as the feeding of the young (Dexter, 1952). Further observations with individually marked birds might show it to be of regular occurrence in *brachyura*. The origin of such cooperation is not clear. It may result from a shortage of nest sites as Snow (1962)

suggests, from the inability of some birds to find mates as Dexter
(1952) proposes, or to some other cause. Skutch (1961) feels that
such activities in passerine birds may represent an adaptive curtail-
ment of the reproductive rate favoring the greater survival of fewer
young.

Eggs were usually laid at the rate of one every other day. On a
few occasions disturbances of the nest or inclement weather appeared
to prolong the laying period. Five eggs partially incubated in a single
clutch weighed 1, 1, 1, 1¼, and 1½ grams. The range in size of
seven eggs was from 17 to 18¾ mm in length and from 12 to 13 mm
in width. They lacked any appreciable taper. Fresh eggs were a pure
white; well incubated ones were at times slightly discolored.

Cypseloides rutilus

As in all *Cypseloides* swifts, clutch size in *rutilus* is very small. Of
25 clutches observed from 1962 to 1964, 23 were of 2 and 2 of 1 egg,
the average clutch size being 1.9. Of 32 clutches Snow (1962) ob-
served only one case of a clutch of a single egg was noticed and that
seemed attributable to a bird breeding for the first time.

The interval between the laying of the two eggs was slightly more
irregular than for *brachyura.* The second egg of the clutch was
usually laid 2 days after the first, but occasionally an interval of as
much as 5 days occurred, during which the first egg was left un-
covered.

The eggs from two clutches weighed 2¼, 2¾, 2¾ grams and,
like those of *brachyura,* were white and became noticeably discolored
during the course of incubation. The one egg of *rutilus* measured in
Trinidad was 20.5 mm long and 15 mm wide and lacked any appreci-
able taper. Clutches Rowley (1966) measured in Mexico ranged from
23.5 by 15.2 mm and 24.2 by 15.0 mm to 22.6 by 15.2 mm and 21.9
by 15.4 mm.

No extra-parental cooperation was observed in this species.

INCUBATION AND HATCHING SUCCESS

The incubation period was calculated from the laying of the last
egg to the hatching of the last young. For *Ch. brachyura* the 17-18
day period determined by Snow (1962) was confirmed, except in one
case when the period was only 16 days. Hatching of the entire clutch
usually involved a period of 48-72 hours between the hatching out of
the first and last young.

The incubation period for all *Cyp. rutilus* clutches agreed with the 22-23 day period Snow (1962) determined. The young in the broods of two usually hatched within 24 hours of each other.

Although substantial losses often occurred during the incubation period, the percentage of hatching was high among those eggs of both species that reached the expected date of hatching (Table 6). The figure recorded in this study for *rutilus* (84.3 per cent) is lower than that of Snow (93.1 per cent) because of the desertion of a clutch, which may in turn have resulted from the greater frequency of disturbing visits in this study. Thus the higher value is probably more characteristic of undisturbed nests. The hatching rate based on the total number of eggs laid is rather low for both species compared with similar values reported for other swifts (Table 6). Comparable data for tropical congenors is however lacking. Those species showing a high hatching success are also those with the more inaccessible nest sites. The higher hatching success of *Cyp. rutilus* as compared to *Ch. brachyura* probably similarly reflects the fact that *Cyp. rutilus* nests overhang water on smooth surfaces or inaccessible ledges, and

Table 6. AVERAGE HATCHING AND FLEDGING SUCCESS OF SWIFT SPECIES

Species	Eggs hatched of No. completely incubated (%)	Eggs hatched of No. laid (%)	Young fledging of No. eggs hatching (%)	Young fledging of No. eggs laid (%)
Apus apus[1]				
(England)	— —	74.0[11]	74.5	59.0
Apus apus[2]				
(Switzerland)	— —	76.0	85.8	65.2
Apus melba[3]	94.4	86.0	80.9	76.0
Apus caffer[4]	98.9	88.6	86.0	76.2
(Kenya)				
Apus caffer[5]	— —	81.0	70.3	57.0
(South Africa)				
Cypsiurus parvus[6]	— —	54.2	31.5	17.1
Chaetura pelagica[7]	— —	89.5	96.1	86.0
Chaetura brachyura[8]	95.0	51.7	53.5	26.7
Cypseloides rutilus[9]	93.1	— —	— —	— —
Cypseloides rutilus[8]	84.3	65.8	68.4	36.1
Collocalia maxima[10]	— —	29.2	65.4	— —
Collocalia esculenta[10]	— —	76.1	74.7	— —
Collocalia salangana[10]	— —	51.5	78.5	— —

[1]Lack and Lack, 1951. [2]Weitnauer, 1947. [3]Lack and Arn, 1947. [4]Moreau, 1942a. [5]Schmidt, 1965. [6]Moreau, 1941. [7]Fischer, 1958. [8]This study. [9]Snow, 1962. [10]Medway, 1962a. [11]78.0 per cent when eggs ejected prior to start of incubation are omitted.

are less often disturbed by predators than the nests of *Ch. brachyura* in manholes or hollow trees. Several of the "inaccessible" sites mentioned for other species were in man-made structures and may not reflect mortality rates when under natural conditions.

PARENTAL CARE

The period when the young are under parental care is divided into nestling and fledgling periods. The nestling period includes the time the young are in the nest. The fledgling period is when the young are out of the nest but incapable of flying and are still being fed by the adults. These periods are quite different in the two species of swifts in this study; in *brachyura* the nestling and fledgling periods are well defined while in *rutilus* the two periods overlap.

Chaetura brachyura

Nestling period.—The young of *brachyura* spend the first 3 weeks of their lives in the nest. Some birds leave the nest as early as day 20 but most remain in it until 22 or 23 days after hatching. Those in larger broods tend to leave the nest sooner than those in smaller ones.

Fledgling period.—The *brachyura* fledgling period lasts about 2 weeks, during which the young are out of the nest clinging to the walls of the nest cavity. Most of the fledglings remain in the nest cavity until they are 30-36 days old, and occasional individuals stay until they are about 40 days old, even though they may be capable of leaving as early as 26 days after hatching. In one extreme case two young birds were still roosting in the nest cavity and being fed by the adults 49 and 50 days after hatching respectively.

The ultimate factor governing departure of the fledglings is probably cessation of feeding by the adults. Young birds quite capable of flying were observed to spend much or all of the day roosting in the nest cavity so long as the adults continued to feed them. Several birds that escaped while being handled flew away successfully, and were found again roosting on subsequent daytime visits. Snow (1962) also observed young birds to "return to their nest hole by day after their first flight." It is quite possible that young birds more than 30 days old, still found roosting by day, were making occasional short flights before abandoning the nest cavity entirely. Two 35-day-old swifts, caught roosting in their nest cavity, were fully capable of sustained flight at this age and

returned successfully when released at a point 9 miles away. The earlier observations by Snow (1962) indicated that "the young can fly if disturbed as early as 28 days after hatching; if undisturbed, they do not usually leave until they are 30-40 days old."

Cypseloides rutilus

In *Cyp. rutilus*, as in all swifts except species of *Chaetura*, no separation of the nestling and fledgling periods is apparent, as the young remain in the nest until the time they can fly and feed themselves. This combined nestling-fledgling period in *Cyp. rutilus* is somewhat longer than in *Ch. brachyura*, being closer to 40 days. All available figures exceed 35 days, and most fall between 37-43 days. These figures are in agreement with those determined by Snow (1962). Young *rutilus* have been seen on occasion to exercise their wings while "hanging to the outer rim of the nest" (Snow, 1962). Any attempt to clamber about on the rocky wall adjoining the nest might be fatal, as these surfaces are usually smooth and often wet and slippery.

OTHER SPECIES

The combined nestling-fledgling periods for most swifts are between 35-45 days, with larger species requiring slightly longer periods than smaller ones. Unusually short periods of 29-32 days were noted for *Cypsiurus parvus* (Litchenstein) and 30 days for *Chaetura pelagica* (Moreau, 1941; Fischer, 1958). Slight geographic variation in the nestling-fledgling period has been noted in *Apus caffer* (Lichtenstein), which averages 42 days in Kenya and 46 days in South Africa (Moreau, 1942a; Schmidt, 1965). Weather conditions can also affect the length of the period, bad weather extending it as much as two days (Lack, 1956b).

BROODING

Until they are about two weeks old, nestlings of both swift species are brooded at night by one or both parents. After two weeks time the young are too large for the adults to cover effectivley. During the first days of nestling life *brachyura* nestlings are brooded regularly by day for long periods and for shorter periods up to 20 minutes long as late as 8 days after hatching. As early as the second day after hatching, however, both adults are sometimes absent, presumably foraging for the young. Nestlings of *rutilus* are usually brooded continuously during the daytime for the first 10-11 days, and occasionally as late as 13 days after hatching.

Most swift species brood during the daytime for most of the first week of nestling life, although both adults may be absent for short periods, particularly around dusk. Thereafter daytime brooding is sporadic and highly variable in duration. In England Lack and Lack (1952) record daytime brooding in *Apus apus* for 98 per cent of the time during the first week of nestling life, up to 52 per cent during the second week, and 7 per cent or less thereafter.

FLEDGING SUCCESS

The mortality during the nestling and fledgling periods for *Ch. brachyura* was approximately equal to that during incubation (Table 6). Only 53.5 per cent of the 58 hatching fledged successfully, and only 26.7 per cent of the 112 eggs laid resulted in fledged young. For *Cyp. rutilus* the mortality rates of eggs and nestlings were also about equal, with 68.4 per cent of the 19 hatchlings fledging successfully, or 36.1 per cent of the total 36 eggs laid.

As indicated by Snow (1962), the figures for *brachyura* may not be typical of nests other than in man-made structures, and some additional mortality may well have resulted from the frequent visits and repeated handling that were part of this study. No information is available for any species of *Chaetura* in a natural nest site. The only information on other *Cypseloides* swifts is for *niger*, which had a similarly high rate of nest failures, particularly in the nestling stage (Hunter and Baldwin, 1962).

The causes of egg and nestling losses are not clear. At least one *niger* nestling was seen to fall from the nest (Knorr, 1961:168), and possibly many of the *rutilus* losses are similarly due to young birds accidentally falling out of the nest. This is less likely in *brachyura* nestlings because their strong feet enable them to hold tenaciously to the nest at a very early age.

No predation of eggs or nestlings was actually observed for either species. Two nestlings *brachyura* and one of *rutilus* were found that had been badly chewed by some animal. As these nests were inaccessible to terrestrial predators, possibly the culprits were bats of one of the several species that commonly roosted close to the swift nests. Other losses of both nestlings and eggs might also be attributable to bat predation. Skutch (1964) suspected bats to be responsible for the disappearance of eggs and nestlings and for the wounding of a nestling hermit hummingbird.

In recent studies of three species of *Cypseloides* swifts in Mexico, including *rutilus*, numerous broken eggs were found amid the litter

that accumulated under nests and roosts (Rowley, 1966; Rowley and Orr, 1962, 1965). Altough some of these may have been dropped by females, particularly early in the breeding season, most were probably accidentally ejected from nests by adults. Rowley (1966) considered *rutilus* "clumsy on [their] nests" and that consequently eggs were often accidentally rolled over the edge of the shallow nests and destroyed. Accidental ejection of eggs from a nest by an adult has been observed in *Chaetura* brachyura (pers. obs.) and in two species of *Apus* (Lack and Lack, 1951; Moreau, 1942a).

GROWTH

BODY WEIGHT

A total of 321 *brachyura* nestling weights was obtained in the field, from 57 chicks in 15 nests (Fig. 8); from 1-15 weights were obtained from single nestlings. A total of 165 weights of *rutilus* nestlings was obtained from 25 individuals weighed between 1 and 16 times each (Fig. 9).

At hatching the average weight of *brachyura* nestlings was 1.6 grams; 18 days later they reached a maximum average weight of 21.2
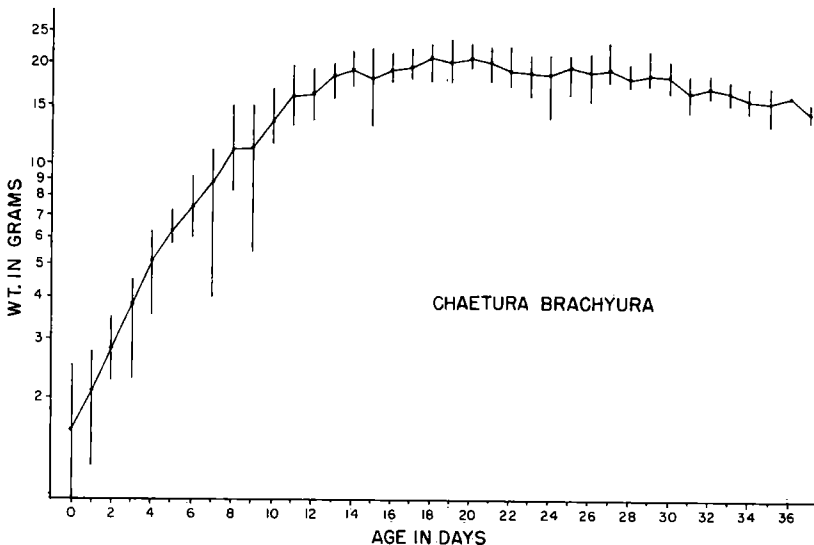

Figure 8.--Growth curve of *Chaetura brachyura*. Semi-log plot, vertical lines represent range of daily weights, curve connects daily means.

grams, a 13.3-fold increase. At fledging they had reached approxi-
mately 87 per cent of their adult weight.

The average weight of *rutilus* at hatching was 2.1 grams, and they
reached a maximum average weight of 26.2 grams on day 29, a 12.4-
fold increase. At fledging *rutilus* weighed approximately 119 per cent
of their adult weight.

The instantaneous percentage growth rate calculated for each day
(Brody, 1945: 508) tended to decrease in both species after an initial
rise (Table 7, 8). *Ch. brachyura* had its peak growth rate on the 4th
day after hatching, but the peak for *rutilus* did not occur until the 7th
day. The average weight gain per day and the average per cent
growth rate per day calculated for seven 5-day periods during the
nestling life of these two species (Table 9) show that *brachyura*
has an initially higher average daily weight gain and average per cent
growth rate that subsequently decline rapidly. After approximately 3
weeks of nestling life the young begin to lose weight, particularly
when they first leave the nest and again later when they begin to
fly. *Cyp. rutilus*, on the other hand, has an initially lower average
daily weight gain and average per cent growth rate which also
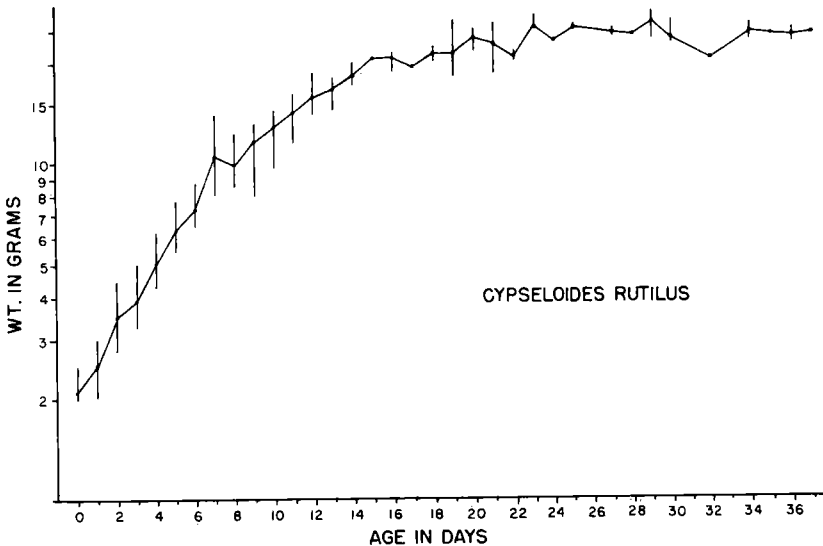declines, although at a slower rate so that the nestlings do not begin

Figure 9.—Growth curve of *Cypseloides rutilus*. Semi-log plot, vertical lines
represent range of daily weights, curve connects daily means.

Table 7. DAILY WEIGHT (GRAMS) AND RELATIVE GROWTH RATE (PER CENT) OF *Chaetura brachyura*.

Days from hatching	No.	Mean weight	Range	Mean weight change	Per cent relative growth per day
0	20	1.6	1 - 2½	.....	....
1	18	2.1	1¼ - 2⅜	0.5	27.1
2	13	2.8	2¼ - 3½	0.7	28.7
3	10	3.7	2¼ - 4½	0.9	27.8
4	10	5.1	3½ - 6¼	1.4	34.0
5	10	6.3	5¾ - 7¼	1.2	19.1
6	8	7.4	6 - 9	1.1	16.0
7	9	8.7	4 - 11	1.3	16.1
8	16	11.1	8¼ - 15	2.4	24.3
9	9	11.2	5½ - 15	0.1	0.8
10	15	13.5	11½ - 16¾	2.3	18.6
11	14	16.1	13 - 19½	2.6	17.6
12	14	16.2	13½ - 19	0.1	0.6
13	7	18.3	15¾ - 20	2.1	12.1
14	9	19.0	17½ - 21¾	0.7	3.7
15	11	18.1	13 - 22¼	−0.9	− 8.6
16	8	19.1	17½ - 21½	1.0	13.9
17	7	19.6	18 - 22	0.5	2.5
18	6	22.2	17¾ - 22½	2.6	12.4
19	7	20.2	17½ - 23¾	−2.0	− 9.4
20	5	20.9	19½ - 23	0.7	3.4
21	7	20.2	17¾ - 22½	−0.7	− 3.4
22	6	19.0	17¼ - 22½	−1.2	− 9.5
23	5	18.9	16 - 21	−0.1	− 0.5
24	8	18.8	13¾ - 21¼	−0.1	− 0.5
25	11	19.7	16 - 21	0.9	4.6
26	7	19.0	15½ - 21¼	−0.7	− 3.6
27	7	19.4	17½ - 23	0.4	2.0
28	6	18.0	17 - 20	−1.4	− 7.4
29	6	18.7	17¼ - 21¾	0.7	3.9
30	6	18.4	16¼ - 20¼	−0.3	− 1.6
31	7	16.5	14¼ - 18½	−1.9	−10.8
32	3	17.0	16 - 18½	0.5	2.9
33	5	16.6	15 - 17¾	−0.4	− 2.3
34	4	15.7	14¼ - 17	−0.9	− 5.5
35	4	15.4	13 - 17	−0.3	− 1.9
36	1	16.0	..... -	0.6	3.8
37	2	14.3	13½ - 15	−1.7	−11.2

Table 8. DAILY WEIGHT (GRAMS) AND RELATIVE GROWTH RATE (PER CENT) OF *Cypseloides rutilus*.

Days from hatching	No.	Mean weight	Range		Mean weight change	Per cent relative growth per day
0	7	2.1	2	- 2½	--	--
1	10	2.5	2	- 3	0.4	17.4
2	7	3.5	2¾ -	4½	1.0	33.6
3	10	3.9	3¼ -	5	0.4	10.8
4	8	5.0	4¼ -	6¼	1.1	24.8
5	13	6.3	5½ -	7¾	1.3	23.1
6	7	7.3	6½ -	8¾	1.0	14.7
7	7	10.6	8	- 14½	3.3	38.2
8	4	9.8	8½ - 12¼		−0.8	- 8.7
9	10	11.6	8	- 13	1.8	16.8
10	3	12.8	9¾ - 14¼		1.2	9.8
11	7	14.1	11½ - 16		1.3	9.6
12	6	15.8	14	- 18½	1.7	11.3
13	6	16.6	14½ - 17¾		0.8	4.9
14	4	18.2	17	- 19¾	1.6	9.2
15	1	20.5	.... -		2.3	11.9
16	6	20.7	18½ - 21½		0.2	0.9
17	1	19.3	.... -		−1.4	- 7.0
18	6	21.0	20	- 22	1.7	8.4
19	4	21.2	18	- 26¾	0.2	9.3
20	4	23.9	21½ - 24¾		2.7	11.9
21	6	22.5	18½ - 26		−1.4	- 6.0
22	2	20.8	20¼ - 21¼		−1.7	- 7.8
23	3	25.5	25	- 27½	4.7	20.3
24	1	23.0	.... -		−2.5	−10.3
25	3	25.2	24¾ - 25¾		2.2	9.1
26	....	....	.... -		--	--
27	3	24.2	24	- 25	−1.0	- 4.0
28	1	24.0	.... -		−0.2	- 0.8
29	3	26.2	23¼ - 28¾		2.2	8.7
30	4	23.6	22½ - 26¼		−2.6	−10.4
31	....	....	.... -		--	--
32	1	20.3	.... -		4.1	−15.0
33	....	....	.... -		−3.3	--
34	3	24.4	23	- 26½	--	18.3
35	1	24.0	.... -		−0.4	- 1.6
36	2	23.9	22½ - 25¼		−0.1	- 0.4
37	1	24.3	.... -		0.4	1.6

Table 9. AVERAGE DAILY GROWTH RATE (GRAMS) AND RELATIVE GROWTH RATE (PER CENT) FOR 5-DAY INTERVALS FOR *Cypseloides rutilus* AND *Chaetura brachyura*.

| Age | C. brachyura | | C. rutilus | |
	Mean daily weight change	Mean daily relative growth rate	Mean daily weight change	Mean daily relative growth rate
0-4	0.9	29.4	0.7	21.7
5-9	1.2	15.3	1.3	16.8
10-14	1.6	10.5	1.3	9.0
15-19	0.2	2.5	0.6	4.7
20-24	–0.3	– 2.1	0.4	1.6
25-29	–0.02	– 0.1	0.8	3.3
30-34	–0.6	– 3.5	–0.4	– 2.3

to lose weight until approximately 4½ weeks after hatching.

The general pattern of growth shown by these two swifts is similar to that reported for most altricial birds, particularly those with longer periods of development (Dawson and Evans, 1957, 1960; Maher, 1964; Kahl, 1958). *Ch. brachyura* is nearly identical in growth pattern to the only previously studied *Chaetura* species, *pelagica* and *vauxi* (Fischer, 1958; Baldwin and Zaczkowski, 1963). *Cyp. rutilus* is most similar in growth pattern to European species in the genus *Apus* with similarly long fledging periods (Lack and Lack, 1951; Weitnauer, 1947). No information is available for any other *Cypseloides* species.

GENERAL DEVELOPMENT

Feathers.–Like other species of swifts, *brachyura* and *rutilus* hatch naked. Approximately 4 days after hatching the developing contour feathers appear under the skin as dark dots along the feather tracts. The remiges are first to break through the skin, usually doing so around day 4-5. The rectrices are somewhat slower, emerging on about day 6-7, followed by the contour plumage when the birds are about 8 days old. The feathers of the dorsal tract grow somewhat faster than those of the cervical, capital, and ventral tracts and begin to emerge from their sheaths about 15-16 days after hatching. Emergence in the remaining tracts is somewhat later. The flight feathers begin to break out of their sheaths 12-13 days after hatching. The growth of the wing is shown in Fig. 10 and the tail in Fig. 11. The tail completes its growth about 26-27 days after hatching, but the wing does not reach full length until shortly after fledging.
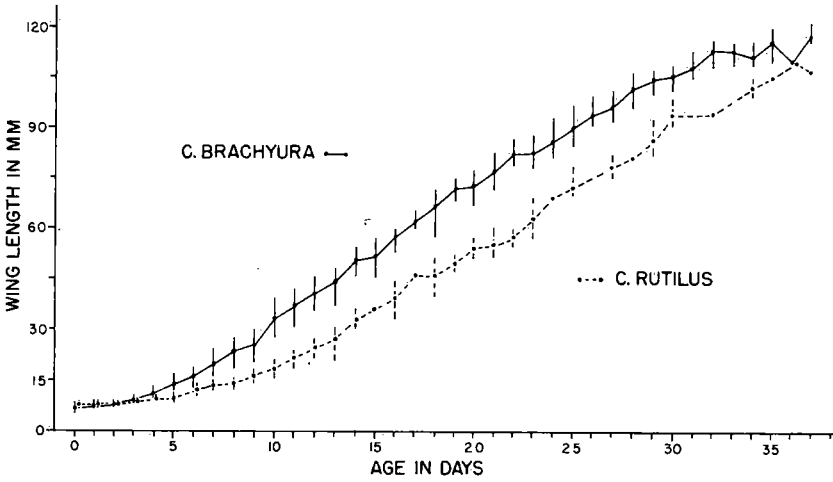
Figure 10.—Growth of the wing of *Chaetura brachyura* and *Cypseloides rutilus*. Vertical lines represent ranges, curves connect daily means. Wing length measured along chord from carpal joint to tip of longest primary.
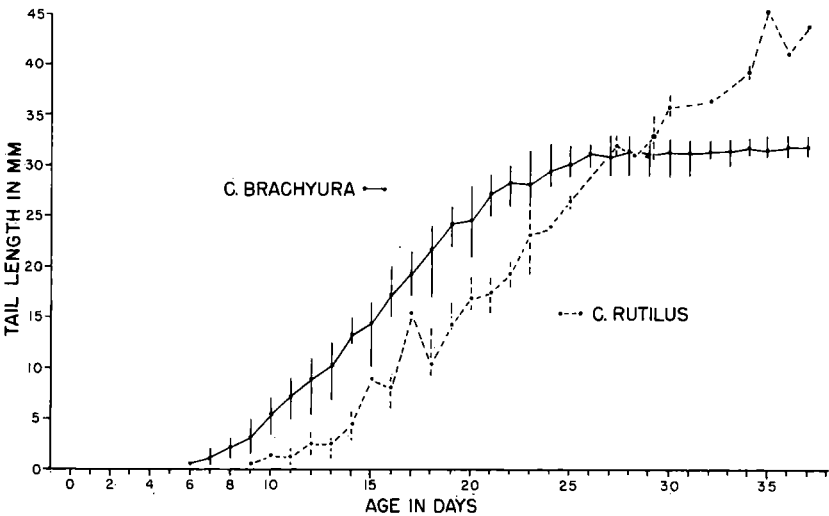

Figure 11.—Growth of tail of *Chaetura brachyura* and *Cypseloides rutilus*. Vertical lines represent ranges, curves connect daily means.

Cyp. rutilus acquires its feather covering in a sequence generally similar to that of *Ch. brachyura* but it differs slightly in timing. The remiges first break through the skin on about day 5 and the rectrices about 9 days after hatching. The contour plumage first appears as dark subcutaneous streaks and emerges through the skin at about day 10-11. The flight feathers begin to emerge from their sheaths about 13-14 days after hatching, about one day later than noted for *brachyura*. The contour feathers, however, begin to break through their sheaths much earlier in *rutilus* despite their having emerged through the skin somewhat later than in *brachyura*. These feathers begin to erupt in 13 days as opposed to day 15-16 for *brachyura*. The contour feathers of *rutilus* on the cervical, capital, and ventral tracts develop somewhat more slowly than those of the dorsal tract, as also noted for *brachyura*. The tail reaches its full length about the time the young fledges (Fig. 11), but the wing does not complete its growth until early in the post-fledging period (Fig. 10).

A major difference in the plumage development of *Chaetura* and *Cypseloides* species is the appearance in the latter group of a dark gray, down-like covering early in nestling life, prior to the appearance of the regular contour feathers. Although referred to as natal down by earlier observers, it consists of a loose-webbed semiplume type of feather and forms part of the first teleoptile plumage (Collins, 1963). These feathers appear as subcutaneous dots as early as the first day of nestling life. They may break through the skin as early as 5-6 days after hatching although usually somewhat later. They routinely emerge earlier than the previous estimate of 8-9 days after hatching.

These semiplumes are freed of their sheaths for more than half their length shortly after they erupt from the skin, and thus the nestling soon takes on a downy appearance (Collins, 1963; Fig. 3). The semiplumes seem to reach their full length of about 13-14 mm by day 19 and are entirely freed of their sheaths by day 26. They are covered over by the emerging contour plumage at about 28 days after hatching. Semiplumes are longest on the back and rump and shorter on the head and underparts. They are found on the margins of the pterylae, particularly on the dorsal aspect of the body. Although semiplumes are generally absent from the wings occasionally a few appear along the lateral margin of the humeral tract and in a short row in the apterium between the lesser secondary coverts and the marginal coverts (Collins, 1965). A similar down-like plumage has been recorded for other *Cypseloides* species (Hunter and Baldwin, 1962; Orr, in litt.) and one probably occurs in all members of the genus. The semiplume

covering and the early emergence of the contour feathers from their sheaths appear to be aids to thermoregulation in nestlings living in a cooler microclimate.

Eyes.—The two species differ noticeably in the development of the eyes. Those of *Chaetura* are partially open on day 16 and completely open on day 18, which is slightly later than has been observed for *pelagica* and *vauxi* (Fischer, 1958; Baldwin and Zaczkowski, 1963). In *Cypseloides rutilus* they open gradually with an interval of more than a week between the first partial and the complete opening; the eyes may open partially as early as day 7, but usually this first occurs on· day 8-9; they are not fully open until about day 16-17.

Bill and Feet.—The newly hatched swifts of both species are pale flesh pink except for the bill and claws, which have a slight gray pigmentation at the tip, especially noticeable in *brachyura*. The lining of the mouth is also a flesh pink and lacks the bright pigmentation observed in many other avian groups, particularly the passerines. A prominent egg tooth is present on the upper mandible. Parkes and Clark (1964) report similar structures in other genera and the lower mandible has a hardened whitish cap. The egg teeth gradually disappear during the first weeks of nestling life. Both egg teeth are generally unobservable by day 14, although a slight roughness on the culmen sometimes can be detected on slightly older birds.

Grasping with the feet was noticed on the first day after hatching in both species. The legs of *brachyura* seem to be particularly well developed very early in life and are capable of supporting the nestling on a vertical surface within 48 hours of hatching. The feet of *rutilus* cannot support a nestling this way until about day 14. Michael (1933) similarly notices that *Cypseloides niger* has "the dainty feet and slender legs of a songbird" and not the stronger limbs characteristic of the White-throated Swift, *Aeronautes saxatilis* (Woodhouse). In their study of *Chaetura vauxi*, Baldwin and Hunter (1963) also comment on the particularly sharp claws and strong toes as compared to *Cypseloides niger*. The young of *brachyura* hold on to the twigs of the nest so tenaciously that claws are apt to be pulled off it care is not taken in removing them from the nest. An unexplained loss of claws of *vauxi* nestlings noted by Baldwin and Hunter (1963) probably occurred during their removal from the nest for observation. Their stronger feet enable to *Chaetura* species to raise larger broods in their small nests. The ability to hold tightly to the nest reduces the chances of a nestling being jostled out of the crowded nest, particularly when defecating. As the nestlings grow and overcrowd the

Figure 12.—*Chaetura brachyura* nestlings shortly before leaving the nest.

nest. (Fig. 12) they can climb out and cling to the wall nearby until actual fledging (Fig. 13).

Behavior. The vocalizations of these nestling swifts are rather limited. *Cypseloides rutilus* nestlings only make a very soft twittering when disturbed and practically no noise during feeding, but *brachyura* nestlings utter a prolonged loud rasping rattle that can be heard at some distance whenever disturbed and particularly during feeding. This call starts and stops abruptly, and if one bird starts, its nestmates are quick to join in. This 'disturbance' call (Fischer, 1958) is normally restricted to feeding and associated activities and excitement once the eyes are open. Prior to this the slightest disturbance, whether an external stimulus or merely the sudden activity of one member of the brood, is apt to trigger several seconds of this calling.

Neither of these swifts foul the nest. The nestlings carefully void fecal wastes over the nest rim. As other workers have noted, this often results in large accumulations of trash, particularly the chitinous remains of their insect food, under the nests. This indigestable chitin is passed completely through the digestive tract and not regurgitated in the form of pellets as in some other insectivorous birds.
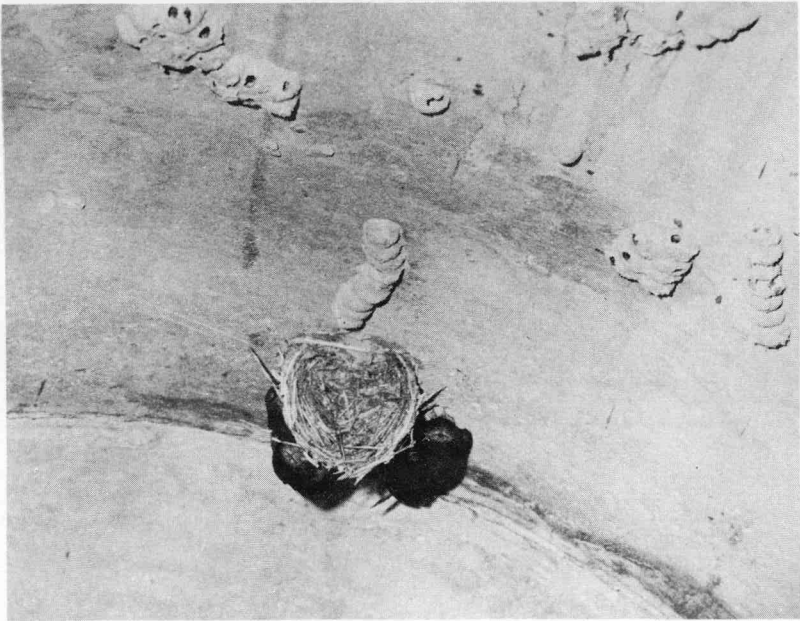
Figure 13.—*Chaetura brachyura* fledglings hanging on wall near nest. Nearby are the mud nests of the potter wasp, *Eumenes canaliculatus.*

DEVELOPMENT OF HOMEOTHERMY

Young swifts of both species essentially lack any thermoregulatory capacity at hatching. When they are not brooded their body temperature quickly drops to near ambient temperatures (Figs. 14-15). Body temperatures as low as 25-27°C were recorded for *rutilus;* the lowest body temperature recorded for *brachyura* nestlings was 31.9°C. The thermoregulatory capacity of both species improves as they grow older, and at the end of the third week of nestling life the body temperature declines very little, even during extended periods of exposure.

Nestlings tested in a cold chamber (Fig. 2) at approximately 5°C showed rapid decreases in body temperature, as much as 9.8 degrees within 5 minutes. A total of 101 tests were made on 31 *brachyura* nestlings and 72 tests on 12 *rutilus* nestlings. The rate at which body temperature dropped lessened sharply with increasing age (Fig. 16). This lessening in temperature decline represented an increase in the thermoregulatory capacity of the nestlings through both an increased capacity for thermogenesis and decreased heat loss. The decrease in body heat loss could be due to the appearance of an insulating feather coat or a decrease in the nestlings' surface to volume ratio. *Cyp.*

Figure 14.—Body temperature of nestlings of *Chaetura brachyura* when un-brooded. Vertical lines represent daily range in body temperatures, curve connects daily means. Typical daily range in ambient temperature 26.0-30.5 C.
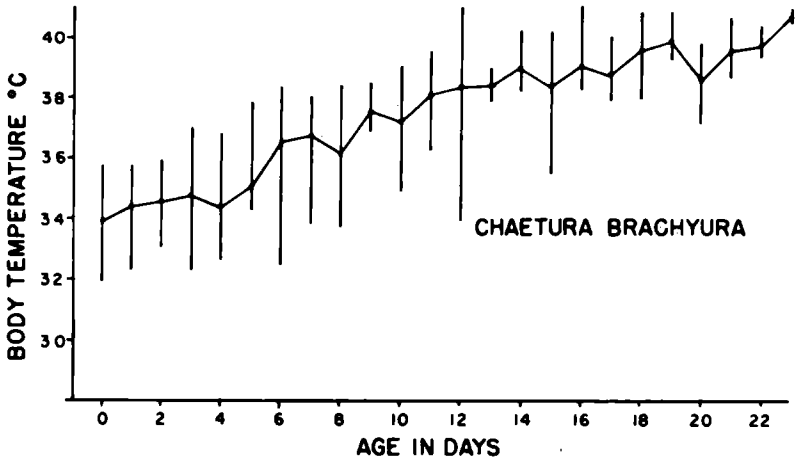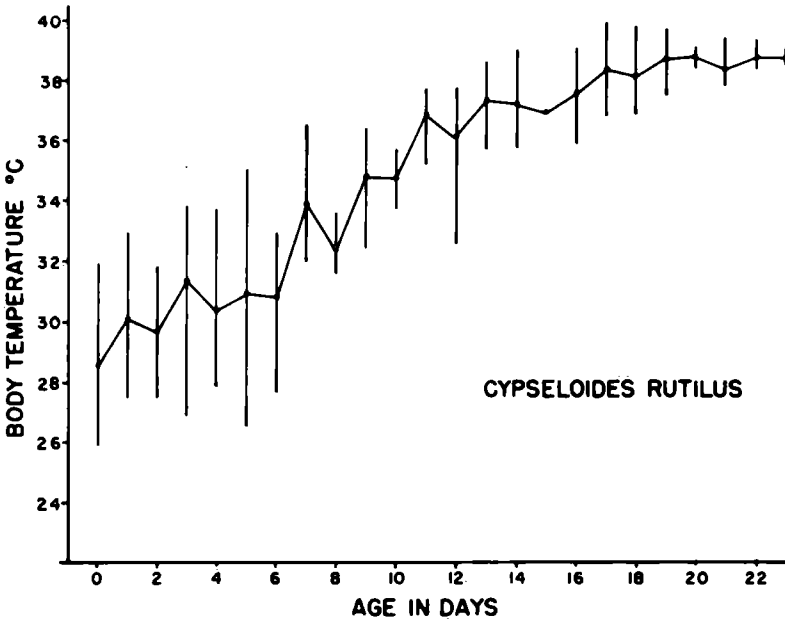

Figure 15.—Body temperature of nestlings of *Cypseloides rutilus* when un-brooded. Vertical lines represent daily range in body temperatures, curve connects daily means. Typical daily range in ambient temperature 21.0-25.0 C.

rutilus seem to have an efficient coat of insulation early in nestling life in its downlike semiplume covering. In addition its contour plumage grows in very rapidly. Both *rutilus* and *brachyura*, however, perfect their thermoregulatory capacities at about the same rate and show little difference in their body weights, and hence surface to volume ratios, during their first 2 weeks of life. Thus *brachyura* evidently must depend upon increased heat production to counteract the effect of cold. As the ambient temperatures of their nest sites are usually quite warm, they are only rarely exposed to cold and the need for increased thermogenesis.

TORPOR

The insect food of swifts may be affected markedly by varying weather conditions. In temperate regions, where acute food shortages lasting several days are of common occurrence, both adult and nestling swifts routinely drop their body temperatures at night and enter a state of torpor (Koskimies, 1950; Bartholomew, Howell, and Cade, 1957). Young *Apus apus* can fast as long as 9 days by utilizing their stored fat deposits and decreasing their body temperature and metabolism at night (Koskimies, 1950). Similar reactions have been observed
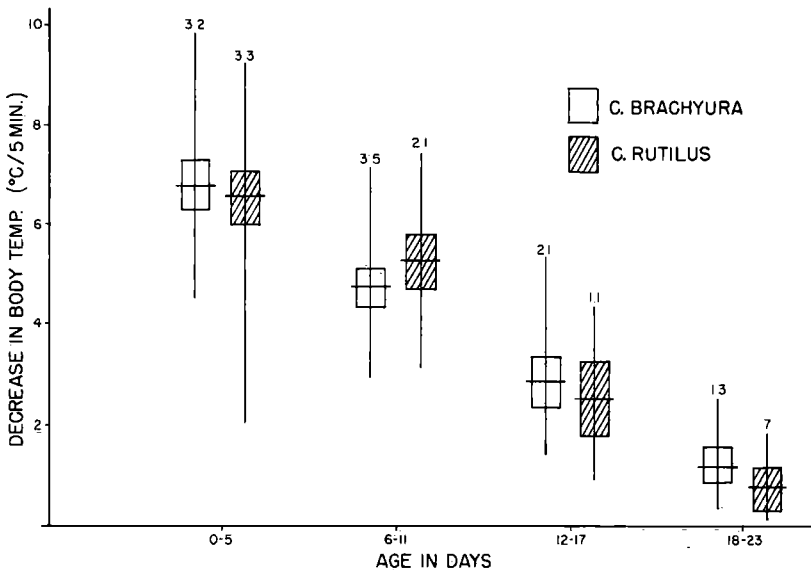

Figure 16.—Decrease in body temperature of nestling swifts under cold stress. Vertical line represents the range, and rectangles two standard errors on either side of the mean.

in several species of tropical swifts when deprived of food for several days in captivity (Howell, 1961; pers. obser.). Under natural conditions no healthy adult or nestling of either *brachyura* or *rutilus* exhibited a body temperature below the maximum that it was capable of maintaining, and none appeared to be in less than a fully active, awake condition. Several times nestlings that appeared to be injured or in an extremely weakened condition had abnormally low body temperatures, and usually these young were dead or missing from the nest at the next visit. The capacity for dropping into torpor may exist in all swifts, but neither *brachyura* nor *rutilus* seem to use it in the normal course of events.

ADULT WEIGHT

A sample of 240 individual weighings showed the average adult weight of *brachyura* to be 18.3 grams with a range of 15.5-22.0 grams. Snow (1962) reported an average weight of 19.8 grams, but this value was clearly influenced by the inclusion of one female weighing 30 grams, 8 grams heavier than any other recorded for *Ch. brachyura* This value is within the expected weight range of the larger but extremely similar species, *Chaetura chapmani,* Hellmayr, to which perhaps it should be attributed. The average weight of 24 juveniles of *brachyura,* captured with roosting flocks of adults during September and October 1964, was not appreciably different from that of the adults, although a few juvenile individuals ranged as low as 14-15 grams, well below the minimal weight recorded for any adult.

The average adult weight of *rutilus* was 20.2 grams and ranged from 17¾ to 24¼ grams in a sample of 45 individual weighings. A slight sexual dimorphism in weight was apparent; 24 males averaged 20.6 grams and ranged from 19¼ to 22¼ grams, while 19 females averaged 19.6 grams with a range of 17¾ to 24¼ grams. This difference is significant ($P < .02$).

Monthly mean weights for both sexes of *brachyura* varied between a low of 17.1 grams (Oct. 1964) and a high of 18.7 grams (Aug. 1964). Somewhat higher (18.9, 19.0 g) daily means were also recorded during August 1964. Monthly mean weights of both sexes of *C. rutilus* varied from a low of 19.6 grams to a high of 20.7 grams, while daily sample averages varied from a low of 19.0 to a high of 21.1 grams, both in October 1964. Eighteen individuals of *brachyura* and eight of *rutilus* weighed on two to four separate occasions varied as little as ¼ gram and as much as 2½ grams between weighings.

These weight variations are explainable in terms of temporal variations in food availability. Gladwin and Nau (1964) recorded similar weight changes in *Apus apus* in England and correlated sharp decreases in body weight with prolonged cold or rainy weather, which greatly decreases the swifts aerial food supply (Lack and Owen, 1955). No marked seasonal change in weight was apparent between April and November in either *brachyura* or *rutilus*, as is typical in migrant species such as *pelagica* in temperate North America (Coffey, 1958).

FOOD AND FEEDING HABITS

A poorly known aspect of swift biology is their feeding habits. Although some information exists on the types of food collected and the rate at which it is brought to the young, information on where and at what rate it is collected is only fragmentary.

In Trinidad during clear, sunny weather, mixed flocks of swifts are commonly seen moving up and down the valleys of the northern range, overhead at one instant, several miles away in a matter of minutes, and back overhead shortly thereafter. During the (summer) rainy season these birds are often observed on the advancing edge of the abundant intermittant showers. The flocks may contain up to seven of the nine species of swifts recorded in Trinidad. These are only temporary associations, and if the birds are watched over longer periods certain specific feeding patterns become discernible.

Chaetura brachyura is by far the most widely distributed species in Trinidad and is found at almost all elevations. The only *Chaetura* that regularly forages over the savanna areas, it is decidedly more plentiful there and over the lower parts of the northern range than over those areas above 1200 feet elevation. One pair feeding young in a nest at an elevation of 500 feet in Arima Valley "used to fly off down the valley in the direction of the savanna three miles away. They would return from the same direction" (Snow, 1962).

Cypseloides rutilus was less often observed in flight and then only in the upper part of Arima Valley or over the higher parts of the northern range. Even though it nests in caves at sea level on the north coast and at elevations of 500-1100 feet in Arima Valley, it seems to forage exclusively over the forest at higher elevations. Although the feeding ranges of the two species overlap at the lower elevations around 500 feet, *rutilus* is also commonly observed at higher elevations including the summit of El Tucuche (3,068 feet), whereas *Ch. brachyura* is uncommon above 1200 feet. Conversely I have never observed *rutilus* over the savanna areas. In addition to feeding at

higher elevations, *rutilus* and another swift, *Panyptila cayennensis* (Gmelin), seem at all elevations to feed farther above the ground than most species of *Chaetura*. This tendency was also observed for *rutilus* in Trinidad by Snow (1962) and in Costa Rica by Slud (1964), and elsewhere for *niger* by Rathbun (1925). As this characteristic of feeding at higher altitudes was most commonly noted during fine weather and particularly when both *rutilus* and *cayennensis* were part of mixed flocks containing one or more species of *Chaetura*, it may be less diagnostic of their day to day feeding activities when not in association with other species.

In England *Apus apus* generally feeds in the immediate vicinity of the nests (Lack and Owen, 1955), whereas in Washington *Cypseloides niger* makes daily trips of several miles from mountain nesting sites to lowland feeding areas (Rathbun, 1925). During the breeding season both species also make long-range movements of several hundred miles to avoid prolonged adverse weather conditions (Lack, 1955; Udvardy, 1954). Fischer (1958) reports seeing *Chaetura pelagica* in New York foraging over a field about $\frac{1}{4}$ mile from the nest and regularly bringing in Ephemeroptera, presumably collected over a stream $\frac{1}{8}$ mile away. He also saw two color-marked birds foraging $2\frac{3}{4}$ and 4 miles, respectively, from their nests.

Weather-influenced differences in feeding attitude have been noticed for *Apus apus* and *Cyp. niger*, which feed higher in the air on sunny days and low over the ground or water during rainy or cloudy weather (Lack and Owen, 1955; Rathbun, 1925).

Day to day variations in feeding habits have been noticed for many species of swifts as they exploit temporary abundances in their air-born insect prey. They do not merely fly through the air with mouths open to catch whatever happens to get scooped in, but if watched closely can be seen to change their flight direction to snap up attractive prey items. Additional confirmation of this is provided by the comparison of food samples with random samples of aeroplankton; the swift-gathered samples are clearly richer in the larger species that are less characteristic of true aeroplankton (Lack and Owen, 1955).

The foraging habits of *brachyura* and *rutilus* did not change noticeably from day to day, although both species often descended to nearly ground level during wet weather to feed on the large flights of winged reproductive termites. Feeding on this temporary plethora of food was not confined to the swifts. Many species, ranging in size from house wrens (*Troglodytes aedon*) to caciques (*Psarocolius decu-*

manus), also preyed on them. Eisenmann (1961) noted a similar array of birds feeding on termite swarms in Panama.

In Brazil Carvalho (1962) observed *Ch. brachyura* and *Ch. spinicauda* (Temminck) "rubbing" against dry twigs and plants in bloom in search of insects or nest material. Several times I saw somewhat similar behavior by *brachyura* in Trinidad. The birds seemed to bank sharply up and flutter briefly near the outermost branches of trees extending above the forest canopy, apparently picking insects or spiders off the leaves. Fischer (1958) noticed similar foraging behavior in *pelagica* and it may well be widespread among the swifts.

Other swifts have also been noted feeding in several less typical ways. Meikeljohn (1928) reports *Apus apus* landing on the wall of a house and gathering spiders under the eaves, and Gilbert (1944) saw them foraging for insects and perhaps nest parasites in old swallow nests.

The stomach contents of the swifts collected during this study were mostly masses of partly digested insect remains, difficult to identify. On the other hand, the food they brought the nestlings was easily identified and probably was the same food the adults consumed. The adults brought the food to the nests in their throats as a compact mass of undigested insects partly glued together by saliva. by manipulating the food from the throat of recently fed nestlings I collected 21 samples of nestling food, 17 from *brachyura* and 4 from *rutilus*. This method, used earlier by Lack and Owen (1955), does not injure the birds if done carefully, and was not repeated often enough to disrupt the pattern of normal growth.

These samples varied (Table 10) from a nearly complete food ball of 326 insects to only a few remnants of a meal. Eight were homogeneous masses of either winged ants or winged reproductive termites. Heterogeneous samples varied from one or two types of insects to a mixture of some 40 species representing 6 orders of insects and 9 families of spiders. Daily variation in the food brought in by a single pair of adults was extensive and usually included both homogeneous and heterogeneous samples.

Interspecific differences in the type of food collected by these swifts is hard to assess because of the difficulties encountered in collecting samples from *rutilus*. Seemingly *brachyura* utilized a great variety of food items and *rutilus* only a few. This difference probably results from the fortuitous collecting of nearly homogeneous samples of winged ants and termites from *rutilus*; possibly more samples would have shown a diversity of prey items equal to that of *brachyura*.

TABLE 10.   CONTENTS OF FOOD BALLS COLLECTED FROM NESTLINGS OF *Chaetura brachyura* AND *Cypseloides rutilus*.

Food item	Number of samples in which it occurred	Number of individuals
A. Chaetura brachyura		
Araneae	2	94
Lycosidae	1	1
Tetragnathidae	1	1
Linyphiidae	1	1
Clubionidae	1	12
Micryphantidae	1	2
Oxyopidae	1	2
Thomisidae	1	16
Salticidae	1	34
Theridiidae	1	1
Araneidae	1	3
unidentified	1	21
Coleoptera	6	73
Curculionidae	3	14
Apion sp.	1	1
Ceutorhynchus sp.	1	12
unidentified	1	1
Scolytidae	3	9
Cocotrypes sp.	2	7
unidentified	2	2
Cryptophagidae	1	2
Chrysomelidae	3	13
Lema sp.	1	3
Chaetocnema sp.	1	2
Systena sp.	2	2
Unidentified	1	2
Altica sp.	1	2
Platypodidae	3	28
Platypus sp.	3	28
Staphylinidae	2	3
Coccinellidae	1	1
Nitidulidae	3	3
Stelidota sp.	1	1
Carpophilus sp.	2	2
Orthoptera	1	1

TABLE 10 CONTINUED—

Food item	Number of samples in which it occurred	Number of individuals
Hemiptera	2	10
Saldidae	1	1
Tingidae	1	9
Homoptera	2	16
Membracidae	1	2
Aphidae	1	1
Cicadellidae	1	5
Deltocaphalus flavicosta	1	1
Unidentified	1	4
Delphacidae	2	8
Peregrinus maidus	1	1
Sogata sp.	1	1
unidentified	1	6
Diptera	12	402
Hymenoptera	16	203
Formicidae	12	128
Camponotus sp.	6	41
Trachymyrmex sp.	2	6
Leptalae elongata	2	15
unidentified	4	75
Isoptera	4	49
Kalotermitidae	1	1
Calcaritermes nigriceps	1	1
Rhinotermitidae	2	32
Coptotermes testareus	2	32
Termitidae	1	16
Nasutitermes costalis	1	16
B. *Cypseloides rutilus*		
Hymenoptera	2	19
Formicidae	2	19
Dorymyrmex sp.	2	19
unidentified	1	7
Isoptera	2	25
Rhinotermitidae	1	20
Dolichorhinotermes longilabius	1	20
Termitidae	1	5
Anoplotermes meridianus	1	2
Anoplotermes sp.	1	3

Homogeneous food samples reported for several other swift species were in no case typical of the normal day-to-day diet. These simply corroborate what has already been observed from the foraging behavior. Swifts are quick to feed on any temporarily abundant prey item such as mayflies (Ephemeroptera) or aphids (Homoptera: Aphidae) in temperate areas or winged ants (Hymenoptera: Formicidae) or termites (Isoptera) in the tropics.

Swifts feed not only on many different kinds of insects, but on a wide range of sizes as well. Even so the sizes of prey items any species of swift takes seem to have certain limits. The upper limit probably depends upon the size of the bird and what it can comfortably swallow.

All food items of *brachyura* and *rutilus* were measured to check for possible size differences in their prey. The total length from the head to the tip of the abdomen, exclusive of antennae and legs, was taken to be the best available indication of total size. All fractional measurements were read to the next whole millimeter. The range of sizes and abundance of each size food item is shown in Fig. 17. As was true for the prey species diversity, *brachyura* appears to feed on a wider range of prey items than *rutilus*. Again it seems likely that this seeming difference is an artifact of the sampling. If only the
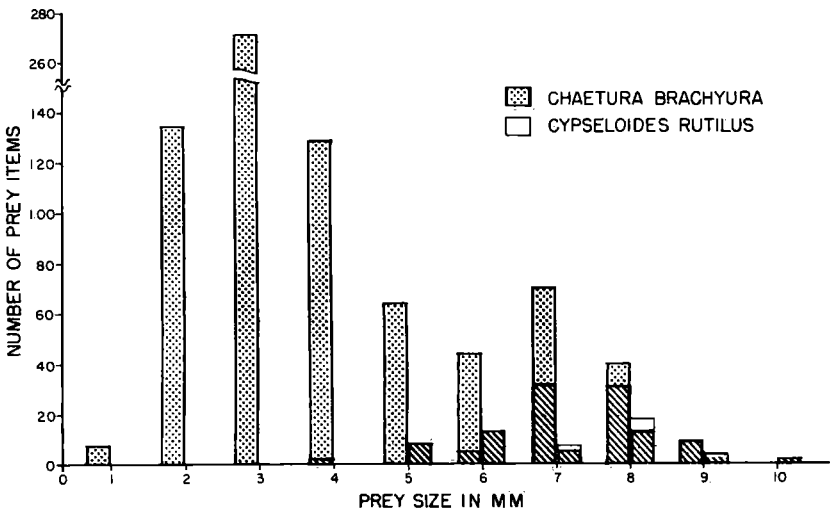

Figure 17.—Size of prey selected by *Chaetura brachyura* and *Cypseloides rutilus*. Diagonal shaded areas represent the portion of the sample consisting of winged ants and termites.

similar food items (winged ants and termites) of the two swift species are compared (Fig. 17), the interspecific differences in the size of prey selected are not significant. Winged ants and termites appear in the food samples throughout the breeding season, and the absence of any differences in size of these food items the swifts selected may indicate a similar absence of difference in size of other food items selected. If so, *rutilus* and *brachyura* would appear to select similar kinds and sizes of food items, although their foraging ranges only partially overlap.

In England *Apus apus* usually takes food items ranging in size from 2-10 mm, rarely larger or smaller. Within this range it tends to take larger items from 5-8 mm long during fine weather when insects are plentiful. During rainy or cold weather fewer insects of all sizes are available, and the swift includes more of the smaller prey items from 2-5 mm in its diet (Lack and Owen, 1955).

From this it seems that larger swifts such as *Apus apus* may occasionally select food items larger than any taken by either *brachyura* or *rutilus* and rarely take prey as small as some these smaller swifts take regularly. Similarly, 276 food items collected by another large swift, *Cypseloides niger*, in Veracruz, Mexico, ranged from 2-12 mm in length, with the most frequent sizes selected being 9 and 10 mm, or about the maximum size recorded for either *brachyura* or *rutilus* (Collins, unpubl.). If extended to other situations, two species of similar size would expectedly feed on insects within similar size ranges. The food habits of *Apus apus* and *A. pallidus* (Shelley) support this idea. These two swifts are nearly equal in size and select similar sized prey items (G. E. Watson, pers. comm.).

FEEDING OF YOUNG

The feeding of the nestlings was seen on several occasions but never at close enough range to be sure of details. Presumably it is similar to that reported for other swifts, in that the adult carries the food to the nest in the mouth or throat, inserts its bill into the nestling's mouth, and passes the food to it (see Arn-Willi, 1960; Plate 22-23). Food items are often brought to the nest glued together with saliva into a compact wad or "food ball". Very young birds generally receive only part of a food ball, the rest being shared with other nestlings or retained by the adult. When older a single nestling usually receives the entire food ball.

The rate of feeding of *brachyura* is similar to that of other species of *Chaetura* for which there is information. The intervals between

visits of adults to the nest range from 2.5-45 minutes and average 20.5 minutes.

Like other swifts of its genus, *Cypseloides rutilus* is characteristically absent from the nest for extended periods of time, particularly after brooding has ended. The feeding intervals of *rutilus* appears to be long and irregular. The one interval for which an exact time was obtained was 36 minutes. All other intervals recorded were in excess of 100 minutes, although the exact duration could not be determined.

Smith (1928) reports the best studied species of *Cypseloides, Cyp. niger*, may leave the nest at dawn and not return to feed the nestling until nearly dusk. Some feedings have been observed in the morning hours and indicate higher feeding rates at certain times, possibly when the nestling is very young. Michael (1927) watched an adult of this species feed the nestling, brood it, and then regurgitate a second meal for the young swift several hours after the initial feeding. Two adults collected at nighttime roosts still had large amounts of food in their throats, which would have enabled them to feed the nestling a second time (Collins, unpubl.).

The most complete information is that for *Apus affinis* in Kenya (Moreau, 1942b). This swift fed the young birds at intervals ranging from less than 8 up to 254 minutes, but averaged one feeding trip every 118 minutes for a brood of two. Broods of one were fed at a slower rate and broods of three at a significantly faster rate than either the broods of one or two. Despite acceleration of feeding rate with increased brood size, the rate per individual nestling decreased in larger broods.

In many species a flurry of feeding activity begins shortly before evening roosting, with the adults making many trips to the nest in a short time. Both Fischer (1958) and Sherman (1952) found that *pelagica* brought smaller quantities of food per trip during such visits, occasionally only a single insect.

An increase in feeding rate with increasing age of the nestlings is indicated in some swifts (Kendeigh, 1952: 97-98). This is particularly true in times of good weather and abundant food, when the young swifts tend to build up large reserves of subcutaneous fat. Lack (1956c) reports the adults tended to stay away from the nest longer when the young were well fed and consequently did not beg as enthusiastically when adults returned with food.

ADULT BEHAVIOR

Flocking.—Both *brachyura* and *rutilus* are most frequently observed flying in company with other swifts of either the same species or in mixed flocks of several species. Flocks made up of but one species are less characteristic and have been observed for *brachyura* only in savanna areas and for *rutilus* only in the vicinity of the summit of El Tucuche (elevation 3,075 ft.), one of the two highest peaks in Trinidad (Snow, 1962; pers. obs.). Although at times these flocks seemed to be primarily socially oriented, with individuals gliding in lazy circles and occasionally executing steep dives, they most often appeared to be loose aggregations of actively feeding birds. I have observed both single-species and mixed-species flocks during all parts of the year.

Roosting.—During the breeding season adults of both *brachyura* and *rutilus* roost on or very near their nests. In *brachyura,* other adults of the same species were sometimes found in the same manhole site with a nesting pair, but roosting at some distance from the nest. Adults and their late stage young out of the nest usually roosted in a single tight clump near the nest.

After the breeding season individuals of both species tended to unite in communal roosting flocks. In *brachyura* these postbreeding roosting flocks were sometimes as small as 6-10 birds, perhaps representing but one or two family groups, occasionally as large as 375 birds. The manhole a roosting flock selected changed from year to year and was not dependent on its having been used as a nest site that year. Frequently several roosting flocks, both large and small, occupied manholes less than 50 yards apart on the same night. Postbreeding roosting flocks of *brachyura* often included from 1-6 individuals of *Chaetura chapmani* (Fig. 18), an uncommon resident in Trinidad (Collins, MS.), and twice one or two individuals of *Chaetura spinicauda* (Snow, 1962; pers. obs.).

In Trinidad the post-breeding roosting flocks of *rutilus* were usually only small groups of 2-6 birds, and some pairs continued to roost apart at their nest site (Fig. 19). In Mexico Rowley (1966:131) observed large roosting flocks of this species, one of which he estimated to contain 300 birds. No other species of swift has been recorded roosting with *rutilus.*

In both species as the breeding season approaches these roosting flocks tend to break up and the various pairs spend the night adjacent to their prospective nest sites. Further information is needed on

Figure 18.—Roosting flock of *Chaetura brachyura* in manhole nest site, Waller Field, Trinidad. One individual of *Chaetura chapmani*, with the light throat, can be seen at the top center.

the exact timing and sequence of this dispersal of the breeding pairs.

Display and copulation.—Owing to the difficulty of observing any individual flying swift for more than a few moments, the display behavior of swifts is very poorly known. Like other members of its genus, *brachyura* was often seen flying in pairs or trios in the vicinity of the nesting sites. Though it was never possible to determine the sexes of the birds involved, this type of display is generally assumed to be associated with pair formation (Fischer, 1958). The "V-ing" display commonly noted in *pelagica* was not observed during this study.

Copulation in *pelagica* has been observed only when adults were

Figure 19.—Roosting pair of *Cypseloides rutilus* on nest, Arima Valley, Trinidad.

roosting at the nest site (Fischer, 1958), but for other species it has also been observed frequently while the birds were in flight (Dupond, 1943; Smith, 1950; Lack, 1956c; Rowley and Orr, 1962). Twice I saw two *brachyura* tumble downward end over end while clinging together, separate a few feet above the ground, and fly away in different directions. Similar actions have been noted in *Ch. pelagica* (pers. obs.) and *Aeronautes saxatilis* (Bent, 1940). Two such pairs of *saxatilis* collected each proved to be male and female in full breeding condition (Bradbury, 1918).

A wing-clattering or wing-clapping threat display at the nest or roost has been recorded for several species of *Chaetura*. In its usual form, as Fischer (1958) describes it in *pelagica*, the bird slowly raises its wings above its back, leaps backward into flight, and snaps or claps its wings together three to six times before landing near its original starting point. The wing-clapping display of *brachyura* is noticeably

different from that of *pelagica* and *chapmani* (Collins, MS) but similar to that of *andrei* (Sick, 1959), in which the wings are raised in the same fashion but the feet usually do not leave the wall and the clapping is confined to a single downward clap, seemingly more against the wall of the roost than against the opposite wing.

This sort of threat display was not shown by *rutilus* when similarly disturbed at its roost sites, nor was any aerial display or copulatory behavior by it noted during this study.

MOLT

Both *brachyura* and *rutilus* have a single complete annual molt which follows the breeding season. Some birds, particularly those raising second broods, were found in the early stages of this molt while they still had eggs or young in the nest. Molting birds were observed from August to early December.

In general the molt pattern is similar in both *brachyura* and *rutilus* and in agreement with the sequence Snow (1962) outlined for *Chaetura* species. The annual molt starts with the primaries, which are replaced in sequence from the innermost outward. The secondaries begin to be replaced after the primary molt is well advanced. The replacement of the tail is centripetal and begins after the wing molt has reached about the 4th or 5th primary. Body molt begins soon after the start of the primary molt and spans the whole duration of the molt period. It starts in the head and neck regions and progresses posteriorly over the body, a bit more rapidly on the dorsum than on the venter.

Juvenal birds do not molt either remiges or rectrices their first fall. Some light body molt observed in these birds in late September and October may represent a partial postjuvenal molt of the body feathers.

PARASITES AND PREDATORS

Ectoparasites in the form of mites (Acarina) and feather lice (Mallophaga) were collected from both species. Mallophaga were abundant on nestlings when their feathers were first emerging from the sheath, and their eggs were clustered on the dorsal feathers of the head and neck. M i t e s were noticed only on the remiges, mainly on the vanes of the outer primaries. Although these collections have not yet been identified, the mallophagan species *Dennyus brevicapitis* has been reported from *brachyura* in Trinidad, and *Dennyus brunne-*

itorques and *Eureum yepezi* from *rutilus* in other parts of its range (Carriker, 1954, 1958).

One specimen of a flea, *Polygenis dunni,* was caught on a young nestling *brachyura.* This species has previously been collected from several rodents in Trinidad and northern South America (Johnson, 1957).

The only endoparasites observed were tapeworms (*Taenia* sp.) collected from the intestines of both swifts.

Adult mortality in swifts is generally lower than in smaller and slower-flying species of passerines (Lack, 1954). No predators of adult swifts were observed during this study. Beebe (1950) watched a pair of nesting Bat Falcons in Venezuela preying heavily on the smaller swifts, including both *brachyura* and *rutilus.*

DISCUSSION

In their general biology *Chaetura brachyura* and *Cypseloides rutilus* appear similar to most swifts for which information is available. They are almost exclusively aerial in their activities and feed on airborne arthropods, mostly insects.

The breeding season of both swifts coincides with the abundance of aerial food associated with the summer rainy season. Many other species of Trinidadian birds have similarly adjusted their reproductive cycles so that they breed when suitable food is most plentiful. For the swallows, as for the swifts, the breeding peak and the maximal abundance of food both occur early in the rainy season. For the nectar feeding hummingbirds and the Bananaquit (*Coereba flaveola*), however, the maximal food abundance and the breeding peak occur at the height of the dry season (December-May) when many forest trees and vines are in flower (Snow and Snow, 1964). The absence of a pronounced peak in food abundance may permit an extended breeding season as in two species of thrushes (Snow and Snow, 1963). Beyond the tropics, a similar adaptive relationship often exists between breeding season and maximal food abundance. It can be seen in a great variety of bird species including both temperate zone tits of the genus *Parus* and arctic sandpipers of the genus *Calidris* (Gibb, 1954; Holmes, 1966). Previously the explanation of this synchronization was that "breeding seasons are adapted to the environmental cycle in such a way as to secure that the maximum supply of appropriate food will be available when the young are hatched and for a sufficient time after they are first on the wing" (Thompson, 1950:179). More recent studies have shown that another important factor in-

fluencing the timing of breeding is "the female's obtaining enough food to form eggs" (Lack, 1966; 273).

The pattern of nestling growth in both species is typical of altricial birds, although greatly prolonged in comparison to the several small passerines Maher (1964) reviews. Snow (1962) suggests that nest inaccessibility has allowed a relaxation of selection for the accelerated growth of nestlings so typical of most passerine birds nesting in the open.

Chaetura brachyura shows a pronounced similarity in all aspects of its biology to all other New World species of *Chaetura* that have been studied. In nest form, clutch size, nestling growth pattern, feeding habits, and general behavior only minor specific differences exist. For the most part these result from the timing of events during development. This general similarity is shown by an array of species that inhabit the area from temperate North America south to sub-equatorial South America including both sedentary and migratory species.

An equal degree of similarity exists between *Cypseloides rutilus* and other congeneric species, although the little information available relates mainly to *niger*.

Although both species studied show similarities to various congeners, several pronounced intergeneric differences are manifest in their reproductive activities. The nest site of *rutilus* is colder and darker than that of brachyura, less accessible to predators, and suffers fewer losses of both eggs and nestlings. At the same time this environment imposes several hardships on the development of the young. At hatching the young swift's capacity for temperature regulation is poorly developed, and it improves rather slowly during the first weeks of nestling life. If left unbrooded in the cold environment of the nest, *rutilus* nestlings rapidly lose heat to the environment, and much of the energy available for growth is expended in wasteful thermogenesis. To prevent such energy-draining heat loss, the adults brood the nestlings until their capacity for thermoregulation reaches a stage where the heat lost without brooding will no longer slow growth and development appreciably. In *rutilus* and its congeners thermoregulation is aided by the early appearance of an insulating feather coat. This includes the normal contour feathers which break out of the sheath at an early date, as well as a down-like semiplume portion of the first teleoptile plumage, which also grows in rapidly. Thus the intergeneric differences in nestling development and adult behavior represent adaptations that enable *rutilus* and other species of *Cypseloides* to

contend with the cold environment of the nest site.

The regulation of clutch size in birds has been studied in diverse taxa in many parts of the world. The most complete information is based on studies of temperate passerine species in which the clutch size "has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food" (Lack, 1954:31). Studies on Old World temperate and tropical swifts have shown these birds to be similarly food limited and their clutch size adapted to the number of young that can be raised under average conditions (Lack and Lack, 1951; Lack and Arn, 1947; Lack, 1966; Perrins, 1964; Moreau, 1941, 1942a, 1942b). The same factors doubtless regulate clutch size in other swifts in both temperate and tropical parts of the New World.

As shown above, the clutch size of *brachyura* resembles that of other species of *Chaetura* and is nearly double the clutch size of *Cypseloides rutilus*. Thus *rutilus* in Trinidad seems capable of obtaining food enough to nourish only two young, while *brachyura* can gather nearly double that amount. As noted earlier the feeding ranges of these two swifts overlap only partially, with *rutilus* feeding at higher elevations and higher altitudes. Even so, it is hard to accept the corollary that the food decreases in abundance by nearly 50 per cent with such shifts in feeding ecology, and hence is entirely responsible for the reduced clutch size in *rutilus*. It is equally hard to accept that *rutilus* is only half as efficient at gathering food as *brachyura*. However *rutilus* has to brood the young longer and more continuously than *brachyura* to contend with the colder environment of its nest site, which reduces the nestlings' food by restricting the foraging to one adult at a time. The absolute abundance of food may be the same or only slightly diminished in its foraging range, but the effective food supply available to the nestlings is much less.

In other species of *Cypseloides* a clutch size of two is typical except in *niger*, which nests in extremely cold environments at high elevations in the temperate zone, where it has to contend with an even less dependable food supply because of prolonged periods of bad weather in its breeding area. Like other swifts facing similar conditions it shows a further reduction in clutch size, namely to a single egg. It would be interesting to know what size clutch this bird lays in less rigorous environments in Central America and the West Indies.

Snow (1962) suggests that the small size of *rutilus* nests provides room for only two nestlings with consequent selection for a clutch of only two. This seems doubtful unless a maximum nest size for *Cypse-*

loides can be demonstrated, which seems unlikely in view of the fact that *Cypseloides semicollaris* builds no nest and lays only two eggs (Rowley and Orr, 1962).

In feeding both *brachyura* and *rutilus* apparently select food items within the same size ranges, but forage in slightly different areas. This may well represent an efficient mechanism to avoid interspecific competition between similarly sized swifts. As noted earlier, differently sized swifts tend to select different sizes of prey items. Thus where two differently sized species share a foraging range the size differences in the food items selected may be enough to avoid interspecific food competition. In support of this hypothesis it would be interesting to know the size prey ranges selected by an extremely large species such as *Cypseloides semicollaris* or *zonaris* and any of the tiny species of *Collocalia* or *Micropanyptila furcata* Sutton.

Feeding at higher altitudes by one species may further reduce interspecific competition within a given foraging range. *Cypseloides rutilus* and *Panyptila cayennensis* exhibit this habit in Trinidad, and *Collocalia maxima* Hume reduces possible interspecific competition with the several other sympatric species of *Collocalia* by similarly foraging at higher altitudes and specializing on the larger higher-flying insects in Malaysia (Medway, 1962a). Additional studies will undoubtably further clarify the ecological and behavioral differences existing between sympatric species of aerial foraging insectivorous birds.

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PREPARATION OF MANUSCRIPT

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Conference of Biological Editors, Committee on Form and Style.
1960. Style manual for biological journals.
Amer. Inst. Biol. Sci., Washington. 92 p.

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Florida State Museum
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