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# The North American Grouse: Their Biology and Behavior

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# *The North American Grouse*

## *Their Biology and Behavior*

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## Abstract

The ten currently recognized species of grouse in North America have played an important role in America's history, from the famous but ill-fated heath hen, a primary source of meat for the earliest New England immigrants, to the ruffed grouse, currently one of the most abundant and sought-after upland game birds in more than 40 states and provinces. This book summarizes the ecology, reproductive biology, and social behavior of all ten of the extant North American grouse species. It also describes the current status of grouse populations, some of which are perilously close to extinction. The social behavior of grouse is of special biological interest because among these ten species there is a complete mating system spectrum, from seasonally monogamous pair-bonding to highly promiscuous mating patterns. The latter group illustrates the strong structural and behavioral effects of sexual selection resulting from nonmonogamous mating. These influences reach a peak in the development by some grouse species of engaging in mating "leks," arena-like competitions performed by males while attempting to attract fertile females, and also provide opportunities for females to select optimum mating partners. These sexual competitions also promote strong differences evolving in sexual signaling behaviors ("displays") among closely related species. Nevertheless, a relatively high incidence of mating errors and resulting hybridization often occurs in spite of these marked behavioral differences. In addition to a text of 101,000 words, the book includes 16 range maps, 37 line drawings, and 38 photographs by the author, as well as nearly 1,400 literature citations.

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# Preface

When I published *Grouse and Quails of North America* more than four decades ago (1973), I thought it would be my only contribution to the then already extensive literature of gallinaceous bird biology. However, over the following 25 years I added to it with worldwide surveys of the grouse (1983); pheasant (1986, 1999); and quail, partridge, and francolin (1988) families. The biology and behavior of grouse have continued to remain a major interest of mine during the past four decades, and I have long hoped somebody else might someday take on the formidable task of summarizing the massive biological literature that has accumulated on the North American grouse since the mid-1970s.

That hope has not yet materialized, although the ten individual species accounts in *The Birds of North America* monograph series sponsored by the American Ornithologists' Union since the early1990s have gone a long way toward providing a collection of fairly recent monographs on grouse biology. Yet, purchasing this entire series represents a very expensive investment, and it is not available in most city libraries. Even buying only the individual species accounts that include all the North American grouse requires a significant cash outlay.

After I published a short book in 2002 describing the grassland grouse of North America and their ominous recent population declines (*Grassland Grouse and Their Conservation*), I again began thinking that an updated overall review of the biology and conservation status of all the North American grouse would be useful. I thus decided to extract much of what I had written about the North American grouse from my 1975 book and update it so far as my available time and more limited research opportunities allowed. Mostly for my own preference, I have left the species accounts in their original sequence, which does not conform to the current American Ornithologists' Union sequence, although the taxonomic names used here have been updated, with the older vernacular names parenthetically noted.

The technical and popular literature on these fascinating but increasingly vulnerable birds has continued to grow rapidly, and although my 1973 book had only about 300 references pertaining to grouse, the present one includes some 1,400 titles. I have been unable to investigate more than a small percentage of these additional sources but hope that their presence in the literature section will provide a useful guide to future researchers.

As for several of my earlier books, the DigitalCommons and Zea Books publication program at the University of Nebraska–Lincoln Libraries (digitalcommons.unl.edu) has provided me with a very convenient means of assembling and publishing updates and expansions of several of my earlier books as well as original research. For these opportunities I am highly indebted and deeply grateful to Paul Royster, Coordinator for Scholarly Communications, who has invariably cheerfully accepted these manuscripts and rapidly converted them into attractive and readily available publications.

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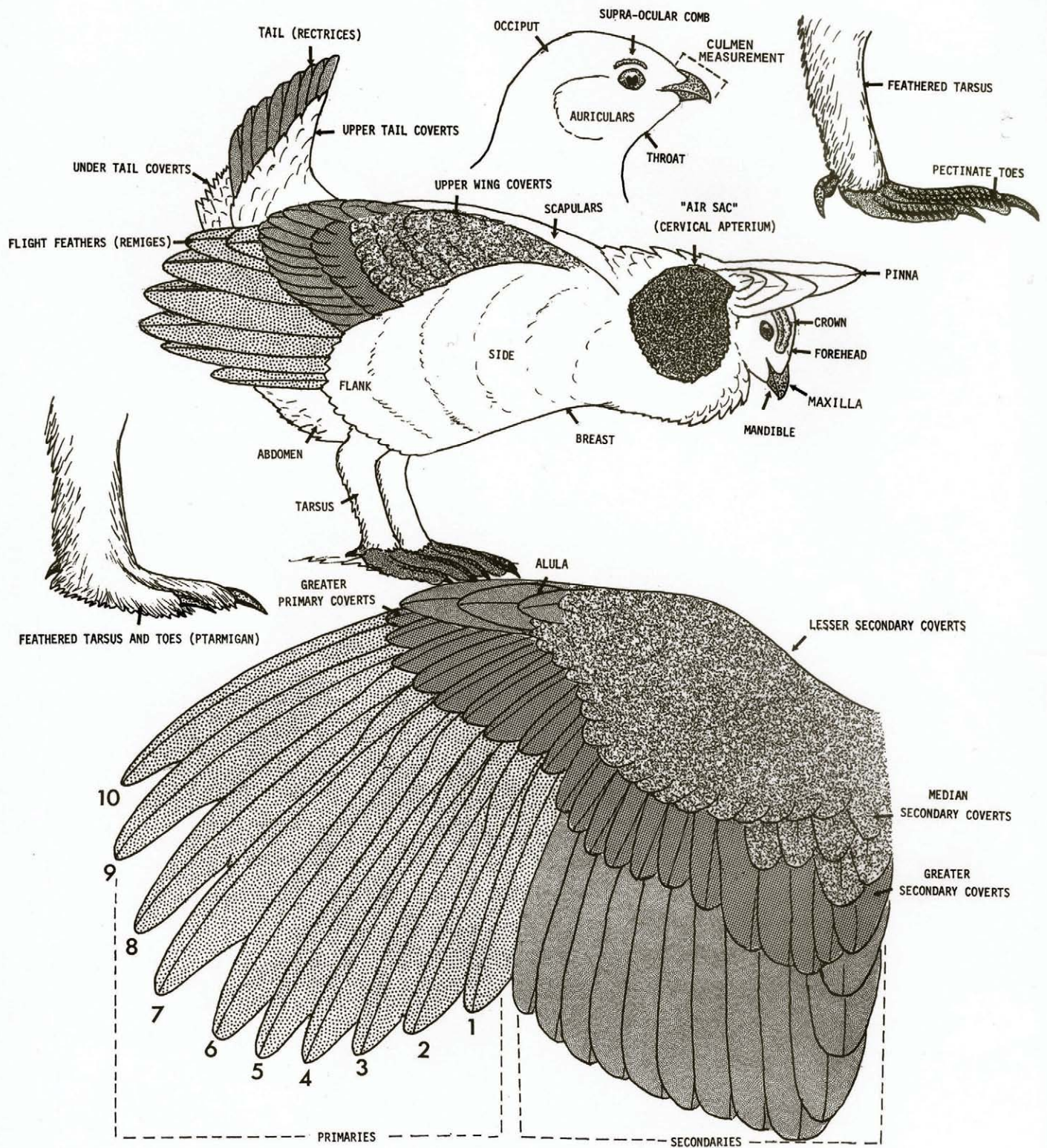
Fig. 1. Body regions and feather areas of a typical grouse (above) and the wing regions (below),
with the numbering of primary feathers indicated.

# I. Introduction to the North American Grouse

All of the grouse, quails, and partridges of North America share a number of anatomical traits that provide the basis for their common classification within the order Galliformes and the term gallinaceous birds. Among these are the facts that they all have fowl-like beaks and four toes. In all the North American gallinaceous species, the hind toe is elevated and quite short, and thus is poorly adapted for perching. In this general group there are always ten primary (outer wing) feathers, 13 to 21 secondary (inner wing) feathers, and 12 to 22 rectrices (tail feathers). In grouse, down feathers are rare, but fluffy aftershafts are attached to the bases of the larger contour (body) feathers. These aid in body insulation, as do short feathers that extend down the legs to the bases of the toes, or even (in ptarmigan) to their tips. Dense feathers also surround the nostrils and probably reduce heat losses while breathing. A large crop is present, in association with the highly herbivorous (leaf- and bud-eating) diets of grouse. A muscular stomach (gizzard) serves to help grind hard foods, and long blind sacs (caeca) in the small intestine help in bacterial digestion of cellulose-rich foods.

Grouse eggs vary in basic color from pastel or earth tones (buff to reddish brown), with darker brownish spotting prevalent in those species having generally darker eggs, such as ptarmigan. A simple nest is scratched out on the ground, often amid dense grasses or under low shrubs. Clutch sizes vary considerably, with the smallest clutches in ptarmigan (4–11 eggs) and the largest (11–14) in prairie grouse. Incubation by the female begins immediately after the completion of the clutch and requires 20 to 27 days. The chicks are covered with down, precocial, leave the nest within hours after hatching, and are often able to fly short distances in less than two weeks. They are cared for by the female (in most grouse) or by both parents (in some ptarmigan); coveys of related birds often thus form and may persist through winter. A number of external structural characteristics typical of grouse are shown in figure 1.

## Visual and Acoustic Adaptations for Reproduction

No North American grouse exhibits brightly colored feathers or elaborate crests, but several have special tracts of decorative feathers on the neck, such as elongated and erectile pinnae in prairie-chickens and airy filoplumes in sage-grouse. In the ruffed grouse, the special "ruff" feathers are borne on the lateral branches of the lower cervical feather tract. The dozen or so tapering feathers making up the pinnae of prairie-chickens are similarly borne on each side of the neck, below which is a large area of colored skin lacking feathers, the apterium.

In the greater prairie-chicken this skin is yellowish in color, presumably because of subcutaneous fat, whereas in the lesser prairie-chicken the skin is more reddish. The sharp-tailed grouse has a similar apterium, with skin that appears reddish to violet when expanded by esophageal inflation. Male sage-grouse exhibit a large and somewhat oval apterium on each side of the neck, located quite low and somewhat frontally. These areas of exposed skin measure about 2 inches by 1 inch in older greater sage-grouse males and are much smaller in females (Brooks, 1930). The exposed skin is olive gray but becomes yellowish when expanded during display. Most grouse also exhibit bare skin above their eyes ("eye-combs"), which in males become larger and more colorful when engorged with blood during display.

The lower and laterally adjacent breast feathers of male sage-grouse are curiously bristly, which was once thought to be a result of wear until Brooks (1930) discovered that newly grown feathers have the same appearance. They produce the rasping or squeaking sounds made when the front surfaces of the grouse's wings are brushed over the lower breast during display (Lumsden, 1968).

Dusky and sooty grouse males similarly expose rounded areas of neck skin during "hooting," which are surrounded by conspicuous whitish bases of surrounding dark neck feathers. These exposed skin areas vary from being flesh colored to purplish red (in the dusky) to appearing more thickened, wrinkled, and deep yellow in the sooty. Such variations presumably result from differences in subcutaneous fat deposits, which become less evident during nonbreeding periods (Brooks, 1926).

The sharp-tailed grouse and prairie-chicken expose similar areas of neck skin during their displays, and Lumsden (1965) noted that the sharp-tail's tail feathers are unusually adapted to the tail-rattling noises made during its display. The rectrices in males are very stout basally but taper rapidly. Ventrally the shaft projects in two keels, but dorsally the shaft is rounded and projects only slightly. The outer webs of the vanes are stiff and curve sharply downward, and the inner webs are also thickened. Each clicking sound is produced by lateral feather movements, during which the inner web catches on the ventrally projecting shaft of the inwardly adjacent feather web, and after some resistance the two disengage, producing a click. Simultaneously the curved outer webs brush over the dorsal surface of the next outwardly adjacent feather, producing a scraping sound. Additional nonvocal sounds by males of these species may be produced by foot stamping. The greater, Attwater's, and lesser prairie-chickens also perform feather-scraping or tail-clicking noises that are species-typical during display (Sharpe, 1968).

Few if any grouse vocalizations are pure tones; a basic or fundamental sound frequency (pitch) is generated by the vibrations of paired sound-producing (tympaniform) membranes of the vocal structure (syrinx), which is located at the junction of the windpipe (trachea) and bronchi. There are

usually also several higher overtones or harmonics generated, which are progressive multiples of the fundamental frequency, making the sounds richer and probably more individually distinctive. These harmonics are in turn differentially amplified or dampened by the resonating characteristics (length and volume) of the tracheal tube, throat (especially the inflatable "air sacs" of some species), and mouth. The overall acoustical effects of all these structures help tune the bird's vocalizations to a resonant frequency (timbre) that may serve to identify the species, sex, and possibly even the identity of the individual producing it. These features may help ensure same-species matings and reduce the danger of possible hybridization.

## Grouse Reproductive Behavior

The size of the male's territory and the length of time during which it is defended vary considerably among grouse. One extreme is that of defending throughout the breeding season a fairly large territory, within which a single female not only nests but she and her brood are also defended by the male. From that point one may trace the progressive development of a reduced territorial size that is defended only until after fertilization of females has been completed, and the females neither nest within the territorial boundaries nor are they or their broods defended by the males. This trend toward the evolution of a polygamous or promiscuous mating system is associated with many parallel evolutionary trends. There is an increased pressure on males for enhancing their attraction value to females; thus a tendency exists for more elaborate or more conspicuous sexual signal systems among males. Since they no longer must remain near the female and the nest, pressures for protective coloration are countered by those of sexual selection, and increased behavioral and plumage dimorphism is to be expected.

Conspicuousness in male sexual displays can be enhanced not only by an increase in body size and the exhibition of elaborate visual and acoustical signals in an individual male but also by multiplying such effects through the aggregation of several males. These counterpressures—those favoring the maintenance of definite and maximum territorial areas as a factor of reproductive success and those favoring the aggregation of several displaying males in a limited area to increase the likelihood of female attraction and reduce the danger of predators to individual males—have led directly to the evolution of arena behavior in several grouse species.

This arena-like form of male communal display, in which individual male territories are closely adjacent, are relatively small, and serve only as mating stations, can evolve only under certain circumstances. First, the males must be totally freed from defending areas large enough for the females to nest within and also from defending the female during incubation and brooding. Next, the reproductive efficiency of a group of males must be greater than that of single males, either because of their greater attraction to females or be-

cause the assembled males are relatively safer from predators than are those displaying solitarily. Further, to assure assortative mating there must be enough individual variation among the males in aggressiveness that territorial size or location is directly related to breeding success; these variations are perhaps most likely among species that require two or more years to attain full reproductive development. In addition, if male display aggregations are to develop, it must be advantageous for the less successful males to associate with the more successful ones. It may be argued that such early experience increases the male's chances of holding a larger or more centrally located territory that will be more reproductively efficient later in its lifetime. Peripheral males participating in arena displays may be regarded as apprentices that reproductively benefit more from such experience than they would from establishing independent and solitary territories.

Arena displays among grouse might logically be expected to evolve more readily in open-country habitats than in heavily forested ones, so open-country and polygamous species are preadapted for the evolution of arena behavior. It seems quite probable that the arena behavior of sage-grouse evolved independently from that of the prairie grouse (*Tympanuchus*), and the corresponding behavior of the European black grouse (*Tetrao tetrix*) may also have evolved independently. This last species is actually a woodland edge form, but its arena displays occur in open heaths. The communal leks of the black grouse were the earliest of the arena displays of grouse studied, and the term lek is now generally applied to the arena behavior of all grouse and also many other birds and mammals (Johnsgard, 1994). Koivisto (1965) suggested that "display ground: be used to describe the general topographic location in which social display is performed, "arena" used to indicate the specific area (the collective territories), and "lek" be more broadly applied to both the birds and their arena. Similarly, the term "lekking" can be used to indicate the general process of communal male display in grouse.

To illustrate how arena behavior may have gradually evolved from more typical territorial behavior, a series of representative grouse specimens can be given as examples that provide reference points along this behavioral spectrum.

Of all the grouse, the willow ptarmigan's actions come closest to the presumed ancestral (or most generalized) type of reproductive social behavior. In this species the male establishes fairly large territories in the fall (at least in nonmigratory populations). These individual territories are largest for the most aggressive males, and many young or inexperienced males may be unable to establish territories, especially in dense populations. The female is attracted to a displaying male, and a firm pair bond is formed. Sometimes males form a pair bond with two females and may breed with both. Territorial displays and defense continue after the pair bond is established, but such activities are diminished during the nesting season. At that time the male defends the female and nest and after hatching remains with the female and brood. After the brood is reared, the territorial boundaries are again established.
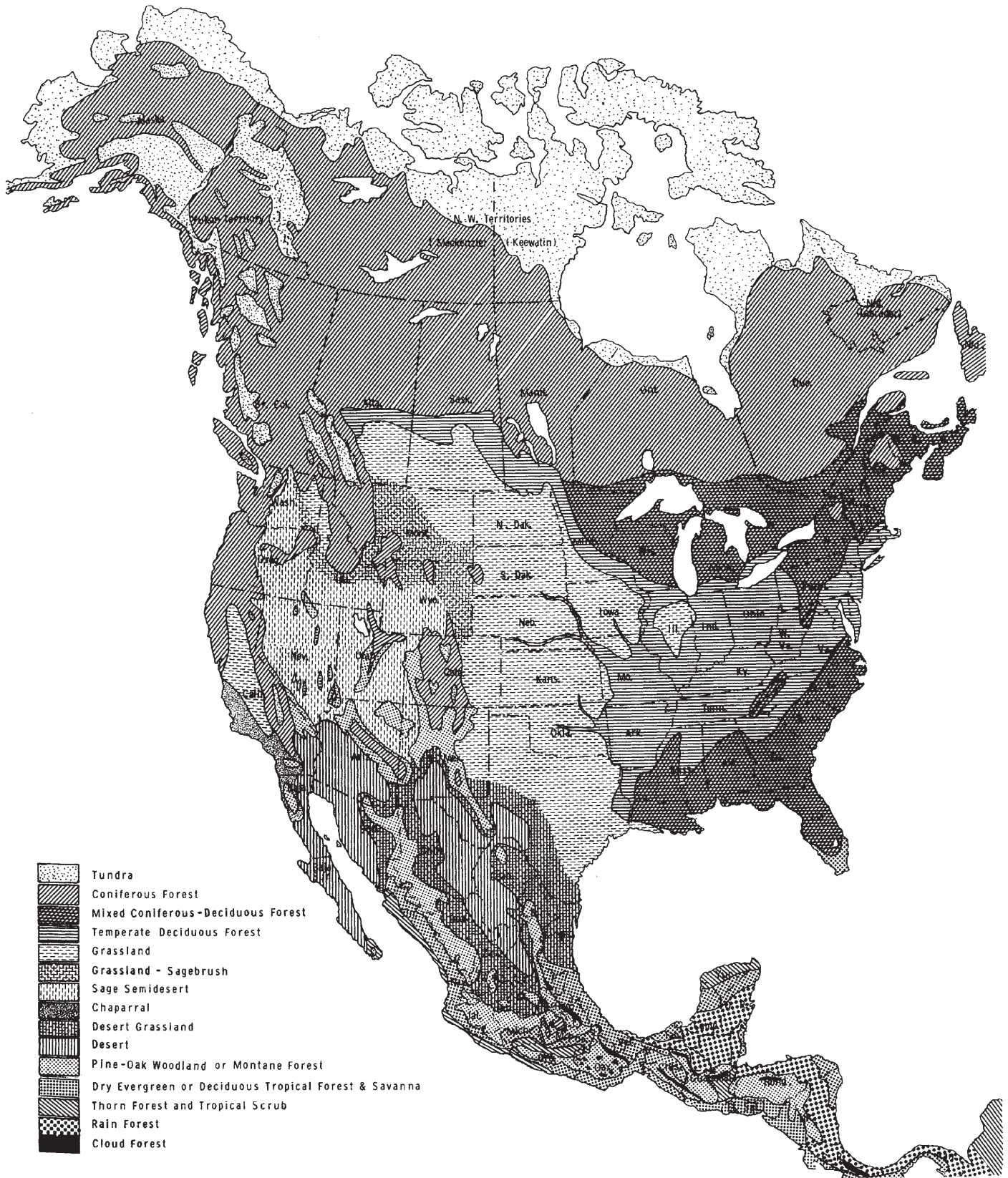
Map 1. Distribution of major natural vegetation communities in North America.

Legend:

- Tundra
- Coniferous Forest
- Mixed Coniferous-Deciduous Forest
- Temperate Deciduous Forest
- Grassland
- Grassland - Sagebrush
- Sage Semidesert
- Chaparral
- Desert Grassland
- Desert
- Pine-Oak Woodland or Montane Forest
- Dry Evergreen or Deciduous Tropical Forest & Savanna
- Thorn Forest and Tropical Scrub
- Rain Forest
- Cloud Forest

In the rock ptarmigan and white-tailed ptarmigan, the pair bond is established in the spring. At least in the rock ptarmigan, two or three females may sometimes be associated with a single territorial male, and Choate (1960b) found some indications of polygamy or promiscuity in the white-tailed ptarmigan. The male continues to defend the territory while the female is incubating, although with reduced intensity, and the territory is abandoned about the time of hatching. The female and young may remain in the male's territory but are only infrequently accompanied by him, and he usually takes no part in defending the young. In the rock ptarmigan the male reestablishes his territory in the fall, while in the white-tailed ptarmigan this evidently does not occur until spring (Watson, 1965b; Choate, 1963b).

In the monogamous European hazel grouse (*Bonasa bonasia*), the male reportedly establishes his territory in the fall, with those in optimum habitats being the most successful in attracting females. A male usually remains on his territory, defending both it and the female during incubation and brooding periods, but he only atypically performs distraction displays or utters warning calls to the female (Pynnonen, 1954). Some observers have, nonetheless, reported seeing males attending broods with females.

The dusky and sooty grouse exhibit a clearly intermediate stage between the one extreme of a monogamous or nearly monogamous pair bond associated with the establishment of a territory large enough to support the rearing of a brood and the other extreme of complete promiscuity and territorial defense limited to an area serving to attract females and provide a mating station. Other North American species that fall into this general category are the ruffed grouse and the spruce grouse.

Because of their winter migrations, dusky and sooty grouse males probably first establish territories in spring. Although these areas may cover several acres, hooting is limited to particular places within the territorial boundaries. The home ranges occupied by females associated with territorial males may overlap the boundaries of several male territories. The typical mating system of these grouse may thus be considered polygamous or promiscuous (Bendell, 1955b; Bendell and Elliott, 1967), but in local populations at least some birds may form strong pair bonds that persist until after the young hatch (Blackford, 1958, 1963). The location of the female's nest is not associated with the male's hooting sites, and the male does not defend the nest or brood. In general, male hooting sites are well separated and their territories are not contiguous, but in a few cases apparently communal male displays involving four or more males have been observed (Blackford, 1958, 1963). Males remain on their territories until their late summer migration, well after active territorial defense ceases.

The forest-dwelling capercaillie (*Tetrao urogallus*) of Europe provides a slightly more advanced stage in the evolution of communal displays, judging from such reports as those of Lumsden (1961). He studied an arena with three territories (varying from 300 to 1,000 square yards in area) that did not have contiguous boundaries but were separated by 20 to 40 yards. Four nonterritorial males visited the arena, all of which were apparently yearlings; they performed partial sexual displays and sometimes threatened one another but were ignored by the territorial cocks between whose territories they moved at will. Up to nine females visited the display ground at one time and, of 13 copulations seen, 12 were performed by a single male. Dementiev and Gladkov (1967) found that 66 display grounds contained 630 males, collectively averaging 9.5 males per display ground (individual arena averages ranged from 2 to 12 males).

In the related black grouse, the seasonal maximum number of males occupying a display ground averaged about 9 and ranged from 3 to 26, the strongest one or two of which ("first-class") occupied relatively central territories (Koivisto, 1965). The territories of this species were nearly contiguous and ranged in size from 100 to 300 square meters (Kruijt and Hogan, 1967). Koivisto (1965) estimated that territories of this species may range up to 200 square meters, with no significant differences in the sizes of territories of first-class and second-class males. Immature males, which make up about one-third of the population, are either nonterritorial and are not tolerated by territorial males, or they occupy small and peripheral territories ("third-class" males).

Koivisto believed that the primary survival value of these immature birds for the group is their tendency to warn the actively displaying males of the presence of danger. He found that there is a direct relationship between age and hierarchical position in the arena, the first-class males being mature birds that are the most fit for reproduction and also are the most successful in attracting females. Of 47 copulations he observed, first-class males performed 56 percent. The value to the species of such assortative mating and the relative protection first-class males gained from the presence of the other categories of males appeared to Koivisto to be the primary evolutionary advantages of communal male display.

Among the North American grouse, corresponding arena behavior occurs in prairie-chickens, sharp-tailed grouse, and sage-grouse. In the prairie-chickens and sharp-tailed grouse the average number of males occupying display grounds in general equals or exceeds the number reported for the black grouse. Copelin (1963) indicated that in the display grounds he studied the number of male lesser prairie-chickens ranged from 1 to 43, and active grounds averaged 13.7 males over an 11-year period. Robel's greater prairie-chicken study area (1967) had from 17 to 25 resident males present over a 3-year period. He found (1966) that 10 marked territorial males defended areas of 164 to 1,069 square meters (averaging 518 square meters), and that the two males defending the largest territories over two years of study accounted for 72.5 percent of 54 observed copulations.

Numbers of male sharp-tailed grouse present on display grounds vary considerably with population density in Ne-

braska; leks of both this species and greater prairie-chickens average about 10 males but sometimes exceed 20 and rarely reach 40 or more. Hart, Lee, and Low (1952) reported that up to 100 male sharp-tailed grouse were observed on display grounds in Utah, but the average on 29 grounds was 12.2 males. Evans (1961) confirmed that females select the most dominant males for matings, and Lumsden (1965) reported that on a display ground he studied, 1 male accounted for 76 percent of 17 observed attempted or completed copulations. Scott (1950) concluded that the social organization of sharp-tailed grouse is more highly developed than that of the pinnated grouse but is not as complex as that of sage-grouse.

The greater sage-grouse provides the final stage in this evolutionary sequence; it exhibits a higher degree of size dimorphism than any other species of North American grouse (adult weight ratio of females to males being 1:1.6–1.9), the display areas have a larger average number of participating males, and the central territories are among the smallest of any grouse species. Scott (1942) was the first to recognize the hierarchical nature of the species' territorial distribution pattern and to describe first-rank or master cocks, which were responsible for 74 percent of the 174 copulations that he observed. Dalke et al. (1960) reported that the territories held by master cocks were often 40 feet or less in diameter, and Lumsden (1965) diagrammed the territorial distribution of 19 males that exhibited an average distance between nearest neighbors of about 40 feet. In Colorado, 407 counts of strutting grounds indicated an average maximum number of 27.1 males present (Rogers, 1964). Patterson (1952) provided figures indicating that 8,479 males were counted over a three-year period on Wyoming display grounds, which averaged about 70 males per display ground. Patterson described one enormous ground containing 400 males, and Scott's observations (1942) were made on a lek of similar size.

Lumsden (1968) found that individual sage-grouse might have strutting areas that overlap those of other males, and that, although entire groups of males might move about somewhat, the relative positions of the males remain the same. Furthermore, large sage-grouse leks may have several centers of social dominance, and Lumsden suggested that these should be called conjunct leks. He believes that yearling males are not tolerated by old males in the center of the lek but can move about fairly freely near the edges of the arena. They probably do not normally establish territories until their second year, when they may become "attendant" males with territorial status. The remarkably large size and complex social hierarchy of sage-grouse leks, as well as their extraordinarily complicated strutting displays, would seem to qualify this species as representing the ultimate stage in evolutionary trends discernible through the entire group. Since sage-grouse are ecologically isolated from all other grouse species and are known to have hybridized only rarely, it would seem that these complex behavioral adaptations are the result of intraspecific selective pressures, rather than the need for reproductive isolation from closely related forms.

A possible index of the intensity of sexual selection in promoting sexual differences in behavior and morphology of the sage-grouse was mentioned earlier and might be weight differences between adult females and males, which approach female-to-male ratios of 1:2. For the essentially monogamous ptarmigan species these ratios range from about 1:1 to 1:1.09. For the dusky/sooty grouse, spruce grouse, and ruffed grouse they range from 1:l.l to 1:1.33, and in the prairie grouse from 1:1.14 to 1:1.31. These data would suggest that the intensity of sexual selection insofar as it might affect weight differences in the sexes is about the same in the lek-forming prairie grouse as in the non-lek-forming but polygamous or promiscuous forest-dwelling species. Data presented by Dementiev and Gladkov (1967) indicate corresponding weight ratios for the black grouse of 1:1.27 to 1:1.38, and for capercaillie the corresponding ratio is 1:2.28, even higher than in sage grouse. Berndt and Meise (1962) similarly reported the adult female-to-male weight ratio in the capercaillie as 1:2.08 to 1:2.25. This species and a closely related one are, by considerable measure, the largest of all grouse, and the ecological implications of both total body size and sexual differences in body size of these two species are still to be discovered.

## Nonvocal Acoustical Signals in Grouse

The feather specializations found in the sharp-tailed grouse that are related to tail-rattling have already been mentioned. Similar tail-rattling also occurs in male sage-grouse, tail-clicking noises are made by pinnated grouse, and a tail-swishing display occurs in Franklin spruce grouse, involving both alternate and simultaneous spreading of the rectrices (MacDonald, 1968). Likewise, foot-stamping sounds are made by males of many species; these are perhaps most apparent in the sharp-tailed grouse but also occur in prairie-chickens, willow ptarmigan ("rapid stamping" of Watson and Jenkins, 1964), and probably other species.

A more interesting kind of nonvocal sexual signal used by male grouse is the drumming and clapping sounds made by various species, which apparently represent variably specialized or ritualized territorial flights. The territorial display flights of male ptarmigan may serve as a starting point from which the increasingly specialized variations of the other species may be derived. In the red grouse (willow ptarmigan), Jenkins and Watson (1964) stated that "the bird (either sex) flies steeply upward for about ten meters, sails for less than a second, and then gradually descends with rapidly beating wings, fanned tail, and extended head and neck. On landing, its primaries often touch the ground, and it then stands high with drooping wing, bobbing its body and fanning its tail in and out." Calling occurs during the ascent, descent, and after landing, with the loudness of the call and length of the flight varying with the bird's relative dominance.

Schmidt (1969) described a similar "scream flight" display of white-tailed ptarmigan, and Choate (1960b) reported once

seeing a male white-tailed ptarmigan fly upward in a nearly vertical flight, hovering, screaming, gliding down in a single spiral, and then landing with another scream about 35 feet from the starting point.

This kind of flight was reported by Bent (1932) for the rock ptarmigan: the male flies upward 30 to 40 feet and then floats downward on stiff wings until he is near the ground, when he checks his descent and may sail up again, calling loudly. MacDonald (1970) also described the rock ptarmigan's flight display in considerable detail.

In the eastern Canadian and Alaskan forms of spruce grouse an apparently corresponding aerial display occurs as the male flies steeply downward out of the tree being used as a display perch, stops his descent about 4 to 8 feet above the ground, and then descends rapidly with strongly beating wings (Lumsden, 1961a; Ellison, 1968b). In the Franklin spruce grouse males fly vertically and slowly up to a perch with whirring wings. They may then rush forward along the branch and spread the wings and tail, make three or four drumlike wing beats while standing upright, or perform an aerial wing-clap display (MacDonald, 1968). In this display the bird takes flight and at some point pauses in midair with a deep wingstroke, following which he sharply strikes the wings together above the back and drops downward to the ground, with a second wing-clap following landing.

Short (1967) noted that males of Franklin spruce grouse have outer primaries that are more indented and more closely approach those of the Siberian spruce grouse (*Falcipennis falcipennis*) than they do those of the eastern race *canadensis*; thus it is probable that similar whirring or wing-clapping sounds are made during aerial displays in the Siberian species.

Corresponding drumming flight behavior is found in the dusky and sooty grouse (Wing, 1946). Bendell and Elliott (1967) reported that a "flutter flight" occurs in both sexes of the sooty grouse, but that the noise produced is a ripping sound and apparently is not so elaborate as in the interior dusky grouse populations such as *richardsonii* and *pallidus*. Blackford (1958, 1963) stated that both sexes of the former race perform a wing-flutter (or flutter-jump) display some 8 to 10 inches off the ground. Males perform more extensive drumming flights; they may also exhibit a fairly sharp whipping of the wings on alighting in a tree and sometimes produce a wing-clap, consisting of a single loud wing note, presumably made in the same manner as by Franklin spruce grouse. In typical drumming flights the male jumps from his display perch, flies strongly upward with whirring wings, and returns after a horseshoe-shaped flight course to a point near where he started (Blackford, 1963).

The well-known drumming display of ruffed grouse would appear to be an exaggerated version of the drumming movements of the Franklin spruce grouse or a ritualized drumming flight in which the male has substituted wing-beating movements for the actual flight. No actual flight displays are known to occur in this species, but the related hazel grouse (*Bonasa bonasia*) exhibits both wing-flapping displays and actual display flights with associated calling (Pynnonen, 1954; Schenkel, 1958). Male vocalizations in these two species are limited: hissing sounds are made by the ruffed grouse, while whistling notes are produced by the hazel hen. The typical flutter-jump display, in which males make short, nearly vertical flights with strongly beating wings and sometimes with associated vocalizations, would appear to be an alternate evolutionary modification of the territorial song flights of ptarmigan. Typical flutter-jump displays occur in the prairie grouse and black grouse (Hamerstrom and Hamerstrom, 1960) as well as in the capercaillie (Lumsden, 1961b). Flutter-jumps of capercaillie, which have loud wing noises, are performed without associated vocalizations. Male sharp-tailed grouse only rarely utter calls at the start of these flights, which nonetheless are conspicuous in their open-country habitat. In prairie-chickens, calls might be uttered before, during, or after the display, and the black grouse utters hissing sounds during flutter-jumping. The sage-grouse lacks a flutter-jump display.

In summary, it would appear that the visually and acoustically conspicuous territorial flights of ptarmigans have, in the forest-dwelling grouse, been replaced by drumming, fluttering, or whirring flights, wing-clapping noises, and sedentary wing-drumming displays. In most of the lekking grouse flying has been restricted to short and often quiet flutter-jumps, which are visually conspicuous in these open-country birds but are limited in length to their typically small territories.

As a final point, these aerial displays occur in both sexes of ptarmigan, are more common and better developed in males than in females of the dusky and sooty grouse species, and are performed only by males in the lek-forming species of grouse. Ultimately, in the heavy-bodied greater sage-grouse, with its closely packed leks, the flutter-jump display has been lost altogether. Lumsden (1968) suggested that the rotary wing movements made during strutting may represent the last remnants of the sage-grouse's flutter-jump display.

## Grouse Hybridization

The study of hybridization between species, under either natural or artificial conditions, provides information of value for a variety of reasons. In general, it may be expected that the incidence of crossbreeding between populations existing under natural conditions will be related to their nearness of relationship, and information of taxonomic interest may be obtained from such study. Furthermore, the relative survival and fertility of the resulting hybrids should provide an indication of the degree of genetic difference between the parental types, and thus genetic information may be available through experimental hybridization studies. Hybrids provide favorable material for studying the chromosomal numbers and configurations among related species, and when they are fertile the degree of phenotypic variation in second or backcross generations may be used to estimate genetic differences
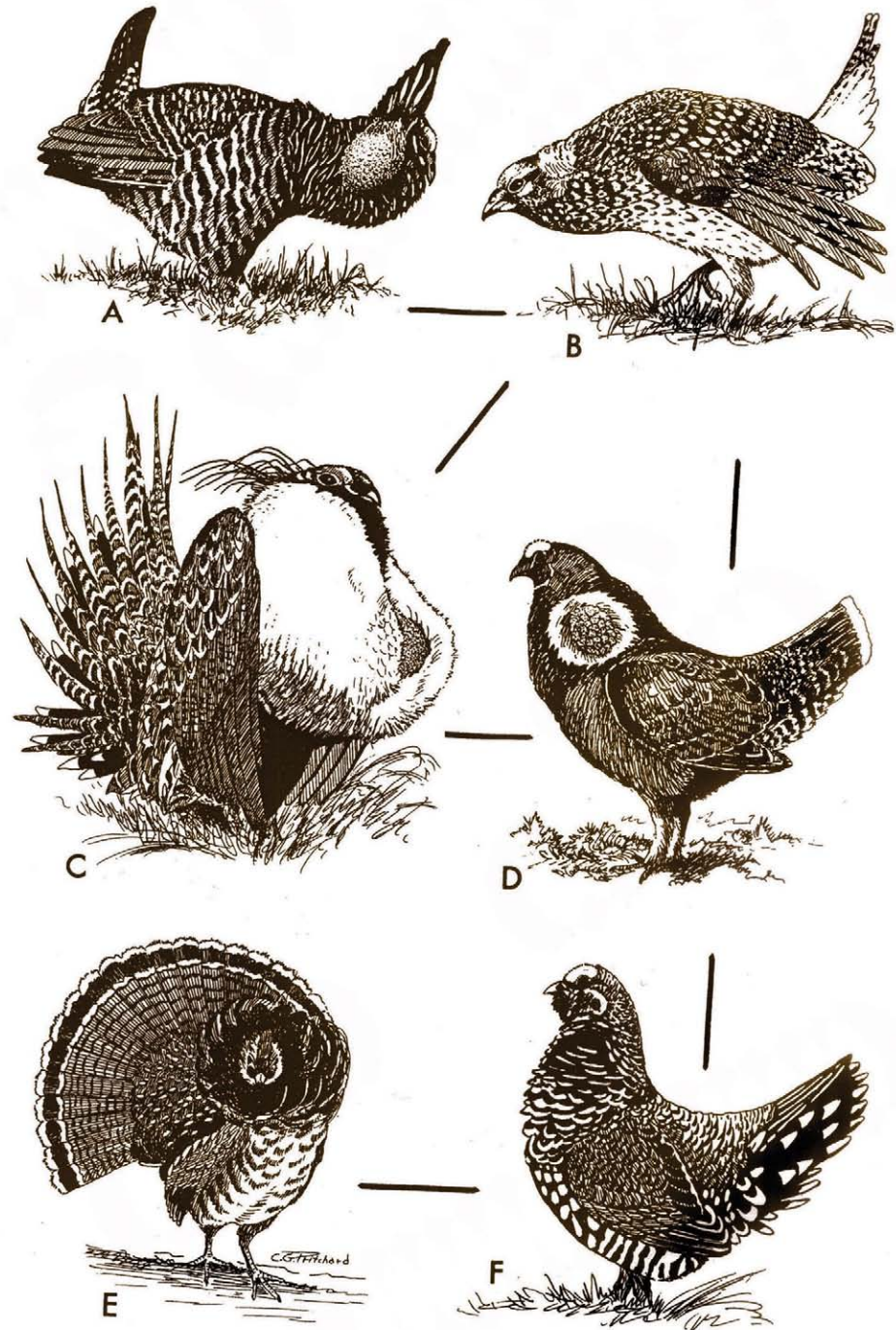
*Fig. 2. Display postures and reported hybridization combinations among six species of North American grouse: (A) greater prairie-chicken, (B) sharp-tailed grouse, (C) greater sage grouse, (D) dusky grouse, (E) ruffed grouse, (F) spruce grouse. Drawing by C. G. Pritchard.*

controlling specific traits. Finally, the presence or absence of natural hybridization between closely related forms occurring in the same habitats may provide a clue as to the degree of niche overlap and interspecies competition.

Nearly all known cases of hybridization among the North American grouse species have involved naturally occurring hybrids. This is largely a reflection of the difficulties of keeping and breeding grouse in captivity. One rare case of hy-

bridization among North American grouse produced under captive conditions (see also Crawford, 1978) was the rearing of several hybrids, including reciprocal crosses, between greater and lesser prairie-chickens by William Lemburg of Cairo, Nebraska. He also attempted unsuccessfully to obtain backcross hybrids from a wild-caught female greater prairie-chicken × sharp-tailed grouse hybrid that he mated with males of both of parental species.

Captive-produced hybrids between greater and lesser prairie-chickens have also been reported (Crawford, 1978), which are reproductively fertile and exhibit intermediate structural and behavioral traits. Wild hybrids of this type have also been found in western Kansas, where the two species have recently come into contact (Bain and Farley, 2002; Thompson et al., 2011).

All of the North American genera of grouse (as now recognized) have been involved in intergeneric hybridization. Intrageneric hybridization has also occurred within *Tympanuchus* and *Lagopus*. Examples of most of the hybrid combinations reported from North American grouse are illustrated in figure 2.

### Intrageneric Hybrids

Hybridization within the genus *Lagopus* is ecologically probable on the basis of the extensive region of geographic contact between the willow and rock ptarmigan, and some hybrids have been reported (Harper, 1953; Todd, 1963).

The other genus of grouse that has been involved in intrageneric hybridization is *Tympanuchus*, and in this case there is no question that hybridization between the sharp-tailed grouse and the greater prairie-chicken has occurred repeatedly under natural conditions. Unlike *Lagopus*, where pair bonds of varying lengths and degrees develop, in *Tympanuchus* a highly structured form of arena (lek) behavior is the rule, and mating choices by females must be made rapidly, owing to competition among females for mating opportunities with favored males ("master cocks"), and males are likely to accept a willing female of almost any grouse species as a mating partner.

In a summary, Johnsgard and Wood (1968) pointed out that natural prairie-chicken × sharp-tailed grouse hybridization had been reported in every state and province where natural contact between these species occurred. These include four Canadian provinces from Ontario to Alberta and at least the Dakotas, Colorado, Nebraska, Iowa, Minnesota, Wisconsin, and Michigan. The highest known incidence of hybridization ever reported was on Manitoulin Island, Ontario, where the two species came into relatively recent contact, and possibly up to 50 percent of the total grouse population there may have been of hybrid origin (Lumsden, 1970), whereas in Nebraska a hybridization rate of 0.3–1.2 percent was estimated (Johnsgard and Wood, 1968). Sparling (1980) reviewed the taxonomic aspects of hybridization in these species.

The complete spectrum of plumage patterns exhibited by these hybrids would indicate a clear capacity to produce second-generation or backcross offspring, but so far little information is available on the relative reproductive success of hybrids as compared to the parental types. Observations made by Lumsden (1965), as well as personal observations, suggest that such hybrids are usually able to occupy only peripheral territories on display grounds that are dominated by phenotypically "pure" birds of either species, and are probably at a considerable reproductive disadvantage because of intermediate display signals and behavior, in spite of their apparent fertility. It is also true that when a single male of a species enters a mixed-species lek otherwise made up of the other species, it may be threatened or attacked by several of the resident males (Johnsgard, 2007).

### Intergeneric Hybrids

#### *Lagopus* × *Dendragapus* Hybridization

At least three specimens of natural hybrids between willow ptarmigan and spruce grouse have been reported (Lumsden, 1969). These two species overlap extensively in their breeding ranges in eastern Labrador, northern Ontario, the Northwest Territories, Yukon Territory, British Columbia, and Alaska, but are ecologically isolated during the breeding season. Lumsden noted that in the area where two of the hybrids occurred, the Hudson Bay region of Ontario, spruce stands near rivers are in close proximity to heath and lichen communities. The last of the three reported hybrids came from York Factory, Manitoba, which is also near Hudson Bay and presumably represents similar habitat. No information is available as to the possible fertility of this cross.

#### *Dendragapus* × *Falcipennis* Hybridization

A single reported specimen representing hybridization between the dusky grouse and spruce grouse has been reported (Jollie, 1955). This bird was obtained in Idaho where, although the ruffed grouse is widespread in the state, both of the parental species are evidently rare locally. These two species overlap extensively in their ranges from western Montana through Idaho and Washington and north to Yukon Territory and apparently occupy generally similar habitats through much of this range.

#### *Dendragapus* × *Tympanuchus* Hybridization

Brooks (1907) described an apparent dusky grouse × sharp-tailed grouse hybrid taken at Osoyoos, British Columbia. In spite of a seemingly substantial overlap in the breeding ranges of these two species, extending from Yukon Territory southeast through parts of British Columbia, Washington, Idaho, western Montana, Utah, and western Colorado, it appears that ecological differences in breeding habitats would only rarely allow for possible interbreeding.

#### *Centrocercus* × *Tympanuchus* Hybridization

Two hybrid greater sage-grouse × sharp-tailed grouse specimens have been described from central Montana (Eng, 1971). Kohn and Kobriger (1986) also described a wild hybrid of this seemingly unlikely combination from western North Dakota.

# II.  Species Accounts
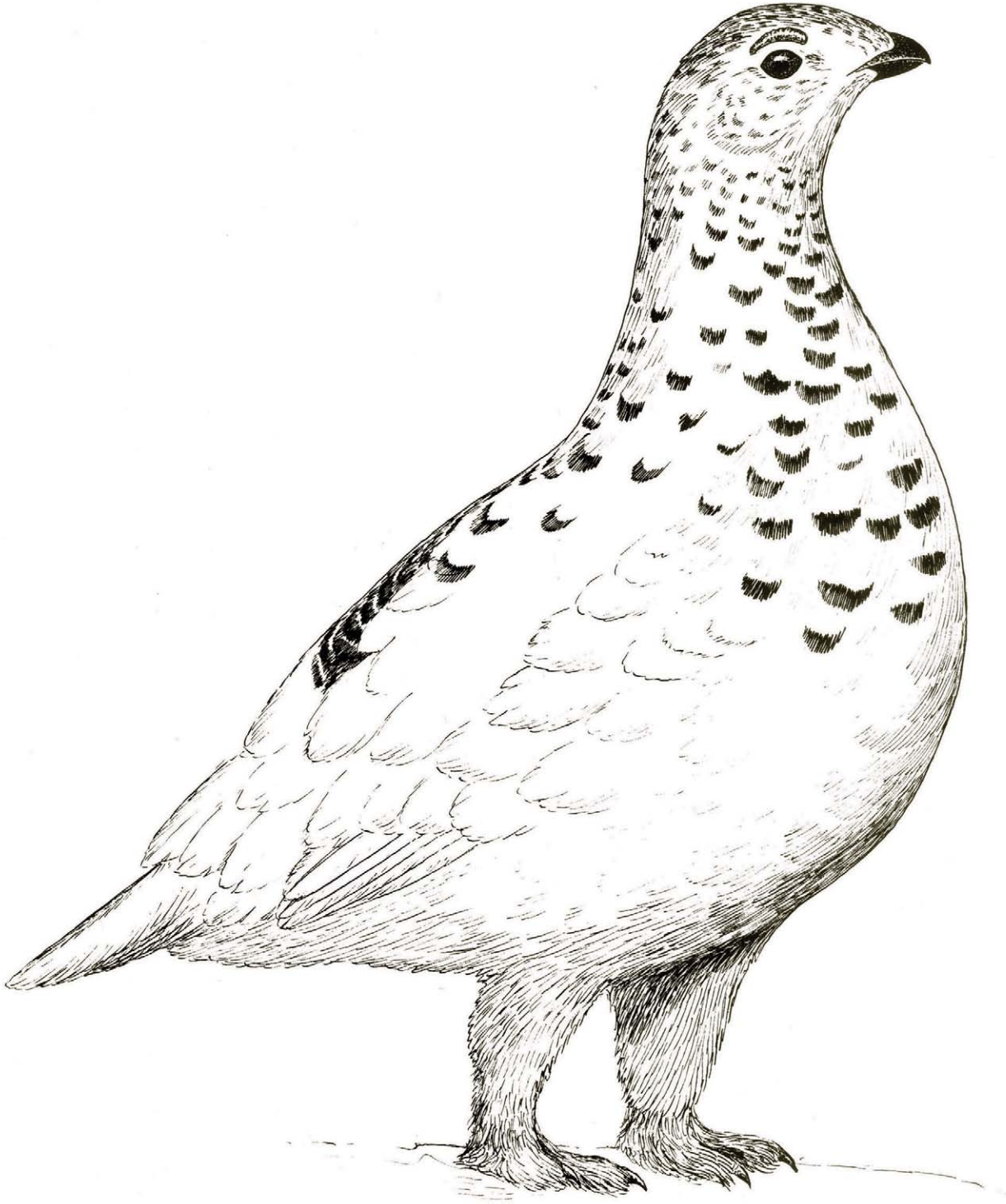
# Greater and Gunnison Sage-Grouse

*Centrocercus urophasianus* (Bonaparte) and *Centrocercus minimus* Young et al.

## Other Vernacular Names

Sage grouse, sage hen, sage cock, sage chicken

## Range

*C. urophasianus* (Bonaparte): Greater sage-grouse. Resident from central Washington south through central and eastern Oregon to northeastern California, and east through the intermountain West to southwestern North Dakota, western South Dakota, Wyoming, and northwestern Colorado. Small peripheral populations also exist in southeastern Alberta and southwestern Saskatchewan; extirpated from British Columbia.

*C. minimus* Young et al. (1999): Gunnison sage-grouse. Resident in the Gunnison Basin of Colorado and nearby upland mesas, with a very small relict population in southeastern Utah. Extirpated from Arizona and New Mexico. Endangered species candidate.

## Subspecies of Greater Sage-Grouse

*C. u. urophasianus* (Bonaparte): Eastern greater sage-grouse. Resident from southern Idaho, eastern Montana, southeastern Alberta, southern Saskatchewan, and western North Dakota south to eastern California, south-central Nevada, Utah, western Colorado, and southeastern Wyoming.

*C. urophasianus phaios* Aldrich: Western greater sage-grouse. Resident from central and eastern Washington south to southeastern Oregon.

## Measurements

### Greater Sage-Grouse

*Folded wing:* Males, 282–323 mm; females, 248–279 mm. Using flattened wings, females 240–285 mm; males 288–334 mm (Crunden, 1963).

*Tail:* Males, 297–332 mm; females, 188–213 mm.

*Mass* (in life): Adult males, range of yearly means (three years): 2,885–3,005 g. Adult females, overall mean from 3 years: 1,626 g (n = 143) (Huff and Braun, 1991).

*Culmen:* Adult males, range of means (three years): 41.0–41.1 mm (Huff and Braun, 1991).

### Gunnison Sage-Grouse

*Mass:* Males, range of yearly means (three years): 2,070–2,217 g. Adult females, overall mean from three years: 1,210 g (n = 13) (Huff and Braun, 1991).

*Culmen:* Adult males, range of means (three years): 32.9–32.9 mm. Adult females, overall mean from three years: 27.5 mm (n = 13) (Huff and Braun, 1991).

## Identification

### Greater Sage-Grouse

Adults, 19–23 inches long (females), 26–30 inches long (males). The large size and sagebrush habitat of the greater sage-grouse make it unique among grouse. Both sexes have narrow, pointed tails, feathering to the base of the toes, and a variegated pattern of grayish brown, buffy, and black on the upper parts of the body, with paler flanks but a diffuse black abdominal pattern. In addition, males have blackish brown throats, narrowly separated by white from a dark V-shaped pattern on the neck, and white breast feathers concealing the two large, frontally directed gular sacs of olive-green skin. Behind the margins of the gular sacs are a group of short white feathers with stiffened shafts that grade into longer and softer white feathers and finally into a number of long, black hairlike feathers that are erected during display. Males also have rather inconspicuous yellow eye-combs that are enlarged during display. Females lack all these specialized structures but otherwise generally resemble males. Their throats are buffy with blackish markings, and their lower throats and breasts are barred with blackish brown.

### Gunnison Sage-Grouse

The Gunnison's adult body mass differences are diagnostic: adult males average 2.0–2.1 kg in spring (versus 2.8–3.0 kg in greaters) and Gunnison females average 1.2 kg (versus 1.6 kg in greaters). Adult male Gunnison also differ from greaters in having thicker, longer, and more conspicuous black feathers on their hindneck that when raised resemble a black ponytail, whereas in greaters their more filament-like festers (filoplumes) form a diffuse halo when erected. The Gunnison's dark brown back and upper wing-coverts have conspicuous white shaft-streaks, but the whitish portions of their vanes are less evident than is true for the more highly mottled wing-coverts of greater sage-grouse. The tail feathers of both sexes of the Gunnison are more contrastingly patterned with conspicuous cross-barring of brown and creamy white, with the pale bars almost as wide as the dark, whereas in the greater the dark bars are much broader than the pale bars.

## Field Marks

The combination of sage habitat, large body size, pointed tail, and black abdomen is adequate for certain identification of both sage-grouse. Males take flight with some difficulty and fly with their bodies held horizontally; females take off more readily and while in flight dip alternately from side to side. When the birds fly, their white under wing-coverts contrast strongly with the blackish abdomen.

## Age and Sex Criteria

### Greater Sage-Grouse

*Females* may readily be separated from adult males by their weight and measurements (see Measurements section), by the absence of black on the upper throat, and by the fact that the white tips of the under tail-coverts extend partway down
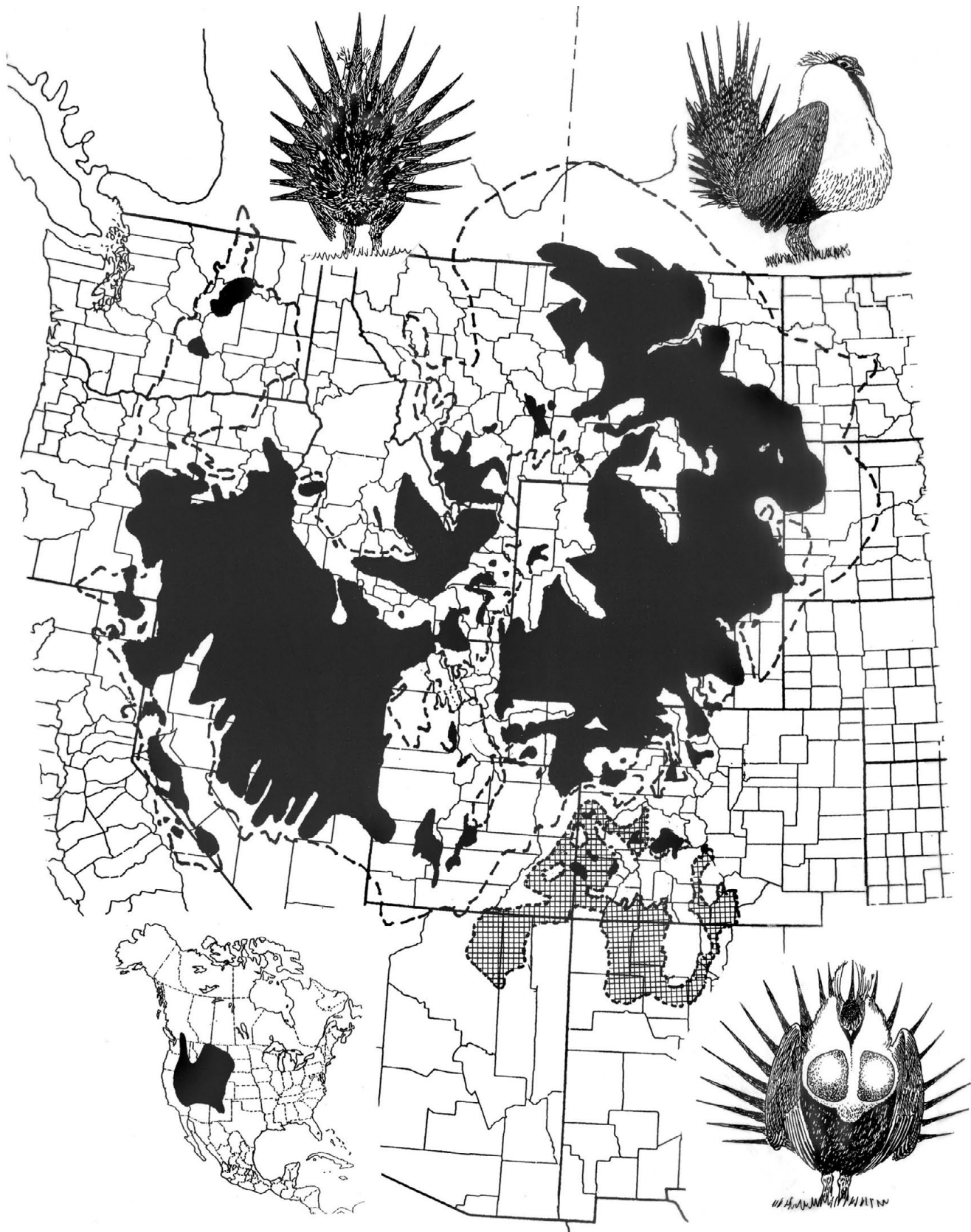
*Map 2. Historical (dashed line) and current distributions (inked) of the greater and Gunnison sage-grouse. The probable historic range of the Gunnison sage-grouse lies within the area indicated by crosshatching. The inset map shows the historical range of big sagebrush (Artemisia tridentata).*

the feather rachis (Pyrah, 1963). Crunden (1963) provides a sex and age key based on primary measurements.

*Immatures* (under one year old) resemble females but are paler. Their outer primaries are more pointed and mottled than the others, and the outer wing-coverts are narrowly pointed and instead of being unmottled dark gray are marked with brown and white with white tips (Petrides, 1942). Immatures also have light yellowish green toes, unlike the dark green toes of adults. Males do not usually achieve their full breeding condition their first year; subadult males have narrower white breast bands than do adults. The tail feathers of immature males are also blunter and tipped with white. During their first fall, immature birds have bursa depths in excess of 10 mm (averaging 18.9 mm in October), whereas adults have maximum bursal depths of 7 mm and average depths of 1.6 mm (Eng, 1955).

*Juveniles* have conspicuous shaft-streaks on their upper body feathers and tail feathers with white central shafts that spread out into narrow terminal white fringes (Ridgway and Friedmann, 1946).

*Downy young* have a distinctive salt-and-pepper appearance dorsally that is devoid of striping and consists of a mottled combination of black, brown, buff, and white. The head is whitish, spotted with brown and black in a fashion similar to blue grouse downies, and the underparts vary from grayish white to buff and brownish on the chest region, where a brown-bordered buff band is usually evident. The malar and nostril spots of this species are unique (Short, 1967), and a definite loral spot is also present. The broken pattern of dark markings on the forehead and crown found in this species probably corresponds to the black border that occurs around the brown crown patch in most other grouse (Short, 1967).

## Distribution and Populations

At one time the greater sage-grouse was found virtually wherever sagebrush (*Artemisia*, especially *A. tridentata*) occurred, throughout many of the western and intermountain states. In early times it occurred in fourteen or fifteen states and was the principal upland game species in nine (Rasmussen and Griner, 1938). However, overgrazing and drought contributed greatly to the species' near demise. By the early 1930s it was a major upland game species in only four states (Montana, Wyoming, Idaho, and Nevada), and by 1937 only Montana retained a regular open season. Restricted hunting was by then still permitted in Nevada and Idaho, but all other states had established closed seasons (Rasmussen and Griner, 1938). After 1943 Montana also established a closed season that lasted nine years. The species eventually became completely extirpated from British Columbia and New Mexico. There are no recent specimen records from Nebraska, although birds may rarely stray across the Wyoming state line. There have been no Oklahoma records since 1920 (Sutton, 1967).

A low ebb in sage-grouse populations in the western states occurred in the middle to late 1940s. Idaho reported an upturn in populations after 1947, and, after four years of protection, reopened hunting in 1948. Nevada reestablished limited hunting in 1949, followed by Washington in 1950. Permit-only seasons were established by Wyoming in 1948 after eleven years of protection and by Utah in 1950. California opened one county (Mono) to hunting in 1950, after five years of protection.

Judging from figures presented by Patterson (1952), the total United States kill in 1951 was less than 75,000 sage-grouse. Except for two years, Colorado maintained a closed season from 1937 until 1953, and in 1952 Montana held its first season since 1943. South Dakota began hunting sage-grouse again in 1955, after nineteen years of protection, and in 1964 North Dakota held its first season since 1922. Alberta initiated a highly restricted season in 1967. Hamerstrom and Hamerstrom (1961) reported estimated hunter-kill figures for 1959 of about 44,000 birds in Wyoming, 23,000 each in Idaho and Montana, 15,000 in Colorado, and 12,000 in Nevada, plus approximately 2,000 each in California, Washington, and Utah, totaling more than 100,000 killed across the entire United States.

Hunter-kill data for 1969 indicated that the sage-grouse was a legal game species in five states and one Canadian province. In 1968 total statewide totals were 55,361 in Wyoming and 53,462 in Montana, and the 1969 kill was 81,729 birds in Idaho and 21,922 in Colorado. Kill estimates for Nevada and Utah were respectively 11,765 (1968) and 11,109 (1969). Smaller numbers were shot in California (3,200 in 1969), Washington (2,300 in 1969), Oregon (4,760 in 1969), and South Dakota (about 2,000 in 1967). Alberta and North Dakota each had totals of a few hundred during those years. The overall national kill was thus about 250,000 birds in 1969.

The densest regional breeding concentrations have historically occurred in the sagebrush scrublands of south-central and southwestern Wyoming. The species is closely associated with sagebrush, which is the primary year-around food and primary nesting cover. Of the several published range maps for sage-grouse (e.g., Aldrich, 1963; Edminster, 1954), that prepared by Patterson (1952) appears to be most representative of distributional patterns as they existed in the mid-twentieth century. Patterson estimated that some 90 million acres of preferred sagebrush-grassland habitat still existed in the early 1950s, and that an additional 40 million acres of peripheral desert scrub habitat were then also present. If the 90-million-acre figure is assumed to be representative of good habitat, it would total about 140,000 square miles. If an average population density of ten birds per square mile is also assumed, the 1950 sage-grouse population might have totaled 1,400,000 birds.

In 1967, Schneegas estimated that 5 million to 6 million acres of sagebrush had been lost during the previous thirty years, which was only a small taste of the changes yet to come. The continued clearing of extensive areas of sage for irrigated farming and industry, and the expanded use of herbicides to improve grazing conditions have greatly re-

duced sage-grouse habitat and populations. In northwestern Colorado, 92 percent of the region's priority sage-grouse habitat (926,700 acres) has already suffered damage or is at significant risk. From an original national sagebrush community covering some 150,000 square miles (96 million acres), probably less than half still exists in good or better condition, and most of what remains has been variously fragmented by roads, transmission lines, and other structures, or otherwise has been degraded biologically by biotoxins. The species has been increasingly impacted by both agricultural and industrial forces, such as road building, mining, irrigation, and other developments, resulting in massive sagebrush removal and destruction.

In 2000 the Washington population of the greater sage-grouse was estimated at 1,100 birds, stimulating two regional conservation groups (The Northwest Ecosystem Alliance and The Biodiversity Foundation) to initiate a legal petition to provide for its protection under the Endangered Species Act's threatened category. In 2001 the U.S. Fish and Wildlife Service (USFWS) determined that a nationally threatened category was warranted but precluded, owing to other priorities. According to Tweit (2000), such a listing would have affected millions of acres of public lands, and thousands of federally managed grazing allotments. Farming, hunting, surface mining, and other activities on federal, state, and private lands would also have been impacted over a broad region of the American West.

Because of continuing habitat losses, greater sage-grouse numbers are falling rapidly. North American Breeding Bird Survey data confirm that the national population has been declining significantly, with a 2.7 percent annual rate of population reduction occurring between 1966 and 2011. Although a threatened federal status is now (2016) biologically even more critically warranted, the legal recognition of the species' plight has been effectively fought for several decades by petroleum, development, ranching, and agricultural interests.

As recently as September 2015, the USFWS withdrew a request for listing the greater sage-grouse as federally "threatened," stating that it "does not now face the risk of extinction now or in the foreseeable future." In Nevada and California, where the total population is about 9,000 birds, the Department of the Interior also decided in 2015 not to list the birds as threatened or endangered. In Washington the sage-grouse is a fully protected and state-listed species, and is limited to two isolated populations near Ellenburg.

The USFWS also amazingly estimated a total U.S. population of 432,000 greater sage-grouse in 2015, distributed across a wildly optimistic 173 million acres of habitat. This imagined area is almost twice as large as the species' range that was estimated to exist more than a half-century earlier (Patterson, 1952). In contrast, an independent estimate of the greater species' total population, based on a decade's data (1990s) of the national Breeding Bird Survey was 150,000 birds (Rich et al., 2004).

In 2012 Wyoming was believed to support the largest sage-grouse population of any state, calculated (using 150,000 as an assumed national total) at about 55,000 birds by Canterbury, Johnsgard, and Dunning (2013). Accepting the USFWS's imagined 432,000 sage-grouse would mean that nearly 380,000 more must be present somewhere in the species' nine remaining states. As of 2015 only eight states (California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, and Wyoming) still had populations deemed large enough to allow hunting of greater sage-grouse. Only five of these states had significant seasons in 2015: Montana (30-day season), Wyoming (3–11 days), Colorado (2–7 days), Idaho (6 days), and Nevada (2–15 days). None of these states allow the killing of more than two birds per day.

Hunting in 2015 was greatly curtailed in California (one bird per season), Utah (two birds per season), and Oregon (two birds per season). In North Dakota, where the population is almost entirely limited to Bowman and Slope counties, hunting has not been allowed since 2008. Lek survey counts there dropped from an average of about 300 total males observed in 1980 to about 75 in 2014. The 2015 season was also closed in South Dakota, where only an estimated 1,500 birds were judged to be alive in 2007. And yet the USFWS sees no long-term national threat to the species.

The Gunnison sage-grouse is in even greater imminent danger of extinction but ironically has recently been removed from consideration by the USFWS as a federally endangered species. This recently (1999) recognized species of sage-grouse is now centered in the Gunnison Basin of Colorado. It evidently also once extended to northern New Mexico but was extirpated by about 1912 (Braun and Williams, 2015). It has also been extirpated from Oklahoma, Arizona, and perhaps up to 15 out of the possibly 22 Colorado counties where it historically occurred (Braun et al., 2015). Its historic occurrence in Kansas is considered doubtful, with a single possible record of a bird shot in Morton County during the 1930s.

As of 2015 this species' range was limited to six or seven Colorado counties, and to at least one adjoining county in eastern Utah. The total world population of the Gunnison sage-grouse at the start of the twenty-first century was estimated at 2,000 birds by Rich et al. (2004). A more recent and only slightly more optimistic estimate suggests that the Gunnison's population during the early 2000s was fewer than 5,000 birds, of which 3,500 to 4,000 occurred in Colorado's Gunnison Basin (Young et al., 2015).

## Population Density

Patterson (1952) estimated greater sage-grouse densities by determining strutting grounds in two study areas that totaled 250 square miles. He reported an average of one strutting ground per 5.7 square miles, and a density of 12.5 males per square mile. This density estimate of course excluded from consideration all females and probably at least some immature males. Edminster (1954) thus calculated that the total spring population of sage-grouse might have been 30 to 50

birds per square mile, or 13 to 21 acres per individual. Rogers (1964) likewise reported that certain counties of Colorado locally supported up to 10 to 30 birds per square mile, while the remaining habitat supported 1 to 10 birds per square mile.

## Habitat Requirements

### Wintering Requirements

During winter, sagebrush provides not only nearly 100 percent of the food that is utilized by greater sage-grouse but is also important escape cover. Edminster (1954) pointed out that during winter sagebrush has the important attributes of being evergreen, tall enough to stand above snow, and highly nutritious. Rogers (1964) indicated that the best wintering areas in Colorado were those at the lowest elevations, where sagebrush was available all winter. Local topography may influence availability of sagebrush, because of snow cover, but sage-grouse may be expected to occur wherever exposed sagebrush may be found through the winter period. Dalke et al. (1963) reported that wintering concentrations of sage-grouse in Idaho usually occurred where snow accumulations were less than six inches deep, which occurred in areas some 30 to 50 miles from the habitats used during fall and spring. Black sage (*Artemisia nova*) is the preferred winter food in eastern Idaho, but it is often covered by snow.

### Spring Habitat Requirements

In late winter, male greater sage-grouse begin to leave their wintering areas and return to their traditional strutting grounds. Among 45 strutting grounds classified by type of land area, Patterson (1952) found that 11 were on windswept ridges and exposed knolls, 10 were on flat sagebrush areas with no openings, 7 were on bare openings on relatively level lands, and the remaining 17 occurred in seven other habitat types. Relatively open, rather than dense, sage cover is clearly the preferred habitat for strutting grounds, as indicated by a number of writers such as Scott (1942) and Dalke et al. (1963).The latter study reported that new strutting grounds could be readily established by clearing areas of 0.25 to 0.5 acre in dense stands of sage.

### Nesting and Brooding Requirements

Patterson (1952) reported that 92 percent of the greater's nests that he found were under sagebrush, usually in cover 10 to 20 inches tall and on drier sites where the shrub cover was less than 50 percent. In Utah, Rasmussen and Griner (1938) found that silver sage (*A. cana*) provided preferred nest cover, with plants of this species 14 to 25 inches tall providing cover for 33 percent of 161 nests, while the more common big sage (*A. tridentata*) of the same height category accounted for 24 percent of the nests. The highest nesting densities (up to 23 nests on 160 acres, or 1 nest per 6.95 acres) occurred in dense second-growth sagebrush. Klebenow (1969) found that 91 percent of 87 nests or nest remains were associated with three-tip sage (*A. tripartita*). He noted that the sagebrush averaged only eight inches tall in nesting habitats, but that taller plants were preferred for nest sites.

No nests were found where the shrub cover exceeded 35 percent. In the best nesting areas, nest densities of up to 1 nest per 10 acres were found.

Brooding habitat requirements are evidently slightly different from the greater sage-grouse's nesting requirements. Klebenow (1969) reported that 83 percent of the broods he observed were in big sagebrush but not in dense stands. All but three of 98 broods recorded were seen in areas of less than 31 percent shrub cover. As the summer progressed, broods moved into moister areas that still contained green plant material, until by late August they had gathered near permanent water sites. However, available water in the form of green vegetation, rain, or dew evidently provides adequate moisture for sage-grouse.

Observations by Martin (1970) of the greater's broods in Montana indicated that, in 158 locations, young broods used areas having less plant density and lower crown cover (9–15 inches high) than did older broods or adults (7–25 inches high). Rogers (1964) also reported that low sage (7–15 inches high) is preferred feeding, nesting, and roosting cover, while taller plants serve for nesting, shade, and escape cover. Spraying with the herbicide 2,4-D in Montana greatly reduced summer usage by greater sage-grouse, apparently by altering vegetational composition, particularly of favored food plants (Martin, 1970). Similarly, Peterson (1970) concluded that components of brood habitat for greater sage-grouse include a diversity of forms and a density of sage of 1 to 20 percent.

## Food and Foraging Behavior

The importance of sagebrush as a food item for adult sage-grouse is impossible to overestimate. Martin, Zim, and Nelson (1951) reported that sage (*Artemisia* spp.) made up 71 percent of the diet in 203 samples and that usage of animal material ranged from 9 percent in summer to 2 percent in spring and fall. Apart from sagebrush, vegetable food consists largely of the leaves of herbaceous legumes and weeds (collectively called forbs) and grasses, which are utilized primarily in late spring and summer (Edminster, 1954). Patterson (1952) reported that sagebrush composed 77 percent (of a total of 95.7 percent plant material) of foods found in 49 samples from adult greater sage-grouse in Wyoming and 47 percent (of a total of 89 percent plant material) from 45 juveniles analyzed. Evidently sage is taken in limited amounts even during the first month of life (Griner, 1939), although like all grouse, newly hatched chicks feed principally on insect life.

During early life, young greater sage-grouse feed heavily on ants, beetles, and weevils and later add grasshoppers to their food intake (Patterson, 1952), although the total animal content of the diet drops from as much as 75 percent to less than 10 percent. The study of Klebenow and Gray (1968) indicates that insects predominate in the diet only during the first week of life, and thereafter forbs become the predominant food, with shrubs only gradually assuming

a place of primary importance. The importance of forbs is also indicated by a study by Trueblood (1954), who found that this food category composed from 54 to 60 percent of the major food items consumed by juvenile sage-grouse in Utah and from 39 to 47 percent in adults. On lands partially reseeded to grass, he found that adults persisted in their preference for shrubs, while juveniles exhibited a preference for forbs and a strong aversion to grasses.

Martin's study (1970) has provided additional evidence of the value of a variety of forbs as a source of summer food for greater sage-grouse. He found that, in a sample of 35 sage-grouse collected from July to September, sage (*Artemisia*) totaled 34 percent of the food, while dandelion (*Taraxacum*) composed 45 percent. Collectively, these plants plus two additional forb genera (*Trifolium* and *Astragalus*) contributed over 90 percent of the food material. Two California studies (Leach and Hensley, 1954; Leach and Browning, 1958) also indicated that weedy forbs such as prickly lettuce (*Lactuca*) and cultivated herbaceous broadleaved plants such as clover and alfalfa play important roles as early fall food sources for sage-grouse.

One of the most complete studies available on juvenile food requirements is by Peterson, who analyzed the food of 127 young up to 12 weeks of age. During that period, forbs composed a total of 75 percent of the diet, and two plant genera (*Taraxacum* and *Tragopogon*) together made up 40 percent of the food consumed. Insect use declined from a high of 60 percent in the first week to only 5 percent by the twelfth week, and sagebrush was used very little by chicks before the age of 11 weeks.

## Mobility and Movements

### Seasonal Movements

One notable study on seasonal movements of greater sage-grouse so far available is that of Dalke et al. (1963). Patterson (1952) had previously summarized the literature on possible migratory movements of these birds, noting that in Oregon a winter migration to lower elevations was followed after nesting by a migration to summer ranges at 8,000-foot elevations. Possible winter movements of Wyoming and Montana birds into South Dakota were discussed by Patterson, and he mentioned a male that was banded in Wyoming and recovered the following fall still in Wyoming but some 75 air miles from its point of banding.

In mountainous country, wintering grounds of greater sage-grouse are often some distance from spring and summer habitats, at considerably lower elevations. With the gradual regression of snow, male grouse on their wintering grounds begin working toward the strutting areas. Dalke et al. (1963) reported that these birds move in small flocks, flying short distances, during this migration. Many such birds in Idaho may move 50 to 100 miles along established routes before reaching their strutting grounds. Adult females evidently reach the strutting grounds at about the same time as adult males, or somewhat later. Patterson (1952) noted that

male greater sage-grouse began to arrive on Wyoming strutting grounds as early as February and were followed in one or two weeks by females. Dalke et al. (1963) found that adult males and even females occupied grounds in late March or early April that were not yet free of snow. A rapid build-up of adult males occurred in early April, while subadult females arrived about a week after adult females, and subadult males did not appear in numbers until most of the females had already left the grounds in late April.

Movements of male greater sage-grouse between strutting grounds is evidently fairly rare, both within one season and from year to year. Dalke et al. (1963) noted that of 78 adult males banded in 1959 and 1960, a total of 14 (18 percent) were observed later on grounds other than those where they had been banded. During the same two years, 107 females were banded, and 6 of these were subsequently observed visiting other strutting grounds. Movements by males between strutting grounds covered distances of from 550 yards to 4.3 miles. Dominant males were only rarely involved in these movements, suggesting that the movements are the result of attempts by subordinate males to establish territories in various locations. Earlier, Dalke et al. (1960) had reported that 70 percent of banded greater sage-grouse that were again observed on strutting grounds in the first three years were seen on their original strutting grounds and no others. Some master cocks occupied nearly identical territories in successive years, while others lost their territorial positions.

It is not well known how far female greater sage-grouse move from strutting grounds to build their nests, but current evidence would suggest that it is usually not very far. Klebenow (1969) noted that on one area of three-tip sage (a favored nesting cover) located more than a mile from the nearest strutting ground no nests were found and only one very young brood was seen. In each of two areas of big sage, nests were found within a half-mile and at only slightly lower elevations. However, unpublished Colorado studies indicate that females regularly move 3 to 4 miles from a display ground to a nest site, and may travel as far as 7 miles.

Following nesting, female sage-grouse gradually move their broods to places where food supplies are plentiful, usually in relatively moist areas such as hay meadows, river bottom lands, irrigated areas, and the like. Patterson (1952) estimated that family units break up and juveniles become relatively independent at about ten to twelve weeks, when they have completed their molt into juvenal plumage.

Spring dissolution of the strutting grounds by male greater sage-grouse is a gradual process, and some subadult males may remain after most adult birds have left for summer ranges (Dalke et al., 1960). However, Eng (1963) found that adult males were the last to leave the strutting area. These are usually at higher elevations, but the birds may move downward into alfalfa fields near irrigated valleys. Schlatterer (1960) reported that the sequence of arrival of birds on the summering areas in Idaho was males, unpro-

ductive females, and productive females. In southern Idaho the summer brood range may be 13 to 27 miles from the nesting grounds, a considerable movement for these recently fledged birds.

Fall movement toward wintering areas is likewise a gradual process, and the rates probably vary according to weather conditions. Pyrah (1954) reported that immature female greater sage-grouse were the first to leave for wintering areas, followed by mature females, then adult males. Immature males associated with immature and mature females. Dalke et al. (1963) reported that birds collected in flocks near water holes as freezing temperatures began and that movements were quite noticeable by the time the daily minimum dropped to 20° Fahrenheit. Birds usually remained in a single place for several days and then moved out in groups. By the time the first snows fell, flocks were usually composed of 50 to 300 birds in loose associations. During severe weather, flocks of up to 1,000 birds could be seen, but in midwinter they normally consisted of less than 50 individuals, with old males often in groups of fewer than 12.

### Daily Movements

Daily movements and activity patterns of greater sage-grouse have yet to be fully documented, but some work with banded birds is of interest. Lumsden (1968) noted the daily locations of several individually marked males on a strutting ground, and confirmed that individual males returned daily to their specific territories. However, their territorial boundaries were rather ill-defined and exhibited considerable overlap. On one occasion, when a cluster of hens formed about 55 meters from Lumsden's blind, six males left their usual territories and moved toward the hens, apparently maintaining their same positions relative to one another. Of 27 individually marked hens, 16 were observed later on the same display ground. Four were seen to visit the ground on three mornings, one was seen twice, and eight only once. Seven were observed mating, in each case only once, and none of these birds was seen again.

Males of greater sage-grouse arrive on the strutting grounds long before dawn and early in the season may actually remain all night. Hens arrive before dawn and usually leave shortly after sunrise. After daybreak, immature males are the first to leave the grounds, followed by successively more dominant males and finally the master cock. The birds normally walk to feeding areas that may be within a half-mile of the strutting grounds (Pyrah, 1954). Hens rarely return to the strutting grounds in the afternoon. Gunnison sage-grouse reportedly stop displaying much earlier in the morning than do greaters and are much harder to observe without disturbing them (N. Paothong, pers. comm.)

Observations on nesting greater sage-grouse hens by Girard (1937) and Nelson (1955) indicate that they normally leave their nests twice a day during incubation. Girard reported that these foraging periods occurred between 9:30 and 11:30 a.m. and between 2:00 and 3:00 p.m., whereas

Nelson reported earlier morning and later afternoon periods. The feeding periods usually lasted 15–25 minutes, according to Nelson.

During late summer, greater sage-grouse roost until about 6:00 a.m., forage until about 10:00 a.m., rest until about 3:00 p.m., forage again until 8:00 p.m., and finally go to roost again about 9:00 p.m. (Girard, 1937). Unlike the prairie grouse, sage-grouse exhibit no fall display activities. During winter, daily movements of sage-grouse have no definite pattern, and apart from foraging, much time is spent resting and preening. Roosting occurs on rocky outcrops (Crawford, 1960; Dalke et al., 1963).

## Reproductive Behavior

### Prenesting Behavior

In a sense, the greater sage-grouse may be regarded as the classic lek-forming species of North American grouse. Not only are the lek sizes the largest in terms of average numbers of males participating but also the degree of segregation according to dominance classes is the most evident. Further, although Scott (1942) was by no means the first to describe the social strutting behavior of greater sage-grouse, his study first recognized the complex social hierarchy of males and designated the most dominant males as master cocks. This term has since been applied to most other lek-forming grouse, such as prairie-chickens and sharp-tailed grouse.

As soon as traditional display grounds are relatively free of snow, male sage-grouse begin to occupy them. In different years conditions may vary, but in the northern United States the birds are usually on their strutting grounds by late February or March. Most studies indicate that the first birds to occupy the grounds are the adult males, which may return to virtually the same territorial site that they occupied in previous years.

It might be assumed that the male sage-grouse behavior patterns exhibited on the strutting grounds perform two separate functions: proclamation and defense of territory on the one hand and attraction and fertilization of females on the other. Although natural selection thus operates through the differential successes of individual males in attracting females, it is of interest that apparently in all grouse the behavior patterns serving to attract females are derived directly from hostile behavior patterns associated with the establishment and defense of territory. As a result, relatively few of the displays performed by male grouse in lek situations serve strictly as male-to-female displays, but rather those postures and calls that function in territorial establishment are for the most part utilized in sexual situations as well. It is therefore generally impractical to fully separate signals associated with attack and escape (agonistic displays) from those which function sexually to attract females (epigamic displays). The resulting close relationship between relative individual success in performing territorial behavior (achieving male-to-male social dominance) and relative individual reproductive success (fertilization of females) provides a basic key to
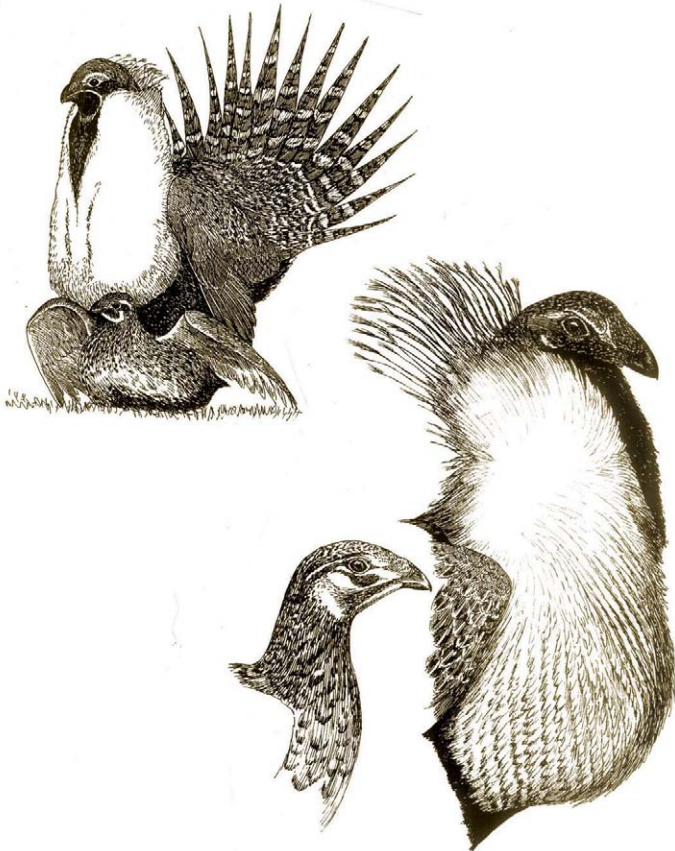
*Fig. 3. Copulation posture and sexual dimorphism
in the greater sage-grouse.*

the understanding of social behavior in lek-forming grouse. This contrasts with the situation in socially displaying duck species, in which agonistic and sexually oriented displays are much more separable, probably because of the absence or insignificance of territoriality during pair-forming processes of waterfowl.

The fact that most male displays performed by lek-forming grouse are derived from hostile responses further complicates their dual role as sexual attractants. Female grouse must not only be attracted to these signals, but must in turn identify themselves as females in order to avoid attack by territorial males. This is usually achieved by submissive postures that in general are associated with inconspicuousness through slimmed plumage, silent movements, and general lack of male-like signals. Thus a kind of paradox may be seen in lek-forming grouse. Whereas in non-lek-forming species of grouse (e.g., ptarmigan) the females may perform fairly elaborate and often male-like displays, in the social species the degree of development of female display is perhaps inversely proportional to the relative development of male displays and other male signals. The role of the female in lek-forming grouse is therefore reduced to simply appearing on the lek, being attracted to particular males, and allowing copulation to occur. This last point is achieved by a precopulatory squat-

ting display with wings partially spread, which is virtually identical in all grouse so far studied. In sage-grouse, where hens often cluster in groups around specific males (master cocks), fighting between hens may sometimes occur, but it is not likely that this occurs in other species.

### *Male Territorial Advertisement Behavior*

#### Greater Sage-Grouse

Although strutting by sage-grouse has been described by many writers, the accounts by Lumsden (1968) and Hjorth (1970) are by far the most complete and accurate. The following summary is therefore in large measure based on their descriptions. Lumsden and Hjorth have confirmed the basic findings of Scott (1942), who discovered the relationship of social dominance to sexual success, with master cocks representing the individuals maintaining a central territory that is selectively sought out by females for copulation. It is important to note, however, that the strutting behavior of master cocks differs in no obvious way from that of birds occupying lower social ranks, such as the secondary status "subcocks" and "guard cocks" or the peripheral attendant males. Strutting by nonterritorial yearling males is, however, poorly developed and may readily be recognized from that of older birds. Such immature birds probably represent the so-called "heteroclite" males described by Scott.

Overt fighting between males is largely but not entirely limited to the edges of territories. Fighting males typically stand 10 to 20 inches apart, head to tail and nearly parallel to one another, with heads upright and feathers usually lowered. The tail may be raised or lowered and is sometimes shaken rapidly, producing a rattling sound that perhaps corresponds to the tail-rattling display of sharp-tailed grouse. Periodically the males attempt to strike each other with their nearer wing, but unlike the prairie grouse, males do not fly into the air and strike with their feet. The associated calls are *kerr* sounds, often in a series of 8 to 12 repeated notes.

Overt fighting is less common in sage-grouse than is ritual fighting, in which the same parallel posture is assumed but the birds remain virtually motionless. At times the birds may actually close their eyes as if sleeping in this posture, which Lumsden interprets as "displacement sleeping." When threatening, males of both sage-grouse species draw up the skin on the sides of the neck, thus erecting the crown's filoplumes and increasing the exposed areas of white feathers. The tail may also be cocked and spread and the body held more upright when in such a threat posture. In general, the amount of white feathers exhibited by a male is a relative index of its aggressive tendencies. It is thus of interest that female grouse lack white areas and that the white neck area of yearling males is smaller than that of adults. When charging, the posture assumed by the adult male is strongly similar to that held during the strutting display. This would suggest that strutting represents a ritualized form of charging, in which the forward body movement component has been almost entirely lost.
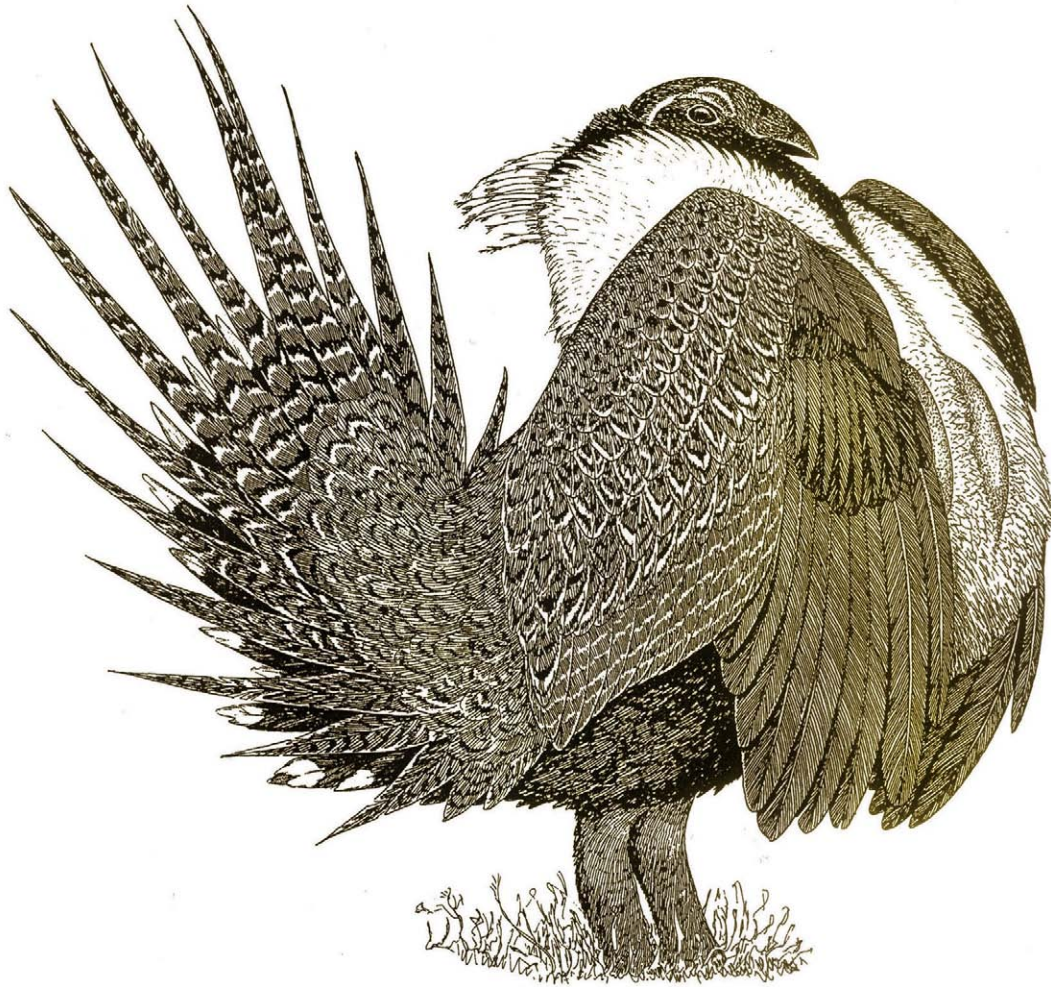
Fig. 4. Strutting posture of male greater sage-grouse.

When on territory and between strutting sequences, the male greater is usually in an "upright" posture (Hjorth, 1970) with tail cocked and spread, wings slightly drooped, neck feathers ruffled, and the esophageal pouch partly inflated and hanging in a pendulous fashion. In this posture he may jerk his head upward and utter a soft snoring note that is apparently associated with the inhaling of air (Hjorth, 1970).

The greater sage-grouse's strutting display ("ventro-forward" of Hjorth, 1970) is a complex sequence of stereo-typed movements (figs. 5 and 6) and sounds, which lasts about three seconds and which Lumsden has divided into ten stages. In the first stage the male assumes an erect posture with the tail fanned and held slightly behind the vertical, lowers his folded wings, and takes a step forward. The back is gradually raised, so that by stage two it is held at a 45-degree angle from the ground. The anterior neck feathers then suddenly part, exposing two olive-green skin patches. The third stage begins as the bird opens his beak and apparently takes a breath. The pendent esophageal bag is then lifted and the skin patches disappear, another step forward is taken, and the folded wings are quickly drawn across the

stiffened feathers at the sides of the neck as it is jerked upward ("first vertical jerk" of Hjorth), producing a brushing sound. In the fourth stage the beak is shut, the wings are moved forward again, and the esophageal bag is lowered. In stage five the neck again swells, the oval skin patches are exposed a second time, but again are not greatly inflated, and a second although silent backward stroke of the wings is performed. In stage six a third step forward is taken, the wings are again moved forward, the skin patches are somewhat more fully expanded, and the esophageal bag begins to move upward again. In stage seven the neck is diagonally extended ("second vertical jerk" of Hjorth), as the esophageal bag is strongly raised, nearly hiding the head, and the wings are again rubbed against the breast feathers as they make their third backward stroke. In stage eight the head is withdrawn into the erected neck feathers, the esophageal bag bounces downward, and the inflated bare skin patches form large oval bulges ("first forward thrust" of Hjorth), while the wings move forward and back a fourth time. In stage nine the head is quickly withdrawn into the neck feathers so that it becomes completely concealed, compressing the esopha-
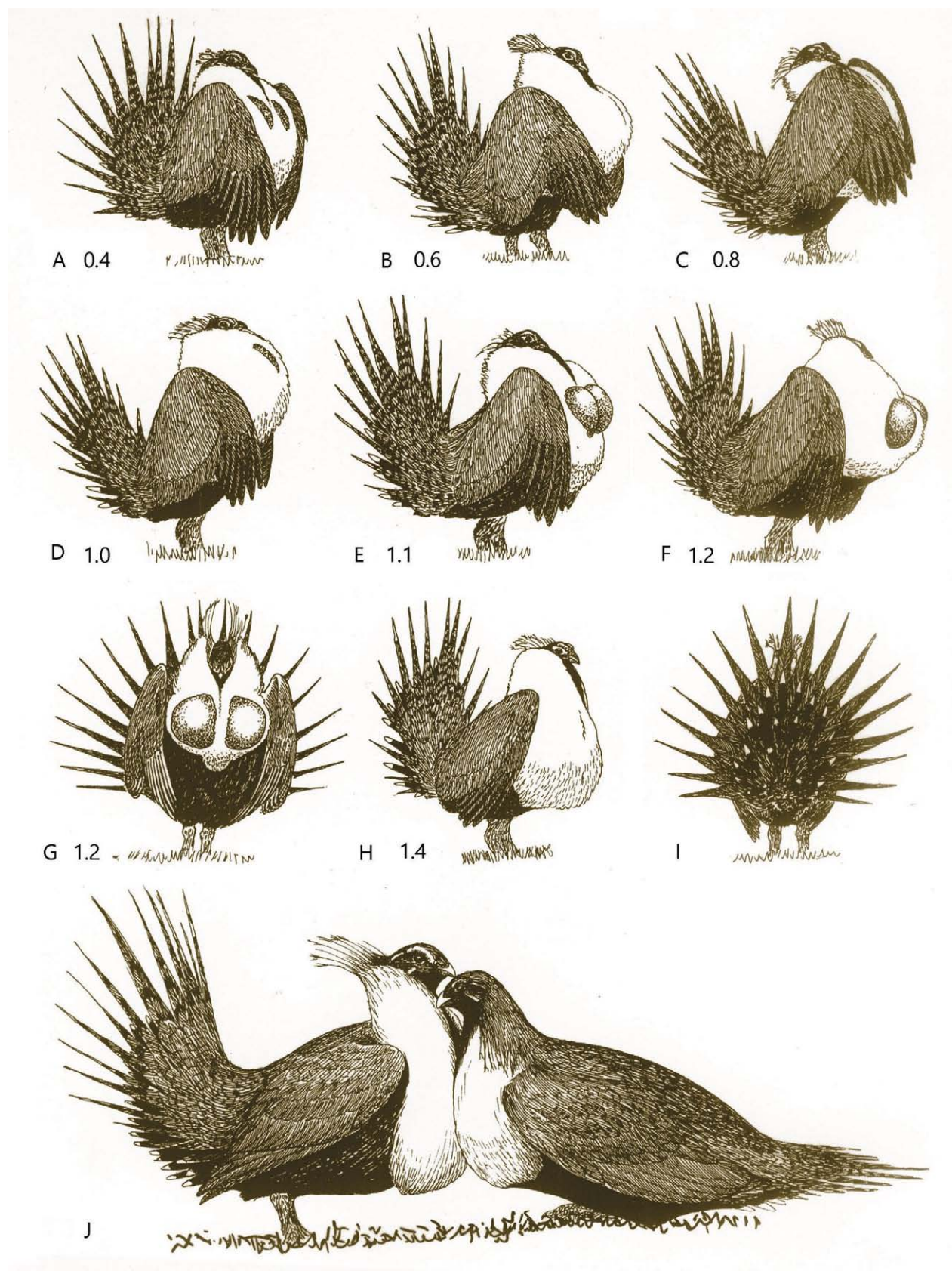
*Fig. 5. Strutting sequence in the male greater sage-grouse, with elapsed time in seconds shown. Threat behavior between two territorial males is also shown. Mostly after Hjorth (1970).*

Start    Wing swish    Cooing/hooting    Wing swish

Cooing/hooting    Air sac plop    Whistle    Air sac plop    End

Air sac plop

Air sac plop

Wing swish

Cooing/hooting

Wing swish

Whistle

Wing swish

Cooing/hooting

*Fig. 6. Sequential stages in the postures (above) and associated vocal and mechanical sounds (two-second sequence) (below) during strutting by male greater sage-grouse.*

geal bag so greatly that the skin patches bulge strongly outward in the shape of hemispheres ("second forward thrust" of Hjorth), and the wings complete a fifth backward stroke. Pressure on the trapped air in the esophagus is now suddenly released, causing the skin to collapse with two plopping sounds, and the head is moved upward toward a normal position. In the tenth and final stage the head returns to the original starting position, the white neck feathers close over the bare skin areas, and the body returns to the stance assumed at the beginning of the display.

The major motor elements of the entire display sequence thus consists of several forward steps (Hjorth reported four to seven), five rotary wing movements, two brushing sounds of the wings against the sides of the breast and neck, and four increasingly greater inflations of the esophagus, with associated expansions of the colored skin patches. The predominant nonvocal sound is a "resonant squeaking, swish-

ing" noise (Lumsden, 1968) that is followed by two plopping sounds. However, a call is also uttered, which Lumsden described as sounding like *wa-urn-poo*, only the last part of which can be heard at any distance. Hjorth (1970) determined that there are actually four vocal notes produced, of which the second is the loudest.

The greater sage-grouse lacks much of the pivoting action of the greater prairie-chicken's booming, but, as Lumsden pointed out, strutting is not a specifically frontal display. Although visually impressive when seen from the front, the long and colorful under tail-coverts are also conspicuous signals when seen from behind. Lumsden found no strong tendency of males to face hens when performing their strutting displays, and often they faced directly away from them.

Apart from the fighting call and that which is uttered during strutting, only one other male call has been reported for male greater sage-grouse. Lumsden noted a deep grunting

sound, which occurred both in threat situations and when near hens, and often as a prelude to fighting. The same call was occasionally heard from hens. Hjorth (1970) called this vocalization a "grunting chatter."

The strutting behavior of males when hens are present is not noticeably different from when they are absent, except perhaps for the greater frequency of displays. Hen sage-grouse typically gather together in tight groups near master cocks; from 50 to 70 hens have been seen in single clusters in large leks. Lumsden noted that, although hens clustered at 20 different locations during his observations, the groups nearly always formed near the most dominant male. Thus, hens are clearly attracted to specific males rather than to specific mating spots on a lek. Clusters of hens evidently serve as a sexual stimulus for females, and precopulatory squatting by one often provides an apparent stimulus for others to behave similarly. Males normally quickly mount any soliciting female, and copulation lasts only a few moments. Unlike other grouse, the male does not normally grasp the female's nape in his beak while mounted, perhaps because of the considerable disparity in size between the sexes.

Most studies indicate that the majority of copulations are achieved by only one, or at most two, males in any center of mating activity. Scott (1942) found that master cocks performed 74 percent of 174 observed copulations, Patterson (1952) found mating success similarly restricted to a few males, and Lumsden (1968) found that two males accounted for more than half of the 51 copulations he observed. However, Hjorth (1970) found that four males took part in the matings he observed on one lek.

Following copulation, the female usually runs a short distance forward, shaking her wings and tail for several seconds before starting to preen. Usually females leave the strutting grounds within a few minutes after copulation. Males usually remain in a motionless squatting position for several seconds after copulation, which Lumsden regards as a ritualized display posture that he believes may function to reduce disruption of the hen cluster.

In contrast to nearly every other North American grouse (the ruffed grouse is the only other case), the greater sage-grouse lacks a flight display. Lumsden is probably correct in explaining this on the basis of the male's large size and poor agility, plus the fact that needs for territorial advertisement are reduced in greater sage-grouse because of the large number of males usually present and the conspicuous nature of individual birds. Lumsden also believed that "call flights" by hens serve to advertise the location of the strutting ground. Such "quacking" calls are uttered by hens when flying toward the ground or when flying from one part of the ground to another. Occasionally the calls are also uttered when the hen flies away from the strutting ground. Lumsden also described a "wing-bar signal" display, which he states may be performed by females in flight prior to landing, perhaps functioning as a landing-intention signal. This display is sometimes, but not always, associated with a call flight, and is produced by drawing the white under wing-coverts



*Fig. 7. Male greater sage-grouse in flight.*

up over the leading edge of the wing so they are visible from above and behind the bird. A somewhat similar "shoulder-spot display" occurs in both sexes of sage-grouse while on the ground. Lumsden regarded this display as an expression of conflict, with fear as one of the components.

Calls of male greater sage-grouse include the strutting call, grunt, and fighting call already mentioned, as well as a high-pitched and repeated *wut* note that is used as an alarm call (Lumsden, 1968). Males, especially yearlings, sometimes also utter a squawking note, perhaps as a flight-intention signal. Hens also have well-developed fighting notes, as well as whining notes in confrontational situations. Both sexes may also hiss when being handled.

### *Male Territorial Advertisement Behavior*

#### Gunnison Sage-Grouse
There are marked differences in the overall plumage appearance, movements, and associated vocal and mechanical sounds produced during male strutting displays of the greater and Gunnison sage-grouse. In both species the white feathers on the sides of the breast and in front of the wings are modified for mechanical sound production by having stiffened shafts that are raised during display so the anterior wing feathers can abrasively scrape over the breast feathers. The forward and backward wing movements of the Gunnison are less extreme, and a substantially larger number of air sac inflations and deflations occur within each strutting sequence, although in both the durations of each sequence are essentially identical, about two seconds (Young et al., 1994, 2000) (figs. 8 and 9).

### *Nesting Behavior*
Once fertilization has been accomplished, the sage-grouse hen apparently leaves the strutting ground for nesting. There

*Fig. 8. Comparison of male feathers and strutting appearance between Gunnison sage-grouse (left) and greater sage-grouse (right). Also shown are a rectrix (above) and upper wing-covert, and (greater sage-grouse only) a filoplume and lower neck feather.*

is no present evidence that a hen requires more than one successful copulation to complete her clutch. Patterson (1952) believed that females begin laying within a few days after mating, although Girard (1937) indicated that from 7 to 12 days may be taken up in locating a nest site and in nest construction. This kind of delay would not seem to be normal, and Dalke et al. (1963) found a good correlation between actual and calculated hatching period by assuming that 10 days would be required to lay an average clutch of 8 eggs, and that 26 more days would be required for incubation, for a total elapsed time of 37 days between mating and hatching.

Estimates of greater sage-grouse clutch sizes usually range from 7 to 8 eggs. Patterson (1952) reported an average clutch of 7.26 eggs in 80 nests during one year, and 7.53 eggs in 74 nests the following year. Griner (1939) reported an average clutch size of 6.8 eggs in Utah, Nelson (1955) reported 7.13 in Oregon, and Keller, Shepherd, and Randall (1941) reported 7.5 in Colorado. Patterson (1952) believed that a very limited amount of renesting might occur, judging from smaller late clutches and the presence of new nests near destroyed or deserted nests. Although Eng (1963) found a second peak of females on strutting grounds in late May, this was not reflected in a second late hatching peak, and

he concluded that reduced male fertility late in the season prevents effective renesting.

Patterson's estimate (1952) of a 25- to 27-day incubation period for greater sage-grouse has generally been supported by later workers such as Pyrah (1963), who utilized data from captive grouse. This contrasts with various earlier estimates of a 20- to 24-day incubation period. Sage-grouse appear to have a high rate of both nest destruction and nest desertion. Gill (1966) summarized data on fates of nests from eight different studies, which ranged in hatching success from 23.7 to 60.3 percent. Predator activity was responsible for a large part of the nesting losses, predators accounting for 26 to 76 percent of the lost nests of six studies summarized by Gill. Of a total of 503 nests represented, 47.7 percent were destroyed by predators. Coyotes, ground squirrels, and badgers are evidently among the more important mammalian predators, while magpies and ravens may be significant avian predators of nests.

## Evolutionary Relationships

For reasons that have never been evident, taxonomists have traditionally regarded the sage-grouse as closely related to the true "prairie grouse," namely the pinnated grouse and
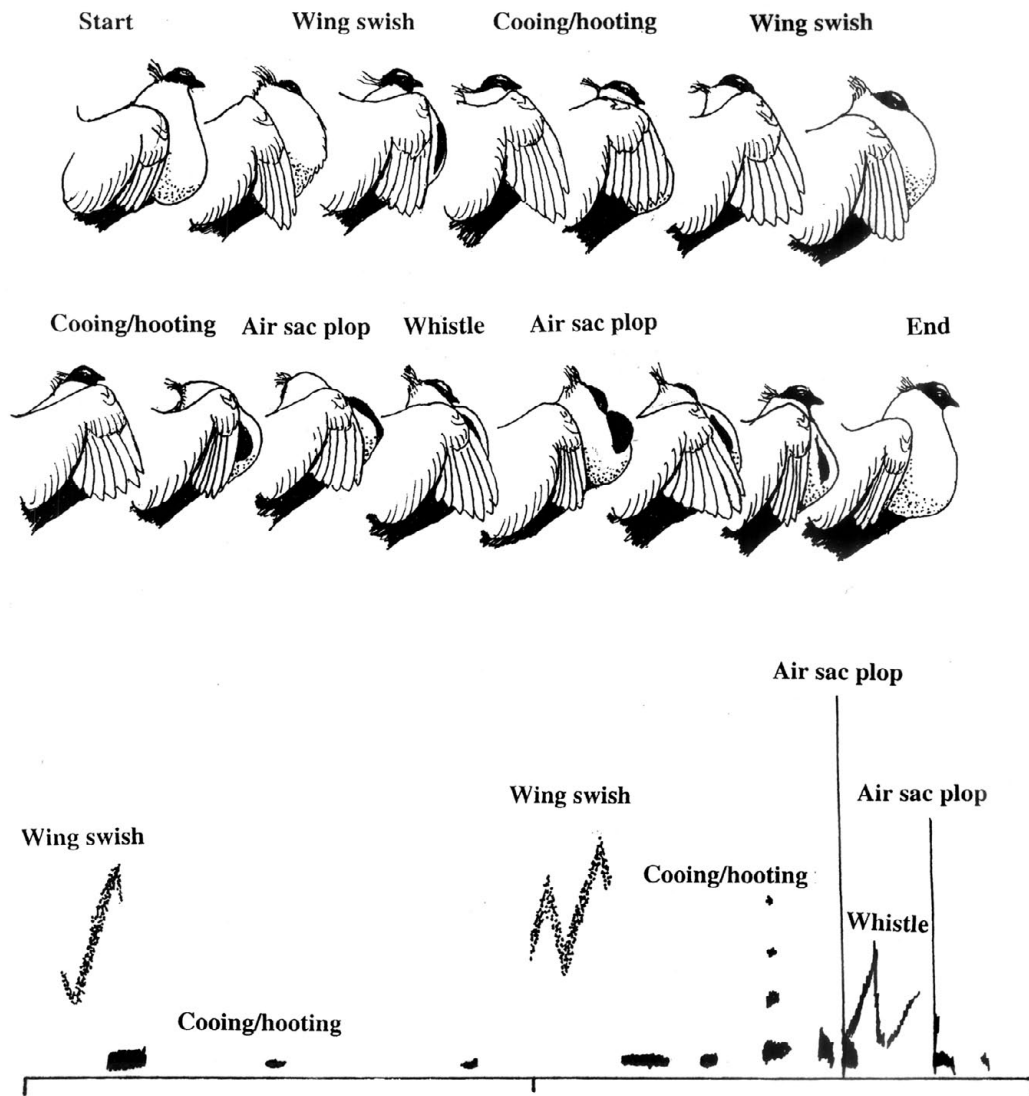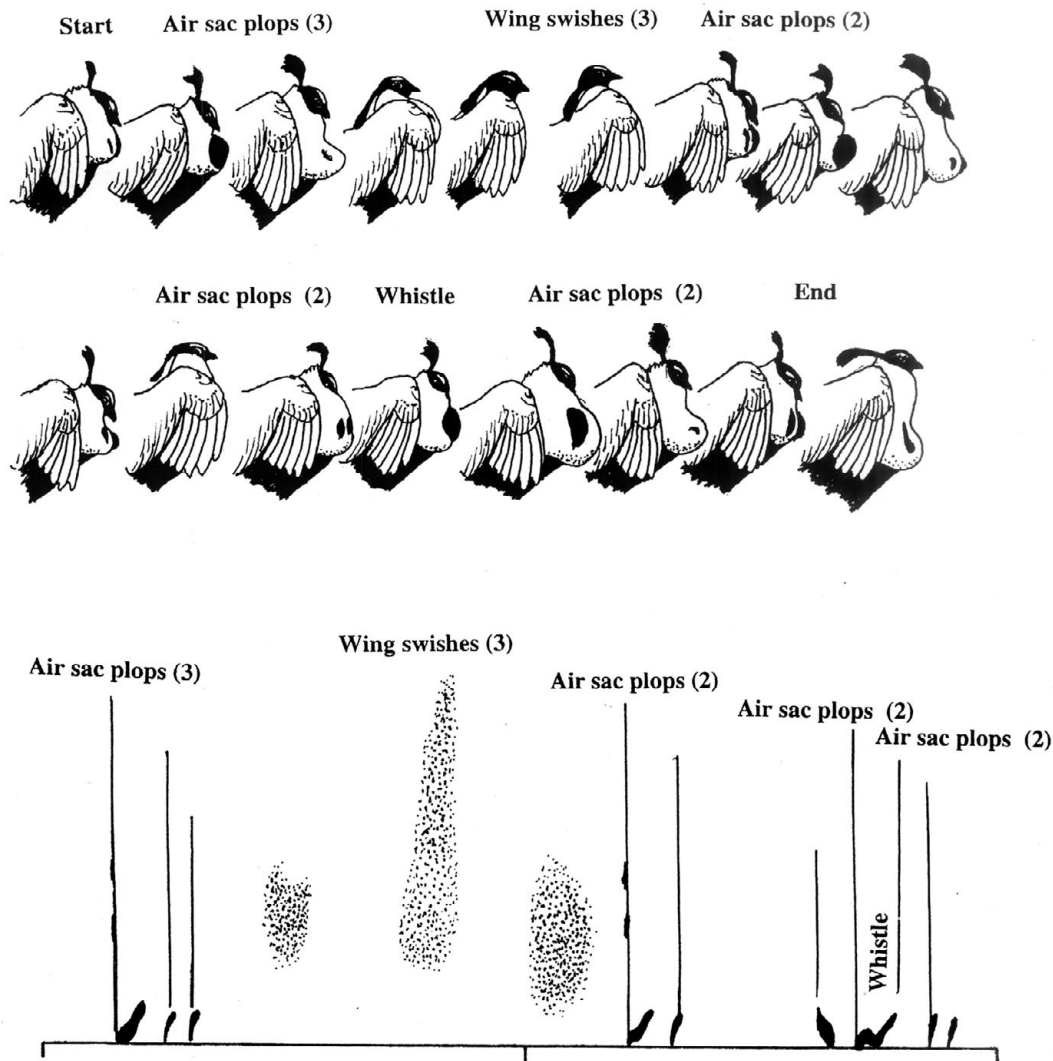
*Fig. 9. Sequential stages in the postures (above) and associated vocal and mechanical sounds during strutting by male Gunnison sage-grouse (below, a two-second sequence).*

the sharp-tailed grouse. Not until the analysis by Hudson and Lanzillotti (1964) was it proposed that the greater sage-grouse may have its nearest affinities with the "forest grouse" instead. Short (1967), using various lines of evidence, supported the view that *Centrocercus* probably evolved from an ancestral type similar to *Dendragapus*, and that *D. obscurus* represents the nearest living relative of the greater sage-grouse. Lumsden's analysis of behavior (1968) also presented this view, and he pointed out that the male greater sage-grouse shares with the dusky/sooty and spruce grouse the characteristic of having a white "V" marking on the throat that apparently has signal value at least in the sage-grouse. Lumsden suggested that the greater sage-grouse and dusky/sooty grouse diverged from a common ancestral type that was a forest-dwelling bird, to which the spruce grouse and Siberian spruce (or sharp-winged) grouse (*Falcipennis*) are the nearest modern equivalents. In contrast, Short suggested that the ancestral grouse was a woodland edge species, of which the earliest offshoot was a grassland-woodland form

ancestral to *Tympanuchus*, followed later by separation of pre-*Dendragapus* and pre-*Centrocercus* types.

I believe that both adult and downy plumage characteristics strongly favor the view that *Dendragapus* and *Centrocercus* are closely related, and that the male sexual displays of sage-grouse and *Dendragapus* grouse have many features in common. The subsequent evolution of lek behavior by the greater and Gunnison sage-grouse produced some convergent similarities to the social displays of prairie grouse, but these should not be regarded as evidence for close common ancestry. However, the American Ornithologists' Union Checklist (1998) places *Centrocercus* between *Bonasa* in taxonomic sequence of the grouse subfamily Tetraoninae, followed by the spruce/sharp-winged grouse genus *Falcipennis*.

*Suggested reading:* Patterson, 1952; Schroder, Young, and Braun, 1999; Johnsgard, 2002; Paothong, 2012; Young et al., 2015

*Plate 1. Greater sage-grouse, male strutting; April.*



*Plate 2. Greater sage-grouse, male strutting to female; April.*

*Plate 3. Greater sage-grouse, male strutting with air-sac inflation; April.*

*Plate 4. Greater sage-grouse lek, master cock (center) and female cluster; April.*



*Plate 5. Greater sage-grouse, female crouching; April.*

# Dusky and Sooty Grouse (Blue Grouse)

*Dendragapus obscurus* (Say) 1823 and *Dendragapus fuliginosus* Ridgway 1873

## Other Vernacular Names

Blue grouse, fool hen, gray grouse, hooter, mountain grouse, pine grouse, pine hen, Richardson grouse (*richardsoni*)

*Note:* In the following descriptive account, the outdated collective name "blue grouse" is used when the specific identity of the taxon mentioned is unknown or when both currently recognized taxa are intended.

## Range

From southeastern Alaska south on the Pacific Slope and along the coast to central California (*fuliginosus*), and from southern Yukon, southwestern Mackenzie, interior British Columbia, and western Alberta southward along the offshore islands to Vancouver, and in the mountains through Utah and Colorado to northern and eastern Arizona and northern and western New Mexico (*obscurus*).

## Subspecies

### Dusky Grouse Subspecies

*D. o. obscurus* (Say): Dusky grouse. Resident in the mountains from central Wyoming and western South Dakota south through eastern Utah and Colorado to northern and eastern Arizona and New Mexico.

*D. obscurus oreinus* Behle and Selander: Great Basin dusky grouse. Resident in mountain ranges of Nevada and Utah.

*D. obscurus howardi* Dickey and van Rossem: Mount Pinos dusky grouse. Resident on the southern Sierra Nevada from about latitude 37°N to the Tehachapi range and west to Mount Pinos, where probably extremely rare.

*D. obscurus richardsonii* (Douglas): Richardson dusky grouse. Resident from the southern Yukon and Alaska south through interior British Columbia to the Okanagan Valley and western Alberta to Idaho, western Montana, and northwestern Wyoming.

*D. obscurus pallidus* Swarth: Oregon dusky grouse. Resident from south-central British Columbia south through eastern Washington to northeastern Oregon.

### Sooty Grouse Subspecies

*D. fuliginosus fuliginosus* (Ridgway): Sooty grouse. Resident from the boundary between Yukon and Alaska south through the mainland of southeastern Alaska, coastal British Columbia including Vancouver Island, western Washington, and western Oregon to northwestern California.

*D. fuliginosus sierrae* Chapman: Sierra sooty grouse. Resident on the eastern slope of the Cascade Mountains of central

Washington south into California and from southern Oregon south along the Sierra Nevada into California and Nevada.

*D. fuliginosus sitkensis* Swarth: Sitkan sooty grouse. Resident in southeastern Alaska south through the coastal islands to Calvert Island and the Queen Charlotte Islands, British Columbia.

## Measurements

*Folded wing* (unflattened): Both species, adult males, 196–248 mm; adult females, 178–235 mm (adult males of all races average over 217 mm; females, under 216 mm).

*Tail* (to insertion): Both species, adult males, 131–201 mm; adult females, 111–159 mm (adult males average over 150 mm; females, under 150 mm).

## Identification

Adults: females 17.2–18.8 inches long, males 18.5–22.5 inches long. These are the largest of the coniferous-forest grouse of the western states and provinces. Sexes differ somewhat in coloration, but both have long, squared, and relatively unbarred tails (pale grayish tips usually occur in both sexes of all races except *richardsonii* and *pallidus*, which sometimes have suggestions of a pale tip). Upperparts of males are mostly grayish or slate colored, extensively vermiculated, and mottled with brown and black markings; the upper wing surfaces are more distinctly brown. White markings are present on the flanks and under tail-coverts, and feathering extends to the base of the middle toe. The bare skin over the eyes of males is yellow to yellow-orange, and the bare neck skin exposed during sexual display varies geographically from a deep yellow and deeply caruncled condition (in *D. fuliginosus*) to purplish and somewhat smoother (in *D. obscurus*). Females have smaller areas of bare skin and are generally browner overall, with barring or mottling on the head, scapulars, chest, and flanks. The three races of sooty grouse (*sitkensis*, *fuliginosus*, and *sierrae*), in addition to the neck skin coloration differences noted for adult males, normally have eighteen rather than twenty rectrices, yellowish rather than grayish downy young, and other minor structural differences.

## Field Marks

Dusky and sooty grouse are likely to be confused only with the similar but smaller spruce grouse, the ranges of which overlap in the Pacific northwest. Males of these forms lack the definite black breast patch of male spruce grouse. Females have relatively unbarred, grayish underparts, as compared with the spruce grouse's white underparts with conspicuous blackish barring. A series of five to seven low hooting notes is frequently uttered by territorial males in spring.

## Age and Sex Criteria

*Females* may be recognized by barring on the top of the head, nape, and interscapulars, which is lacking in adult males (Ridgway and Friedmann, 1946), and by the bases of

the neck feathers around the bare "air sac" skin, which are grayish brown rather than white. The sex of adults may be determined from the wings alone; females have a more extensively mottled brownish pattern on their marginal upper wing-coverts; in males these feathers are gray, with little or no mottling (Mussehl and Leik, 1963).

*Immatures* (in first-winter plumage) may be recognized by one or more of the following criteria: the outer two primaries (retained from the juvenal plumage) are relatively frayed and more pointed (van Rossem, 1925) as well as being lighter and more spotted than the inner ones, the outer tail feathers are narrow and more rounded (up to 0.875 inch wide at 0.5 inch below the tip, as opposed to being at least 1.25 inch wide in adults), and the tail is shorter than in adults (the maximum length of plucked feathers of juvenile males is 152 mm, and of juvenile females, 134 mm, compared with 162 and 138 mm in adult male and female *fuliginosus*, respectively (according to Bendell, 1955a). Immatures of both sexes generally resemble adult females but may usually be recognized by their pale buffy or white breasts, the absence of a gray area on the belly, and (except in *richardsonii* and *pallidus*) the absence of a gray bar at the end of the tail (Taber, in Mosby, 1963). Juveniles may be distinguished by the conspicuous white (tinged with tawny) shaft-streaks of the upperparts, wings, and tail, and the brown rectrices which may be mottled or barred and lack a gray tip (Ridgway and Friedmann, 1946). The juvenal plumage is carried only a very short time in this species, as in other grouse, and the juvenal tail feathers are molted almost as soon as they are fully grown.

*Downy young* of dusky and sooty grouse lack the chestnut crown patch of spruce grouse, exhibiting instead irregular black spotting over the crown and sides of the head and a conspicuous black ear patch. The black head marking in young grouse also includes a central crown mark that connects with frontal spotting, two indefinite lateral stripes, and a faint brownish area posteriorly that is bordered by slightly darker markings (Short, 1967). These species are thus intermediate between the extreme type of head markings found in sage-grouse and the more *Lagopus*-like markings typical of the spruce grouse.

## Range and Habitat

The overall North American range of the dusky and sooty grouse is closely associated with the distribution patterns of true fir (*Abies*) and Douglas-fir (*Pseudotsuga*) in the western states (Beer, 1943). Their ranges more closely conform with that of the Douglas-fir than any other conifer tree species, but this is probably a reflection of both species' being closely adapted to a common climatic and community type rather than any likelihood of their being closely dependent on Douglas-fir. These species actually occupy a fairly broad vertical range in the western mountains, breeding at lower elevations, sometimes as low as the foothills, and spending the fall and winter near timberline or even above it. Rogers (1968) reported that in Colorado the dusky grouse are
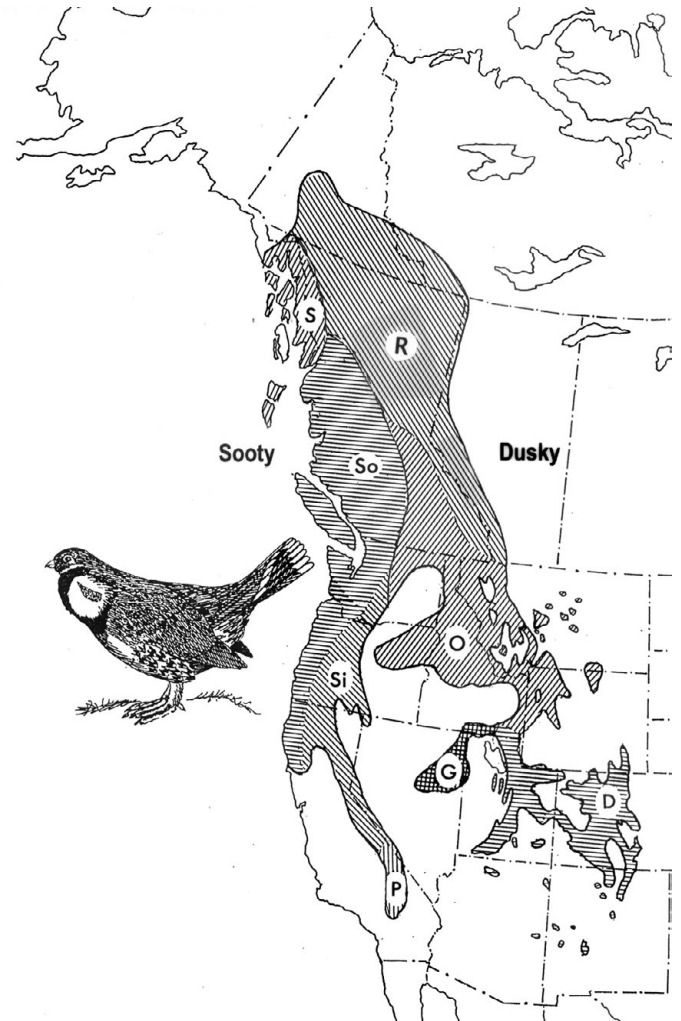


Map 3. Current distribution of the Sitka (S), sooty (So), Sierra (Si), and Mount Pinos (P) races of the sooty grouse, and the dusky (D), Great Basin (G), Oregon (O), and Richardson (R) races of the dusky grouse.

usually found between 7,000 and 10,000 feet but have been seen at elevations as low as 6,100 feet and as high as 12,400 feet, averaging about 9,000 feet. At least in the moist Pacific northwest, lumbering and fire produces a more open forest that improves the breeding habitat of sooty grouse by opening the forest cover, but heavy grazing on lower slopes can be deleterious (Hamerstrom and Hamerstrom, 1961).

In contrast to several grouse species, no major range changes of importance have occurred in the blue grouse in historical times (Aldrich, 1963). In none of the states and provinces where the species occurs is it in danger of extirpation, although the southern populations in New Mexico and Arizona are relatively sparse and scattered. It is an important game species in western Canada. In the 1970s the estimated total annual hunter kill was 140,000 in the United States and 300,000 in Canada (Johnsgard, 1975). As of 2016, in addition to western Canada, "blue" grouse could be legally hunted in Alaska, Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Washington.

Although these forest-adapted grouse depend heavily on coniferous cover for wintering, their preferred habitat also includes a number of deciduous tree species, shrubs, and forbs. Foremost among broadleaf trees are aspens (*Populus*), and a variety of shrubs provide food and escape cover. Rogers (1968) summarized records of dominant trees, shrubs, forbs, and grasses associated with dusky grouse observations in Colorado over a several-year period. In all years, aspen was the dominant tree, snowberry (*Symphoricarpos*) was the dominant shrub, bromegrass (*Bromus*) was the dominant grass, and groundsel (*Senecio*) or vetch (*Astragalus*) were the dominant forbs. Trees recorded less frequently were juniper (*Juniperus*), spruce (*Picea*), Douglas-fir, and ponderosa pine (*Pinus ponderosa*). Although hens and broods were sometimes seen in pinyon pine (*Pinus edulus*) and juniper cover, summer concentrations of males were usually in open coniferous stands of spruce and fir. Rarely were dusky grouse seen more than a mile from trees or shrubs, and females with broods were usually not far from water.

Similar observations on dusky grouse habitat characteristics have been made in southern Idaho by Marshall (1946). There the vertical range used by the species extends from less than 5,000 feet in ponderosa pine–Douglas-fir forest, which is infrequently used, to subalpine forests reaching over 8,000 feet, which provide wintering areas for both sexes and summering habitats for males. In these higher ridges they use the conifers, especially Douglas-fir, for both food and cover. In all but 8 of 25 cases, the grouse were observed to land in conifers upon being flushed, while the remainder landed on the ground. Of 159 observations of birds as to cover type, 87 were in Douglas-fir, 41 were in subalpine cover, 25 were on banks of streams, and the remaining 6 were in grass or brush cover.

A study by Fowle (1960) on Vancouver Island provides comparable data for the coastal population of sooty grouse. Summer habitat there consists of second-growth cover produced by fire and logging of Douglas-fir forests. About 45 percent of the sample areas had no vegetation at all, while in the rest mosses, lichens, ferns, and grasses, as well as a variety of shrubs and forbs, made up most of the cover. Except near water, where alders (*Alnus*), willows (*Salix*), and dogwood (*Cornus*) occurred, trees were only in scattered groups. About 20 percent of the area was covered with important grouse foods, including bracken fern (*Pteridium*), willow, Oregon grape (*Mahonia*), blackberry (*Rubus*), huckleberry (*Vaccinium*), salal (*Gaultheria*), and cat's-ear (*Hypochaeris*). These plants made up a total of more than 90 percent of adult food samples and over 80 percent of juvenile food samples.

By the end of September, the birds move up to higher slopes, and they winter in the coniferous zone (Bendell, 1955b), where they are found primarily in subalpine forests. Zwickel, Buss, and Brigham (1968) point out that winter habitat is probably determined more by cover type than by altitude per se, and may occur in Washington at as low as 4,000 feet, between the ponderosa pine and Douglas-fir zones,

with the critical factor apparently being the presence of interspersed Douglas-fir and true firs.

## Population Density

Estimating dusky and sooty grouse population densities is difficult because of the cover inhabited by the species as well as their generally solitary nature. Rogers (1968) summarized results of Colorado dusky grouse surveys from vehicles; over a three-year period in two study areas they averaged one grouse per 26.07 miles, and ranged from 10.3 and 38.72 miles per grouse in various years.

Using a strip-count census method, Fowle (1960) counted adult sooty grouse on Vancouver Island during two summers. In four areas totaling 272 acres, he determined a density in 1943 of 2.6 acres per bird. Later work in the same area by Bendell and Elliott (1967) indicated that the density of territorial males in dense and sparse populations respectively was approximately from about 2.3 to 7.7 acres per territorial male. Similar counts of territorial male dusky grouse were made by Mussehl and Schladweiler (1969) in Montana on six study areas that were in part exposed to insecticide spraying. Numbers of territorial males on sprayed and unsprayed areas did not appear to differ and averaged about 1 male per 18 acres, ranging from 12 to 24 acres per male.

Whether dusky and sooty grouse are subject to population "cycles" is perhaps questionable, but at least major population fluctuations and corresponding changes in density evidently do occur. Fowle (1960) and Hoffmann (1956) summarized historical data on grouse populations during the 1900s, but neither attempted to explain these fluctuations. Zwickel and Bendell (1967) hypothesized that population fluctuations in sooty grouse are related to the nutritional condition of females, as determined by the summer range conditions, which might affect chick survival and in turn determine subsequent autumn population densities. However, no relationship was found between the number of young in autumn and the breeding density in the following year. They suggested that the death rate or dispersal of juveniles between autumn and early spring is the single most important factor regulating breeding densities. The ten-year grouse cycle phenomenon and its possible basis has more recently been discussed by Page and Bergerud (1998), and Gundarsson (1998) also discussed the possible sources of the ten-year population cycle in Icelandic rock ptarmigan.

A 2004 estimate of the two species' populations combined was 2,600,000 (Rich et al., 2004).

## Habitat Requirements

### Wintering Requirements

Primary wintering needs for the dusky and sooty grouse appear to be sufficient trees to provide roosting and escape cover and a supply of needles from trees of the genera *Abies*, *Tsuga*, or *Pseudotsuga* as a source of food. Beer (1943) reported that adult "blue" grouse subsist almost entirely on needles from November through March. Needles, buds,

twigs, and seeds of Douglas-fir may all be eaten in winter, and needles, buds, and pollen cones of true fir are also used. Where both *Abies* and *Pseudotsuga* are present, the former appears to be preferred. Larches (*Larix*) may be used until its needles are shed, and various species of pines are used for their buds, pollen cones, and seeds. Marshall (1946) noted that 99 percent of the contents of nine birds killed during winter in Idaho consisted of needles and buds of Douglas-fir. Interestingly, grit is evidently retained in the gizzard through the winter, in spite of the deep snow cover. Hoffmann (1956) reported that white fir (*Abies concolor*) provided favored winter roosts for sooty grouse in California.

### Spring Habitat Requirements
As the winter ends, both sexes begin to move downward from the coniferous zones, and males seek out areas suitable for territories. Bendell and Elliott (1966) analyzed the habitats used by both sexes of sooty grouse on Vancouver Island from spring through August, classifying cover as "very open" (40 percent tree, log, stump, and salal cover) or "very dense" (100 percent woody cover). The relative grouse use in two types was 115 in very open cover compared to 18 in very dense cover. The use of the very dense cover was limited to some territorial males that apparently established territories there before it became so heavily vegetated and some females. The authors concluded that the sooty grouse is better adapted to a dry habitat than is the ruffed grouse and may indeed have evolved from a grassland species. Supporting this view was their finding that young captive sooty grouse required only about half as much water as captive ruffed grouse. They concluded that the breeding habitat of sooty grouse might be defined as open and dry, with shrubs and herbs interspersed with bare ground.

In California, Hoffmann (1956) found that the persistence of snow cover determined the onset of sooty grouse hooting in spring and the transition to spring behavior in a study area where virtually no seasonal migration occurred. Blackford's studies (1958, 1963) on Montana provide additional information on territorial requirements for one population (*obscurus*) of the dusky grouse. In this area, hooting occurred either at ground level or in trees during strutting. Strutting areas were in forest-edge habitats with combined grassy, open forest border and a dense coniferous stand. Occasionally, rocky outcrops occurred, and old logs were present on the forest floor. Blackford's observations established that earlier, widely reported differences in territorial defense and strutting behavior between coastal (sooty) and inland (dusky) populations are not in general absolute.

Yearling males may migrate downward to the breeding areas or may remain on the wintering areas through the summer. Bendell and Elliott (1967) estimated that about half of the yearling sooty grouse males moved to the summer range their first year. There they are silent, move about widely, and may be attracted to hooting territorial males. These authors observed two cases of territorial yearling males. Females may return to the same general area of the summer range in subsequent years but are not nearly so

localized in this respect as are males (Bendell, 1955b). Unlike males, females are not particularly aggressive toward one another, and their home ranges may overlap. However, Stirling (1968) suggested that during the squatting and egg-laying periods females do become somewhat aggressive, and this behavior tends to scatter females and perhaps allows for a spacing of nests.

### Nesting and Brooding Requirements
Surprisingly little has been written on specific nesting needs for blue grouse, perhaps because their nests are rather difficult to find. Usually the nest is located near logs or under low tree branches and is fairly well concealed. Bendire (1892) stated that most nests are under old logs or among roots of fallen trees and are generally to be found in more open timber along the outskirts of the forest. He found one nest beside a creek in rye grass some two miles away from timber and another in an alpine meadow under a small fir tree, with no other trees within thirty yards. Bowles (in Bent, 1932) noted that nests are usually in very dry, well-wooded sites, and they are often at the bases of trees or under fallen branches or some other shelter. However, they may be up to 100 yards from trees, with little or no concealment. Lance (1970) found that nests were usually fairly near territorial males but well separated from the nests of other females.

Brooding habitat for dusky and sooty grouse appears to be that which provides ample opportunities for the young to feed on insects and other invertebrates. Beer (1943) suggested that "blue" grouse usually nest in open situations where there will be an abundance of insect life for the newly hatched birds. For the first ten days, the young feed almost exclusively on animal materials, especially ants, beetles, and orthopterans, according to Beer. As the young grow older, berries such as currants (*Ribes*) and juneberries (*Amelanchier*) are sought out, and the young birds and adults gradually move upward as they follow the ripening berry crop.

Wing, Beer, and Tidyman (1944) reported that broods occupy home ranges that were characterized by semi-open vegetation and available water. Relatively open areas were used by newly hatched chicks, while older broods moved into more densely vegetated areas. Mussehl (1963) found that dusky grouse brood cover in Montana was consistently low (averaging 7–8 inches), had little bare ground (8–20 percent), and was predominantly herbaceous in nature, with grasses next in importance, followed by low shrubs and forbs. Woody cover increased in importance for food and escape cover as the birds matured.

## Food and Foraging Behavior

In spite of the rather broad geographic range of these grouse, their food requirements appear to be fairly consistent. Martin, Zim, and Nelson (1951) reported that Douglas-fir was the most important food item in 158 dusky grouse samples from the northern Rocky Mountains, and in 154 samples of birds from the Pacific Northwest, Douglas-fir and true firs provided the major food items. They also listed a

variety of herbaceous plants and sources of berries that are used in summer and fall. Judd (1905b) indicated that winter "blue" grouse foods include ponderosa pine, Douglas-fir, true firs (*Abies concolor* and *A. magnifica*), and hemlocks (*Tsuga heterophylla* and *T. mertensiana*).

Beer (1943) analyzed over 100 crops and gizzards of "blue grouse" mostly from Washington and Oregon, and noted that adult foods were 98 percent plant materials, with conifer needles composing 63.8 percent, berries 17 percent, miscellaneous plant materials 17.2 percent, and animal material 1.7 percent of the materials examined. Beer noted that the grouse reach the peak of their morning feeding by 7 a.m. and stop by 9 a.m. Later feeding periods are just before noon, during late afternoon, and particularly toward evening, when the most intensive foraging of the day occurs. Growing young feed more continuously than adults, but those of all ages forage most heavily during the last three hours of daylight. Similar observations were made by Fowle (1960), who noted that although feeding occurred through the day, the greatest amount of food was consumed in the evening after 6 p.m. Males often alternated feeding with hooting, but females with young evidently restricted their foraging to the evening. Fowle never saw wild grouse drink water and believed it might not be important if berries or other succulent foods are available.

Hoffmann (1961) noted that sooty grouse in California rely during the winter almost entirely on needles of white fir (*Abies concolor*), which he analyzed for protein content. He found that needles from high in the tree had a higher protein content than those from lower branches but that no apparent yearly differences occurred over a three-year period during which the grouse population suffered a major decline.

## Mobility and Movements

### Seasonal Movements

An altitudinal movement of dusky and sooty grouse to coniferous wintering areas has been reported for most areas, the exception being Hoffmann's study in California (1956). Doubtless the horizontal distances involved in movements between summering and wintering areas differ greatly in various regions, but relatively little detailed information is available. One banding study by Zwickel, Buss, and Brigham (1968) in north-central Washington indicated that autumn migrations of dusky grouse may be fairly long. The longest movement recorded by a banded bird was 31 miles, which occurred in less than two months. Of 30 birds recovered, 50 percent had moved over 5 miles, and 30 percent were recovered over 10 miles from where they had been banded. In contrast, Mussehl (1960) reported a maximum fall movement of 3.4 miles in Montana, while Bendell and Elliott (1967) found a maximum fall movement of 10 miles on Vancouver Island. Zwickel, Buss, and Brigham speculated that at least some breeding females leave their broods behind and return to their previous wintering areas, which stimulates wandering by young birds and the possible colonization of new wintering areas.

### Daily Movements

Evidently relatively little daily movement is performed by adult male dusky and sooty grouse from the time they arrive on the summer range and establish territories until they begin their fall movement back to the wintering areas. Males probably establish territories as soon as weather conditions permit, and maintenance activities such as foraging, dusting, and sleeping are all carried out within the territorial boundaries (Bendell and Elliott, 1967). Territorial size presumably varies inversely with population density. In dense populations with about 0.44 male per acre, Bendell and Elliott estimated that territory sizes averaged about 1.5 acres. In sparse populations with about 0.13 male per acre, territories were at least 5 acres in size.

Similarly, female grouse probably exhibit little daily movement, at least after fertilization has occurred. Until then they presumably move about through the territories of males until sufficiently stimulated to permit mating. Various studies of marked broods (Mussehl, 1960; Mussehl and Schladweiler, 1969) indicate that prior to dispersal the broods move about relatively little, and individual brood ranges may overlap considerably.

## Reproductive Behavior

### Territorial Establishment

Male dusky grouse evidently become territorial immediately after their arrival on the breeding range (Blackford, 1963), or as soon as snow-cover conditions permit for sooty grouse (Hoffmann, 1956). Territorial site requirements are somewhat ill-defined and may vary locally or with subspecies. In Colorado, Rogers (1968) stated that dusky grouse display sites may be in aspen–ponderosa pine, mixed fir and aspen, open and dense aspen, mixed shrubs, sagebrush, wheat fields, and on roadbeds, but preference is shown for fairly open stands of trees or shrubs. Physical features include earth mounds, rocks, logs, cut banks, and occasionally tree limbs. Preference is generally given to flat, open ground, although steep slopes are at times also used. Display sites may be near heavy cover, but this is normally used for escape rather than for display. Two observations were made of birds displaying at more than 20 feet, but ground display is more typical of dusky grouse.

In contrast, Hoffmann (1956) found that in a California sooty grouse population the males normally hooted from the tops of white fir or sometimes from Jeffrey pine (*Pinus jeffreyi*) or lodgepole pine (*P. contorta*). Bendell and Elliott (1966, 1967), studying sooty grouse on Vancouver Island, found that many hooting sites were elevated areas on the ground and that territories included diverse cover types, with males hooting from virtually all types of cover within their territory. In dense cover with small openings, territories are related to the location of openings. Thickets within territories are used for resting and concealment. This combination of open areas for display and shelter in the form of fir clumps, logs, or stumps used for hiding and as observation posts provide the basic

territorial requirements. Several display sites may be used within a single territory; Rogers (1968) noted that from 2 to 11 hooting sites for one bird have been recorded.

### Territorial Advertisement

Territorial proclamation by male sooty and dusky grouse is achieved by a combination of postures, vocalizations, and movements that are collectively called hooting. In spite of reported differences in hooting behavior among different populations, current evidence indicates that actual differences are few and tend to be quantitative rather than qualitative. Thus, the interior populations of dusky grouse have much weaker hooting calls that are barely audible more than 50 yards away, whereas the coastal populations of sooty grouse have strong hooting notes that carry several hundred yards. The former typically call from the ground but may use trees, while the latter more often call from tree limbs. The gular sac of dusky grouse males is generally purplish, while that of sooty grouse is more heavily wrinkled and yellowish. The eye-combs of dusky grouse are large and vary from yellow to a bright red under maximum stimulation; those of sooty grouse are smaller and usually are lemon yellow but sometimes also become livid red (Bendell and Elliott, 1967).

   During hooting the male partially raises and spreads his tail and opens the feathers of his neck to expose an oval gular sac that is surrounded by white-based neck feathers, which form a "rosette" pattern. Both wings are slightly drooped toward the ground. In this posture (called the "oblique" by Hjorth, 1970), the gular sac is partially inflated in a pulsing manner as up to seven but usually five (in the dusky grouse) or six (in the sooty grouse) hoot sounds are uttered in fairly rapid succession. These are repeated at frequent intervals. Bent (1932) reported intervals of 12 to 36 seconds between call sequences of *fuliginosus*, Steward (1967) determined a mean interval of 24.2 seconds in *sitkensis*, and Rogers (1968) noted intervals of from 6 to 23 seconds for *obscurus*. Such hooting is uttered at various times during the day but is most prevalent in early morning and again in late evening, primarily from 3 a.m. to 5 a.m. and again from 7 p.m. to 10 p.m. (Bendell, 1955b). Hjorth (1970) noted that although in both subspecies groups the call sequence lasts about 3 seconds, the fundamental frequencies of dusky grouse calls (95–100 Hz) are lower than those of sooty grouse (100–150 Hz) and have much less amplitude. Males may periodically move about between hooting sites, and while walking they keep the head low and the tail cocked and spread, exposing the spotted under tail-coverts ("display walking" of Hjorth, 1970).

### Strutting Displays

When in the presence of another grouse, a sooty and dusky male will stand in an erect posture with his tail tilted toward the other bird ("upright cum tail-tilting" of Hjorth, 1970), the eye-combs enlarged, and the wing away from the intruder drooped in proportion to the amount of tail-tilting. In this posture the male may perform vertical head-jerking
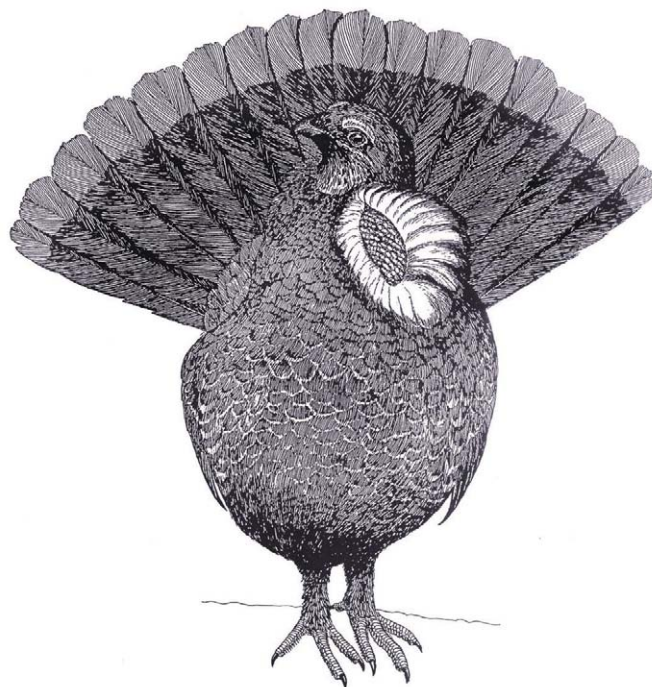


Fig. 10. Male dusky grouse, strutting display while standing.

movements, with the gular "sac" nearer the intruder expanding in synchrony with these head movements (Hjorth, 1970). Hjorth also reported that these downward head movements with exposed gular skin ("bowing cum asymmetric apteria display") might be greater in the dusky grouse than in sooty grouse.
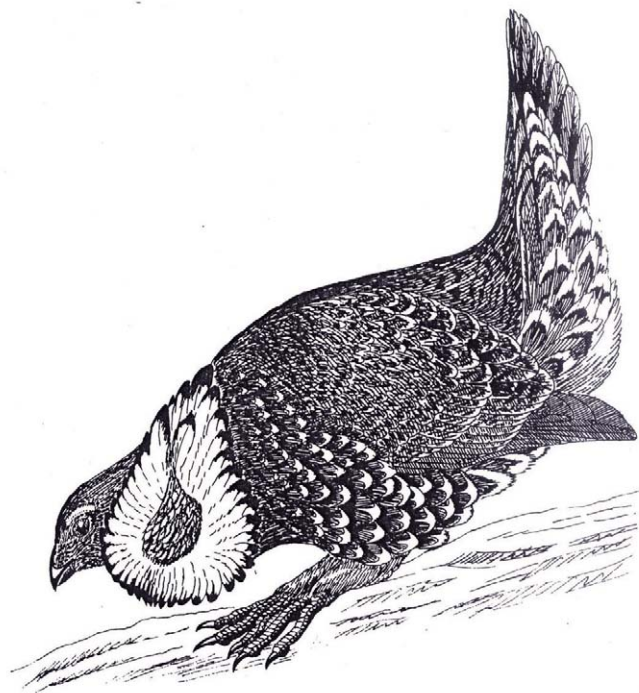


Fig. 11. Male dusky grouse, strutting display while walking.

In this erect and tilted-tail posture, the male typically advances toward the intruder. Bendell and Elliott (1967) stated that in the sooty grouse the head and neck are held broadside to the other bird in such a way as to be framed against the background of the dark tail. Rogers (1968) provided a photograph of the comparable posture of a Colorado dusky grouse. The approach display is climaxed by a quick, arcing dash toward the other bird ("rush cum single hoot" of Hjorth, 1970), which is associated with maximal tail-cocking and spreading, extreme engorgement of the eye-combs, and a drooping of the wings so they drag on the ground.

In this posture the male jerks his head several times and then lowers it and runs forward with short, fast steps, terminating the run with a deep *oop* or *whoot* note. Rogers (1968) noted that this sound could be heard as far as 510 feet away, in contrast to the hooting series in Colorado dusky grouse, which could not be heard beyond 105 feet. Bendell and Elliott (1967), as well as Hjorth (1970), observed that it is actually a double note, with a short squeal or whistle following the deeper sound. Hjorth (1967, 1970) noted that during the forward dash the male deflates his neck, turns his tail toward the other bird, and holds his neck in such a way that the cervical rosette is maximally exposed. The head is held low, the tail is twisted to provide maximum surface exposure, and the wing on the far side is increasingly drooped as the tail is twisted. After the call is uttered the bird gradually assumes a normal posture again.

If the other bird is a receptive female she may remain in place, and the male then displays about her, raising and lowering his body and jerking his head, always keeping the neck rosette and nearer eye-comb in full view of the female. After 2 to 3 minutes of such display, the male moves behind the female and attempts to mount her. During treading, the male grasps the nape of the hen in his beak, and holds her body against his lowered wings as she squats. Following treading the male again assumes his upright display posture (Hjorth, 1970).

### Flight Displays

The other primary aspects of display by male grouse involve fluttering or flying movements, which have been variably ritualized to produce sound and advertise the presence of the male. They are difficult to classify because various observers have described them differently. Blackford (1958, 1963) attempted to classify these aerial displays based on his dusky grouse observations in Montana, which may be summarized as follows:

"Wing-fluttering" is a brief flapping of wings as the bird rises about 8 to 10 inches in the air, producing relatively little noise. It may be performed by either sex, both on the ground and in trees.

"Wing-drumming" is the typical male display flight, or flutter-jump. It is a short, vertical leap into the air as the bird beats his wings strongly a few times before descending. Often one wing is beat much more strongly than the other, producing a rotary movement ("rotational drumming") and causing the bird to make an incomplete turn before landing.

"Wing-clapping," noted only by Blackford, is an upward leap associated with a single, very loud wing note.

"Drumming flight" was distinguished by Blackford from normal wing-drumming by the fact that a circular flight some 10 to 12 feet in diameter is made before landing again near the takeoff point.

Several other possible wing signals were noted by Blackford (1963), including a "double wing flutter," a "perching signal," an "explosive flush," and an "aerial signal." Since they have not been well studied or described by others, they need not be given further consideration here.

### Vocal Signals

Male vocalizations other than the hoot and *oop* calls are relatively few, judging from most accounts. Rogers (1968) reported a "gobbling" sound uttered by a male after making a clapping, wing-beating flight to a branch. This was followed by regular hooting sounds until a single two-note *ca-caw* was uttered about 18 minutes later.

Female vocalizations reported by Blackford (1958) include an in-flight alarm call, *kut-kut-kut*, a low warning note uttered before flight, *kr-r-r*, and an "excitement" call, *kutter-r-r-r*, which fluctuates greatly in pitch. Rogers (1968) noted that the in-flight alarm call of females was the note most commonly heard. Female blue grouse also produce a "whinny" call that is highly effective in stimulating males to begin hooting and to move toward the source of the sound. Use of tape-recordings of such calls is an effective method of censusing blue grouse (Stirling and Bendell, 1966). Likewise, recorded chick distress calls evoke clucking responses from broody hens.

Stirling and Bendell (1970) have reviewed the behavior and vocalizations of adult blue grouse. They described and presented sonograms of three male calls, including the hooting call, the *whoot* call associated with the rush display, and a growling *gugugugug* associated with attack. Females were believed to have two calls related to reproduction: the "whinny," related to copulation readiness, and the "quaver call," or qua-qua, that consists of a pulsed series of notes produced by breeding females just prior to the time that males reach maximal reproductive development, thus possibly synchronizing breeding cycles. Females also utter a "hard cluck," or *bruck-duck* call, which apparently serves as a threat signal.

### Collective Display

Although dusky and sooty grouse are regarded as species that normally defend fairly large territories and display in a solitary fashion, several observations of collective display have been made. Bendell and Elliott (1967) noted that of 420 territorial sooty males studied, the average distance between nearest territorial neighbors in open cover was approximately 600 feet. In 5 percent of the 1,000-foot circular areas they studied, there were 7 or 8 hooting males, which were usually 200 to 500 feet apart and formed a "hooting group" that usually called in chorus. They regarded such hooting groups as indicating a habitat favorable for ter-

1.   0.0

2.   0.1

3.   0.3

4.   0.4

5.   0.8

6.   0.9

7.   2.1
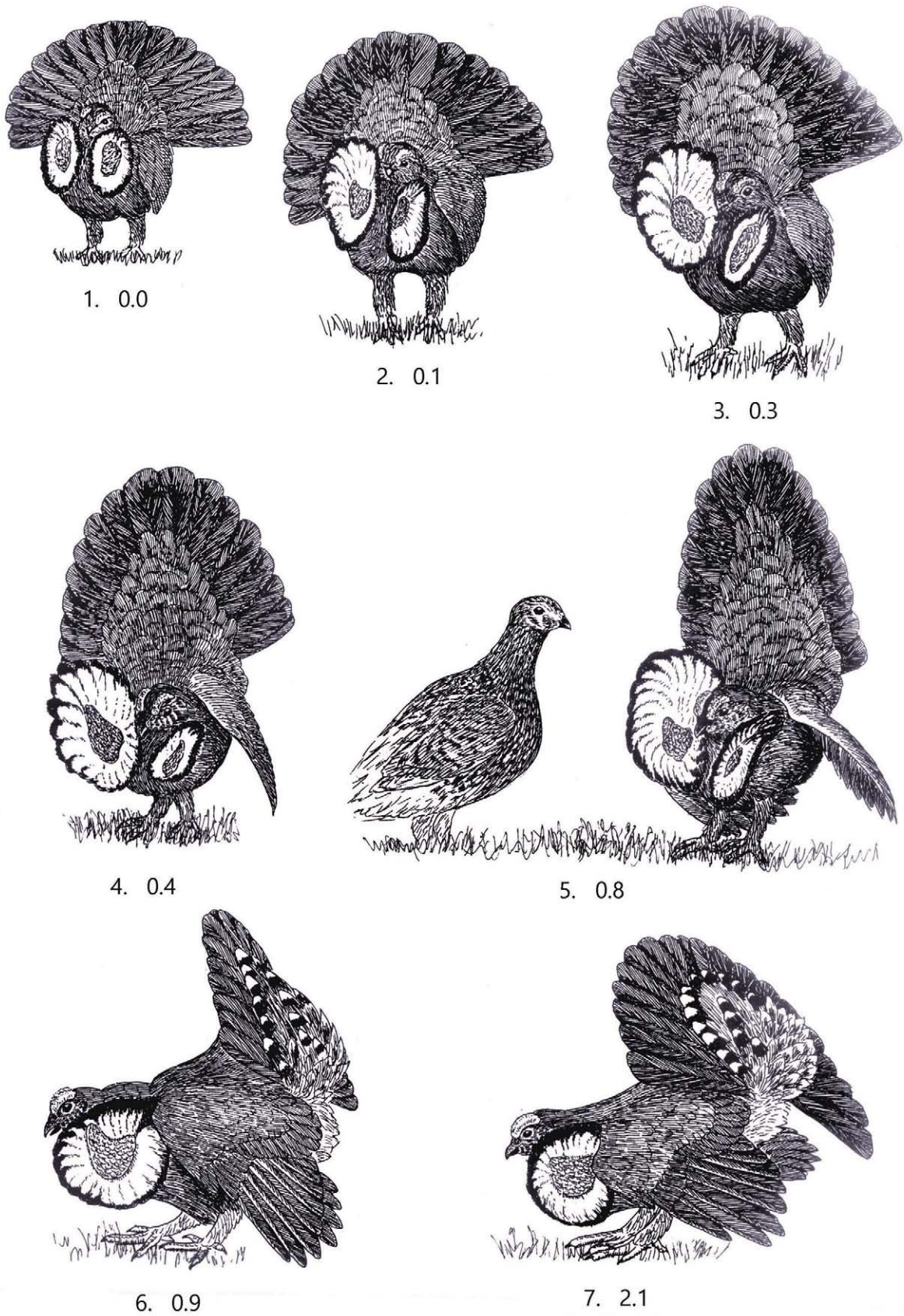
*Fig. 12. Rush display sequence by male Oregon dusky grouse, including elapsed time in seconds. After Hjorth (1970).*

ritories rather than as a variant of lek behavior, since, they pointed out, sooty grouse remain on their territories through the breeding season, in contrast to typical lekking grouse. However, Blackford's observations (1958, 1963) of collective display indicated that dusky grouse males would at times leave their territorial sites and cross over adjacent territories to perform in a "communal court." In one case he noted that at least two males, two females, and one bird of unknown sex converged on the territory of another male, where collective display occurred. This kind of temporary establishment of collective display areas by males which perhaps follow females into the territory of an unusually effective resident male might provide the evolutionary basis for typical lek behavior, provided that such "hooting groups" are more efficient in attracting females than are individual males displaying in a solitary fashion.

### Nesting and Brooding Behavior

Since the male plays no role in nest defense, incubation, or brooding, the female undertakes these duties alone. Evidently nearly all females, including yearlings, attempt to nest (Zwickel and Bendell, 1967). Further, most hens that fail to produce a brood of young do so because of nest destruction rather than nest desertion. Zwickel and Bendell (1967) found that of 30 nests found, 12 hatched successfully, 8 had been deserted, and 10 had been destroyed. The deserted nests were attributed to human disturbance. In that area, foxes and weasels were suggested as principal nest predators. How much renesting might occur after nest destruction or desertion is still uncertain, but Zwickel and Lance (1965) reported two definite instances indicating that renesting might occur even when the first nest is destroyed late in incubation and that a second clutch can be started within about fourteen days after such destruction.

Zwickel and Bendell (1967) found that 51 nests contained 323 eggs, or an average clutch size of 6.3 eggs. Gabrielson and Jewett (1940) reported that 9 Oregon nests contained 74 eggs, averaging 8.2 eggs per clutch. Zwickel and Lance (1965) indicated that the laying rate is 1.5 days per egg and that the incubation period is 26 days.

Upon hatching, the chicks become fairly independent of the female relatively soon. Zwickel (1967a) found that chicks began to eat plant materials at 1 day of age, can fly at 6 to 7 days of age, and by 2 weeks of age can fly up to 60 meters. No chicks older than 11 days were observed being brooded by the hen, and few over 7 days old were seen being brooded. Contrary to other writers, Zwickel (1967b) doubted that chilling by rain or cold days normally plays an important role in chick survival.

Zwickel noted several calls of brooding females. When the chicks wailed loudly with their distress note, the females uttered a low brood call, *cu-cu-cu*. While foraging, hens produced a similar but less audible series of notes that Zwickel termed a contact call. When calling the brood together, the female sometimes produced a high-pitched *kwa-kwa-kwa* call, which the chicks responded to by wailing. When the hen returned to her brood after a considerable absence she would cluck loudly or produce a high-pitched *kweer-kweer-kweer*, which was audible for up to a mile under favorable conditions. Zwickel concluded that vocal signals were highly important in maintaining brood organization and exhibited considerable plasticity to meet varying needs.

Evidently most chick losses occur during the first 2 weeks of age, according to Zwickel and Bendell (1967). These authors presented data indicating that brood sizes for chicks up to 14 days old average from 3.3 to 4.4 young, while brood sizes for chicks estimated to be older than 42 days average 2.9 to 3.7 young. Mussehl's study in Montana (1960) indicated that the movements of 8 marked broods for periods of 19 to 47 days were restricted to areas having maximum diameters of 440 to 1,320 yards. During early July these broods primarily used a mixed grass–forb cover, but with gradual drying of the prairie forbs they moved into deciduous thickets for the remainder of their brooding period. Little use of montane coniferous forest was noted. By the end of August most of the brooding range had been abandoned, and broods began to disperse. Juveniles then moved singly or in small groups, with individual birds making lateral movements of up to 2.1 miles as they worked their way up toward the wintering ranges.

## Evolutionary Relationships

The "blue" grouse presumably had their evolutionary origins in western North America, either in a coniferous forest situation or in a forest-grassland edge habitat. Jehl (1969) concluded that the evolution of ancestral spruce and blue grouse occurred in the western United States in the late Pleistocene, one of which presumably directly gave rise to the modern dusky/sooty grouse. I believe that the ancestral *Dendragapus* grouse probably originated in North America, whereas the ancestral spruce grouse (*Falcipennis*) may have had its origins in eastern Asia, only later coming into contact with *Dendragapus*, as its current placement with the sharp-winged grouse in the genus *Falcipennis* would indicate.

It seems probable that the sage-grouse also had its origin in the western part of North America and may be much more closely related to *Dendragapus* than the adult plumage patterns would suggest. The surprising similarities of the downy young would support this view, and the strutting behavior patterns of the two species are not greatly different. To a much greater extent than is usually appreciated, the breeding habitat of the dusky grouse is relatively arid and open, and the species is in no sense a climax coniferous forest bird.

I would suggest that North America was invaded relatively early from eastern Asia by a *Tetrao*-like ancestral type, which as it moved southward produced the more montane-dwelling dusky/sooty grouse ancestor, and also the intermontane or valley-dwelling sage-grouse ancestor. A second invasion probably brought the spruce grouse into North America, possibly as recently as late Pleistocene times.

*Suggested reading:* Rogers, 1968; Zwickel, 1992; Zwickel and Bendell, 2004

*Plate 6. Dusky grouse, male walking; June.*



*Plate 7. Dusky grouse, male hooting; June.*

*Plate 8. Dusky grouse, male hooting; June.*

# Spruce Grouse

*Falcipennis canadensis* (Linnaeus) 1758

## Other Vernacular Names

Black partridge, Canada grouse, cedar partridge, fool-hen, Franklin grouse, heath hen, mountain grouse, spotted grouse, spruce partridge, swamp partridge, Tyee grouse, wood grouse

## Range

From central Alaska, Yukon, Mackenzie, northern Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Labrador, and Cape Breton Island south to northeastern Oregon, central Idaho, western Montana, northwestern Wyoming, Manitoba, northern Minnesota, northern Wisconsin, Michigan, southern Ontario, northern New York, northern Vermont, northern New Hampshire, Maine, New Brunswick, and Nova Scotia.

## Subspecies

*F. c. canadensis* (Linnaeus): Hudsonian spruce grouse. Resident in east-central British Columbia, central Alberta, central Saskatchewan, southwestern Keewatin, northern Manitoba, northern Ontario, northern Quebec, and Labrador south to central Manitoba, central Ontario, and central Quebec. Introduced into Newfoundland in 1964 (Tuck, 1968).

*F. canadensis franklinii* (Douglas): Franklin spruce grouse. Resident from southeastern Alaska, central British Columbia, and west central Alberta south through the interior of Washington to northeastern Oregon, central Idaho, western Montana, and northwestern Wyoming.

*F. canadensis canace* (Linnaeus): Canada spruce grouse. Resident from southern Ontario, southern Quebec, New Brunswick, and Cape Breton Island south to northern Minnesota, northern Wisconsin, Michigan, northern New York, northern New Hampshire, northern Vermont, northern and eastern Maine, New Brunswick, and Nova Scotia.

*F. canadensis atratus* (Grinnell):Valdez spruce grouse. Resident in the coast region of southern Alaska from Bristol Bay to Cook Inlet, Prince William Sound, and perhaps Kodiak Island.

## Measurements

*Folded wing:* Males, 161–192 mm; females, 159–191 mm (males average 2 mm longer).

*Tail:* Males, 107–144 mm; females, 94–119 mm (adult males of all races average more than 120 mm; females, under 110 mm).

## Identification

Adults, 15–17 inches long. Thus is a species that is associated with coniferous forest throughout its range. The sexes are quite different in coloration, but both have brown or blackish tail feathers that are unbarred and narrowly tipped with white (*franklinii*) or have a broad, pale brownish terminal band. The upper tail-coverts are relatively long (extending to about half the length of the exposed tail) and are either broadly tipped with white (in *franklinii*) or tipped more narrowly with grayish white. The under tail-coverts of both sexes are likewise black with white tips (males) or barred (females). Feathering extends to the base of the toes. Males are generally marked with gray and black above, with a black throat and a well-defined black breast patch that is bordered with white-tipped feathers. The abdomen is mostly blackish, tipped with tawny (laterally) to white markings that become more conspicuous toward the tail. The bare skin above the eyes of males is scarlet; no bare skin is present on the neck. The females are extensively barred on the head and underparts with black, gray, and ocherous buff in varying proportions; the sides are predominantly ocherous and the underparts are mostly white.

## Field Marks

In the eastern states and provinces, spruce grouse are likely to be confused only with the ruffed grouse, from which the spruce grouse can be readily separated by the unbarred tail and the presence of a lighter tip rather than a darker band toward the tip of the tail. The conspicuous black and white markings of the underparts of males distinguish spruce grouse from dusky and sooty grouse, and the predominantly white underparts of female spruce grouse help to distinguish them from these species.

## Age and Sex Criteria

*Females* may be distinguished from adult males by their tawny to whitish throats and breasts, barred with dark brown (these areas are black or black-tipped with white in males). Accurate determination of sex in most races is possible by using either the breast feathers (males' breast feathers are black tipped with white, those of females are barred with brown) or tail feathers (males have black rectrices, tipped and lightly flecked with brown; females' are black or fuscous, heavily barred with brown). In *franklinii* the breast condition is the same, but the tails of females are barred or flecked with buffy or cinnamon brown, while the males have uniformly black tails or black tails flecked with gray (Zwickel and Martinsen, 1967).

*Immatures* resemble adults of their sex but the two outer juvenal primaries are more pointed than the others and (at least in *franklinii*) are narrowly marked with buff rather than whitish on the outer webs (Ridgway and Friedmann, 1946). Ellison (1968a) also reported that the tip of the ninth primary in immature Alaskan spruce grouse is mottled and edged with brown, while in adults it is only narrowly edged with brown.

*Juveniles* resemble adult females but have white or buffy markings at the tips of the upper wing-coverts as well as on their primaries and secondaries. Their tail feathers are dark brown, barred, speckled, and vermiculated with lighter markings (Ridgway and Friedmann, 1946).
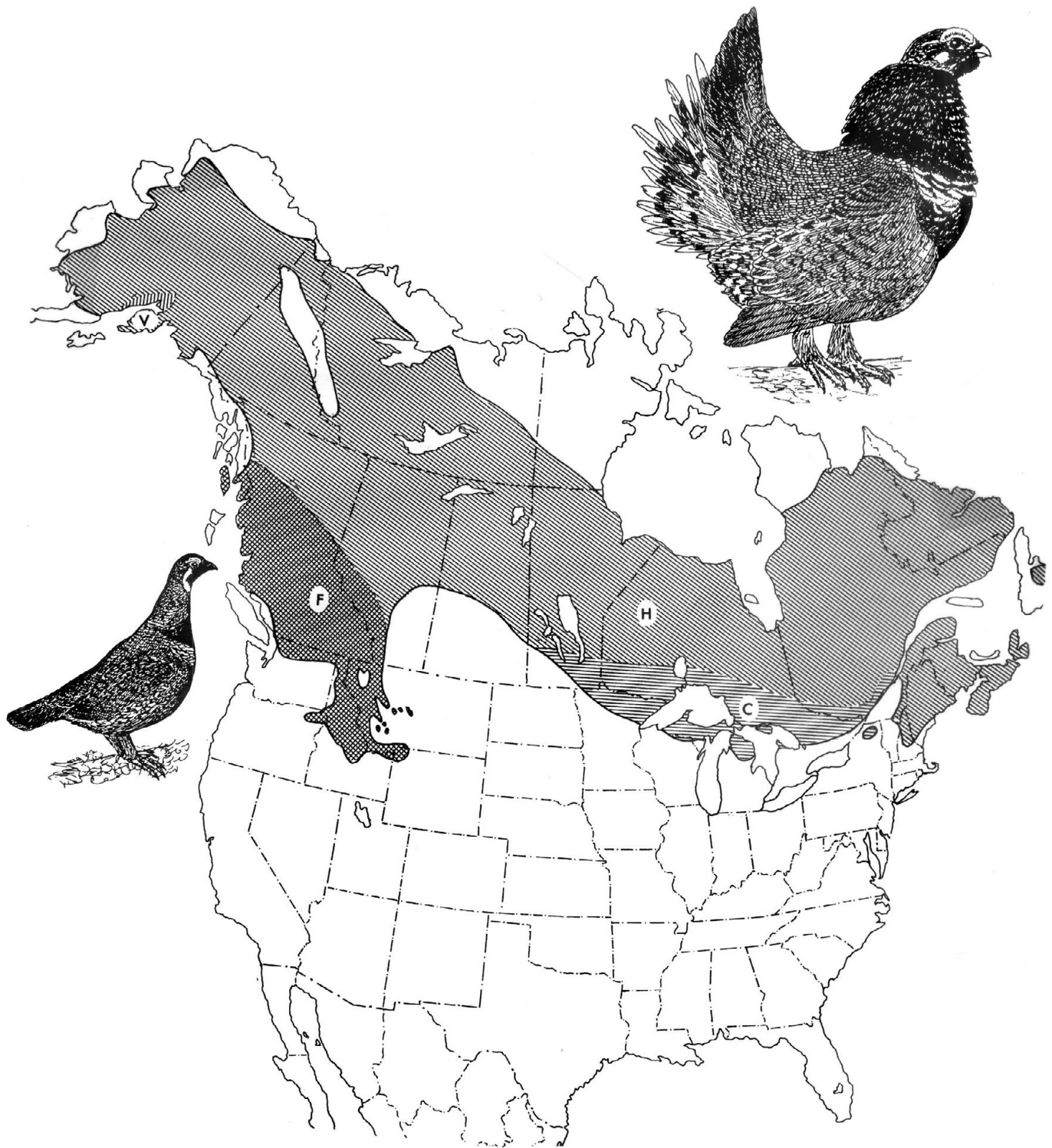
*Map 4. Distribution of Canada (C), Franklin's (F), Hudsonian (H), and Valdez (V) races of the spruce grouse.*

*Downy young* of this species more closely resemble *Lagopus* than do that of the blue grouse, and they have a discrete chestnut brown crown patch margined with black. Downy spruce grouse lack the feathered toes of ptarmigan; however, they are also more generally rufous dorsally and have less definite patterning on the back.

## Distribution and Habitat

The overall geographic distribution of the spruce grouse is a transcontinental band largely conforming to that of the boreal coniferous forest (Aldrich, 1963). East of the Rocky Mountains, the species' range generally conforms to that of the balsam fir (*Abies balsamea*) and also the black and white spruces (*Picea mariana* and *P. glauca*). In the Rocky and Cascade ranges the bird's southern limit occurs well north of the limits of montane and subalpine coniferous forest, suggesting that other limiting factors are influential in that area. What role competition with dusky grouse might play in limiting the western range of the spruce grouse is unknown.

Probably only in the southeastern limits of its range have the populations of spruce grouse undergone serious reduction. In Michigan, where the species was once common to abundant, it had become noticeably reduced as early as 1912 (Ammann, 1963a). They are now uncommon on the Upper Peninsula and rare in six counties of the Lower Peninsula, and hunting was last permitted in 1914. In Michigan they are more often found associated with jack pines (*Pinus banksiana*) than with spruces.

In Minnesota, the spruce grouse was fairly abundant in coniferous forests as late as 1880 but almost completely disappeared with the cutting of this forest (Stenlund and Magnus, 1951). Roberts (1932) believed that the species was doomed to be extirpated from the state "before many years have passed." However, by 1940 the second-growth forest that had grown following lumbering began to develop an understory of conifers (especially black and white spruce) and jack pine, and the spruce grouse again became common in several northern areas (Stenlund and Magnus, 1951). In observations reported by these authors, associated cover type was most commonly jack pine, followed in order by black spruce, balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*). Of 79 observations, 44 percent were made in cover that was completely evergreen, and 72 percent were in upland cover rather than in lowland or swamp cover. Shrader (1944) also noted population gains in the spruce grouse in Minnesota following its near extinction.

The situation in Wisconsin for spruce grouse is apparently still extremely unfavorable. Scott (1943, 1947) documented the historical changes in spruce grouse populations of that state. His map indicated that the species probably originally extended across northern Wisconsin from Polk to Marinette County, but as of 1942 was limited to about ten counties, with an estimated population of 500 to 800 birds.

Finally, in southern Ontario, spruce grouse have nearly disappeared from the area south of Lake Nipissing (Hamerstrom and Hamerstrom, 1961). Lumsden and Weeden (1963) pointed out that in the early 1960s spruce grouse had sufficiently high populations to be hunted in Maine, Montana, Washington, Idaho, Alaska, and all the Canadian provinces and territories except Nova Scotia (where protected) and Prince Albert Island (where it has been extirpated). In 1970 Minnesota allowed the hunting of spruce grouse as well,

but it was still protected in Wisconsin, Michigan, New York, Vermont, and New Hampshire. As of 2016, in addition to being hunted almost throughout nearly all of Canada, spruce grouse could also be legally hunted in Alaska, Idaho, Minnesota, Montana, and Washington.

Some hunter-kill estimates for British Columbia are 32,000 to 58,000 birds, down from estimates of 83,000 to 122,000 in the 1970s but still second only to the ruffed grouse as a target for British Columbian upland game hunters. Estimated annual kills from 1972 to 1974 for the other provinces that made such estimates available are: New Brunswick, up to 40,000, Manitoba, 10,000–22,000, Newfoundland, 12,000–15,000, Saskatchewan 1,300–9,000, and Yukon Territory, 4,600 (Robinson, 1980). Robinson estimated U.S. hunter kills for five states (excluding Alaska) of about 58,000 to 70,000 birds in the early 1970s, and an estimate of 230,000 birds for Canada, for a grand total of 340,000–450,000 for North America, a total very similar to my own (1973) estimate of 440,000. A 2004 estimate of the species' total population during the 1990s was 1,200,000 (Rich et al., 2004), which, if these kill estimates were accurate, would indicate a relatively high annual hunting mortality rate of about 28 to 38 percent.

## Population Density

Few estimates of population densities for spruce grouse are available. Ellison (1968b) reported that a spring census of males in south-central Alaska indicated a density of about 10 males per square mile during two years and 7 per square mile in a third year. He also estimated a density of 20 to 30 birds per square mile on the Kenai Peninsula of Alaska (1974). Robinson (1980) estimated a population of 12 to 24 birds per square mile on a 25-square-mile study area of northern Michigan's Upper Peninsula.

## Habitat Requirements

A careful analysis of the entire habitat needs of the spruce grouse remains to be done, but a study by Robinson (1980) provides a valuable analysis of summer habitat needs. Analyzing tree composition, as well as that of shrubs and low herbs, and comparing locations of spruce grouse sightings obtained a useful indication of habitat selection. Of 430 trees where spruce grouse were seen, 32 percent were spruces, although spruces (*Picea mariana* and *P. glauca*) made up only 3 percent of the tree cover.

On the other hand, jack pines made up 91 percent of the tree composition but accounted for only 51 percent of the sightings. Pure stands of either jack pine or spruce were not used as much as mixed stands. In the shrub layer, young black spruces accounted for a larger proportion of spruce grouse sightings than would be expected from their relative abundance, while jack pines again provided a smaller proportion of sightings. Balsam firs at sighting points were more than seven times as abundant as at random sites. As to low vegetation, blueberry (*Vaccinium*), trailing arbutus (*Epigaea*), black spruce, and logs and stumps all were associated with

higher than expected sightings of spruce grouse. In general, mature stands of either jack pine or spruce were not favored, apparently because of the lack of concealing cover at ground level. Robinson found that molting males used the same habitat in late summer as did females with broods and indeed were often seen accompanying broods. Robinson concluded that populations of spruce grouse in Michigan were highest in areas of boreal forest and jack pine forest. In one such area, the grouse selected habitats that had a mixture of spruces and jack pine, a prevalence of young spruces in the shrub layer, and a varied ground cover that included blueberries, trailing arbutus, and scattered stumps and logs.

In a comparable study of Alaskan spruce grouse, Ellison (1968b) noted that hilltops covered with white spruce, birch (*Betula*), and species of *Populus* were not a preferred habitat, although where an understory of alder was present some brood use and use by molting adults occurred in late summer. Two upland cover types provided preferred habitat. These were a white spruce and birch community with understories of grasses, spiraea, blueberry, and cranberry, and a black spruce community with a blueberry, cranberry, and lichen understory. Grouse sometimes also used dense lowland stands of black spruce, and broods were often found in stunted black spruce borders at the edges of bogs. MacDonald (1968) noted that the habitat of the Franklin race of spruce grouse in Alberta consisted of lodgepole pine forests, with some clumps of aspen and poplar. Somewhat open stands of pines, some 20 to 30 feet tall, were evidently preferred areas for display by territorial males.

Winter habitat needs of the spruce grouse, to judge from their known food habits, consist simply of coniferous trees of various species that provide both food and cover requirements.

### Food and Foraging Behavior

The survey by Martin, Zim, and Nelson (1951) indicated that spruce grouse in Canada and the Northwest feed extensively on the needles of jack pine, white spruce, and larch and on the leaves and fruit of blueberries. A small fall and winter sample from British Columbia included a diverse array of berry species as well as lodgepole pine and spruce needles.

Jonkel and Greer (1963) analyzed crop contents during September and October in Montana and noted that western larch (*Larix occidentalis*) was an important early fall food but that it declined in use during October. Other important foods were needles of pine, spruce, and juniper; clover leaves; the fruits of huckleberry (*Vaccinium*), snowberry (*Symphoricarpos*), and white mandarin (*Streptopus*); and grasshoppers. A study by Crichton (1963) indicated that prior to snowfall in central Ontario, spruce grouse fed mostly on needles of jack pine and tamarack (*Larix laricina*) and the leaves of blueberries. After the shedding of the tamarack needles and the fall of snow, jack pine needles became almost the sole source of food in spite of a high availability of black spruce.

A seasonal analysis of spruce grouse foods in Alberta by

Pendergast and Boag (1970b) indicated that during winter lodgepole pine needles (*Pinus contorts*) made up nearly 100 percent of the food. In spring, the proportion of spruce needles to pine needles increased. The summer diet of adults was mostly ground vegetation, such as *Vaccinium* berries. In the fall the adults returned to feeding on conifers, but berries remained important. In contrast, chicks under a week old apparently subsisted entirely on arthropods. Later, they began to eat *Vaccinium* berries, but arthropods remained an important source of food through August. By October, the juveniles were starting to eat needles, and by November both the adults and young were using needles as a major food item.

A study in Alaska by Ellison (1966) yielded generally similar conclusions, except that the winter diet consisted primarily of needles of both black and white spruce. With spring, spruce was taken in decreasing amounts, and blueberry leaves, buds, and old cranberries were taken, as well as unripe crowberries (*Empetrum*). Summer food consisted largely of berries (crowberry, blueberry, and cranberry), and berry consumption continued into fall, as spruce needles again began to appear in the diet. Ellison reported that the protein content of spruce needles ranged from 5.7 to 6.3 percent, or about the same protein content as has been reported for Douglas-fir and white fir.
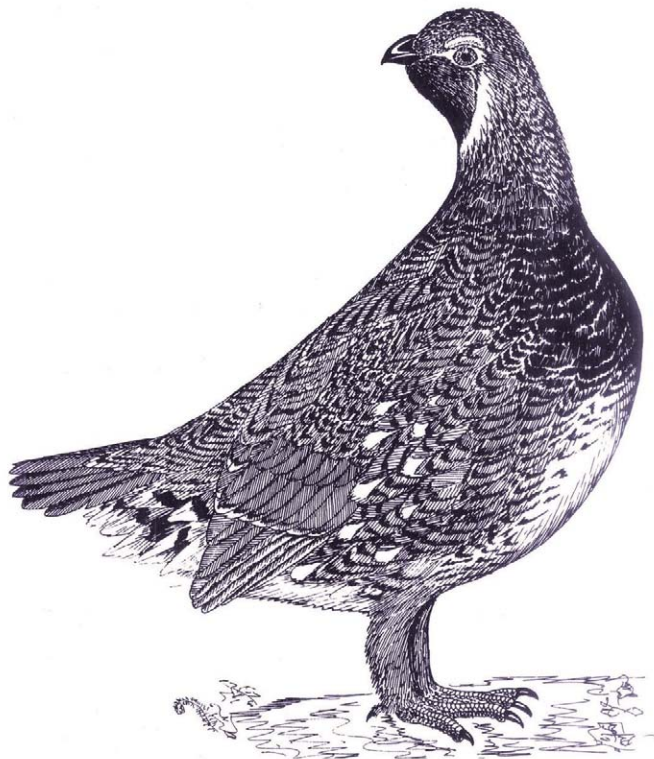


*Fig. 13. Male spruce grouse, in alert posture.*

## Mobility and Movements

### *Spring Movements of Males*

Virtually the only detailed information on spruce grouse movements so far available is that provided by Ellison (1968b), who used radio transmitters to obtain movement data. He found that all adult males, but only some yearling males, established territories and became relatively sedentary. Those birds that were considered territorial remained localized on from 3 to 21 acres of forest during late April and most of May. Immature males considered nonterritorial occupied "activity centers" of 6 to 16 acres during this time but also made fairly long trips of up to 1.25 miles from these centers, frequently entering the territories of other males in the process, evidently being attracted to them by displays. Interestingly, Ellison noted that in each year of the study, juvenile males tended to establish territories on the periphery of territories held by especially active territorial males, a tendency reminiscent of "hooting groups" of blue grouse, which has also been noted in ruffed grouse (Gullion, 1967b). The actual estimated territorial size of four adult males ranged from 4.6 to 8.9 acres and averaged 6.9 acres. After May 21, these same males occupied larger home ranges of from 4.5 to 29.6 acres, averaging 20.1 acres. Considering four immature and territorial males as well, the maximum sizes of the home ranges of all eight males was 61 acres, while three of five nonterritorial males moved about over areas of 270 to 556 acres.

## Reproductive Behavior

### *Territorial Establishment*

Ellison (1968b) reported that spruce grouse males established their territories and activity centers in stands of fairly dense spruce or stands of spruce and birch with trees some 40 to 60 feet tall. Stands of trees up to 80 feet tall, with dense undercover, were sometimes used by nonterritorial males but apparently were not suitable for territorial purposes. MacDonald (1968) indicated that pines from 20 to 30 feet tall and that were not too closely spaced were preferred display sites.

Stoneberg (1967) stated that of four males he studied, three displayed in small openings in dense forest, while one was in less dense forest. He estimated that the four marked males he studied had home ranges of 10 to 15 acres. Two remained in very localized sites during the display period, while one of the other two used several display sites within a 25-yard radius, and the last moved about extensively and used no specific sites. However, this last bird was the only one that had no female on his territory at the time. MacDonald thought that males have favored display sites within their home ranges but that the latter are too large to have definite boundaries except in areas of contact with adjacent males.

Both Stoneberg and Ellison reported that display flights (drumming flights or wing-clapping flights) were performed in openings rather than in dense forest. Ellison described the ground vegetation of such openings as low, rarely more than 1.5 feet in height, and usually consisting of mosses, lichens, and *Vaccinium* species.

### *Territorial Advertisement*

Several detailed accounts of strutting behavior are now available. Displays of the Franklin race of spruce grouse have been described by Stoneberg (1967) and MacDonald (1968), and those of the nominate race by a number of writers, including Bishop (in Bendire, 1892), Breckenridge (in Roberts, 1932), Harper (1958), Lumsden (1961a), and Robinson (1980). Only a few differences appear to be present in the two forms, as will be noted.

The basic male advertisement or "strutting" display consists of a standing posture ("upright" of Hjorth, 1970). In this posture the tail is cocked at an angle of from about 70 to 90 degrees, exposing the white-tipped under tail-coverts that are held out at varying angles; the neck is fairly erect, the wings are slightly drooped, and the crimson eye-combs are engorged. The throat feathers are lowered to form a slight "beard," and the lateral black neck feathers are lifted, as are the lower white-tipped feathers at the sides of the neck and the upper breast. No bare skin is exposed, but the pattern of feather erection is much like that of the male blue grouse. Lumsden has noted that the esophagus is evidently slightly inflated as well, but no hooting sound is normally heard. However, an extremely low-pitched sound (about 85–90 Hz) may be produced by male spruce grouse (Stoneberg, 1967; Greenewalt, 1968). Stoneberg heard series of such notes ranging from one to four, and I have heard similar sounds coming from boxes containing several recently trapped males and females. MacDonald likewise heard hooting sounds apparently produced by a male when it rushed toward a female. However, Hjorth (1970) questioned on anatomical grounds whether male spruce grouse could produce such low-pitched sounds, believing that reports of such calling were the result of confusion with blue grouse hooting.

When in the strutting posture, the male usually walks forward with deliberate paces, typically spreading the rectrices on the opposite side as it raises each foot, making the spread tail asymmetrical ("display walking cum tail-swaying" of Hjorth, 1970). This lateral tail movement, which produces a soft rustling sound, may also occur when the bird is not walking, as has been noted by Stoneberg as well as by me. A similar display is tail-fanning, in which the rectrices of both sides are quickly fanned and shut again. This also produces a rustling sound and may occur during walking or when the bird is standing still, often alternating with tail-flicking. On one occasion I saw a male performing tail-fanning before a female as it uttered a series of low hissing notes that started slowly and gradually speeded up, with a fan of the tail accompanying each note. Lumsden (1961a) described this as occurring when a male observed his reflection in a mirror. A similar tail-fanning during calling is typical of the capercaillie.

When approaching a female in the strutting posture, the male may perform several displays that have been given

*Fig. 14. Male spruce grouse, peering from tree.*

different names by various writers. One is a vertical head-bobbing, which may grade into or alternate with ground-pecking (Harper, 1958; Lumsden, 1961a; Stoneberg, 1967; MacDonald, 1968).

During the pecking movements the male faces the female and often tilts its head to the side, thus exposing both combs to her view. Wing-flicking may likewise occur at this time (Stoneberg); Harper also noticed what appeared to be wing-beating movements suggestive of the ruffed grouse's drumming.

Two other major male displays occur in the situation of close approach to a female by the male. These are the "neck-jerk" display described by Lumsden, which MacDonald preferred to call the "squatting" display, and the "tail-flick" described by Lumsden but which Stoneberg calls the "head-on rush."

The tail-flicking, or head-on rush, display (called the "rush cum momentary tail-fanning" by Hjorth, 1970) is apparently homologous to the short forward rush of the male blue grouse. It begins with the male's making several short and rapid steps toward the female, stopping a few inches away, partially lowering its head, and suddenly snapping its tail open with a swishing sound. The wings are simultaneously lowered to the ground, and a hissing vocalization is uttered, followed by a high-pitched squeak. The wings are then withdrawn, leaving the alulae exposed, the tail is closed, and the head is tipped downward with the neck still extended diagonally. In this rigid posture the tail is fanned a second time and is held open longer. During this display the male is usually oriented so that his head faces the female, exposing to her view the visual effect of the eye-combs, fanned tail, and contrasting breast coloration. In the Franklin race, the white-tipped upper tail-coverts are made conspicuous by the tail movements, but they are not evident in the nominate race. MacDonald noted that during this display (which he described under the general tail-swishing display), a single, soft hooting noise can be heard at very close range.

Males perform the squatting display as a possible pre-copulatory signal according to Lumsden, and MacDonald agreed with this interpretation but notes that it is sometimes omitted from the sequence. As the male approaches the female, the head-on rushes (or "arcing rushes," since MacDonald indicated that the male may move in arcs in front of the hen) increase in frequency until he is quite close to her. After watching her intently for several seconds, the male sinks to the ground in a squatting position, with neck stretched, head nearly parallel to the ground, and tail held in a vertical and partially spread position, while the wings are slightly spread and lowered. This display has been observed only once by the writer, to whom it closely resembled the "nuptial bow" of pinnated grouse, which serves as a precopulatory display in that species. Hjorth (1967) illustrated the posture and agreed that it is homologous to the nuptial bow of prairie grouse. He believed that it is stimulated when the male's displays elicit neither attack nor pairing behavior.

Squatting as described by MacDonald probably does not correspond to the typical head-jerk as described by Lumsden and Stoneberg, since MacDonald mentioned no actual head-
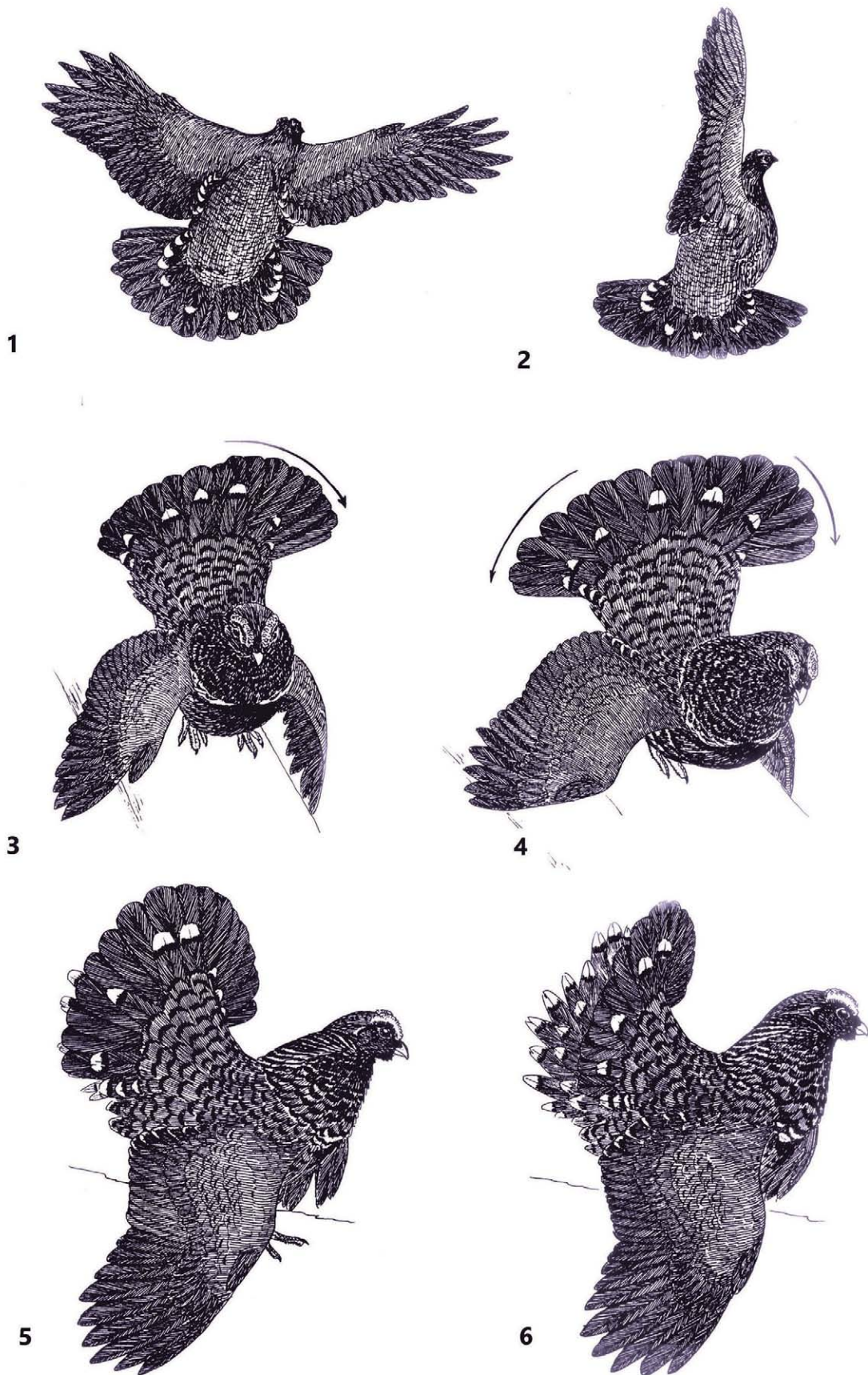
Fig. 15. Male Franklin's spruce grouse, showing aerial wing-clapping (above) and tail-swishing (below). After MacDonald (1965).

jerking movements, and I likewise noted none during one observation of the squatting display. Lumsden mentioned seeing repeated, sudden upward movements of the head, first to one side, then to the other, as well as occasional circular head movements. With each upward movement, the tail was fanned open and again shut, producing the usual rustling sound. Stoneberg noted two types of head-jerking movements, one of which was a rapid tossing of the head from one side to the other for up to three seconds, pausing and repeating it, with the tail kept vertical and the head near the ground. A slower type of head-jerking was associated with strutting, when the bird would stop, facing the female, and jerk the head from one side to the other while fanning or flicking his tail.

Aggressive male displays of the spruce grouse consist of at least two postures. MacDonald reports that when two males meet at a distance the resident territorial male sleeks his plumage, raises his tail, and flashes the lateral rectrices and upper tail-coverts, uttering a series of guttural notes. These notes no doubt correspond to the calls I heard from a male when I interrupted his strutting, which Lumsden described as harsh hissing sounds. Stoneberg describes the rapid notes as "throaty *kuks*." The male then runs toward the opponent with the head low, neck extended, and the tail down (Lumsden's "head and tail down" display posture), with the wings held slightly away from the flanks. MacDonald found that such behavior was enough to cause a trespasser to fly away or at least to fly into a tree. When a mounted male is used or a mirror is set up, actual attack behavior may be elicited. Stoneberg found that by placing bright red pieces of felt on a male skin, he was able to elicit strong attack behavior. The male approached the skin with plumage sleeked except for the chin feathers, paused, then leaped at the skin, beating his wings and pecking at the head and breast. After a second attack, the male had succeeded in removing the combs as well as the feathers and skin from the neck and upper breast.

### Aerial Displays

In contrast to the terrestrial displays of spruce grouse, some population variation may occur in the aerial displays of males. Lumsden summarized his observations of aerial display by the nominate subspecies, which apparently consists of several variations. One of these is a short, vertical flight from a few to about 14 feet in the air, drumming on suspended wings, and fluttering back to the ground. This behavior is closest to the typical flutter-jump of prairie grouse. More commonly, however, the male flies either vertically upward or horizontally toward a tree perch, checks its flight, and either lands on the perch or drops back to earth. If it lands on the elevated perch it may stay there varying lengths of time; Lumsden reported periods as short as 10 seconds and as long as 4 minutes.

The flight back down is always performed in the same manner, by dropping steeply downward until the bird is about four to six feet from the ground, then swinging the body into a nearly vertical position, and descending on strongly beating wings toward the ground. Although the drumming sound produced by the wing-beats can be heard as far as 200 yards away, neither Lumsden nor Ellison (1968b) reported any wing-clapping sounds by males of this race, nor have other prior observers. Apparently no vocal calls are uttered during the flight.

Robinson (1980) noted that he never observed any "fancy" spiraling or dipping between branches during these display flights, and he believed that drumming flights are used both as an advertisement for territorial defense and for attracting a female that is not in sight. He judged that defended territories in his study area ranged from 1.5 to 6.23 acres along bog edges, and 9.9 to 24.7 acres in "broad habitat."

Descriptions of the aerial display flights of the Franklin race are somewhat at variance with this general situation. Stoneberg (1967) stated that the downward phase of the flight is as Lumsden described, except that during the final drop to the ground two loud sounds are produced, apparently by clapping the wings together. Once Stoneberg heard wing-clapping before the bird landed in a tree, and in 2 of 45 cases only one rather than two clapping sounds were produced. The wing-clapping display was most commonly heard near sunrise and sunset but often could be heard during the middle of the day as well. Stoneberg believed that cool temperatures favored performance of the display.

MacDonald's observations of wing-clapping are unusually complete, and he regarded the display as being an advertisement of the location of territorial males. He noted that the wing-clap flight was never started from the ground but always from some elevated site. Flying out from a branch some 10 to 20 feet high, the male moves on shallow wingbeats through the trees, with tail spread and tail-coverts conspicuous. On reaching the edge of a clearing, he rises slightly, makes a deep wingstroke, and brings the wings together above the back, producing a loud cracking sound. A second clap follows as the bird drops vertically toward the ground. The male soon selects another branch overhead and begins the sequence again. MacDonald noted that a resident male wing-clapped in the presence of an intruder, and after it had driven it away, began a sequence of vigorous displays and wing-clapping.

According to MacDonald, the vertical flight to a perch may be followed by display on the perch prior to launching into the wing-clapping display. He reported that after alighting on a branch and prior to the wing-clapping flight, the male might perform either or both of two different displays. These include a short rush along the branch followed by a spreading of the wings and tail, closing them, and again spreading the tail, apparently a variant of the tail-flicking display. A second display consists of three or four shallow wingstrokes, like the drumming of a ruffed grouse, producing a similar thumping sound.

### Vocal Signals

Two distinct vocal signals of males have been mentioned; one of these is the low-pitched "hoot" of a male in a sexual situation. These calls may be uttered as single notes or may occur in a series of notes roughly half a second apart (Greenewalt, 1968). They are notable for their extremely low-frequency characteristics of less than 100 Hz.

Males also utter a series of rather guttural notes in aggressive situations. When I placed an adult and immature male in a box together, both birds produced such calls. These usually consisted of two preliminary low, growling *kwerr* notes, followed by from 2 to 8 more rapidly repeated *kut* notes. Occasionally the two types of calls were uttered independently of one another. The younger male's calls were given at a noticeably higher pitch than those of the adult male.

Female spruce grouse produced at least three different types of notes under caged conditions. The loudest and highest pitched was a repeated squealing or whining *keee'rrr* call that resembled the distress call of various quail species. Females also uttered a softer series of *pit*, *pit*, *pit* notes when disturbed and a fairly low-pitched guttural *kwerrr*, which presumably corresponds to the two types of agonistic male notes just mentioned. When in a tree looking down on a human or other potential enemy, females utter a series of clucking sounds that quickly reveal their presence. Bent (1932) described these as *kruk*, *kruk*, *kruk* sounds, and a *krrrruk* that no doubt corresponds to the *kwerrr* note mentioned above. In-flight alarm calls have not been reported.

### Nesting and Brooding Behavior

There is no evidence that the male spruce grouse participates in nest or brood defense, although males may often be seen with females and well-grown broods in early fall. I observed this in southern Ontario during September of 1970, when at least four males were seen associated with females and broods. However, no attempt was made by the male to defend the brood; instead he simply appeared intent on displaying to the adult female.

Nests of the spruce grouse are usually situated in a well-concealed location, often under low branches, in brush, or in deep moss in or near spruce thickets. Ellison (*Alaska Department of Fish and Game*, *Game Bird Reports*, vols. 7–9, 1966–68) reported on 19 nest locations, 14 of which were in open, mature white spruce, birch, or spruce-birch-alder ecotones, while 2 were in open black spruce, 2 were in moderately dense black spruce, and 1 was in a mixture of alder and grass. Of 21 nests he found, the clutches ranged from 4 to 9 eggs, and averaged 7.4. Tufts (1961) reported clutch sizes for 39 nests, which ranged from 4 to 10 eggs and averaged 5.8. Robinson and Maxwell (1968) could find no authenticated record of a clutch having more than 10 eggs and concluded that earlier reports of larger clutches were in error. One instance of definite renesting was found by Ellison (*Game Bird Reports*, vol. 9, 1968). Pendergast and Boag (1971) reported the incubation period to be 21 days.

Robinson and Maxwell (1968) noted that when hens had chicks younger than 10 days old (when fledging occurs), the female is highly aggressive and may make threatening movements that resemble male strutting behavior. If the attack fails to deter the intruder, a "sneak" distraction display resembling a "broken-wing act" may occur but without actual injury feigning. In the case of hens with older broods, females may utter warning calls, but by that time they are much less aggressive toward intruders.

## Evolutionary Relationships

It would seem that the nearest living relative to the spruce grouse is *Falcipennis falcipennis*, the Siberian sharp-winged grouse, since it not only occupies a very similar habitat but also evidently has nearly identical courtship displays (Short, 1967; Hjorth, 1970). Some similarities in courtship characteristics between the spruce grouse and the blue grouse are also evident, including the short run toward the female followed by a single-note call, the production of very low-pitched hooting sounds, the tail-fanning displays, and the drumming flight behavior. Some interesting features of the male spruce grouse display also suggest affinities with the capercaillie. These include the general posture, the erection of the chin feathers to form a "beard," and calling with simultaneous tail-fanning. The general plumage appearance of both sexes is also very similar in these two species and the Siberian spruce grouse. Similarities between the display of the capercaillie and the Siberian spruce grouse have also been noted (Kaplanov, in Dementiev and Gladkov, 1967).

It seems probable that the evolutionary origin of the spruce grouse was in eastern Asia, where separation into two populations gave rise to the Siberian spruce grouse and the North American spruce grouse, the latter of which gradually moved southward and eastward through boreal forest and western coniferous forests. Contacts in the west with early *Dendragapus* stock may have provided the selective pressure favoring the evolution of conspicuous upper tail-covert patterning and wing-clapping during aerial display as sources of reinforcement of isolating mechanism differences between these two related types. There is apparently no fossil record of either "*Canachites*" or "*Falcipennis*" except for a late Pleistocene specimen from Virginia, whereas typical *Dendragapus* fossil remains are known from several localities in the western states (Jehl, 1969).

*Suggested reading:* Lumsden, 1961; Robinson, 1980; Boag and Schroeder, 1992

*Plate 9. Hudsonian spruce grouse, female; September.*



*Plate 10. Hudsonian spruce grouse, male strutting; September.*

*Plate 11. Hudsonian spruce grouse, male strutting; September.*

# Willow Ptarmigan

*Lagopus lagopus* (Linnaeus) 1758

## Other Vernacular Names

Alaska ptarmigan, Alexander ptarmigan, Allen ptarmigan, Arctic grouse, red grouse (in Great Britain), white grouse, white-shafted ptarmigan, willow grouse, willow partridge

## Range

Circumpolar. In North America from northern Alaska, Banks Island, Melville Island, Victoria Island, Boothia Peninsula, Southampton Island, Baffin Island, and central Greenland south to the Alaska Peninsula, southeastern Alaska, central British Columbia, Alberta, Saskatchewan, Manitoba, central Ontario, central Quebec, and Newfoundland.

## North American Subspecies

*L. l. albus* (Gmelin): Keewatin willow ptarmigan. Breeds from northern Yukon, northwestern and central Mackenzie, northeastern Manitoba, northern Ontario, and south-central Quebec south to central British Columbia, northern Alberta and northern Saskatchewan, and the Gulf of St. Lawrence in Quebec. Wanders farther south in winter.

*L. l. alascensis* Swarth: Alaska willow ptarmigan. Breeds from northern Alaska south through most of Alaska. Winters in southern part of breeding range.

*L. l. alexandrae* Grinnell: Alexander willow ptarmigan. Resident on the Alaska Peninsula south to northwestern British Columbia.

*L. l. ungavus* Riley: Ungava willow ptarmigan. Resident in northern Quebec and northern Labrador south to central Ungava.

*L. l. leucopterus* Taverner: Baffin Island willow ptarmigan. Resident from southern Banks Island and adjacent mainland to Southampton and southern Baffin islands; wanders farther south in winter.

*L. l. alleni* Stejneger: Newfoundland willow ptarmigan. Resident in Newfoundland.

*L. l. muriei* Gabrielson and Lincoln: Aleutian willow ptarmigan. Resident in the Aleutian Islands from Atka to Unimak, the Shumagin Islands, and Kodiak Island.

## Measurements

*Folded wing:* Adult males, 182–216 mm; adult females, 168–214 mm (males average 190 mm or more; females [except Baffin Island race] average less than 190 mm).

*Tail:* Adult males, 108–135 mm; adult females, 94–139 mm (males average 118 mm or more, females 116 mm or less).

## Identification

Adults, 14–17 inches long. All ptarmigan differ from other grouse in that (except during molt) their feet are feathered to the tips of their toes (winter) or base of their toes (mid-summer) and their upper tail-coverts extend to the tips of their tails. The primaries and secondaries of all the North American populations of this species are white in adults throughout the year, while in winter all the feathers are white except for the dark tail feathers, which may be concealed by the long coverts. Males have a scarlet "comb" of bare skin above the eyes (most conspicuous in spring), and during spring and summer are extensively rusty hazel to chestnut with darker barring above except for the wings and tail. The tail feathers (rectrices) are dark brown, tipped with white except for the central pair, which resembles the upper tail-coverts. In summer females lack this chestnut color and are heavily barred with dark brown and ochre. In autumn the male is considerably lighter, and the upperparts are heavily barred with dark brown and ocherous markings, lacking the fine vermiculated pattern found in males of the other ptarmigans at this season. The female in autumn is similar to the male but is more grayish above and more extensively white below. In winter both sexes are entirely white except for the tail feathers, of which all but the central pair are dark brownish black. In addition, the shafts of the primaries are typically dusky and the crown feathers of males are blackish at their bases. In first-winter males and females the bases of these feathers are grayish.

## Field Marks

The dark tail of both sexes at all seasons separates the willow ptarmigan from the white-tailed ptarmigan but not from the rock ptarmigan. In spring and summer the male willow ptarmigan is much more reddish than the rock ptarmigan, and although the females are very similar, the willow ptarmigan's bill is distinctly larger and higher and is grayish at the base. In fall males are more heavily barred than are male rock ptarmigan, and females likewise have stronger markings than do female rock ptarmigan. In winter males lack the black eye markings that occur in male rock ptarmigan, but since this mark may be lacking in females, the heavier bill should be relied upon to distinguish willow ptarmigan.

## Age and Sex Criteria

*Females* lack the conspicuous bright reddish "eyebrows" of adult males, are more grayish brown and more heavily barred on the breast and flanks than are males, and lack the distinctive rusty brown color of males in summer. In fall, females are somewhat grayer above and more heavily barred on the breast and flanks than are males. In winter they are like males, but the concealed bases of the crown feathers are more grayish (Ridgway and Friedmann, 1946). They can be fairly accurately identified at this time by their brown rather than black tail feathers and central upper tail-coverts and by certain wing and tail measurements (Bergerud, Peters, and McGrath, 1963).

*Immatures* in first-winter plumage tend to have the tip of the tenth primary more pointed than the inner ones, but this is not so reliable as the fact that (1) there is little or no difference in the amount of gloss on the three outer pri-

Map 5. North American distribution of the Alaska (A), Alexander (Ax), Aleutian (Al), Baffin Island (B), Keewatin (K), Newfoundland (N), and Ungava (U) races of the willow ptarmigan. Stippled area indicates wintering limits.

maries of adults, whereas immatures have less gloss on the outer two primaries than on the eighth, and (2) there is about the same amount of black pigment on primaries eight and nine (sometimes more on primary eight than nine) of adults, whereas juveniles have more on the ninth than on the eighth (Bergerud, Peters, and McGrath, 1963).

*Juveniles* may be identified by the fact that their secondaries and inner eight primaries are grayish brown with pale pinkish buff margins or barring. However, the late-growing outer two primaries are white, often speckled with black, like the first-winter flight feathers that soon replace the secondaries and inner primaries.

*Downy young* of willow ptarmigan are reported (at least in the Scottish population) to be darker on both the dark and lighter areas, and have less clearcut margins between these areas than downy rock ptarmigan (Watson, Parr, and Lumsden, 1969). These authors mention other differences that may also serve to separate downy young of these two species, although these may not apply equally well to North American populations. For example, in the Labrador population, birds under three weeks are almost impossible to identify as to species, although young willow ptarmigan are slightly darker and somewhat greenish instead of yellowish on the underparts (Bendire, 1892). After three weeks they may be distinguished by differences in the bill.

## Distribution and Habitat

The North American breeding range of the willow ptarmigan is primarily arctic tundra, although it extends southward somewhat in alpine mountain ranges and in tundra-like openings of boreal forest (Aldrich, 1963). The basic habitat consists of low shrub, particularly willow or birch, in lower or moister portions of tundra. Weeden (1965b) has characterized the general breeding habitat of willow ptarmigan as follows: typical terrain is generally level or varies to gentle or moderate slopes but frequently is at the bottom of valleys; vegetation is relatively luxuriant, with shrubs usually three to eight feet high and scattered through areas dominated by grasses, hedges, mosses, dwarf shrubs, and low herbs. The birds usually occur at the upper edge of timberline, among widely scattered trees, or they may occur somewhat below timberline where local treeless areas occur.

Because of the relatively minor effect man has had on tundra to date, there have been few if any major evident changes in the total range of the species.

## Population Density

Ptarmigans are among the arctic-dwelling species that exhibit major fluctuations in yearly abundance and are believed by many to exhibit regular cyclic population changes (Buckley, 1954). In any case, major changes in population density do occur, thus estimates of density may vary greatly by year as well as by locality. Weeden (1963) summarized estimates of population density for various areas in Canada. These estimates ranged from less than 1 adult per square mile (2.5 square miles per adult) to as many as 8 adults per square mile, with the sparser densities generally based on large areas that include much unfavorable habitat. He also reported (1965b) that a study area of 0.75 square miles had spring populations of males ranging in number from 38 to 150 during seven years of study, which represents from 3.2

to 12.3 acres per male. Somewhat comparable density figures have been reported from Newfoundland (Mercer and McGrath, 1963), where spring 1962 populations on Brunette Island were estimated to be 147 to 207 birds per square mile, depending on technique used. Extensive population research has been done on the Scottish red grouse (now considered as conspecific with the willow ptarmigan) by Jenkins, Watson, and Miller (1963), who estimated spring densities of from 4.5 to 9 acres per pair.

A 2004 estimate of the species' total North American population was 11.1 million, out of a world population of 37 million (Rich et al., 2004). In 2016 the only state in which willow ptarmigan could be legally hunted was Alaska, but it is widely hunted in northern Canada. During the 1970s about 300,000 ptarmigan of all species were being shot by hunters in North America (Johnsgard, 1975), so it is unlikely that hunting has any measurable effect on ptarmigan densities.

## Habitat Requirements

### *Wintering Requirements*
Weeden (1965b) reported that winter habitat of willow ptarmigan consists of willow thickets along streams, areas of tall shrubs, and scattered trees around timberline and burns, muskegs, and river banks below timberline. Bent (1932) noted that in winter willow ptarmigan move to interior valleys, river bottoms, and creek beds, where there is available food in the form of tree buds and twigs of willows (primarily), alders and spruces, and such berries and fruits as can be found above the snow. Godfrey (1966) indicated that during winter the birds might be found well south of treeline, in muskegs, lake and river margins, and forest openings.

### *Spring Habitat Requirements*
Weeden (1965b) stated that male habitat preferences for territorial establishment include shrubby and "open" vegetation, with the plants lower than eye-level for ptarmigan. Males use elevated sites such as rocks, trees, or hummocks during display. Resting areas are provided by small clumps of shrubs at the edges of open areas.

At least in Scotland, territorial establishment occurs during fall, although territories may be abandoned temporarily during winter if snow conditions require it. In Alaska some full display and calling also occurs (Weeden, 1965b). Continued residence, however, is not typical in Alaska or probably in any part of the North American breeding range, since considerable seasonal movement is typical. Thus, local topography, as it affects snow deposit and rate of snow thaw exposing territorial sites, may have considerable effect on territorial distribution of birds in arctic North America.

### *Nesting and Brooding Requirements*
Requirements for willow ptarmigan nest sites are apparently fairly generalized. Brandt (in Bent, 1932) reported that nesting may occur anywhere from coastal beaches to mountainous areas, and nests may be placed beside drift logs, in grass clumps, under bushes, in mossy hummocks, or similar sources

of screening protection. Weeden (1965b) indicates that the nest is usually protected from above and the side by shrubby vegetation, while one side borders an open area. The nest is located within the periphery of the male's territory.

Brooding habitat is similar to nesting habitat, according to Weeden (1965b), with chicks using areas of very low vegetation, while older broods use shrub thickets for escape cover. Maher (1959) noted that broods used a variety of habitats with good cover and were common on upland dwarf-shrub and hedge tundra, as well as being sometimes found in riparian shrub and willow shrub at the bases of hills.

## Food and Foraging Behavior

At least in Alaska, willow buds and twigs provide the most important single food source for willow ptarmigan. Weeden (1965b) noted that this source provided almost 80 percent of winter foods found in 160 crops from interior Alaska, and Irving et al. (1967) also indicated that winter foods consisted almost entirely of the buds and twig tips of willow. Weeden noted that dwarf birch buds and catkins were second in importance, and Irving et al. similarly found that in wooded areas some birch catkins and poplar buds are taken. West and Meng (1966) found that 94 percent of the winter diet of willow ptarmigan from northern Alaska consisted of various willow species, and 80 percent was from a single species (*Salix alaxensis*). They also noted that some birch may be used but although alder is often available and has a higher caloric content than willow, it is seldom used.

One exception to the general winter diet of willow for North American willow ptarmigan has been noted, in Peters's study (1958) of the Newfoundland population. He found that the winter diet consists almost entirely of the buds and twigs of *Vaccinium* species, the buds and catkins of birch and alder, and the buds of sweet gale (*Myrica*).

With spring, the willow ptarmigan's dependence on willow declines in Alaska, and in addition to the leaves of willow, the birds begin to eat a larger variety of leafy materials (Weeden, 1965b). Peters (1958) also noted a spring return to fruit and leafy materials and the berry seeds of crowberry (*Empetrum*) and *Vaccinium*.

Summer foods in Alaska consist of various berries, especially blueberries, willow and blueberry leaves, and the tips of horsetail (*Equisetum*), which grows in willow thickets near streams (Weeden, 1965b). Peters noted that crowberries, blueberries, and the leaves of *Vaccinium* species, especially *V. angustifolium*, provided major sources of summer foods in Newfoundland.

In the fall, as the berry supplies are exhausted and leaves fall from *Vaccinium* bushes, the ptarmigan in Newfoundland return to a diet of buds and twigs (Peters, 1958). The same situation applies to Alaska, although it is willow, rather than *Vaccinium* buds and twigs, that is eaten (Weeden, 1965b). Irving et al. (1967) found a gradual increase in total crop contents of Alaskan ptarmigan from October to January, followed by reduced contents until April. This population migrates southward in October and November and northward from January until May. Evidently feeding is related to changing patterns of daylight rather than temperature cycles or the cycle of migratory activities.

## Mobility and Movements

The willow ptarmigan and its relative the rock ptarmigan are perhaps the most migratory of all North American upland game. Snyder (1957) reported that the willow ptarmigan is migratory to a considerable extent, occasionally wandering as far as the southern parts of the prairie provinces, northern Minnesota, the north shore of Lake Superior, southern Ontario, and southern Quebec. To some degree these southern movements may be related to unusually dense populations in the northern areas (Buckley, 1954). Evidently considerable differential movement according to sex occurs in Alaska (Weeden, 1964). At Anaktuvuk Pass, for example, most wintering willow ptarmigan are males, while many of the wintering birds in timbered areas to the south are females. Likewise, males mostly use alpine-fringe areas of the Alaska Range and the Tanana Hills during winter, whereas females are to be found abundantly in the Tanana Valley (Weeden, 1965b). Weeden (1964) suggested that this differential movement may represent a dispersal mechanism or serve as a means of reducing food competition, or perhaps indicates that females may survive better in forested areas under winter conditions.

Irving et al. (1967) have documented the migration of willow ptarmigan through Anaktuvuk Pass in the Brooks Range. Although few ptarmigan nest there, some 50,000 birds pass through this point each year. The fall migration reaches a peak in October and is over by December, while the spring migration starts in January and early February, subsides in March, and is renewed in April. The early fall migrants are mostly juvenile males and females, whereas the number of adult males gradually increases to a maximum in March, or two months later than the maximum movement of juvenile males. The authors reported no clear indication of cyclic changes in population numbers annually. A spruce forest area occurring 35 miles south of the pass is one of the areas used for wintering, and breeding occurs on the north slope of the Brooks Range and beyond to the Arctic coast. Some of these breeding areas may not be occupied until late in May.

So far, virtually nothing is known of daily movements of willow ptarmigan, and such information will require detailed studies of individually marked birds. Jenkins, Watson, and Miller (1963), studying red grouse, found the birds to be remarkably sedentary in this nonmigratory population. Of 739 birds banded as chicks, only 5 were recovered more than 5 kilometers away that season, and some of this movement may have been caused by the birds' being driven for hunting purposes. Of 290 birds banded as chicks but recovered as adults, 230 were obtained within 1.5 kilometers of the banding location. It would thus appear that willow ptarmigan move only as far as is necessary to maintain a source of

food and cover during the coldest parts of the year. Weeden (1965b) reported that a male and its mate were both found a year after they were banded as adults defending a brood about 100 yards away from the original banding point a year previously, which would attest to considerable site fidelity in this species. Bergerud (1970b) reported that females are more mobile than males, with one banded female moving 61 kilometers in about three months.

## Reproductive Behavior

### Territorial Establishment

Most observations of territorial behavior in this species derive from studies of the red grouse in Scotland by Watson, Jenkins, and their associates. Likewise, display descriptions are also based on this population, unless otherwise indicated.

Territorial behavior and the success of territorial establishment appear to be crucial factors in the biology of red grouse populations, judging from the work of Jenkins and Watson. Territories in red grouse are established in early fall, and the numbers of such territorial males that can be accommodated on a habitat apparently limits the density of the breeding population. Nonterritorial males are forced out of the preferred areas into marginal habitats, where they are more heavily exposed to predation, starvation, and disease. However, such losses play little if any role in the success of the population. Since juvenile birds are rarely able to attain territorial status their first fall, early territorial establishment would favor reproduction by mature males.

Territorial establishment in the North American willow ptarmigan is presumably in spring, although some fall display and calling by males may occur (Weeden, 1965b). However, it is not until late April or May that the willow ptarmigan have acquired their striking nuptial plumage, which presumably provides important visual signals for territorial proclamation and attraction of females. Weeden (1965b) has made the interesting point that whereas the male willow ptarmigan undergoes courtship in this bright brown and white plumage, the rock ptarmigan is still in completely white plumage during courtship, which perhaps provides important visual distinction for species recognition between the two species.

Territorial size has been studied intensively by Jenkins, Watson, and Miller (1963) for red grouse. They found that in each year, some individual territories were larger than others, but in years of high grouse populations the territories in general averaged smaller sizes than in years of lower densities. Territories selected by previous residents were usually larger than could later be defended against newly colonizing birds. Sketched maps presented by these authors indicate that territorial size rarely exceeded a maximum diameter of 300 yards, and most were much smaller. One study area of 56 hectares (138 acres) supported 24 territorial males (2 of which were unmated) in 1961, thus territorial sizes averaged 5.7 acres in the area during that year. In 1960, 16 males (2 unmated) occupied the same area, and in 1958 there were over 40 territorial males (10 unmated) on it. For the study areas as a whole, the breeding density over the years varied from one pair to about five acres, in 1957 and 1958, to about one pair per 15 acres in 1960.

### Agonistic and Sexual Behavior

In contrast to the species considered previously, it is almost impossible to differentiate completely between male and female behavior patterns in the ptarmigan. This is primarily a reflection of their monogamous or nearly monogamous pair bond and a subsequent reduction of sexual selection pressures for dimorphic behavior patterns. Watson and Jenkins (1964) have provided a detailed account of behavior patterns in the red grouse, which will be summarized here in the belief that their findings should apply to the North American willow ptarmigan with little or no modification. Although they also discussed comfort behavior, maintenance activities, and other behaviors, only those patterns directly concerned with reproduction will be mentioned here.

Agonistic behavior patterns of males associated with establishment and defense of territories include sitting on an exposed lookout, such as a hillock or stone, where most of the territory can be seen. Intruders are approached in an attack-intention posture characterized by erect combs, the head and neck stretched forward, the body near the ground, the wings held in the flanks, and the bill open. Prior to such an approach the bird may fan its tail and droop its wings in a manner resembling the waltzing display. A lesser type of threat consists of standing in one place and uttering *kohway* and *kohwayo* calls. A still weaker threat consists of standing and uttering a *krrow* call, which in turn grades into watchful behavior, flight intention, and finally fleeing by running or flying away.

Several kinds of aggressive encounters may occur. Brief encounters may last only a few seconds and involve birds of either sex, which may or may not occur on a territory. "Jumping" is a communal encounter that also is not limited as to sex and not related to territory. In this, two or more aggressive birds will begin to jump about with wing-flapping, causing them to become more fully separated. Prolonged chases may occur when a dominant male follows a subordinate bird for great distances, often beyond its territory, and may in fact kill or wound it. "Facing" occurs when two equally dominant birds face each other with combs erect, heads forward, and wings flicking, with neither one showing signs of retreat. When actual fighting occurs the birds usually do not face each other but rather face in the same direction and strike each other from the side with their bills, wings, and feet. "Walking-in-line" consists of two birds walking side by side some 20 inches apart. While so walking they utter *kohway* and *ko-ko-ko* calls that indicate attack intention, and they may also utter the *krrow* threat call. Such displays by two males often occur at the edges of territories, and hens may perform the same display anywhere in the territory. Occasionally the display occurs outside breeding territories, where up to six birds may participate.
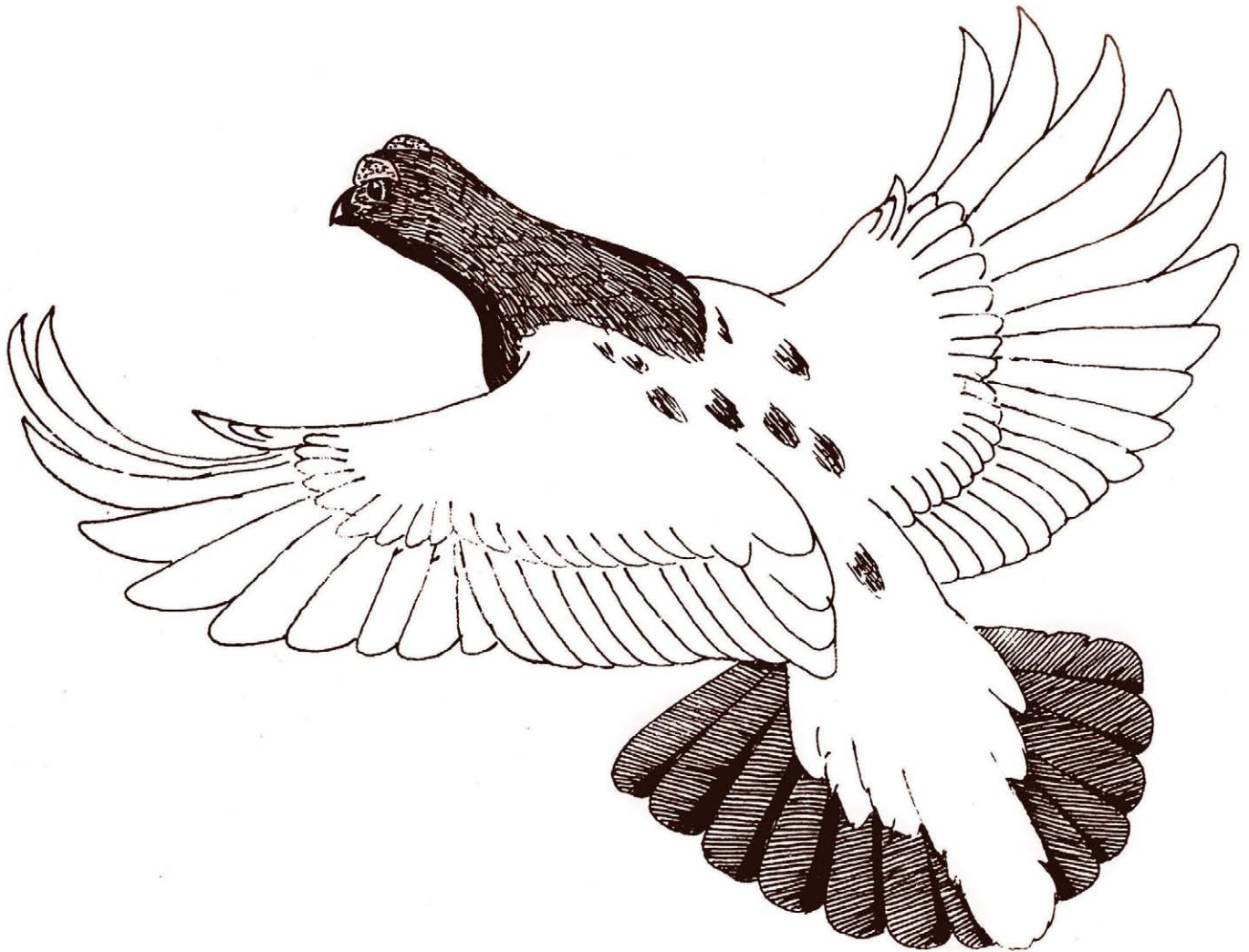
*Fig. 16. Male willow ptarmigan, landing after song-flight.*

Sexual patterns involve pair formation behavior and copulatory behavior. Pair formation is achieved by the males' advertising their territories, and the females being attracted to the more vigorous males. On arriving on a territory, the female may utter a *krrow* call and look for a displaying male to approach. If there is none, she may fly to another territory, until a resident male makes a song-flight landing near her and begins to strut towards her. The female then flees but may be driven back to the territory by the male. Sexual activity occurs in Scotland every month but is most common from February to April, and many pair bonds that had been established earlier are only temporary and may be easily disrupted. When in breeding condition, the male has a highly conspicuous red eye-comb that can be erected to about 1 centimeter. Although the hen's combs are much smaller and paler, they too can be erected.

The male's approach to another bird of either sex is essentially a threatening one, and in the case of a receptive hen the response is one of submissive gestures. Thus the sexual differences in display are not so much qualitative as they are quantitative, in terms of relative dominance and submission. Sex recognition is probably also achieved by the different voice, plumage, and comb development of the hen.

The postures performed by a male in the presence of a female but not elicited in the presence of other males may be considered "courtship" displays. Watson and Jenkins (1964) listed five such displays: tail-fanning, waltzing, rapid-stamping, bowing, and head-wagging.

Tail-fanning is performed by a male when approaching a hen. While cocking his tail, he may fan it with a rapid flick, at the same time lowering his wings and scraping the primaries on the ground as he moves forward. In this stage, the wings are drooped equally and the tail is not tilted. Often the male moves in a slight curve in front of the female, or he may pass in front of her alternately from both sides. Sometimes the under tail-coverts are exposed by his turning away from the hen. Such movements grade into "waltzing," during which the male circles the female closely,

pivoting around her with short, high steps and drooping the wing nearer her, at the same time tilting the tail to expose its upper surface more fully to her view. The body may be tilted toward the hen as well. During "rapid-stamping" the male runs toward the hen with his tail slightly fanned, his neck thickened and arched, and his head held low with the bill wide open. In this posture he might pass close beside the other bird and appear to be attacking her, but the differences in wing and neck positions make it possible to distinguish these two types of behavior easily. If the hen does not flee and mounting does not occur at that time, the male will often raise and lower his head, with his body still held low, the tail partly fanned and the nape feathers raised, in a display called "bowing."

The last of the courtship displays is head-wagging, which both sexes perform. The bird crouches near its mate, extends its neck forward, and quickly wags its head in lateral fashion, exposing its eye combs and twisting its head slightly with each wag. When a hen approaches a cock, the male may also crouch low, erect his combs, and lower his head, producing a posture strongly suggestive of the precopulatory "nuptial bow" of prairie grouse. Although both sexes perform head-wagging, it is not a mutual display, and instead the birds often perform it alternately. When the female performs it, the male may attempt to mount her. However, during actual solicitation, the female crouches without head-wagging, opens her wings, and holds her head up. The male immediately mounts, drooping his wings around the hen during copulation. Afterward, the male utters several threat calls, displays strongly for a few minutes, and often moves to a lookout post.

### Vocal Signals

Watson and Jenkins (1964) described fifteen different vocal signals of adults that are uttered by both sexes, although the hen's calls may be recognized by their higher pitch. Song flight, or "becking," is uttered as the bird takes off, flies steeply upward for 30 feet or more, sails, and then descends gradually while fanning its tail and beating its wings rapidly. On landing the bird may stand erect, droop its wings, fan its tail, and bob its head. During the ascent phase, the call is a loud, barking *aa*, while a *ka-ka-ka-ka* is uttered some 8 to 12 times with gradually slower cadence. After landing, a gruffer and slower call *kohwa-kohwa-kohwa* (also interpreted as *go-back*, *kowhayo*, and *tobacco*) is uttered for a varying length of time. Hens and nonterritorial males do not fly as high or call as loudly as territorial males, and no doubt this call is important in territorial proclamation.

In calling on the ground, a similar signal is uttered, often from a song post such as a stone. The bird stretches his neck diagonally upward and utters a vibrating *ko-ko-ko-ko-krrrrr*, up to about 20 syllables, increasingly faster toward the end. Such calls may be used to threaten approaching animals or birds flying overhead and are largely but not entirely territorial advertisement.

During attack, the birds utter a *kowha* sound, like the last part of the flight song but without preliminary notes. It may be given during attack, when trying to mount hens, or immediately after copulation. A similar call, *koway*, is an attack-intention, or threat, call and is rapidly repeated as a series of hurried notes. A variant is *kohwayo*, also repeated but indicating less aggressiveness than the last call. Still less aggressive notes are *krrow* and *ko-ko-ko*, the latter representing a flight-intention call. This call is given by a bird about to fly or one being handled by a human and may stimulate other birds to take flight.

When a grouse is charging another bird, a single note, *kok*, may be uttered, especially by the chased bird. The same call may be used as an in-flight alarm note. A similar *kok* note serves as a mammalian predator alarm note, while a *chorrow* note serves for an aerial raptor warning signal. A sexual note, *koah*, the emphasis on the first syllable, is used between members of a pair when crouching and head-wagging, when examining nest sites, or when bathing. Hens may also utter it when a nest is approached, but hissing is more often elicited under these conditions. Hissing may also occur when a bird is being handled. A *krow* note is used during distraction display by parents, causing the young to crouch, while a *korrr* or *koo-ee-oo* serves as a call to chicks, especially those uttering distress calls. Finally, a harsh, chattering *krrr* note is used as a defense against avian predators that are attacking the bird or its family.

Watson and Jenkins reported that the distress cheep of chicks is uttered until the young are nearly full-grown, when it gradually changes to a *kyow* note, and finally to the adult *krrow*, and probably then serves as a contact call. Even newly hatched chicks will utter a chattering call that evidently is aggressive in nature and apparently develops into the adult "ground song." By the age of 10 to 12 weeks the male begins to acquire a voice that differs from that of females, resembling more the voice of an adult cock.

### Nesting and Brooding Behavior

The only available analysis of nest-site selection behavior is that of Jenkins, Watson, and Miller (1963) for Scottish red grouse. They studied 163 nests, nearly all of which were in heather cover (*Calluna*). The average height of the heather cover was 378 centimeters (149 inches), compared with a mean cover height of 17 centimeters (7 inches). Most nests were partly overhung with vegetation, but 17 percent were completely uncovered, and 12 percent were completely covered. Most were on hard, well-drained ground, and 67 percent were on flat ground. Most were shallow scrapes, sparsely lined with various plants, including grasses and heather. Usually the nests were within 500 feet of grit sources, water, and mossy or grassy areas where the chicks could feed. The clutch size of this population varied in different years and in different study areas from 6.1 to 8.1 eggs (the average of 395 nests was 7.1 eggs), and the estimated incubation period was 22 days.
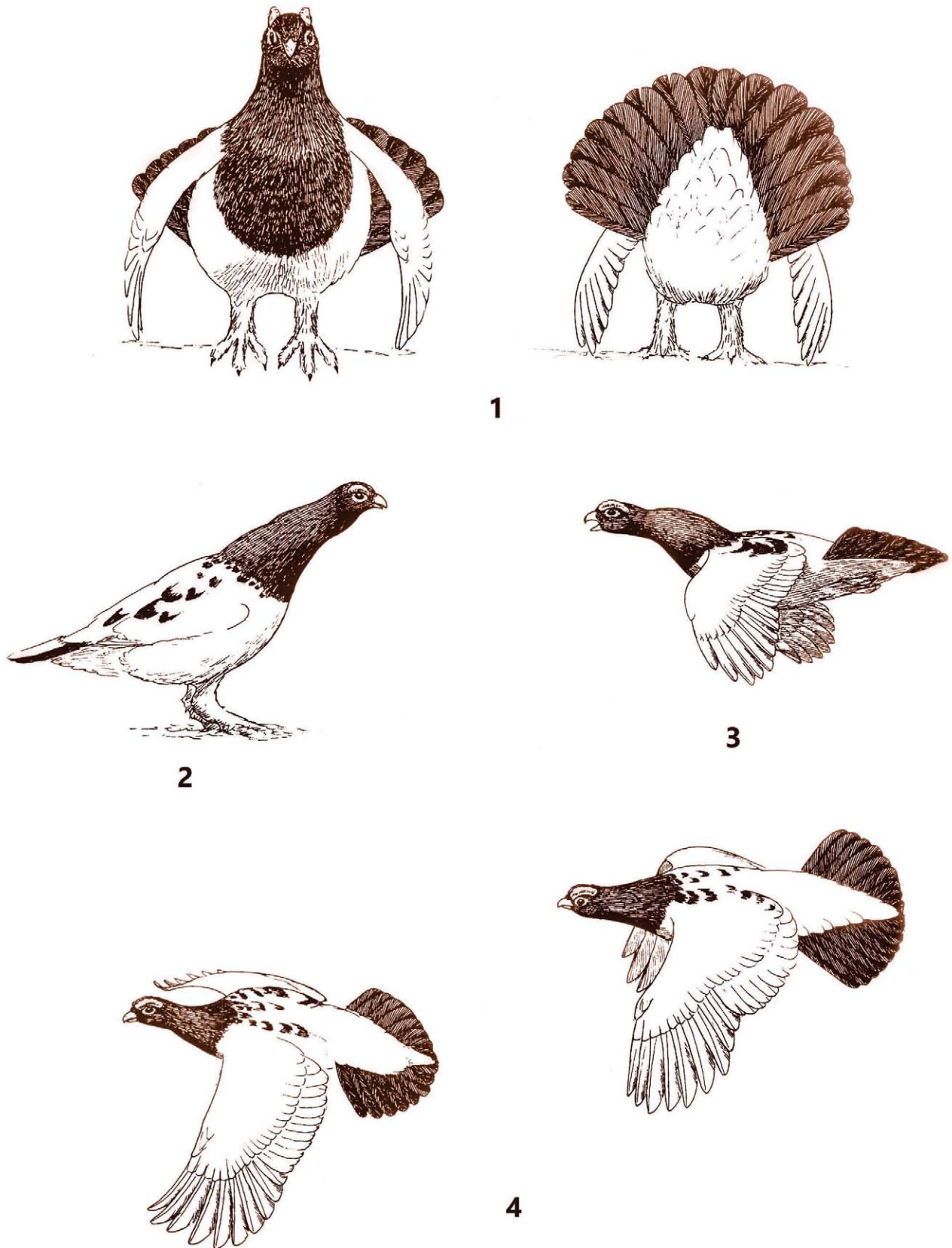
Fig. 17. Male willow ptarmigan, showing (1) front and rear views of tail-fanning and wing-drooping, (2) calling posture of territorial male, (3) song-flight, and (4) aerial chasing. Various sources.

Some comparable information is available for North American willow ptarmigan. Kessel and Schaller (1960) reported that five nests in Alaska had 6 to 7 eggs, averaging 6.8. Eight clutches from northern Alaska averaged 7.8 eggs. Bergerud (1970b) reported an average clutch of 10.2 eggs in 106 Newfoundland nests. Nests containing up to 17 eggs would appear to be the work of at least two females. The incubation period of the North American birds is likewise 21 to 22 days, and the egg-laying interval is somewhat greater than 24 hours (Westerskov, 1956). Bergerud (1970b) judged that in Newfoundland renesting probably accounted for 12 to 18 percent of the young produced.

Unlike the other species of ptarmigan, the male typically remains with the female through the incubation period and assists in brood defense. Jenkins, Watson, and Miller (1963) reported that the percentage of broods observed with both parents in attendance ranged from 61 to 90 percent in various years and areas. In good breeding years, most broods were attended by both parents until they were at least two months old, while in poor breeding years 30 to 40 percent were not attended by parents at any stage. The percentage of parents observed performing distraction display ranged from 4 to 72 percent. Individual brood sizes ranged to as many as 12, and averages varied greatly in different years. Roberts (1963) reported an average brood size of 6.3 chicks for Alaskan willow ptarmigan. This figure is higher than any yearly average reported by Jenkins, Watson, and Miller, whose highest reported brood size was 5.2 for one study area in 1960.

## Evolutionary Relationships

Evolutionary relationships of the genus *Lagopus* as a whole would seem to be very close to both *Dendragapus* and *Tetrao*, as Short (1967) has already suggested. It is perhaps impossible to judge which of these two genera *Lagopus* most closely approaches, and presumably all three genera differentiated from common stock at about the same time.

Relationships within the genus *Lagopus* represent another problem. The white-tailed ptarmigan differs from the rock and willow ptarmigans in several respects, which have been enumerated by Short (1967), and it is clearly the most isolated of the three species. Höhn (1969) suggested such an early offshoot of ancestral white-tailed ptarmigan stock in North America, with which I am in agreement. Höhn judged that the willow and rock ptarmigan ancestral stock also diverged in North America, with the rock ptarmigan moving east to Greenland and both species moving west across the Bering Strait into Eurasia. This kind of speciation model seem unlikely to me, as I can visualize no major barriers that might have allowed for separation of ancestral willow and rock ptarmigan stock in northern North America.

It seems more likely to me that one of these types developed in Eurasia and the other in North America after a splitting of common gene pools, and after secondary contact the rather marked ecological differences between them allowed the development of the extensive geographic contact between them that now exists. In contrast, Johansen (1956) suggested that the genus *Lagopus* originated in Asia and reached North America at an early date, during which the ancestral white-tailed ptarmigan separated from pre-*mutus* stock.

In a strictly behavioral sense, I would regard the willow ptarmigan as more primitive than the other two ptarmigan, in both of which a breakdown on strong pair bonds and a tendency toward polygamy may be seen. It seems probable to me that the evolution of mating patterns in the grouse was from an originally monogamous situation to a polygamous or promiscuous one, rather than to believe that the monogamous situation of the willow ptarmigan is derived from a nonmonogamous mating type. The retention of monogamy or near monogamy in the ptarmigans seems to me to be an ecological artifact, resulting from the greater needs for intensive parental care in an arctic situation than in a subarctic or temperate one, in which the duties of incubation and brood-rearing can be more effectively undertaken by the female alone. This latter arrangement thus frees the male to fertilize a potentially larger number of females, and these resulting reproductive advantages have led to reduced pair bonds or to promiscuous matings.

It is curious, however, that the willow ptarmigan, rather than the rock ptarmigan, has more strongly retained a monogamous and prolonged pair bond, since the rock ptarmigan has an even more northerly breeding distribution and must nest under equally severe breeding conditions. Arnthor Gardnarsson (pers. comm.) has found that in Iceland the males suffer a much higher rate of predation by gyrfalcons than do females, apparently as a result of the male's more conspicuous plumage during the breeding season. The mating system there is an essentially promiscuous one, since the females do not closely associate with males or their territories. Such differential sexual predation pressures might account for the rock ptarmigan's less strongly monogamous mating system and the reduced period of contact between the sexes.

*Suggested reading:* Weeden, 1965; Mercer, 1967; Hanson, Eason, and Martin, 1998

*Plate 12. Newfoundland willow ptarmigan, territorial male; May.*



*Plate 13. Alaska willow ptarmigan, territorial male, molting male; August.*

*Plate 14. Alaska willow ptarmigan, molting immature; August.*



*Plate 15. Keewatin willow ptarmigan, female nest-distraction display; June.*

*Plate 16. Keewatin willow ptarmigan, female standing; June.*

# Rock Ptarmigan

*Lagopus mutus* (Montin) 1776

## Other Vernacular Names

Arctic grouse, barren-ground bird, Chamberlain ptarmigan, Dixon ptarmigan, Nelson ptarmigan, Reinhardt ptarmigan, rocker (in Newfoundland), snow grouse, Townsend ptarmigan, white grouse

## Range

Circumpolar. In North America from northern Alaska, northwestern Mackenzie, Melville Island, northern Ellesmere Island, and northern Greenland south to the Aleutian Islands, Kodiak Island, southwestern and central British Columbia, southern Mackenzie, Keewatin, northern Quebec, southern Labrador, and Newfoundland.

## North American Subspecies (excluding Greenland)

*L. m. evermanni* Elliot: Attu rock ptarmigan. Resident on Attu Island, Aleutian Islands.

*L. m. townsendi* Elliot: Kiska rock ptarmigan. Resident on Kiska and Little Kiska islands, Aleutian Islands.

*L. m. gabrielsoni* Murie: Amchitka rock ptarmigan. Resident on Amchitka, Little Sitkin, and Rat islands, Aleutian Islands.

*L. m. sanfordi* Bent: Tanaga rock ptarmigan. Breeds on Tanaga and Kanaga islands, Aleutian Islands.

*L. m. chamberlaini* Clark: Adak rock ptarmigan. Resident on Adak Island, Aleutian Islands.

*L. m. atkhensis* Turner: Atka rock ptarmigan. Resident on Atka Island, Aleutian Islands.

*L. m. yunaskensis* Gabrielson and Lincoln: Yunaska rock ptarmigan. Resident on Yunaska Island, Aleutian Islands.

*L. m. nelsoni* Stejneger: Alaska rock ptarmigan. Resident in northern Alaska and northern Yukon south to the eastern Aleutians, the Alaska and Kenai peninsulas, and Kodiak Island and east to the western Yukon.

*L. m. rupestris* (Gmelin): Canada rock ptarmigan. Breeds from northern Mackenzie, Melville Island, northern Ellesmere Island, and southern Greenland south to central British Columbia, southern Mackenzie, southern Keewatin, Southampton Island, northern Quebec, and Labrador.

*L. m. dixoni* Grinnell: Coastal rock ptarmigan. Resident on the islands and coastal mainland of the Glacier Bay region of Alaska and on the mountains of extreme northwestern British Columbia south to Baranof and Admiralty islands.

*L. m. welchi* Brewster: Newfoundland rock ptarmigan. Resident in Newfoundland.

## Measurements

*Folded wing:* Adult males, 172–202 mm; adult females, 163–95 mm (males average nine mm longer than females).

*Tail:* Adult males, 97–120 mm; adult females, 85–115 mm (males of all races average 104 mm or more, females usually average under 104 mm).

## Identification

Adults, 12.8 to 15.5 inches long. Both sexes carry blackish tails throughout the year, and although the scarlet comb of males is most evident during the spring, it is also apparent to some extent through the summer. In the summer males are extensively but rather finely marked with brownish black and various shades of brown and lack the rich chestnut tone of male willow ptarmigan. In summer females are more coarsely barred and are generally lighter overall but have somewhat finer markings than do female willow ptarmigan. Females have definite barring extending to the throat and breast, rather than having these areas finely barred or vermiculated as in males. In autumn males are generally pale above, with tones of ashy gray predominating (tawny brown predominating in some Aleutian races), and females at this time have relatively more brown and fewer black markings, plus a sprinkling of white winter feathers. Both sexes in winter are mostly white with blackish tails; males (and most females) also have a black streak connecting the bill with the eye and extending somewhat behind the eye.

## Field Marks

The smaller, relatively weaker, and entirely black bill of the rock ptarmigan serves to separate this species from the willow ptarmigan in all seasons and is sometimes detectable in the field. In the winter, the presence of a black line through the eyes is also diagnostic, but its absence does not exclude this species. For plumage distinctions useful in separating the willow and rock ptarmigans, see the account of the preceding species. During the breeding season the rock ptarmigan is found in higher, rockier, and drier country than the willow ptarmigan, but they may occur together during winter and intermediate periods. In all seasons the dark tail distinguishes the rock ptarmigan from the white-tailed ptarmigan.

## Age and Sex Criteria

*Females* lack the reddish skin combs or "eyebrows" of adult males and in summer are more heavily barred with dark markings both above and below. In autumn the barring is reduced in the female, which is still somewhat more heavily marked than the grayish and finely vermiculated male. In winter the sexes are nearly identical, but females usually lack the black stripe through the eye that is present in males (Godfrey, 1966).

*Immature* females are browner and more narrowly barred with blackish brown above and on the breast than are adult females in autumn (Ridgway and Friedmann, 1946). The pointed condition of the outer primaries has been reported to be an unreliable indicator (Weeden, 1961). Instead, young rock ptarmigan may be distinguished by the fact that in adults the ninth primary (second from outside) has the same amount of pigment as the eighth, or less, whereas immature birds have more pigment on the ninth (Weeden and Watson, 1967).

*Juveniles* may readily be recognized by the presence of at least one brown primary or secondary feather (the eighth

primary is the last to be molted). These feathers are typically mottled with pale buff (Ridgway and Friedmann, 1946).

*Downy young* are usually paler throughout than those of willow ptarmigan, and the crown is lighter and more chestnut colored than the blackish brown crown of the willow ptarmigan (Watson, Parr, and Lumsden, 1969). See willow ptarmigan account.

## Distribution and Habitat

The most arctic-adapted of all the grouse, the rock ptarmigan is more widely distributed in the high arctic than is the willow ptarmigan. It also extends south to Hudson Bay during the breeding season and undertakes considerable southward movement during winter, sometimes occurring as far south as James Bay. Unlike the willow ptarmigan, the rock ptarmigan breeds as far north as Ellesmere Island and on adjacent Greenland to its northern limits at approximately 83°N latitude. Also unlike the willow ptarmigan, this species can survive in the rocky desertlike habitat of the high arctic, which may be a limiting factor in the northern distribution of the willow ptarmigan. Weeden (1965b) reported that typical breeding terrain of the rock ptarmigan consists of moderately sloping ground in hilly country, such as the middle slopes of mountains. Typically, the vegetation is fairly complete but may be sparse on the highest and driest slopes. Shrubs are usually from 1 to 4 feet tall and are concentrated in ravines or other protected sites, while most plants are usually less than 1 foot tall. Many creeping or decumbent woody plants are typical, as well as rosette forms, while sedges and lichens are usually abundant. Breeding terrain rarely extends below the upper limits of timberline and usually occurs from 100 to 1,000 feet above timberline in hilly country.

There have probably been few changes in the distribution of rock ptarmigan in historical times, since it is the species least likely to be affected by human activities. Considerable population fluctuations are known to occur, but those occurring in Greenland and Iceland have been interpreted as representing a ten-year cycle. Buckley (1954) concluded that ptarmigan populations in Alaska are also cyclic in nature, but data to prove this view were inadequate (Weeden, 1963).

## Population Density

Weeden (1963) has summarized population density figures for rock ptarmigan based on various studies in the Northwest Territories. These estimates range from as many as 8 adults per square mile to 4,000 adults on 12,500 square miles (1 bird per 3.1 square miles). Based on a five-year intensive study on a 15-square-mile study area in Alaska, Weeden (1965a, 1965b) reported yearly spring densities of males varying from 5.9 to 11.3 per square mile. Slightly lower estimates of female populations were obtained for the same period.

In a study of Scottish ptarmigan, Watson (1965a) estimated spring populations to be as high as one pair per 2 to 3 hectares (approximately 5 to 7.5 acres) in peak years on the best habitats. However, unlike the fairly uniform heather

(*Calluna*) habitats favored by red grouse, the arctic-alpine breeding vegetation is typically more varied, and an area of 100 or more acres rarely contains no unfavorable habitat. Thus, extrapolations of local density data to large areas is unprofitable; this also helps explain the wide differences in densities reported on small, favorable areas and those estimates based on large regional surveys. Watson estimated that in peak years, spring numbers on his study area of 1,220 acres were as high as 15 to 18 birds per 100 hectares (247 acres) and as low as 5 in one year.

As of 2016, the only state in which rock ptarmigan could be legally hunted is Alaska.

## Habitat Requirements

### *Wintering Requirements*

In Alaska, rock ptarmigan winter in such locations as shrubby slopes at timberline, in large forest openings where shrubs, especially birch, project above snow level, and, more rarely, in riparian willow thickets (Weeden, 1965b). Watson (1965a) noted that in Scotland the birds moved down from their arctic-alpine breeding grounds into a moorland zone of heather that was used by red grouse during the breeding season. Ptarmigan can scratch through a few inches of soft snow to reach plants, but Watson did not find them burrowing under the snow to forage. Local variations in topography caused areas to be blown fairly free of snow periodically, exposing food plants, and the birds move from one such area to another in search of food. Little if any competition for food between ptarmigan and red grouse was noted by Watson, since the two species remained almost completely separated during winter. As mentioned in the willow ptarmigan account, considerable separation of the sexes occurs in North American willow and rock ptarmigans during winter, with males remaining in more alpine-like habitats, while the females tend to move into relatively protected situations.

### *Spring Habitat Requirements*

Territorial requirements for the rock ptarmigan consist of a larger proportion of relatively open vegetation than is the case for willow ptarmigan (Weeden, 1965b). Some territories contain no shrubs at all, and males utilize rocks, knolls, or similar elevations for territorial display and for resting. Watson (1965a) reported that ptarmigan were most common where large boulders or outcrops occurred on stunted heath or a mixture of stunted heath and grassy vegetation. The birds rarely took territories on pure grassland, tall heaths, bogs, or stone fields without healthy vegetation. Favorite areas for territorial establishment were usually on varied heaths or a mixture of varied heaths and grasses. The highest territorial densities occurred on areas of nearly continuous heath broken up by large boulders, slightly lower densities were found on scattered patches of heath, and much lower densities occurred on areas of continuous heath with only a few boulders present. Territorial densities were lowest on bare, gravelly places with only scattered vegetation and boulders.

Map 6. North American distribution of the Adak (Ad), Amchitka (Am), Atka (At), Attu (Au), Canada (C), coastal (Co), Iceland (I), Kiska (K), northern (N), Newfoundland (Ne), North Greenland (No), South Greenland (So), Tanaga (T), West Greenland (W), and Yunaska (Y) races of the rock ptarmigan. Stippled area indicates wintering limits.

### Nesting and Brooding Requirements

Nest sites for the rock ptarmigan may have less overhead concealment than those of willow ptarmigan, but some overhead protection is usually present (Watson, 1965b). Parmelee, Stephens, and Schmidt (1967) indicated that the nesting habitat is usually dry and rocky and sometimes is barren and high but may consist of wet tundra sites with heavy vegetation where willow ptarmigan also breed.

Brooding habitat is similar to nesting habitat, but broods tend to gather in swales on ridges and upper slopes (Weeden, 1965b). They avoid dense shrubs and after beginning to fly at 10 to 11 days of age escape by flying out of sight over knoll ridges.

## Food and Foraging Behavior

The best source of information on rock ptarmigan food habits in North America is that of Weeden (1965b), based on 482 crop samples from interior Alaska. Winter foods there consist primarily of dwarf birch buds (*Betula*) and catkins, followed by willow buds and twigs (*Salix*). Dried leaves of shrubs extending above the snow are also taken in limited quantities.

Spring foods, based on relatively few samples, appear to consist of a variety of plant materials, including the new growth of shrubs, horsetail tips (*Equisetum*), and a small amount of birch and willow materials. Summer foods include an even greater array of plant foods, which consist largely of leaves and flowers in early summer, and berries and seeds later on. Blueberries (*Vaccinium*), crowberries (*Empetrum*), and mountain avens (*Geum*) provide important food sources during this time. During fall, blueberries and heads of sedges (*Carex*) are important, and dwarf birch begins to assume the great importance that will continue throughout winter.

Reporting on birds taken on Baffin Island, Sutton and Parmelee (1956) noted that in the crops of eight adults taken in May about 60 percent of the total food materials consisted of buds and twigs of willow, 32 percent was the leaves and twigs of dryas (*Dryas*), and the remainder consisted of *Saxifraga*, *Draba*, and the galls of willows. A newly hatched chick had eaten leaves of crowberry (*Empetrum*).

Moss (1968) made an interesting nutritional comparison of rock ptarmigan foods taken by birds of the Icelandic and Scottish populations. In Iceland, the birds have a diet predominantly of twigs of willow, leaves of dryas, the leaves and bulbils of *Polygonum*, which are relatively high in nitrogen and phosphorus, and berries of *Empetrum*, which are high in soluble carbohydrates. By comparison, the Scottish ptarmigan subsist on a relatively nutrition-poor diet of heather (*Calluna*), *Vaccinium*, and *Empetrum*. Correlated with this is the fact that in Iceland the ptarmigan have an average clutch size of about 11 eggs, whereas in Scotland the clutch is usually 6 to 7 eggs, averaging 6.6. The average clutch size in Alaska, based on studies made by Weeden (1965a), is essentially the same as in Scotland. Significant annual differences in clutch sizes do occur in Alaska and apparently also in Scotland, but they have not yet been adequately correlated with population density or food quality. Lack (1966) suggested such a possible correlation between clutch size and heather conditions. Watson (1965a) believed that annual differences in clutch sizes were unimportant compared with variations in chick survival. At least in the red grouse, chick survival may be related to the physical condition of the hens as determined by food supplies.

A possibly significant point related to food supplies and reproductive success is the fact that although the rock ptarmigan is the most northerly breeding of the ptarmigans, it is considerably smaller than the willow ptarmigan. Likewise, the alpine-breeding white-tailed ptarmigan is much smaller than either the rock or the willow ptarmigan, in contrast to what might be expected with arctic-breeding birds (Bergmann's principle). The possibility exists, therefore, that smaller body size in the rock and white-tailed ptarmigans is an adaptation to reduced food supplies and has evolved relatively independently of selective pressures related to environmental temperatures. Yet Irving (1960) reported that willow ptarmigan collected in arctic localities of Alaska averaged 90 grams heavier than those from subarctic points some 600 miles south. Further, winter birds tended to be heavier than summer birds, and males, which averaged 10 to 49 grams heavier than females, wintered in more hostile environments.

Although Irving (1960) found that the willow ptarmigan at Anaktuvuk Pass to be migratory, the rock ptarmigan there are not, and in winter they feed on high, rounded slopes where low vegetation is exposed. Also, although willow ptarmigan often retreat with their crops filled with 50 to 100 grams of food into burrows 1.5 to 2 feet under the snow, this behavior is apparently not typical of rock ptarmigan. Manniche (cited in Bent, 1932) indicated that in Greenland the birds may spend the night in holes about 20 centimeters deep on the lee side of rocks or in narrow snow-filled ravines in the rocks. MacDonald (1970) noted that they dug roosting forms deep enough that only their heads remained above the snow, or would use the depressions caused by humans walking across the snow.

## Mobility and Movements

The relatively large heart size (Johnson and Lockner, 1968) of the rock ptarmigan suggests that it may be capable of considerable movements, but there is little detailed information on actual daily or seasonal movements in the species. Snyder (1957) stated that the bird is migratory to an appreciable degree in arctic Canada, and Weeden (1964, 1965b) reported that some low-altitude wintering grounds of the species are at a minimum of 10, and probably 15 to 20, miles from the nearest alpine breeding areas. Weeden believed that, at least in the lower parts of the wintering range, rock ptarmigan move in an unpredictable fashion. By March and April, however, movements are quite limited and consist of visits to various feeding areas separated by distances of up to half a mile or more, the stay at each area lasting varying lengths of time. Irving (1960) reported that at Old Crow, Alaska, winter-
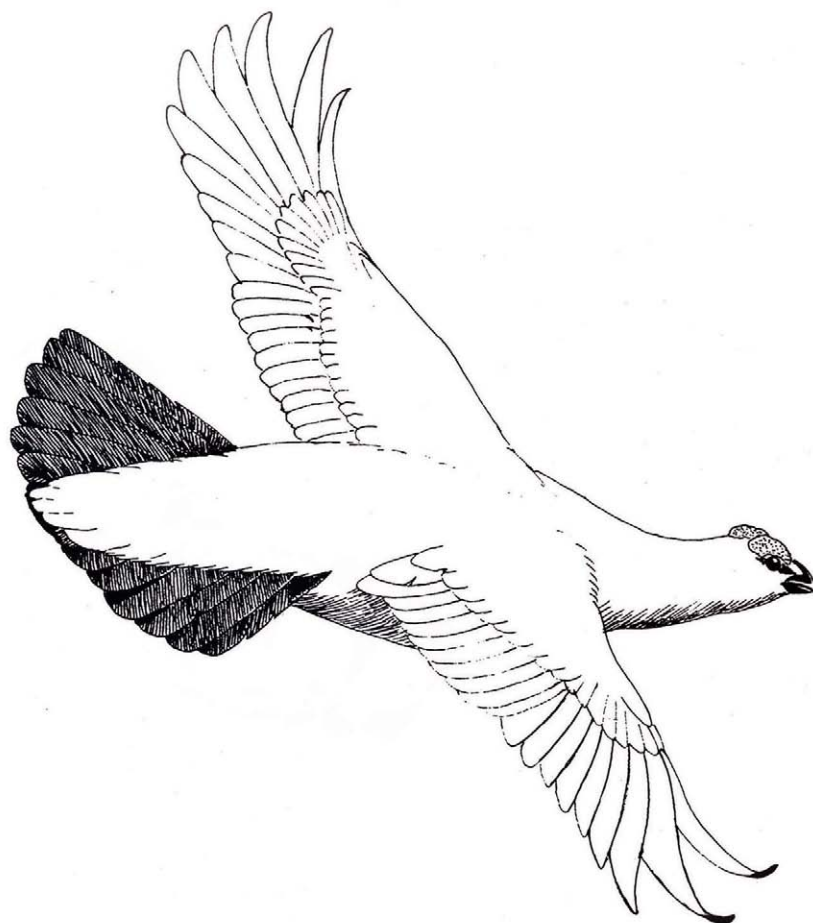
*Fig. 18. Male rock ptarmigan in song-flight.*

ing birds might convene from a nesting area some 30 miles in diameter, but no actual evidence for a regular migratory pattern was indicated. Bent (1932) indicated that although the majority of the rock ptarmigan withdraw from the northern limits of their summer range, they do not usually retreat beyond the southern limits of their breeding range. Nelson (cited in Bent, 1932) reported a regular fall evening migratory movement across Norton Sound, via Stuart Island, and a comparable spring flight in April.

Weeden (1965b) noted that in Alaska the rock ptarmigan disappear from their wintering areas at low altitudes in March and April, and that in 1962 the first migrants arrived at their Eagle Creek breeding ground study areas on March 29. This movement continued through April, and during April males began establishing territories in advance of the arrival of most hens. In the study area, located northeast of Fairbanks, egg laying begins in the second to fourth week of May. Farther north, at Old Crow and Anaktuvuk Pass, the males become territorial in late April and May. By comparison, the first flocks of rock ptarmigan which Parmelee, Stephens, and Schmidt (1967) saw on Victoria Island arrived in mid-May and were all males. The first territorial flights there were noted on May 19, and the first female was seen May 23. Fresh eggs were noted from June 3 until late June, or nearly a

month later than in central Alaska. Interestingly, the weights of spring males collected on Victoria Island averaged about 100 grams more than Irving reported for Anaktuvuk Pass and Old Crow, and females averaged about 90 grams heavier.

## Reproductive Behavior

### Territorial Establishment

The period of breakup of winter flocks and establishment of territories probably varies greatly by locality and year. In Scotland, Watson (1965a) noted that this behavioral transition occurs with the coming of spring thaws and sunny weather, which may be as early as the first part of January or as late as the end of April. In North America, where the birds usually move out of their breeding areas during the winter period, there is probably a fairly short lag between the arrival of the males on the breeding ground and the establishment of territories. The observations of Parmelee, Stephens, and Schmidt (1967) indicate that this lag may be as short as a few days. Both yearling and adult male ptarmigan participate in territorial establishment; Weeden (1965a) found that the percentage of first-year ptarmigan in male breeding populations varied from 41 to 67 percent. Yearling females composed from 17 to 75 percent of the breeding populations, and there was no evidence of any nonbreeding by females.
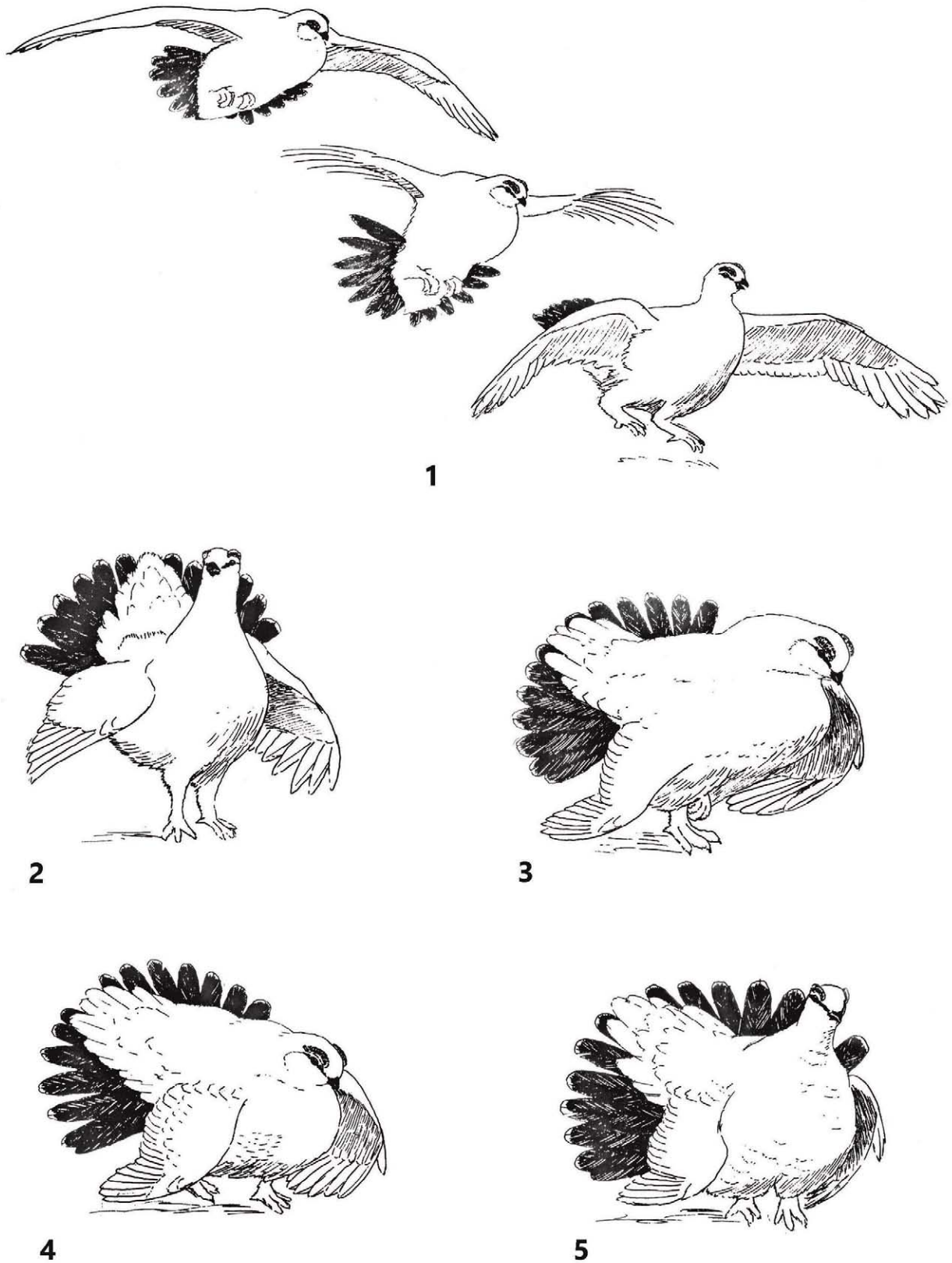
Fig. 19. Male rock ptarmigan displays, including (1) parachuting descent after a song-flight display, (2) posture assumed after landing, and (3–5) later stages in ground display. After MacDonald (1970).

### Agonistic and Sexual Behavior

MacDonald's observations (1970) on Bathurst Island indicated that individual males there defend surprisingly large areas of about one square mile, which include several lookout prominences adjacent to moist hummocky tundra with heavy vegetation. From these points the male watches for other ptarmigan, attacking males and courting females. During the early stages of territoriality the male spends much of his time advertising his location with song flight displays. As his aggressiveness increases, the size and brilliance of his eye-combs also increase. Territorial males, on seeing a rival male, engage in aerial chases with tails spread, combs erected, and their bodies rocking from side to side while in flight. Aerial chases of females were not seen by MacDonald but have been reported by Weeden.

The basic territorial advertisement display of the rock ptarmigan is the song flight. MacDonald noted that the height of this display flight varies from as little as about four feet early in the season to an estimated 250 feet observed in a highly aggressive male. The display may be performed spontaneously or may be elicited by a disturbance of some kind within hearing or visual range of the male. The bird typically leaps into the air, uttering a loud belching call, and swiftly flies forward and upward with alternate wing-flapping and sailing. At the end of the climbing flight, the male sets his wings, fans his tail, and begins an upward soaring glide until he finally reaches stalling speed. At this point he swells his neck and begins to utter a series of staccato, belching notes. As the bird begins his descent on bowed wings a second series of belching notes is uttered and he slowly parachutes downward toward the ground. Just before landing the male tilts his spread tail vertically downward, and as he alights he quickly cocks it back upward to a near-vertical position. The wings are held to the side of the body and are drooped toward the ground, as the male stands with an erect neck or runs forward a short distance while uttering a staccato call. Then the male's neck is deflated, the primaries are lowered so that they drag on the ground, and the tail is fully spread while being tilted at an angle of 45 degrees.

Next, the bird begins a short forward run, simultaneously extending his neck and making a single, slow bowing movement with his head. When a female is newly present on his territory, the male may run in an arc toward her, tilting his tail toward her and extending one wing away from her. The head is also tilted toward the female, exposing the enlarged eye-combs. After a female has become established on a male's territory, this ground display is omitted. Females evidently gradually associate themselves with a specific male and his territory, initially following the male in flight and later being followed by the male. MacDonald noted that at least one male mated with three females in one season, all of which nested in the male's territory.

When two territorial males meet, violent fights may ensue. Threats may be uttered as the birds sleek their plumage, inflate their necks, and close their tails so that they are nearly hidden. The crown may be raised or lowered, and the bright red combs erected or concealed. During attacks the birds attempt to grasp each other with their bills, while striking with the wings. Often feathers from the neck may be pulled out, and sometimes the fleshy eye-combs are torn.

Pair formation in rock ptarmigan is apparently a gradual process, judging from MacDonald's observations. He noted that while the resident male drives other males off his territory, the female becomes more submissive and dependent on him, relying increasingly on the male to warn her of danger. When near the female he continuously utters a contact call consisting of ticking notes, which change to a ratchet-like alarm call when alert to possible danger. When a female is thus alerted, she flushes and is immediately followed by the male, which may perform a song flight before landing. As the male returns to the female following the song flight he may perform the head-bowing and tail-tilting display described earlier. He typically circles the female at a distance of up to two feet, with his head held low, his wings dragging, and his tail tilted toward her. Apparently he attempts in this manner to direct the female into a tundra depression, seemingly trying to induce the female to crouch in it. In four observed instances of copulation, the female crouched in such a depression, partially extending her wings and exposing her white wrists. The male then stepped on her back and pecked at her nape but did not grasp her neck feathers. Rather, he remained with his body in a rather upright posture during copulation, finally bending forward and walking off her back over her shoulder. Then, with his head lowered and held forward, his tail spread and held vertically toward the female, and his wings dragging, he walked in a circular path around the female, with his combs greatly enlarged and his bill open. The female remained crouched for a time, then stood up, shook her plumage, and preened. In two cases the female ran from the male before he completed his postcopulatory display, while in one case the male circled around her twice while the female remained crouched.

MacDonald obtained some data indicating that males were more highly attracted to mounted specimens of females that had piebald brown and while plumage than to whiter females, which is of special interest since females molt into their brown nuptial plumage much earlier than males, which remain white and highly conspicuous throughout the pair-forming period.

### Vocal Signals

MacDonald (1970) reported that although the territorial male has at least six different vocalizations, the sounds nearly defy description. In all cases, they appear to be variations of pulsed clicking sounds that resemble the noise produced by drawing a stick over the slats of a picket fence. The predominant frequencies are low, which is of interest in view of the fact that MacDonald discovered a seemingly unique membranous, inflatable sac on the dorsal side of the trachea in males. During vocalizations, not only the esophagus but presumably also

this tracheal air sac may be inflated, which would facilitate the amplification of low-frequency sounds. The value of low-frequency sounds to the rock ptarmigan would seem to be correlated with the apparently large territories that they hold and associated with their long-distance visual signals in the form of the black and white plumage pattern.

MacDonald also noted that female rock ptarmigan produce at least three different vocalizations, which he described as whining, clucking, and a high-pitched screech, the latter apparently being an alarm call. He also noted a hissing produced during nest defense.

### *Nesting and Brooding Behavior*

Female ptarmigan locate their nests within the territorial boundaries of the male. In Scotland at least, the numbers of females associated with territorial males is rarely more than 50 percent (Watson, 1965a), thus few if any males are normally likely to acquire more than one female. Weeden (1965b) reports that in Alaska two females may sometimes mate with a single cock, and presumably both hens nest within the territorial area of the male. To what extent the male defends the female and her nest is still not very clear for the rock ptarmigan. Höhn (1957) described how, when two female rock ptarmigan were shot, the male quickly approached and displayed to the corpses, but this kind of behavior clearly does not belong in the category of female defense. Weeden (1965b) noted that about one brood in 20 will have a male in attendance, but he never observed any actual brood defense by males. However, MacDonald (1970) reported several cases of brood defense by males, including both attack and distraction behavior.

Rock ptarmigan females build simple, shallow nests, the depressions often being little more than might be caused by the weight and movements of the brooding hen (Weeden, 1965b). Clutch sizes vary considerably by locality and by year. Weeden (1965a and unpublished *Game Bird Reports*, vols. 7–10) noted that clutch sizes varied annually (1960–69) from 6.4 to 9 eggs; the average size of 195 clutches was 7.2 eggs. In the more arctic-like environment of Victoria Island, Parmelee, Stephens, and Schmidt (1967) found three nests, two containing 11 and one containing 13 eggs, suggestive of somewhat larger clutch sizes at higher latitudes. Judging from Weeden's data (1965a), about two-thirds of the nests hatched during an average year. Renesting is apparently not common enough to affect overall productivity. Weeden (1965a) provided data indicating an average brood size in August of 5.3 among 208 broods, with yearly averages (1960–64) ranging from 4.8 to 6.1. By comparison, Watson found that the average annual sizes of full-grown broods (1945–63) varied from 1.2 to 6.2 young. Watson found that an average of 38 percent of the females went broodless each year, but among different years it varied from none to over 80 percent. Weeden (unpublished *Alaska Fish and Game Department Game Bird Report*, vol. 8, 1967) reported that, between 1963 and 1966, 60 percent

of 130 year-old females were seen with young, while 77 percent of 185 older females were observed with young; thus, incubating or brooding efficiency evidently increases with age of the female.

The female is highly attentive to her young and, when disturbed by humans, utters a throaty *krrr* during distraction behavior (Sutton and Parmelee, 1956). When calling chicks toward her, she utters a clucking *kit* or *krit* call. Weeden (1965b) indicates that by imitating the distress peeping of a chick, he could elicit a low, crooning note that could be heard up to 100 yards and helped locate broody hens.

Weeden (1965b) noted that one brood seen in 1960 moved about 4,200 feet in five days, while another was found only about 50 feet from the point where it had been seen ten days before. In the case of two broods that were seen again after 28 days, one had moved about 50 feet and the other family 7,800 feet. In general, the broods stayed within an area of about one-half square mile but did not appear to be attracted by the male's former territory. By late July, most broods had moved to areas higher than the nesting sites, congregating on moist and gentle slopes where sedges, grasses, forbs, and low shrubs predominated in the vegetation. Weeden also found several indications of transfer of individual chicks between broods. Hens that had lost their clutches or broods joined the flocks of males that gather on high, rocky ridges or in streamside willow thickets. As the broods mature, they tended to combine, and these flocks in turn attracted groups of males and nonproductive hens. In time, flocks of 50 to 300 individuals may build up. However, at the same time, there is some calling and displaying among the males and an apparent resurgence of territoriality. The possible significance of this fall behavior is still unknown.

### Evolutionary Relationships

Some general statements as to the evolutionary history of the ptarmigans have been mentioned in the willow ptarmigan account. In addition, it might be noted that the rock ptarmigan is not only the most northerly and most widely distributed of all the ptarmigan species but also might perhaps be considered as most representative of an ancestral ptarmigan type adapted for high arctic breeding. From such a type the later evolution of an alpine offshoot, as represented by the white-tailed ptarmigan, and a subarctic type, represented by the willow ptarmigan, might easily be imagined. A 2004 estimate of the species' total North American population was 4.1 million out of a world population of 8.2 million (Rich et al., 2004).

*Suggested reading:* Weeden, 1965b; MacDonald, 1970; Holder and Montgomerie, 1998

*Plate 17. Newfoundland rock ptarmigan, territorial male calling; May.*



*Plate 18. Newfoundland rock ptarmigan, territorial confrontation; May.*

# White-tailed Ptarmigan

*Lagopus leucurus* (Richardson) 1831

## Other Vernacular Names

None in general use.

## Range

From central Alaska, northern Yukon, and southwestern Mackenzie south to the Kenai Peninsula, Vancouver Island, the Cascade Mountains of Washington, and along the Rocky Mountains from British Columbia and Alberta south to northern New Mexico.

## Subspecies

*L. l. leucurus* (Richardson): Northern white-tailed ptarmigan. Resident above timberline from northern Yukon, western Mackenzie, British Columbia, and west central Alberta south to the northern border of the United States.

*L. l. peninsularis* Chapman: Kenai white-tailed ptarmigan. Resident above timberline from south central Alaska to Cook Inlet and the Kenai Peninsula, extending east and southeast to Glacier Bay and White Pass.

*L. l. saxatilis* Cowan: Vancouver white-tailed ptarmigan. Resident above timberline on Vancouver Island, British Columbia.

*L. l. rainierensis* Taylor: Mount Rainier white-tailed ptarmigan. Resident above timberline in Washington from Mount Baker south to Mount Adams and Mount St. Helens.

*L. l. altipetens* Osgood: Southern white-tailed ptarmigan. Resident above timberline in the Rocky Mountains from Montana south through Wyoming and Colorado to northern New Mexico.

## Measurements

*Folded wing:* Adult males, 164–194 mm; adult females, 155–192 mm (males average 5 mm longer than females).

*Tail:* Adult males, 85–109 mm; adult females, 83–98 mm (males average 8 mm longer than females).

## Identification

Adults, 12 to 13.5 inches long. In any nonjuvenile plumage the white tail serves to separate this species from the other two ptarmigans. Adult males in summer plumage are vermiculated and barred or mottled with black, buffy, and white dorsally, with a buffy or pale fulvous tone predominating on the lower back, rump, and upper tail-coverts, and the underparts are mostly white. Unlike the other ptarmigans, the wings as well as the tail (except for the central pair of feathers) are completely white at this season. Females are similar in plumage but have a heavily spotted and more yellowish color dorsally. In the fall both sexes are mostly pale cinnamon-rufous above, with fine spotting and vermiculations of brownish black and with a lighter head and neck. A few breast feathers are usually marked with white, and the abdomen, under tail-coverts, tail, and wings are white. In the winter both sexes are pure white except for a black bill, eyes, and claws.

## Field Marks

This species is a small alpine ptarmigan with white wings and tail in summer or an entirely white plumage in winter. It is usually extremely difficult to see against a lichen-covered rocky background; therefore, it is overlooked unless something forces a bird to fly.

## Age and Sex Criteria

*Females* exhibit eye-combs (unlike the two other ptarmigan species) virtually identical to those of adult males, but in summer hens are more coarsely and regularly barred with black and rich ocherous buff markings on their brownish back and side feathers, while feathers of males in these areas are finely vermiculated with brown and black. In addition, although males retain their white lower breast, abdomen, and under tail-coverts through the summer, females have yellowish buffy brown feathers with some black barring present in these areas (Braun and Rogers, 1967a). In the autumn differences between the sexes diminish, but for a time females retain a few of their coarsely barred nuptial plumage feathers, especially on the nape, sides, inner wing, and upper tail-coverts. In winter birds of both sexes are identical in plumage but may differ slightly in length of the wing, outer five primaries, and outer rectrix (Braun and Rogers, 1967a). In spring, males can be recognized by their distinctive black-tipped head and neck feathers, which provide a "hooded" effect that is lacking in females, as they gradually acquire their brown, black, and yellow nuptial plumage (Braun, 1969).

*Immatures* may be recognized by the pigmentation of their two outer primaries (Taber, in Mosby, 1963). If black pigment occurs on either the ninth or tenth primary, the bird may confidently be called an immature. Likewise pigmentation on the outer primary covert is an indication of an immature bird, whereas lack of pigmentation in these areas is typical of adults (Braun and Rogers, 1967a).

*Juveniles* have tail feathers that are yellowish brown centrally or white with mottled brown edges (Ridgway and Friedmann, 1946). Until they are all molted, the secondaries and inner eight primaries are also brownish in juveniles (see willow ptarmigan account).

*Downy young* are the least rufous dorsally of all the ptarmigans and have only a suggestion of the usual chestnut crown with its black margin. The two black dorsal stripes are also indistinct, and instead the back has an indefinite blending of buff, gray, sepia, and black shades. Their feathered toes separate downies of this species from any non-*Lagopus* forms.

## Distribution and Habitat

The current distribution of the white-tailed ptarmigan in North America closely conforms to that of alpine tundra,

Map 7. Current distribution of Kenai (K), northern (N), Mount Rainier (R), southern (S), and Vancouver (V) races of the white-tailed ptarmigan. Populations in Utah, Oregon, and California are the result of introductions and are of uncertain status.

although it does not extend southward along the Cascade and Sierra ranges into Oregon or California, nor does it apparently include the Brooks Range of northern Alaska, both of which would seem to provide suitable habitat opportunities for the species. In the Rocky Mountains of the western states the range of the species is highly disjunctive because of the limited elevations above timberline, and it must be presumed that these southern populations became isolated during Pleistocene times. These southernmost populations are probably those most vulnerable to possible extirpation. Ligon (1961) noted that although the New Mexican range of this species once included all the alpine ridges of the Sangre de Cristo range from Lake Peak to the Colorado line, the birds were then found on only a few peaks near the Colorado line. Braun (1970) reported finding them on Costilla Peak in 1970 and has also verified their occurrence on Baldy Peak near Santa Fe. Braun (1969) concluded that although the birds may once have occurred in Oregon, Idaho, and Utah, their recent natural occurrence in these states is unproved. Apparently unsuccessful attempts have been made to introduce them in northeastern Oregon.

Except for Alaska, Colorado is the state with perhaps the greatest number of white-tailed ptarmigan range in the United States. Rogers and Braun (1968) estimated that this ptarmigan occupied more than 4,000 square miles in the state.

Weeden (1965b) reported that typical terrain of this species consists of steep slopes and ridges, often around cirques and stony benches, where ledges, cliffs, and outcrops commonly occur. The vegetation is generally sparse, with shrubs nearly absent and dwarfed when present. The birds in Alaska are usually from 500–2,000 feet above timberline. In Montana, Choate (1963) found that ptarmigan are not present in timber or in shrubby vegetation more than 18 inches high. Rather, they prefer areas of rocks and moist ledges with alpine vegetation that is low growing but well developed. Rocks from 6 to 24 inches in diameter provide optimum habitat, since they provide protection from bad weather and cover from visual predators. Ptarmigan are never found in boggy areas or areas where the vegetation is taller than the birds themselves. They usually frequent gently sloping areas where moisture is abundant and vegetation is present. Preferred cover plants, which also are among the most important food plants, include willow, heath (*Phyllodoce* and *Cassiope*), and mosses.

Braun (1969, 1970) concluded that in Colorado the distribution and abundance of alpine willow is the key factor determining ptarmigan distribution. Willow not only represents the majority of the ptarmigan's food from late September until May, but its occurrence in snow-free areas in late May is an essential component of breeding territories.

As of 2016, the only states in which white-tailed ptarmigan could be legally hunted are Alaska, California, Colorado, and Utah.

## Population Density

Relatively little information is available on breeding densities. Choate (1963) reported the overall density of breeding birds on a 2-square-mile plot at 17.5 birds per square mile, but if unsuitable habitats are excluded from consideration, the density could be calculated as 50 breeding birds per square mile. On study areas totaling 8.41 square miles, Rogers and Braun (1968) reported 52 and 56 breeding pairs plus 11 to 25 unmated birds in 1966 and 1967, or 15.2 to 15.5 birds per square mile. In 1968 there were 55 pairs and 21 unmated males on areas totaling 6.93 square miles, or 19.2 birds per square mile, and in 1969 there were 60 pairs and 28 unmated males on 8.41 square miles, or 17.8 birds per square mile (*Colorado Game Research Review*, 1968 and 1969).

## Habitat Requirements

### Wintering Requirements
Braun (1969, 1970) reported that wintering areas for ptarmigan in Colorado must contain alpine willows (*Salix nivalis* and *S. anglorum*), and alpine areas lacking these species cannot support ptarmigan for prolonged periods. Braun and Pattie (1969) reported that the Beartooth Plateau of Wyoming almost completely lacks willow in this timberline zone, and willow stands that do occur are snow-covered during winter. The birds evidently do not occur there or in certain northern New Mexico peaks where willow is also absent (Braun, 1970).

### Spring Habitat Requirements
Braun (1969, 1970) reported that the presence of willow is essential to the habitat characteristics of successful male territories. In Colorado, breeding territories are adjacent to the spruce-willow alpine timberline (*krummholz*) zone and also include small windblown areas. In the Beartooth region of Wyoming this combination of habitat characteristics in the alpine zone is lacking, thus the area is apparently unsuitable as a breeding ground (Braun and Pattie, 1969). In Colorado, territories are established in suitable habitats where the snow is gone by early May (Braun, 1969).

### Nesting and Brooding Requirements
Nest site characteristics for the white-tailed ptarmigan are evidently rather broad, judging from the diversity of nest sites that have been found (Schmidt, 1969). Probably more important than specific nest sites during the summer period is the accessibility of suitable brooding areas. Brooding areas for females and suitable summering areas for post-territorial males as well as unsuccessful hens occur where the vegetation is short and rocks six inches or larger cover more than 50 percent of the ground surface (Braun, 1969). The vegetation of suitable meadow areas adjacent to rock fields consists principally of hedges (*Carex*) and forbs such as *Geum* and *Polygonum*. During late summer, adults and young move to snow accumulation areas between the summering and wintering habitats, which provide the last source of green plants in the alpine zone and also offer the best protection for intermediate-plumaged birds.

## Food and Foraging Behavior

Weeden (1967) reported on the analysis of 167 crops of this species collected from Colorado to Alaska. Winter foods of Alaskan populations differ from those in Colorado in that alder (*Alnus*) catkins are an important part of the winter diet, with willow (*Salix*) and birch (*Betula*) of secondary importance. In contrast, Colorado ptarmigan subsist largely on the buds and woody twigs of various alpine willows (Quick, 1947). Weeden attributed this difference to the increased availability of alder in northern areas, and to possible competition from other species of ptarmigan in Alaska.

May and Braun (1969) reported that among 40 winter food samples from Colorado, willow occurred with a 100 percent frequency, but alder also occurred in samples from areas where that species was locally abundant. Coniferous food sources (*Picea*, *Pinus*, *Abies*), although readily available, are rarely taken in winter (May, 1970). With spring, a diversity of green leaves and flowers are consumed, although willow remains the most important food. The leaves and flowers of *Potentilla*, *Ranunculus*, *Saxifraga*, and *Dryas*, all of which are high in protein, were other important spring foods. During summer a diverse array of leaves and seeds are also consumed, and the bulbils of *Polygonum viviparum* are an important summer food for adults. During their first two weeks juveniles feed largely on invertebrate foods, then they too begin to feed extensively on these bulbils. Gradually, willow gains importance over *Polygonum* for both juveniles and adults, and eventually the birds go back to a diet consisting almost entirely of *Salix* buds and twigs (May and Braun, 1970; May, 1970).

## Mobility and Movements

Relatively little is known of white-tailed ptarmigan movements but certainly little lateral movement is normally typical. During winter, the birds typically descend to the edge of treeline, where food is more readily available. In Colorado, ptarmigan gather in flocks of 5 to 30 birds in high alpine basins where willows are abundant (Quick, 1947). Single birds also sometimes occur in alpine fir (*Abies lasiocarpa*), limber pine (*Pinus flexilis*), or on steep rock slopes during winter, but when flushed usually drop down into the snow basins below. Weeden (1965b) indicated that in Alaska most birds remain above the timberline, feeding in areas such as steep cliffs, ridgetops, and benches that are blown fairly free of snow. In parts of southwestern Colorado the birds go to low valleys every winter, regardless of snow cover (Braun and Rogers, 1967b). During early winter in Colorado, flocks of up to 50 ptarmigan can be found in areas containing available willow, but later the sexes tend to segregate, with males occurring nearer timberline and females remaining in the larger willow expanses at lower elevations (Braun and Rogers, 1968). Birds may move as much as a mile in a day during winter and up to 15 miles on a longer basis (Braun and Rogers, 1967b).

In spring, Colorado ptarmigan move back up to the breeding areas, which in the case of males may be a distance of less than a mile. Movements of both sexes are very restricted during the breeding and nesting periods, with birds rarely moving more than 500 yards (Braun and Rogers, 1967b). When broods appear, males and broodless females move uphill into higher rocky summering areas that may be up to two miles from nesting areas, where the birds once again become fairly sedentary. Hens may also move their broods as much as one-third mile to such summer brood-rearing areas (Braun and Rogers, 1967b). Subadult males and unsuccessful hens move considerably farther than adult males or brooding females, and fall movements of females may exceed ten miles (Braun, 1969).

Daily movements probably differ considerably according to sex, age, and time of year, and with varying weather conditions. Minimal daily movements may occur among brooding females caring for young chicks. Schmidt (1969) noted that one brood moved about 800 yards in ten hours, and another moved 300 to 400 yards in three hours. Similarly, males on breeding territories move very little. Schmidt found in 1967 that males had an average territory size of 19 acres, with maximum use occurring in 5.3 acres, and in 1968, with a better sample, territories averaged 36 acres, with maximum use in a 9.5-acre area. These territorial areas were used over a 2.5-month period, or the entire period of the pair bond.

## Reproductive Behavior

### Prenesting Behavior

Most of what is known of the reproductive behavior of the white-tailed ptarmigan consists of the work of Schmidt (1969; 1988). The following summary is based on Schmidt's observations.
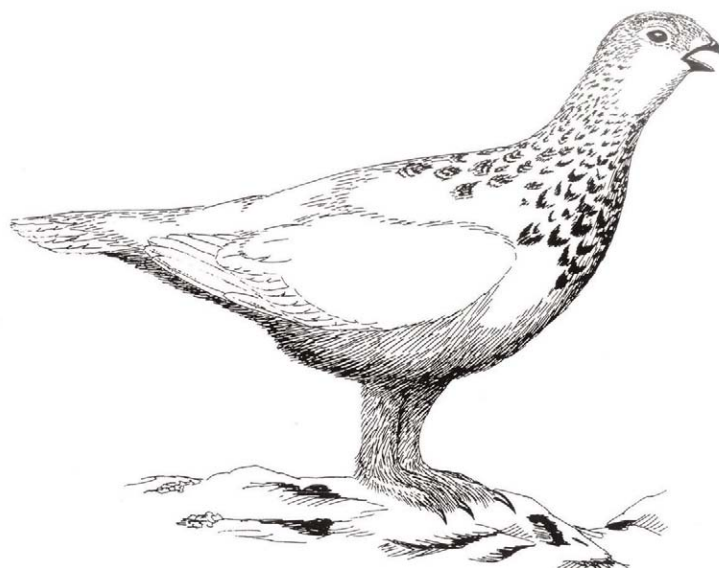


*Fig. 20. White-tailed ptarmigan, territorial male calling.*
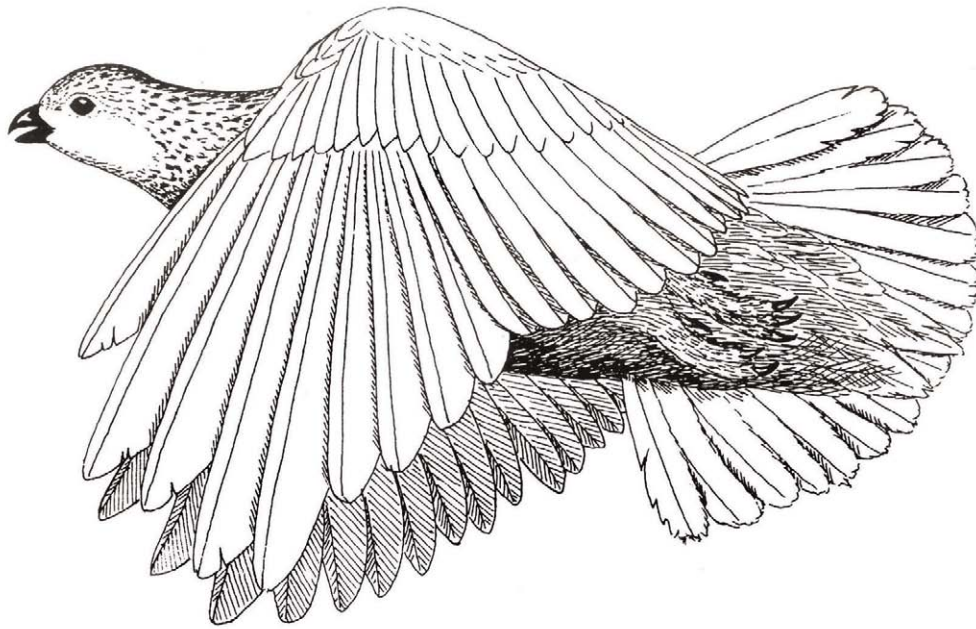
Fig. 21. White-tailed ptarmigan, male in flight.

### Territorial Establishment

With the return of the males from their timberline wintering areas to the alpine breeding grounds, territories were gradually established, which ranged in size from 16 to 47 acres. Within these fairly large defended areas, which overlapped slightly, males were usually to be found in areas of maximum use of from 3.2 to 15.7 acres. Males typically returned to their same territories of past years, and females usually returned to the same territory and the same male each spring. Territorial activity was not strong until the arrival of the females on the breeding areas, and males would often feed together until that time.

Males were typically monogamous, and Schmidt found that although males were sometimes found with two females, this was less common than seeing unpaired males. Territories were usually held by males at least 22 months old, with subadults successful in obtaining territories only if they were vacated by older birds. Territorial defense and proclamation became spirited in late April or early May when the females arrived, and the pair-forming period occurred at the same time. The most intensive territorial activity was typically in very early morning or after feeding in the evening, but during foggy periods or snow squalls activity was intense, apparently as a result of restricted visibility.

### Male Territorial and Pair-Forming Behavior

Male displays and calls may be discussed according to whether they serve the dual purpose of warding off other males from the territory and attracting females, or whether they are performed only in a sexual situation. The basically agonistic territorial signals may be considered first.

Schmidt classified the territorial behavior of males into three general types, the "screen flight," "ground challenging,"

and intimidation displays, noting, however, that they form a continuum of functions and have certain merging characteristics. The male scream flight, which corresponds to the song flight of willow ptarmigan, consists of the birds taking off and uttering a raucous call containing four syllables, *ku-ku-KIIII-KIIERR*, lasting about one second and being repeated at intervals of about one to three seconds. Choate (1960) had noted that this flight was sometimes characterized by a steep rise followed by a shallow glide, which Schmidt did not see. This display clearly attracted females and warned rival males of the territorial location. However, the display was sometimes seen in midsummer after territories had been abandoned, and females sometimes uttered a homologous call while the male was calling or when defending chicks.

Ground challenging was uttered from convenient calling posts, and the associated call varied considerably in emphasis, such as *duk-duk-DAAK-duk-duk* or *DAAK-DAAK-duk-DAAK-duk-duk-duk*. Some "long ground screams" closely resemble the flight scream in their last four notes. Intimidation displays performed on the ground included two major postures. These were a flat posture assumed during running and an upright threat posture held during slow walking or while standing still. During these displays the eye-comb was exposed by raising crown feathers, and low clucking sounds were typically uttered. During territorial border disputes males would usually face one another at distances of from 5 to 30 feet in upright postures, sometimes making short flights while calling. Aerial chases occurred occasionally.

With the arrival of females on a territory, the responses of resident males changed. Males would chase the individual females that entered their territories and perform several specific postures and calls. The "courtship chase" and associated strutting was much like an aggressive attack toward
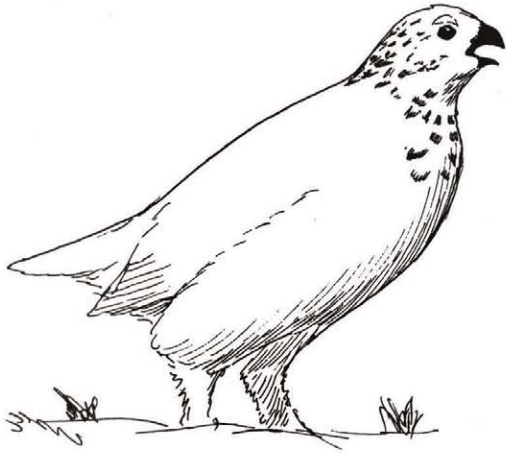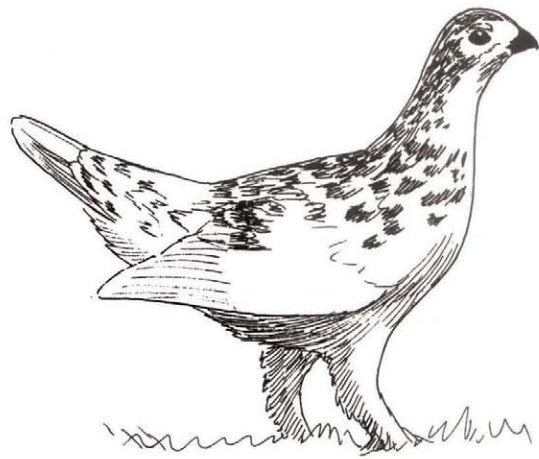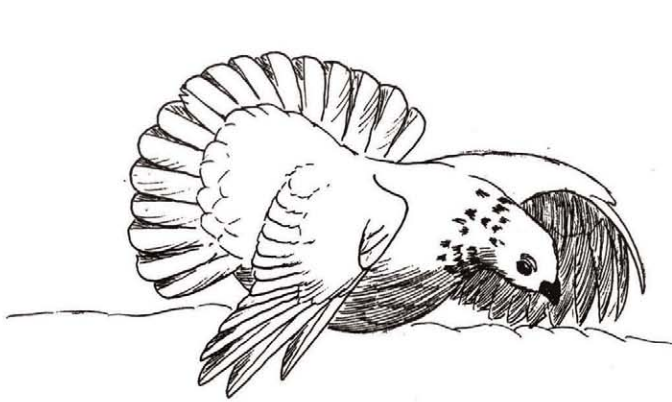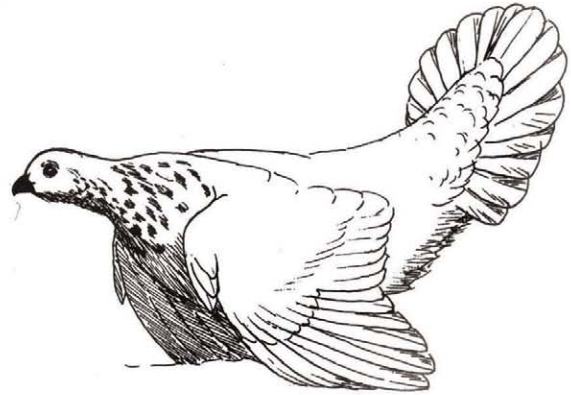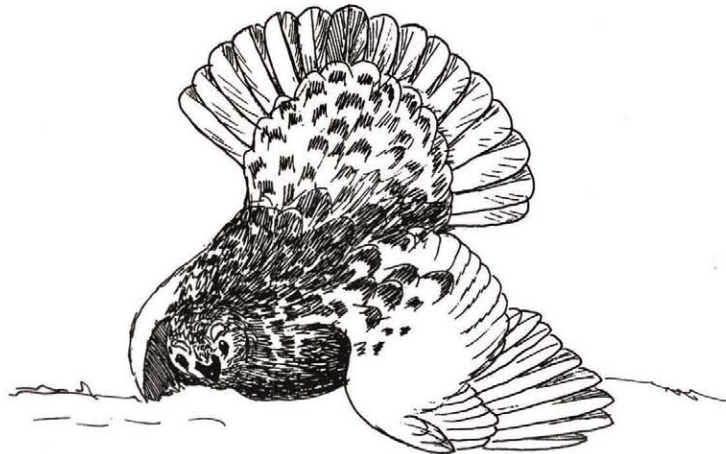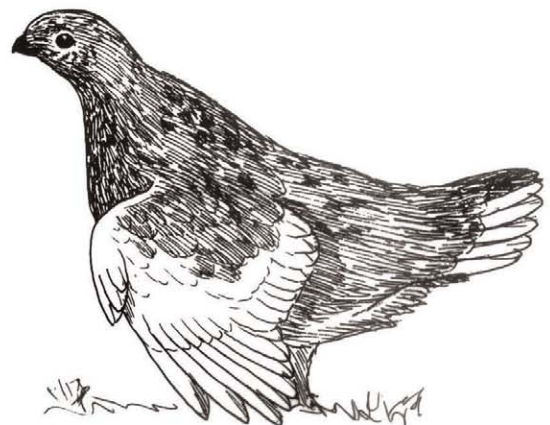
Fig. 22. Male white-tailed ptarmigan displays, including (1) ground challenge posture, (2) upright intimidation posture, (3) strutting while circling female, (4) pursuit strutting, (5) post-copulatory posture, and (6) attack posture of brooding female. After Schmidt (1969).

another male, but the head was held more upright, the tail and under tail-coverts were more strongly lifted, the breast feathers were fluffed, and the wings were slightly drooped. When the female attempted to escape from the approaching male, chases typically ensued.

Males sometimes varied their strutting approach to females with a slow approach and a rhythmic "head-bowing" that resembled the ground-pecking "displacement" display of male spruce grouse, but the bill was lowered only part way toward the ground. Frequently the male performed a "waltzing" display as he approached the female and attempted to circle in front of her. While so doing, he tilted the tail toward the female and dragged both wings, with the wing nearer the female held lower than the more distant one. This waltzing display lasted from 1 to 5 seconds and was usually repeated several times in a 20- to 40-second interval. No calling was heard during this display.

Evidently pair-formation was achieved by the repeated performance of these displays, after which the female followed the male closely, the two birds feeding and resting at the same times. While the female fed, Schmidt heard the male utter "assurance clucks" from 50 to 80 times a minute. When the female rested near the base of a rock, the male typically stood on the top of that rock or an adjacent one.

Copulation and the associated behavior patterns were observed only a few times and occurred just prior to the period of egg laying and incubation. On one occasion Braun (cited in Schmidt) observed an apparent instance of precopulatory invitational "tidbitting," during which the male pecked the ground and uttered a series of low-pitched clucking sounds that stimulated the female to rush over and join in the pecking. As the pair began pecking head to head, the male raised his head, exposed his eye-combs, fluffed his feathers, and drooped his wings. He then began bowing his head over the female while uttering "churring sounds." Then he walked around the female and grabbed her nape, causing the hen to drop to the ground with her neck extended forward. When mounting and during copulation the male lowered his wings and crouched down on the female. When released, the female ran forward in several short dashes, stopping between dashes to shake. The post-copulatory display of the male resembled normal strutting, but the wings were more strongly drooped, and the bird walked in slow steps. In each of four cases, the male moved from 10 to 50 feet before resuming normal feeding. In one case, several short dashes were made by the male as well.

One other display noted by Schmidt (1969; 1988) was "tail-wagging," which apparently occurred as an apparent displacement activity during times of stress. Feeding movements were also noted in stress situations. Schmidt found that it occurred in adults of both sexes and in young only six weeks old. Females typically performed tail-wagging when approached by a courting male but only when approached from the side or behind.

## Vocal Signals

In addition to the several calls mentioned earlier, Schmidt noted several other vocal signals. Females uttered hissing sounds when defending the nest, and when performing distraction displays typically uttered a harsh *craaow* note that apparently served as an alarm call to the chicks. Females also uttered a loud *brrrt*, apparently of similar function. When the young were older, females uttered "alert calls," running to the cheeping distress calls of young, and uttering high clucks in an upright alert posture. Females also uttered soft contact calls in the presence of their broods, and while pecking made cackling noises that served to attract the young. Schmidt noted that such functional tidbitting behavior had earlier been reported for both willow ptarmigan and greater sage-grouse. It is of interest that so far only in the white-tailed ptarmigan has tidbitting been reported as an adult display pattern, where it possibly serves as a precopulatory attraction signal.

## Nesting and Brooding Behavior

Relatively few nesting studies have been made of this species. Choate (1963) reported on 11 nests in Montana that had from 3 to 9 eggs, averaging 5.2. Bradbury (1915) mentioned 6 Colorado nests containing from 5 to 7 eggs. Braun (1969) noted that 19 nests in Colorado had from 4 to 7 eggs, averaging slightly under 6. Choate (1963) found one known instance of renesting in Montana, and Braun (1969) concluded that renesting was also probable in Colorado. He estimated an egg-laying interval of slightly under one and one-half days and an incubation period of 22 to 23 days.

Choate (1963) found an incubation success of 70 percent for nests studied in Montana, and a hatching success of 85.5 percent of eggs observed. Braun (1969) reported a nearly identical hatching success of 81.1 percent in Colorado.

The male apparently normally remains with the female until the time of hatching, judging from observations of Schmidt and Braun in Colorado, although Choate (1963) indicated that the pair bond may last only two or three weeks. Females regularly perform strong nest and brood defense displays, and Schmidt (1969; 1988) noted that males may also defend the nest site. Early in the incubation period, a female disturbed from the nest typically skitters over the ground for from 10 to 50 feet, with her wings dragging and her head low in a distraction display. As hatching approaches the female is more likely to remain at the nest, hissing and spreading her wings. Schmidt never found a male defending a brood, but female brood defense may take several forms. She may attack the intruder, with expanded eye-combs and exposed white carpals, running with the wings extended and head raised and uttering hissing sounds. When the chicks were still very young the female often performed distraction behavior and lead the intruder from the brood. When the chicks were older, the female usually uttered "alert calling" or would place herself between the observer and the brood, running back and forth
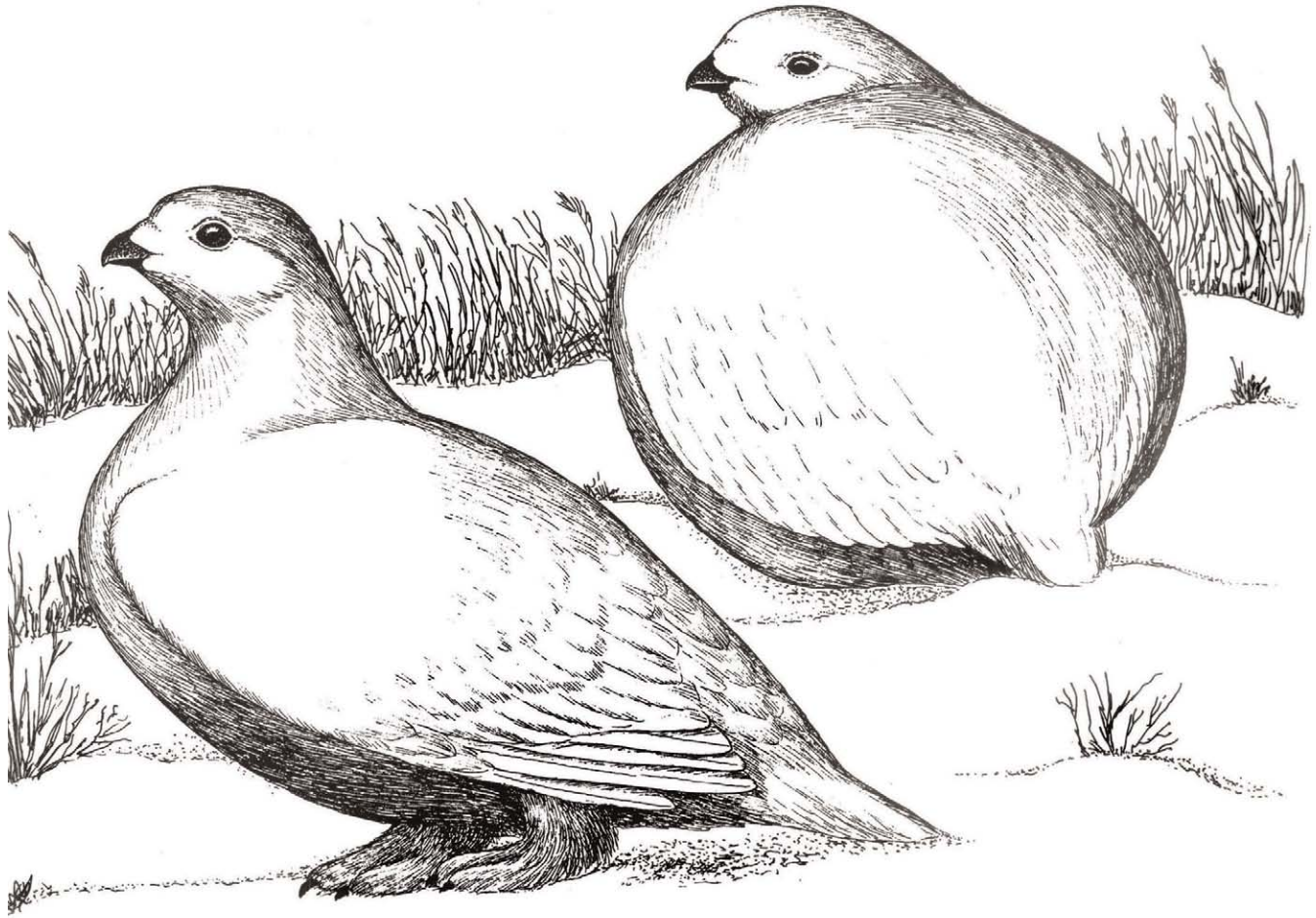
*Fig. 23. White-tailed ptarmigan, pair in winter plumage.*

and hissing. When they were from 10 to 21 days old the chicks could fly from 20 to 150 feet, after which they would run and utter cheeping calls. Loud calls were also uttered by lost chicks, which gradually changed to hoarse cheer-up sounds in older birds. When captured, birds up to 12 months old would sometimes utter similar sounds.

Concentration of females with broods occurred on certain favored areas that provided a combination of rocky habitat and an abundance of low, rapidly growing herbaceous vegetation. Brood mixing commonly occurred on such areas. Hens remained with well-grown young through the autumn period, as the birds gradually moved closer to wintering areas (Braun, 1969).

### Evolutionary Relationships

General comments about ptarmigan relationships have already been made (see willow ptarmigan account). Some authorities (Höhn, 1969; Braun, 1969) appear to agree that the white-tailed ptarmigan must have been derived from a relatively early offshoot of ptarmigan stock that became isolated in western North America. Braun also agreed with Johansen (1956), who thought that the white-tailed ptarmigan originated from ancestral stock of *Lagopus mutus*, which arrived very early in North America. Judging from plumage characteristics of downy young as well as adults, I would favor the view that such a separation of pre-*leucurus* stock occurred before a subsequent splitting of gene pools that gave rise to the modern rock and willow ptarmigans; thus I believe that these two species are more closely related to one another than either is to the white-tailed ptarmigan. Differences in bill size among the three species where they occur together in Alaska and western Canada may be advantageous in reducing foraging competition; thus, indirectly, selection for differences in body size among the three species may have occurred. Weeden (1967) has suggested that winter foods taken by white-tailed ptarmigan in Alaska may be influenced by competition from the two other species of Alaskan ptarmigans.

*Suggested reading:* Weeden, 1965b; Braun and Rogers, 1971; Braun, Marten, and Robb, 1993

*Plate 19. Southern white-tailed ptarmigan, adult pair, female foraging; June.*



*Plate 20. Southern white-tailed ptarmigan, adult pair, female crouching; June.*

# Ruffed Grouse

*Bonasa umbellus* (Linnaeus) 1776

## Other Vernacular Names

Birch partridge, drummer, drumming grouse, long-tailed grouse, mountain pheasant, partridge, pine hen, pheasant, tippet, white-flesher, willow grouse, wood grouse, woods pheasant

## Range

Resident in the forested areas from central Alaska, central Yukon, southern Mackenzie, central Saskatchewan, central Manitoba, northern Ontario, southern Quebec, southern Labrador, New Brunswick, and Nova Scotia south to northern California, northeastern Oregon, central Idaho, central Utah, western Wyoming, western South Dakota, northern North Dakota, Minnesota, central Arkansas, Tennessee, northern Georgia, western South Carolina, western North Carolina, northeastern Virginia, and western Maryland. Introduced in Nevada and Newfoundland.

## Subspecies

*B. u. umbellus* (Linnaeus): Eastern ruffed grouse. Resident in wooded areas of two regions, from east-central Minnesota, southern Wisconsin, and southwestern Michigan south to central Arkansas, extreme western Tennessee, western Kentucky, and central Indiana (this population is sometimes separated as *B. u. mediana* Todd 1940), and from central New York and central Massachusetts south to eastern Pennsylvania, eastern Maryland (formerly), and New Jersey.

*B. u. monticola* Todd: Appalachian ruffed grouse. Resident from southeastern Michigan, northeastern Ohio, and the western half of Pennsylvania south to northern Georgia, northwestern South Carolina, western North Carolina, western Virginia, and western Maryland.

*B. u. sabini* (Douglas): Pacific ruffed grouse. Resident of southwestern British Columbia (except Vancouver Island and the adjacent mainland) southwest of the Cascade Range, through west-central Washington and Oregon to northwestern California.

*B. u. castanea* Aldrich and Friedmann: Olympic ruffed grouse. Resident of the Olympic Peninsula and the shores of Puget Sound south to western Oregon.

*B. u. brunnescens* Conover: Vancouver Island ruffed grouse. Resident of Vancouver Island and adjacent mainland south to Puget Sound and north at least to Lund.

*B. u. togata* (Linnaeus): Canadian ruffed grouse. Resident from northeastern Minnesota, southern Ontario, southern Quebec, New Brunswick, and Nova Scotia south to northern Wisconsin, central Michigan, southeastern Ontario, central New York, western and northern Massachusetts, and northwestern Connecticut.

*B. u. affinis* Aldrich and Friedmann: Columbian ruffed grouse. Resident from central Oregon northward, east of the Cascades through the interior of British Columbia to the vicinity of Juneau, Alaska.

*B. u. phaia* Aldrich and Friedmann: Idaho ruffed grouse. Resident from southeastern British Columbia, eastern Washington, and northern Idaho south to eastern Oregon and on the western slopes of the Rocky Mountains to south-central Idaho.

*B. u. incana* Aldrich and Friedmann: Hoary ruffed grouse. Resident from extreme southeastern Idaho, west-central Wyoming, and northeastern North Dakota south to central Utah, northwestern Colorado (rarely), and western South Dakota.

*B. u. yukonensis* Grinnell: Yukon ruffed grouse. Resident from western Alaska east, chiefly in the valleys of the Yukon and Kuskokwim rivers, across central Yukon to southern Mackenzie, northern Alberta, and northwestern Saskatchewan.

*B. u. umbelloides* (Douglas): Gray ruffed grouse. Resident from extreme southeastern Alaska, northern British Columbia, north-central Alberta, central Saskatchewan, central Manitoba, northern Ontario, and central Quebec southeast of the range of *affinis* and *phaia*, to western Montana, southeastern Idaho, extreme northwestern Wyoming, southern Saskatchewan, southern Manitoba, southern Ontario, and across south-central Quebec to the north shore of the Gulf of St. Lawrence, probably to southeastern Labrador.

## Measurements

*Folded wing:* Adult males, 171–193 mm; adult females, 165–190 mm (males of all races average 178 mm or more; females usually average under 178 mm).

*Tail:* Adult males, 130–181 mm; adult females, 119–159 mm (males average more than 147 mm; females average less than 142 mm).

## Identification

Adults, 16–19 inches long. Both sexes have relatively long, slightly rounded tails that are extensively barred above and have a conspicuous subterminal dark band. The neck lacks large areas of bare skin, but both sexes have dark ruffs. Feathering of the legs does not reach the base of the toes; the lower half of the tarsus is essentially nude. Both sexes are definitely crested, but the feathers are not distinctively colored. In addition males have a small comb above the eyes that is orange red and most evident in spring. Most races (*castanea* is perhaps the only exception) exist in both gray and red (rufous) plumage morphs, which are most evident in the rectrices and appear with the first-winter plumage. Otherwise, little seasonal, sexual, or age variation occurs. The birds are generally wood brown above, with blackish ruffs (less conspicuous in females and immatures) on the sides of the neck, and with small eye-spot markings on the lower back and rump (less conspicuous in females). The tails

of both sexes have seven to nine alternating narrow bands of black, brown, and buff, followed by a wider subterminal blackish band that is bordered on both sides with gray and is less perfect centrally in females and some (presumably first-year) males. In winter, both sexes develop horny tooth-like pectinations on the sides of their toes, which are more conspicuous than in most other species.

## Field Marks

The fan-shaped and distinctively banded tail and neck ruffs of both sexes make field identification easy. The birds usually take off with a conspicuous whirring of wings, and in spring males are much more often heard drumming than they are seen.

## Age and Sex Criteria

*Females* have shorter tails than do males (see Measurements section), and their central tail feathers lack complete subterminal bands near the middle of the tail. A mottled pattern on the central tail feathers (which occur in about 15 percent of the population) can indicate either sex, but a bird with this characteristic is twice as likely to be a male as a female (Hale, Wendt, and Halazon, 1954). Females also have little or no color on the bare skin over the eye, whereas in males this area is orange to reddish orange (Haber, in Mosby, 1963). Davis (1969a) reported that the length of the plucked and dried central rectrices provides a 99 percent effective means of determining sex of both adult and immature ruffed grouse, but specific separation points for these groups vary with populations.

   *Immatures* can be identified by the pointed condition of their two outer primaries, especially the outermost one. Davis (1969a) stated that during the hunting season the condition of the tenth primary was useful for determining age of nearly 60 percent of the birds, with only a 2 percent error. However, the presence of sheathing at the base of the outer two primaries (adults) or on the eighth but not the ninth or tenth primaries (immatures) separated 79 percent of the birds examined with a 3 percent error. Immature males can be distinguished from adults by their shorter central tail feathers (length of plucked feather is 159 mm or less, compared to at least 170 mm in adults) as well as various other criteria (Dorney and Holzer, 1957). Ridgway and Friedmann (1946) reported that the two outer primaries of immatures have outer webs that are pale fuscous and mottled or stippled with lighter buff, instead of being buff or whitish with darker brown markings.

   *Juveniles* resemble the adult female but have barred tail feathers that lack the heavy subterminal band and have the gray tips poorly developed (Ridgway and Friedmann, 1946). Juveniles also have white rather than buff chins and primaries with more mottling on their outer webs (Dwight, 1900).

   *Downy young* can readily be identified by the restriction of black on the head to an elongated ear-patch that is narrowly connected to the eyes and a few mid-crown spots. The crown is otherwise a uniform ocherous tawny, gradually blending with the buffy face color. The back lacks definite patterning and varies from russet or dark brown dorsally to pale buff or yellow ventrally.

## Distribution and Habitat

The distribution of the ruffed grouse in North America covers a surprising variety of climax forest community types, from temperate coniferous rain forest to relatively arid deciduous forest types. The unifying criterion, however, is that successional or climax stages include deciduous trees, especially of the genera *Betula* and *Populus*. For example, the range of the balsam poplar (*Populus balsamifera*) bears a surprising similarity to that of the ruffed grouse, as does that of the paper birch (*Betula papyrifera*). Aldrich (1963) correlated racial variation in the ruffed grouse with major plant formations. He indicated that *togata* occurs in northern hardwood–conifer ecotone area; *umbellus* and *monticola* in eastern deciduous forest; *mediana* in oak–savanna woodland; *umbelloides* in typical boreal forest; *yukonensis* in northern or "open" boreal areas; *incana* in drier montane woodlands and aspen parklands; *brunnescens*, *castanea*, and s*abini* in the Pacific coast rain forest; and *phaia* in the corresponding wet interior forest. The relatively drier montane woodlands of the Pacific Northwest are occupied by *affinis*. Not only is there a correlation between the relative wetness and dryness of these general habitat types and associated darkness or paleness of the body plumage but also there are some relationships between climate or vegetation and plumes color. The gray morph of ruffed grouse is typically associated with northern areas or higher altitudes, while the reddish brown morph is more characteristic of southern and lower altitude populations. Gullion and Marshall (1968) discussed the ecological significance of color morphs ("phases") in ruffed grouse, and they suggested that gray-morph birds are perhaps physiologically better adapted to cold than are red-morph birds, and predominate in conifers and aspen-birch forest of these colder areas. They also suggest that gray-morph birds may be less conspicuous in boreal forests, while in the hardwood forests, where raptors have poorer hunting conditions and mammalian predators are more important, the plumage color may not be significant. However, their data indicate that gray-morph birds survive relatively better in hardwood than do red-morphs, and both morphs survive better in hardwoods than in conifers.

   Gullion (1969) has pointed out that continentwide the areas of highest population density of ruffed grouse correspond to the distributional patterns of aspens (*Populus* spp.), which he related to winter as well as summer food use by adults, as well as their value as brooding habitat. Weeden (1965b) reported that ruffed grouse habitat in Alaska typically contains large amounts of aspen and usually also contains white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). Where ruffed and spruce grouse occur together in Alaska, the ruffed are found in earlier stages of succession,

Map 8. Current distribution of the Appalachian (A), Canadian (C), Columbian (Co), eastern (E), gray (G), hoary (H), Idaho (I), Olympic (O), Pacific (P), Vancouver (V), and Yukon (Y) races of the ruffed grouse. Regions of uncertain racial designation are indicated by crosshatching.

frequenting edges, shrubby ravines, and similar openings. Likewise in southern Ontario I have noticed that both species may be found within 100 yards or less of one another, but ruffed grouse are always associated with birch or poplar, while spruce grouse are usually to be found under coniferous cover such as jack pine.

Edminster (1947) analyzed the general shelter requirements of the ruffed grouse in the northeastern states according to vegetational succession stages. Open land types dominated by herbaceous plants provide some food sources for grouse but are of secondary importance to the grouse. Overgrown fields with shrubs and saplings include single-species stands of high-quality quaking aspen cover (*Populus tremuloides*), pin cherry (*Prunus*), scrub oak (*Quercus*), or alder (*Alnus*) cover of moderate quality, and low-quality gray birch or hardhack cover. Other important cover types include mixed-species stands of hardwood shrubs and trees and mixtures of hardwood and coniferous species. Slashings following lumbering activities produce an early succession stage dominated by many shrubs and herbaceous species, especially blackberries and raspberries (*Rubus* spp.), and are of considerable value to grouse. A later, thicker stand of saplings and taller trees is of less value, especially for young birds.

Older forest stands in the northeast include hardwood types, mixed hardwoods and conifers, and predominantly coniferous forest types. Edminster reported that younger hardwood stands have better understory cover for grouse than older stands, and that scattered openings improve the value of either age class. Pasturing also may affect the undercover development. Edminster believed that hardwoods with about 20 percent coniferous species provides better cover than pure hardwood stands, and that those woodlands with from 20 to 70 percent conifers provide both food and cover at all seasons, although summer cover may be less perfect. Predominantly coniferous stands of trees may be food-deficient in younger stages, but for mature stands with a hardwood understory this is not the case.

A study by Dorney (1959) in Wisconsin provides some additional information on grouse-forest relationships. Dorney concluded that mixtures of hardwoods and conifers have greater ruffed grouse use than do hardwoods alone, but Wisconsin grouse appear to be less dependent on conifers for cover than is the case in New York. A heavy shrub understory is needed by grouse for drumming sites, and an absence of shrubs in young hardwood stands causes rapid loss of drumming territories.

Gullion (1969) reported that in Minnesota young aspen stands first become habitable by adult ruffed grouse about 4 to 12 years after regeneration following logging or fire, when the trees are 25 to 30 feet tall, and the stem densities are less than 6,000 per acre.

Grouse continue to use the habitat throughout the year for the next 10 to 15 years, until stem densities drop below about 2,000 per acre. Older stands of aspen provide impor-

tant winter food in the form of male flower buds besides providing nesting habitats.

The importance of small clearings in deciduous forest, as found by Edminster, was proved by Sharp (1963), who established a number of small clearings up to one acre in size in half of a 1,470-acre pole timber forest. These changes were initiated in 1950, and during the next five years 7 to 21 broods used the managed area, while only 2 to 3 used the unmanaged portion of the forest. After ten years, the openings in the forest had filled in, and the value of the area for brood use had declined.

Probably the overall range of the ruffed grouse has not changed greatly in historical times. Slight additions to the range have occurred with introductions. Wild-trapped grouse from Nova Scotia, Wisconsin, and Maine have apparently been successfully introduced into Newfoundland (Tuck, 1968), and they have also been successfully introduced in the Ruby Mountain range of northeastern Nevada (McColm, 1970).

Restrictions in ranges have occurred in a number of states, as indicated by Aldrich (1963). Although it once occurred in northeastern Nebraska, the ruffed grouse is now completely extirpated from the state. It is also gone from northeastern Kansas and northeastern Alabama. Reintroduction efforts in Kansas have apparently been failures. The population in Missouri was probably never high and may have declined to less than 100 birds by the 1930s, although attempts at reintroduction have had some success (Lewis, McGowan, and Baskett, 1968). By 1930 the once extensive Iowa population was also nearly gone except for a remnant in northeastern Iowa. This population still persists locally, and hunting for the first time in 45 years was allowed in 1968 (Klonglan and Hlavka, 1969). In Ohio, where grouse once ranged over the entire state, a low ebb was reached in about 1900, and the species was protected for 32 of 34 years following 1902 (Davis, 1969b). Remnant populations occur in southern Illinois, where the species is protected. The species is also protected in northwestern South Carolina, which is at the extreme southern limit of the species' range. Although limited to a small area of southern Indiana, the grouse population there is distributed through about 1,100 square miles in five counties.

As of 2016, ruffed grouse could be legally hunted in 34 states and in virtually all the Canadian provinces. It is by far the most popular target for grouse hunters in the United States and Canada, with about 3.7 million birds killed annually (2.7 million in the U.S.) in the 1970s (Johnsgard, 1975).

## Population Density

Grouse populations have been intensively studied in New York by Bump et al. (1947), who reported breeding densities of from 8 to 22 acres per bird near Ithaca, and from 21 to 38 acres per bird in the Adirondacks. Maximum fall densities in the two areas ranged from 5 to 20 birds per acre in various years. Gullion (1969) estimated that maximum breeding den-

sity in Minnesota allowed by territorial behavior is one pair (i.e., one territorial male) per 8 to 10 acres, although normal area-wide densities are more commonly 4 to 6 birds per 100 acres. Slightly lower breeding densities of 2 to 4 birds per 100 acres occur in Ohio (Davis, 1968). Porath (cited in Klonglan and Hlavka, 1969) estimated a spring breeding density of 30 to 35 birds per square mile (4.5 to 5.3 birds per 100 acres) in northeastern Iowa, while late summer populations were approximately 90 to 135 birds per square mile in the same area. In Indiana, Thurman (1966) reported a spring density of 18 males per square mile.

Consideration of ruffed grouse densities are not complete without mention of the well-known cycles of population abundance that have been reported for several grouse species, but are especially often attributed to the ruffed grouse. Keith (1963) made an intensive survey of population fluctuations in a variety of birds and mammals in northern North America, and his conclusions appear to be well founded. He believed that the ruffed grouse has undergone fairly synchronous ten-year population cycles at local, regional, and continental levels over most of its North American range, with the exception of the eastern United States and New Brunswick. His book summarizes population density figures from a variety of studies in Minnesota, Michigan, and Wisconsin that indicate peak-year fall densities of from 123 to 180 birds per square mile in Michigan and up to 353 birds per square mile in Minnesota. The average ratios between densities of peak years and those of the subsequent low ones range from a ratio of 3:l to as much as 15:1, with 12 such estimates averaging about 8:l.

In seven studies of local grouse populations, the ruffed grouse had peak populations or initial declines the same year as prairie grouse and spruce grouse, in two cases the ruffed grouse peaked or declined a year before the others, and in four cases the other grouse peaked or began declines one to three years before the ruffed. Likewise, at state or provincial population levels, the ruffed grouse peaked or began declines the same year as the prairie grouse in 6 of 14 cases, while in 6 cases the other grouse peaked or declined one to three years before the ruffed grouse, and in the remaining 2 cases the ruffed grouse peaked or began its decline a year before the others (Keith, 1963). A genetic explanation for the ten-year grouse cycle has been proposed by Page and Bergerud (1988).

## Habitat Requirements

### Wintering Requirements
Although the ruffed grouse is one of the most temperate-adapted of all North American grouse, as indicated by its distribution in the southeastern states, it is well adapted to withstand cold weather. Edminster (1947) indicated that cold weather alone, if not accompanied by snow or sleet, does not materially affect grouse survival. However, during stormy weather, the grouse resort to coniferous trees or to roosting beneath the snow, where they may remain several days.

Although the birds are rarely if ever frozen into such snow roosts, they become highly vulnerable to predation by mammals such as foxes, and Edminster reported mortality rates from 25 to 100 percent higher than normal during a year of unusually heavy snow-roosting activity.

Although conifers provide valuable winter roosting cover for ruffed grouse in New York, the birds continue to rely on hardwood trees for their food, particularly buds and twigs of such trees as poplars, apples (*Malus*), birches, oaks, and cherries (*Prunus*). When available, understory shrubs and vines such as grapes (*Vitis*), greenbrier (*Smilax*), laurel (*Kalmia*), blueberry (*Vaccinium*), and wintergreen (*Gaultheria*) also provide important sources of winter food and cover (Edminster, 1947).

### Spring Habitat Requirements
The spring habitat needs of ruffed grouse appear to be closely tied to ecological situations associated with suitable drumming sites, or "activity centers" (Gullion and Marshall, 1968). Within a general activity center, a specific display site, or "drumming stage" must be present, and Gullion and Marshall believed that two factors govern the choice of such a site. These are the presence of a number of forty- to fifty-year-old aspens near or within sight of a drumming log and also a tradition of occupancy of the site by male grouse. They concluded that the presence of aspens is the most important aspect of cover, which regulates the choice of activity centers, and they found strong relationships between cover types and male survival. Males survived best in hardwoods completely lacking evergreen conifers (in contrast to conclusions mentioned earlier by Edminster), but the presence of spruce and balsam fir (*Abies balsamea*) did not reduce survival. However, survival did decrease as the density of mature pines increased, and male grouse did not survive as well in edge situations as in uniform forest types.

Boag and Sumanik (1969) gathered evidence supporting the view that ruffed grouse do not select drumming sites at random, but that the nature of the surrounding vegetation plays an important role. Comparing 80 drumming sites with 98 similar sites that were not used, they found shrub sizes greater at used than unused sites, and canopy coverage as well as the frequency of young white spruce trees was higher at used sites. Only at used sites was aspen the predominant tree species in the tree layer. They believed that selective pressure for the male to choose open and visually effective sites for drumming is counterbalanced by selection favoring sites protected from predators. The result has been selection favoring sites which give the males sufficient height above the ground from which to observe other grouse or large ground predators, sufficient openings in the shrub layer to see at least 20 yards in most directions, and sufficient canopy and stem coverage to screen the birds from aerial predators. These conditions are met in Alberta in those areas where the density of young hardwood trees and the density and canopy coverage of young spruce are the highest.

The specific drumming stage is usually but not always a log, thus the presence of logs in suitable habitats is an important component of spring ruffed grouse habitat. Palmer (1963) analyzed 40 drumming logs in Michigan that had been regularly used by male grouse. Of the total, 34 were old, decayed conifers, primarily pines. Males always drummed near the larger end of these, usually about five feet from the end. The logs ranged from 7 to 21 inches in height at the drumming position, and none was shorter than 5.5 feet long. Vegetation over eight feet high was significantly denser near the logs used than in the surrounding cover, and among the larger shrubs, speckled alder (*Alnus incana*) composed about three-fourths of the sampled stems. In general, drumming sites were associated with ground vegetation less dense, and large shrub and tree cover denser than was typical of the surrounding general vegetation.

Several studies have indicated that a male grouse may utilize more than one log in his territory for drumming purposes, but one is typically favored. Gullion (1967a) called this log the "primary log," and designated additional drumming sites as "alternate logs." Disturbance may force the bird to use yet other "secondary logs." Logs and activity sites may also be classified as perennial if they are used through the lifetimes of a succession of grouse, or transient if they are used by one grouse and not used again for several years by other birds. Although perennial logs apparently supply the appropriate ecological conditions that attract male grouse, Gullion and Marshall (1968) have found that male grouse using such sites suffer higher mortality as an apparent result of predators' learning the locations of favored display areas.

### Nesting and Brooding Requirements

Habitats selected by female grouse for nesting have been analyzed by Edminster (1947), based on the study of 1,270 nests in New York. Medium-aged stands of hardwoods, with a few conifers, was most commonly used for nesting habitat, followed by medium-aged stands of mixed hardwoods and conifers. When consideration is given to relative cover availability, slashings were also found to be of importance as grouse nesting habitat in New York. Middle-aged stands of hardwoods or mixed stands were found to be considerably more valuable as nesting habitat than were mature forest habitats.

As to specific nest sites, the bases of trees appeared to be the most favorable site, being used about two-thirds of the time. Most of these trees were hardwoods, and nearly all were of considerable size. Most of the remaining nest sites were at the bases of tree stumps, under logs, bushes, or brush piles. Edminster concluded that nest sites are chosen to provide a combination of visibility, protection, an escape route, and proximity to edges and to satisfy an apparent desire for sunlight. The undergrowth nearby is usually open and the canopy density is also relatively open. More than half of the nests were within fifty feet of a forest opening, often the edge of a road. Slope considerations are evidently not important, except that steep slopes are avoided.

Gullion (1967b, 1969), summarizing research done at Cloquet, Minnesota, reported that female grouse probably begin a search for a clone of male aspen trees after mating, near which they locate their nests. These trees are then used by the incubating hens for foraging during incubation.

Brood habitat analyses have also been made by Edminster (1947). Based on studies of 1,515 broods in New York, it was clear that females with broods showed a preference for brushy habitats, especially overgrown land, followed by slashings. Hardwood stands that have been "spot-lumbered" exhibited a high brood usage, as has been later confirmed by studies in Pennsylvania by Sharp (1963). At the same time, hardwood forests continue to receive heavy use from adult grouse (males and unsuccessful females) during the summer, while mixed woods and coniferous forest types serve for escape from extreme heat and summer storms.

### Food and Foraging Behavior

Korschgen (1966) analyzed the nutritional value of seasonal foods of ruffed grouse in Missouri and concluded that high-protein foods are taken in greatest amounts during summer, foods high in fat and carbohydrate were taken most during winter, and the largest amounts of mineral sources were taken during times of reproduction. Evidently grouse select food to fulfill seasonal nutritional needs. Korschgen summarized the principal ruffed grouse foods indicated by 24 published studies. Aspen and poplars are listed as principal foods in 17 of these studies, birch in 11, and all other food sources were mentioned less often, with apple, grape, sumac, beech, and alder all being listed in several studies. In analyses of foods from six areas in the eastern United States, Martin, Zim, and Nelson (1951) listed aspen as being of first or second importance in five areas, and lacking only in samples from the Virginia Alleghenies. Other plants listed in several studies were clover, greenbrier, hazelnut, and grape.

Winter foods of the ruffed grouse consist largely of buds and twigs of trees. Edminster (1954) listed the following major winter sources of such foods: birches (several species), apple, hop hornbeam (*Ostrya*), poplar, cherry, and blueberry. In the Cloquet area of Minnesota, aspens (*Populus tremuloides* and *P. grandidentata*) are usually the most important source of winter foods, and with the appearance of the male catkins in late winter these trees provide the most nutritious food source available to ruffed grouse as long as snow is on the ground (Gullion, 1969).

A study in Utah by Phillips (1967) indicated that chokecherry (*Prunus virginiana*) was the most preferred winter food there, followed closely by aspen and maple (*Acer*). Aspen was also the second most important fall food, but hips from roses (*Rosa*) had higher usage. In Ohio, Gilfillan and Bezdek (1944) found that the fruit and leaves of greenbrier (*Smilax*) had high winter use, as well as aspen buds, fruit of dogwood (*Cornus*), grape (*Vitis*), sumac (*Rhus*), beech (*Fagus*), and other plants. Winter food in Maine, as reported by Brown (1946), consisted primarily of buds of aspens, followed by buds and leaves of willows, catkins and buds of hazelnut

*Fig. 24. Male ruffed grouse, posture preceding drumming display.*

(*Corylus*), and the buds of wild cherry and apple.

Following winter, as ground vegetation is exposed, food consumption of ruffed grouse becomes more diversified, but at least in New York the buds of poplar, birch, cherry, hop hornbeam, and blueberry are still consumed well into May (Edminster, 1947). Likewise in Maine the buds and catkins of poplar are a primary spring food, in addition to buds and catkins of birch, willow buds, and the leaves of strawberry (*Fragaria*) and wintergreen (*Gaultheria*). In Minnesota, male grouse sometimes continue to feed almost entirely on the male catkins of aspens long after snow melt allows succulent evergreen herbaceous plants to become available (Gullion, 1969). Quaking aspen in this region is preferred over big-toothed aspen by a ratio of more than 2 to 1.

The diet of adult grouse changes drastically in early summer as berries and fruits become available (Edminster, 1947). These fruits include strawberries, raspberries, and related species of the genus *Rubus*, cherries, blueberries, and june-berries (*Amelanchier*). Insects compose a small percentage of adult foods at this time, rarely if ever exceeding 10 percent.

In contrast, the basic food of ruffed grouse chicks for at least the first week or ten days of life consists of insects. Bump et al. (1947) reported that 70 percent of the food taken in the first two weeks consists of insects, compared to 30 percent during the third and fourth week, and dropping to 5 percent by the end of July. Ants are among the most frequent food items, but a variety of other insect types, including sawflies, ichneumon flies, beetles, spiders, grasshoppers, and various caterpillar species make up the remainder of chick foods from animal sources. As dependence on insects declines with age, the amount of plant foods, particularly the fruit of strawberries, raspberries, blackberries, and cherries increases correspondingly (Bump et al., 1947).

Fall foods for juvenile and adult birds include a variety of fruiting shrubs, such as viburnums, dogwoods, thorn apples, grapes, greenbriers, sumacs, and roses (Edminster, 1954). The availability of many of these persists into winter, when they supplement the standard diet of buds, twigs, and catkins.

Gullion (1966) has emphasized that the abundance of data on fall food intake by game birds is often misleading in that the diversity of foraging indicated during that time of year is not representative of the critical dietary sources needed for the population's survival through the winter. Thus, the availability of a winter source of male catkins of birch, alder, hazel, and particularly aspen is probably the most important single factor influencing the wintering abilities of ruffed grouse.

Gullion believed that quantitative or qualitative difference in these winter foods might account for major population fluctuations in Minnesota ruffed grouse. Lauckhart (1957) had earlier pointed out that periodic heavy seed crops in trees may sap the nutrients from buds and stems for a several-year period between such crops, causing a nutrient deficiency for animals highly dependent on these trees. The usual cycle of aspen seed crops is 4 to 5 years; thus an interaction of this cycle and some other factor or factors might account for the ten-year grouse "cycle." Clearly this idea has great promise and should be investigated thoroughly before being discarded.

The importance of water, either in the form of standing water, dew, or succulent plants, also should not be overlooked for ruffed grouse. Bump et al. indicate that captive grouse can easily survive for at least 12 days without food if they are provided with water but in the absence of both food and water will live only a few days. Since most grouse foods contain considerable water, it is probable that the birds can normally survive indefinitely in the absence of standing water.

## Mobility and Movements

Ruffed grouse do not perform any movements that might be considered migratory, although there are some seasonal variations in mobility. Little movement is normally exhibited by ruffed grouse broods prior to the brood's breaking up and dispersing; Chambers and Sharp (1958) reported that the cruising radius of most marked broods was no more than a quarter mile. With the dispersal of the broods, more than half of the juveniles moved distances of more than a mile, in one case up to 7.5 miles. Similarly, Hale and Dorney (1963) reported that about one-fourth of the juveniles they banded had moved more than one mile from the banding site at the time of recovery. One grouse they banded as a three-month-old juvenile was shot 31 days later some 12 miles from the banding site. Apparently these fall movements were independent of population densities and were unrelated to so-called "crazy flight" behavior, during which young grouse may make long and erratic movements apparently related to inexperience and perhaps fright.

By winter, movements of both young and adult grouse decline, and the birds become virtually sedentary by spring. Hale and Dorney (1963) found that males banded on drumming sites were highly sedentary and normally returned to the same site each year. Chambers and Sharp (1958) likewise reported that grouse become sedentary as they mature, with males only rarely moving more than one-fourth mile, while females sometimes moved more than a mile. Hale and Dorney likewise reported that, except during winter, females were consistently more mobile than males. Gullion and Marshall (1968) noted a high degree of fidelity by adult male ruffed grouse, not only to a particular territory but also to a specific display site. Only about 36 percent of 168 males that lived at least 12 months or longer moved to another log during their drumming lifetimes, and such movements

averaged only about 300 feet. At least 20 males, however, moved to new activity centers.

Movements by female ruffed grouse during the spring season are of equal interest and have been studied by Brander (1967). By studying the daily movements of three females in early May, Brander found that the females moved from their established winter home ranges of 7 to 26 acres toward male drumming sites, apparently stimulated by the drumming behavior, particularly drumming sounds. One female was apparently attracted to three different males on different days before copulation occurred, and the pair remained together no more than a few hours. Since the male continued to drum after her departure, Brander concluded that the ruffed grouse mating pattern should be regarded as a promiscuous one. He estimated that the three females each remained in a state of receptivity for only four days, ending the day before the first egg was laid. The hen located her nest in each case within the area of her movements of the previous week to ten days. As mentioned previously, the female usually seeks out a clone of male aspen near which she establishes her nest (Gullion, 1969).

## Reproductive Behavior

### Territorial Establishment and Advertisement

According to Bump et al. (1947), captive male grouse begin to exhibit aggressiveness as early as the first of March, although they have sometimes been seen strutting on warm days in winter. Edminster (1947) reported that drumming has been heard every month of the year and every hour of the day and night, but the most intensive drumming in New York occurs in early spring during late March and April, tapering off in May.

The two basic aspects of male reproductive display are drumming ("wing-beating" of Hjorth, 1970) and strutting ("upright," "bowing," and "rush" sequence of Hjorth, 1970). There is no doubt that drumming is primarily an acoustic display and serves to advertise the location of the male in fairly dense forest cover. Strutting, however, is a predominantly visual display and is probably not normally released except in the visual presence of another grouse or similar stimulus. Undoubtedly both displays are essentially agonistic or aggressive in origin, serving for territorial proclamation and establishment of dominance. Since drumming is the basic means of territorial advertisement, it will be discussed first.

The motor patterns of the drumming display are well described in Bent (1932) and many other references and need little amplification here. The male typically stands on a small log, facing the same direction and at virtually the same location on each occasion. With his tail braced against the log and his claws firmly in the wood, he begins a series of strong wingstrokes. These strokes, which start slowly at about 1-second intervals, rapidly speed up, with a complete series lasting about 8 (Allen, in Bent, 1932) to 11 seconds (Hjorth, 1970). Hjorth found that in a sample of drumming displays from Alberta there were consistently 47 wingstrokes, while
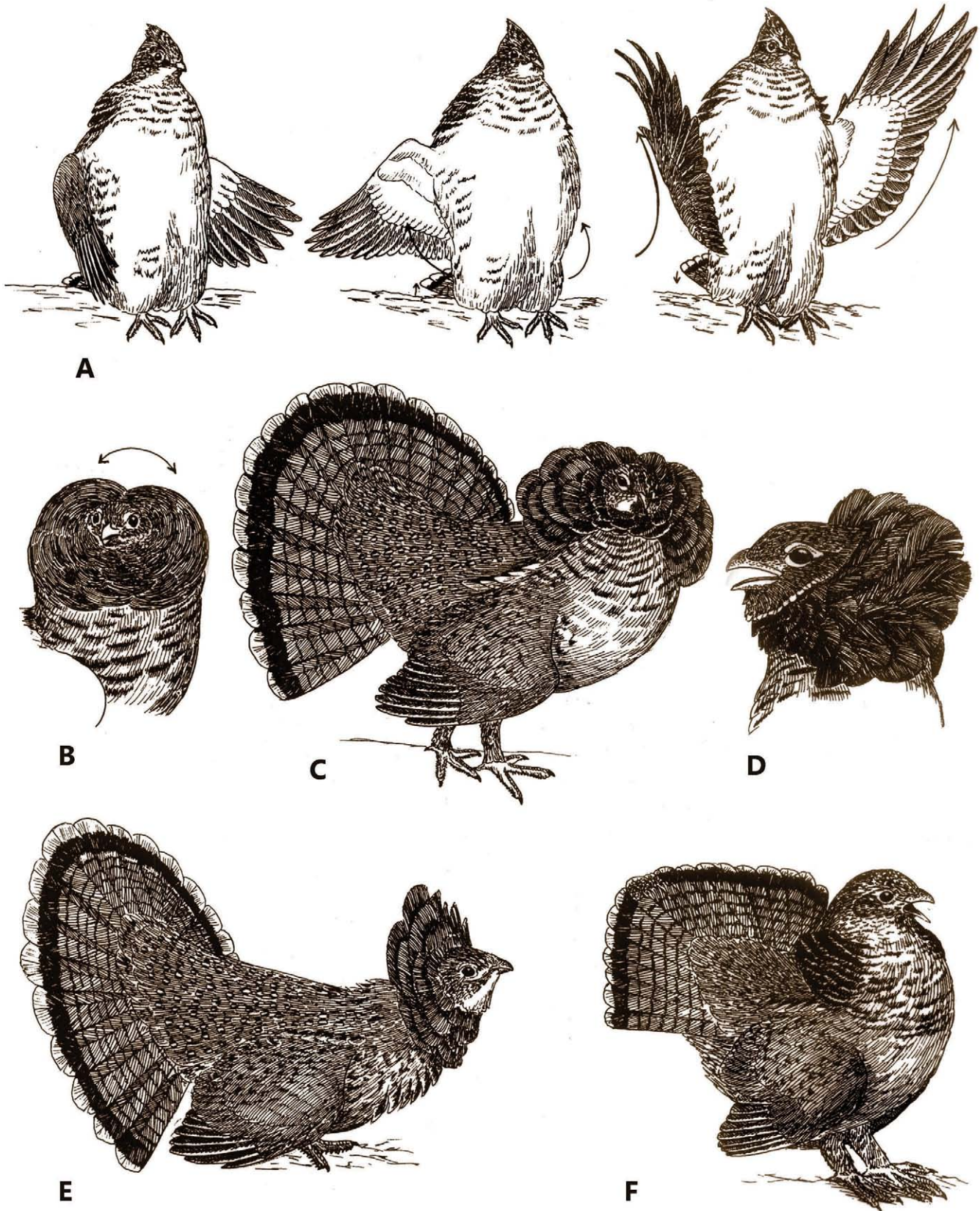
Fig. 25. Male ruffed grouse displays, including (A) drumming sequence, (B) rotary head-shaking, (C) strutting, (D) ruff erection, (E) final phase of rush display, and (F) posture of female defending a brood. Various sources.

one from Ohio had 51. Aubin (1970) noted that among six ruffed grouse studied in southwestern Alberta the number of wingstrokes varied only from 44 to 49 in his samples and was even more consistent for individual birds. Allen hypothesized that the muffled drumming sound produced by the wings resulted from the forward and upward thrust rather than the return stroke. This strong forward thrust produces a counter-pressure that forces the bird backward, thus explaining the need for the brace provided by the tail and the importance of clutching the log with the claws. At the end of the last stroke this pressure is released, and the bird tips forward on its perch. As Allen noted, the wings do not touch each other during the drumming, and the noise simply results from air compression, which accounts for the dull throbbing nature of the sound. Hjorth (1970) advanced the idea that the downstroke rather than the upstroke may be responsible for this sound.

Drumming usually begins well before daylight and may continue until somewhat after sunrise. It usually begins again about an hour before twilight and may continue until dark (Bump et al., 1947). The usual interval between drumming displays is three to five minutes, but this interval varies from a few seconds to much longer periods.

As noted earlier, most males use a single log on which to drum, but some may use more than one. Bump et al. (1947) reported an average of 1.33 logs per male used by 1,173 grouse, Aubin (1970) found that from 1.5 to 1.7 logs per male were used in different years and independently of population densities, while as noted earlier Gullion and Marshall (1968) noted a certain amount of movement among display sites of male grouse.

Gullion (1967a) found that only a few male grouse es-tablish drumming logs their first fall, and a few also fail to become established the following spring. Most birds oc-cupying logs in his study area were full adults, at least 22 months old. He also found a hierarchy of dominance among males. An established male on a drumming log is a "domi-nant drummer," and within his activity center a second, or "alternate," drummer may occur and take over the site of the dominant drummer if it is killed. Nearby rivals on adjacent activity centers are called "satellite drummers," but these are fairly rare. However, other males are "nondrummers," and drum infrequently or not at all. These are presumably young grouse that have been unable to establish drumming sites. Gullion reported that males remain closely associated with their display sites during the summer and that fall drumming may approach or even exceed spring drumming activity. At least a few young males, no older than 17 to 20 weeks, may become established at this time.

Gullion also found "activity clusters" of males, consisting of from about 4 to 8 males occupying sites in fairly close proximity. These seem to represent an expanded collective display ground, similar to those that have been described for other forest grouse.



*Fig. 26. Ruffed grouse, male drumming display.*

### Male Strutting Behavior

Presumably the normal releaser for strutting rather than drumming is the appearance of another grouse near the display log. Edminster (1947) indicated that the drumming male will then strut very slowly toward the intruder with tail erect and spread. The ruffs on the side of the neck are raised ("upright cum ruff display" of Hjorth, 1970), and the male begins to emit hissing sounds that parallel the tempo of the drumming display. With each hiss the head is lowered and shaken in a rotary fashion ("bowing cum head-twisting and panted hissing" of Hjorth, 1970), giving the impression of a locomotive getting underway (Bump et al., 1947). The display ends with a blur of head-shaking and hissing, followed by a short, quick run toward the other bird as both wings are dragged along the ground ("rush cum prolonged hiss" of Hjorth, 1970). Photographs of this display suggest that in the early stages it is oriented laterally, with the tail and upper part of the body tilted toward the object of the display and the head turned in the same direction. However, the short rush is in a shallow arc toward the other bird (Hjorth, 1970). The similarities of this display to the short rushes of the sooty grouse and the spruce grouse are clearly evident. Unlike the spruce grouse, however, the tail is neither shaken nor fanned to produce sound.

Bump et al. (1947) described a "gentle phase" following the strutting phase, which in turn was followed by a "fighting phase" of males. However, their data do not support such a strict interpretation of male behavior patterns, nor would such a sequence seem biologically probable. The strutting behavior of males serves equally well as a preliminary threat

display toward other males prior to fighting and as a preliminary to attempted copulation with females. The means by which males recognize the sex of intruders on their territories is still uncertain, but in all likelihood there is a differential sexual response of males and females to strutting in another bird. Hjorth (1970) gave the posture associated with this reputed "gentle phase" the name "slender upright cum head-shaking."

The period of receptivity of females is apparently only from three to seven days (Bump et al., 1947; Brander, 1967) and probably is terminated as soon as a successful copulation is achieved. Assumption of the typical receptive posture of grouse, with the wings drooped and slightly spread and the tail slightly raised, while the body feathers are depressed, will stimulate copulation attempts by the male.

### Vocal Signals

Hissing is performed by both sexes. Males hiss during their head-shaking and short-rush displays, and females hiss when defending a brood (Bump et al., 1947). Females also utter a squeal during distraction display and quiet their hiding chicks with a downward-inflected scolding note. After any danger is past, they call the brood together with a low, humming call (Bump et al., 1947). Adult grouse of both sexes utter a startled *pete-pete-pete* note, and a chirping *perrck* note, which Bump et al. attributed to "curiosity." A variety of "conversational" notes are also present.

Chicks have four principal call-notes, according to Bump et al. (1947). These include alarm calls, two different notes uttered by scattered chicks, and a warning signal of several descending notes that is uttered by older chicks.

### Nesting and Brooding Behavior

Typical nest sites for the ruffed grouse have already been mentioned (see the Nesting and Brooding Requirements section). Bump et al. (1947) reported that the female lays her eggs at an average rate of 2 eggs every 3 days, thus taking 17 days to complete an average clutch of 11 eggs. The attachment of the female to the nest increases as the clutch size increases, but incubation does not begin until the last egg is laid. The period of incubation is from 23 to 24 days, but low environmental temperatures may delay hatching a few days beyond this time, Bump et al. found that during incubation the female will leave the nest for from 20 to 40 minutes, or only rarely longer, to feed. Evidently feeding may occur twice each day under normal conditions, but during stormy weather the bird may remain on the nest continuously. Much enlarged "clocker" droppings are typical of incubating females; these are usually found in the vicinity of nests near the usual foraging areas.

Bump et al. (1947) reported that although the average clutch size for 1,473 first nests was 11.5 eggs, 149 renesting attempts averaged only 7.5 eggs. Since no cases of second renesting attempts were found, these authors estimated that the maximum number of eggs that a female might lay in a single season is about 19. There is no evidence that second broods are ever raised by this or any other species of grouse in North America.

Female ruffed grouse exhibit strong nest and brood defense tendencies and will often resort to a disablement display, feigning a broken wing, especially prior to hatching time. Following hatching, the female more often stands her ground, spreads her tail, and assumes a posture similar to the male's strutting posture as she hisses or utters squealing sounds. When the chicks gain the power of flight after 10 to 12 days, the usual response of both hen and chick is to fly when disturbed. By mid-September, when the chicks are 12 or more weeks old, the families begin to break up and dispersal of the juvenile birds begins.

## Evolutionary Relationships

In his revision of grouse genera, Short (1967) merged the monotypic genus *Bonasa* with the Eurasian genus *Tetrastes*, which contained two species of "hazel grouse." The two Eurasian species lack neck ruffs but otherwise are very similar to the ruffed grouse, and Short considered that, of the two, the European hazel hen (*T. bonasia*) is nearest to the North American ruffed grouse. The habitat of this bird in Europe is one of mixed hill woodlands and thickets, and it is especially prevalent in aspen and birch, which strongly suggests a common ecological niche. The winter diet of the Siberian hazel hen (*T. b. sibiricus*) consists of from 70 to 80 percent buds and catkins of birches (Dementiev and Gladkov, 1967), which further attests to the strong ecological similarities of these species and certainly suggests a common evolutionary descent.

In contrast to the ruffed grouse, the hazel hen is apparently monogamous and forms a pair bond that lasts at least until hatching and sometimes beyond. An additional behavioral difference is that the male display consists largely of whistling calls (Dementiev and Gladkov, 1967). There is no drumming display, but apparently an aerial display involving the whirring of wings does occur (Hjorth, 1970). It would seem that the evolution of a promiscuous mating system, development of nonvocal acoustical signals rather than reliance on vocal whistles, and the correlated ritualization of aerial display flights into a sedentary drumming display all occurred after the separation of ancestral ruffed grouse stock.

Short (1967) concluded that the nearest relationships of the genus *Bonasa* (in the broad sense) are with *Dendragapus* and that the former genus probably arose from pre-*Dendragapus* stock. I agree that modern species of *Dendragapus* or *Tetrao* probably represent the nearest living relatives of *Bonasa*. However, the American Ornithologists' Union Checklist (1998) places *Bonasa* first in taxonomic sequence of the grouse subfamily Tetraoninae, followed by *Centrocercus*. A 2004 estimate of the ruffed grouse's total population was 8,300,000 (Rich et al., 2004).

*Suggested reading:* Bump et al., 1947; Edminster, 1947; Attwater and Schnell, 1989; Rusch et al., 2000

*Plate 21. Hoary ruffed grouse, male (rufous morph) on drumming log; May.*



*Plate 22. Hoary ruffed grouse, female; May.*

*Plate 23. Hoary ruffed grouse, male (rufous morph) drumming; May.*

# Greater and Lesser Prairie-chickens (Pinnated Grouse)

*Tympanuchus cupido* (L.) 1758 and *T. pallidicinctus* (Ridgway) 1873

## Other Vernacular Names

Prairie-chicken, prairie cock, prairie grouse, prairie hen

## Range

Current resident of remnant prairie areas of Michigan, Wisconsin, and Illinois and from southern Manitoba southward to western Missouri and Oklahoma and portions of the coastal plain of Texas. Also (*T. pallidicinctus*) from southeastern Colorado and adjacent Kansas south to eastern New Mexico and northwestern Texas.

## Species

*T. cupido* (Brewster): Greater prairie-chicken. Historically widespread in taller grasslands and woodland scrub forests of eastern and interior North America; now restricted to generally isolated populations from North Dakota south to Texas, and east to Wisconsin.

*T. pallidicinctus* (Ridgway): Lesser prairie-chicken. Currently limited to arid grasslands of southeastern Colorado and southwestern Kansas southward through Oklahoma to extreme eastern New Mexico and northwestern Texas.

## Subspecies

*T. c. cupido* (Linnaeus): Heath hen or eastern greater prairie-chicken. Extinct since 1932. Formerly resident along the Atlantic Coast from southern Maine south to Maryland.

*T. c. pinnatus* (Brewster): Interior greater prairie-chicken. Currently limited to the grasslands of eastern North Dakota, western Minnesota, central South Dakota, central and southern Nebraska, eastern Kansas, northeastern Colorado (reintroduced), and northeastern Oklahoma. Relict or reintroduced populations exist in western Missouri and central Wisconsin, southern Illinois, and southern Iowa.

*T. c. attwateri* Bendire: Attwater's greater prairie-chicken. Currently limited to two relict populations along the coast of Texas, including Galveston Bay Prairie Preserve near Texas City (Galveston County) and Attwater's Prairie Chicken National Wildlife Refuge, near Eagle Lake (Colorado County).

## Measurements

### Greater Prairie-chicken

*Folded wing:* Males, 217–241 mm (average 226 mm); females, 208–220 mm (average 219 mm).

*Tail:* Males, 90–103 mm (average 96 mm); females, 87–93 mm (average 90 mm).

### Lesser Prairie-chicken

*Folded wing:* Males, 207–220 mm (average 212 mm); females, 195–201 mm (average 198 mm).

*Tail:* Males, 88–95 mm (average 92 mm); females, 81–87 mm (average 84 mm).

## Identification

### Greater Prairie-chicken

Adults, 16 to 18.8 inches long. Both sexes are nearly identical in plumage. The tail is short, somewhat rounded, and the longer under (but not upper) tail-coverts extend to its tip. The neck of both sexes has elongated "pinnae" made up of about ten graduated feathers that may be relatively pointed (in *cupido*) or somewhat truncated (other races) in shape and are much longer in males than in females. Males have a conspicuous yellow comb above the eyes and bare areas of yellowish skin below the pinnae that are exposed and expanded during sexual display. The upperparts are extensively barred with brown, buffy, and blackish, while the underparts are more extensively buffy on the abdomen and whitish under the tail. Transverse barring of the feathers is much more regular in this species than in the sharp-tailed grouse, which has V-shaped darker markings and relatively more white exposed ventrally.

### Lesser Prairie-chicken

Adults, 15 to 16 inches long. In general, like the greater prairie-chicken, but the darker, blackish bars of the back and rump typical of greater prairie-chickens are replaced by brown bars (the black forming narrow margins); the breast feathers are more extensively barred with brown and white; and the flank feathers are barred with brown and dusky instead of only brown. Males have reddish rather than yellowish skin in the area of the gular sacs and during display their yellow combs are more conspicuously enlarged than those of greater prairie-chickens. As in that form, females have relatively shorter pinnae and are more extensively barred on the tail.

## Field Marks

The only species easily confused with either the greater or lesser prairie-chicken is the sharp-tailed grouse, which often occurs in the same areas where greater prairie-chickens are found. Sharp-tailed grouse can readily be recognized by their pointed tails, which except for the central pair of feathers are buffy white, and by their whiter underparts as well as a more "frosty" upper plumage pattern, which results from white spotting that is lacking in the prairie-chickens.

## Age and Sex Criteria

### Greater Prairie-chicken

*Females* may readily be recognized by their shorter pinnae (females of *pinnatus* average 38 mm, maximum 44 mm; males average 70 mm, minimum 63 mm) and their extensively barred outer (rather than only central) tail feathers. The central crown feathers of females are marked with alternating

buffy and darker cross-bars, whereas males have dark crown feathers with only a narrow buffy edging (Henderson et al., 1967). In the Attwater's prairie-chicken the pinnae of females are about 9/16 inch (14 mm) long, while those of males are over 2 inches (53 mm), according to Lehmann (1941).

*Immatures* may be recognized by the pointed, faded, and frayed condition of the outer two pairs of primaries (see sharp-tailed grouse account). The pinnae length of first-autumn males is not correlated with age (Petrides, 1942).

*Juveniles* may be recognized by the prominent white shaft-streaks, which widen toward the tip, present in such areas as the scapulars and interscapulars.

*Downy young* are scarcely separable from those of lesser prairie-chickens (see that account) and also resemble young sharp-tailed grouse. However, prairie-chickens have a somewhat more rusty tone on the crown and the upper parts of the body and richer colors throughout. There are usually three (one small and two large) dark spots between the eye and the ear region and several small dark spots on the crown and forehead. Short (1967) mentions, however, that at least some downy specimens of *attwateri* have only one or two tiny postocular black markings, which thus would closely approach the markings of downy sharp-tailed grouse.

### Lesser Prairie-chicken

*Females* may be identified by the lack of a comb over the eyes and their brown barred under tail-coverts, which in males are black with a white "eye" near the tip (Davison, in Ammann, 1957). Males have blackish tails, with only the central feathers mottled or barred, while the tails of females are extensively barred (Copelin, 1963).

*Immatures* can usually be identified by the pointed condition of the two outer pairs of primaries. The outermost primary of young birds is spotted to its tip, while that of adults is spotted only to within an inch or so of the tip. In addition, the upper covert of the outer primary is white in the distal portion of the shaft, whereas in adults the shafts of these feathers are entirely dark (Copelin, 1963).

*Juveniles* are more rufescent than the corresponding stage of the greater prairie-chicken or the adults. The tail feathers are bright tawny olive and have terminal tear-shaped pale shaft-streaks (Ridgway and Friedmann, 1946).

*Downy young* are nearly identical to those of the greater prairie-chicken (Short, 1967) but are slightly paler and less brownish on the underparts. On the upperparts, the brown spotting is less rufescent and paler, lacking a definite mid-dorsal streak (Sutton, 1968).

## Distribution and Habitat

### Greater Prairie-chicken

The original distributions of prairie-chickens differ markedly from recent distribution patterns; without doubt they are the grouse species most affected by human activities in North America.

### Heath Hen

Aldrich (1963) identified the habitat of the now extinct greater prairie-chicken's eastern race, the heath hen, as fire-created "prairies" or blueberry barrens associated with sandy soils from Maryland to New Hampshire or Maine. The presence of oak "barrens" or parklands may have also been an integral part of the heath hen's habitat, particularly in providing acorns as a source of winter foods (Sharpe, 1968).

### Attwater's Prairie-chicken

The range of the Attwater's prairie-chicken once extended over much of the Gulf coastal prairie from Rockport, Texas, northward as far as Abbeville, Louisiana, an area of more than 6 million acres (Lehmann and Mauermann, 1963). Lehmann (1941) reported spring densities of about 10 Attwater's prairie-chickens per square mile in Texas during the late 1930s. A 1967 survey of this population indicated that 645 birds were then present on about 136,000 acres, a density of 3 birds per square mile. In 2005 there were 40 birds on 12,000 protected acres, or 300 acres per bird.

Of the still-surviving forms of prairie-chickens, the Attwater's prairie-chicken is clearly in the greatest danger of extinction. The race became extirpated from Louisiana in about 1919, and between 1937 and 1963 the Texas population declined from about 8,700 to 1,335 birds (Lehmann and Mauermann, 1963). The remaining population suffered from a badly distorted sex ratio, intensified farming practices, predators, fire exclusion, pesticides, bad drainage practices, and relatively little area set aside specifically for their protection.

The purchase of 3,420 acres of land in Colorado County by the World Wildlife Fund in the mid-1960s (now the Galveston Bay Prairie Preserve of the Nature Conservancy) was the best hope for the retention of a remnant population. By 1965, when the total Texas population was estimated to be 750 to 1,000 birds, the estimated refuge population was 100 birds.

Lehmann (1968) provided a useful summary of the status of this bird as of the 1960s. As of 1967 an estimated 1,070 birds occupied some 234,000 acres, which represents a habitat loss of 50 percent since 1937 and a population reduction of 85 percent during the same time.

By 2000 the total population numbered less than 100 birds, all confined to the Galveston Bay Prairie Preserve and the Attwater's Prairie Chicken National Wildlife Refuge (Johnsgard, 2002). All the birds remaining on that refuge were probably gone, by 1998, as no wild birds were seen that spring (Silvy et al., 1999). These authors also judged that the Refugio County population would be extinct by 2000. The release of captive-raised birds into national wildlife refuges in Brazoria and Aransas counties, and into a Nature Conservancy preserve (Mad Island) in Matagorda County had offered the Attwater's prairie-chicken its very last chance for surviving into the twenty-first century (Silvy et al., 1999). The spring census of 2005 provided an estimate of 40 birds in the wild, on 12,000 acres of land in Galveston and Colorado counties, or 0.2 percent of their original 6-million-acre range.

*Map 9. Historic distribution of the heath hen (solid line). Dashed line shows possible extension of the race's distribution into southern Maine. Inked areas indicate areas of historic scrub barrens or coastal prairie habitats in the bird's known and probable distributions; stippling shows pine-oak barrens outside the race's known historic range. Upper drawing is based on a historic photo.*

### Interior Greater Prairie-chicken

The interior greater prairie-chicken originally occurred in the moister and taller climax grasslands of the eastern Great Plains from approximately the 100th meridian eastward to Kentucky, Ohio, and Tennessee, and northward to Michigan, Wisconsin, Minnesota, and South Dakota (Sharpe, 1968). Sharpe suggested that the presence of oak woodlands or gallery forests throughout much of this range, and the more extensive oak-hickory forests to the east of it may have been an important part of the greater prairie-chicken's habitat. Their absence in the western and northwestern grasslands may have made those areas originally unsuitable for prairie-chickens.

With the breaking of the virgin prairies in the central part of North America, and their conversion to small grain cultivation, greater prairie-chickens responded greatly and moved into regions previously inhabited only by the sharp-tailed grouse (Johnsgard and Wood, 1968). Thus they moved into northern Michigan and southern Ontario, into northern Wisconsin and much of Minnesota, into the three prairie provinces on Manitoba, Saskatchewan, and Alberta, and westward through all or nearly all of North Dakota, South Dakota, and Kansas to the eastern limits of Montana, Wyoming, and Colorado.

At the same time the lesser prairie-chicken may have undergone a temporary extension northward into western
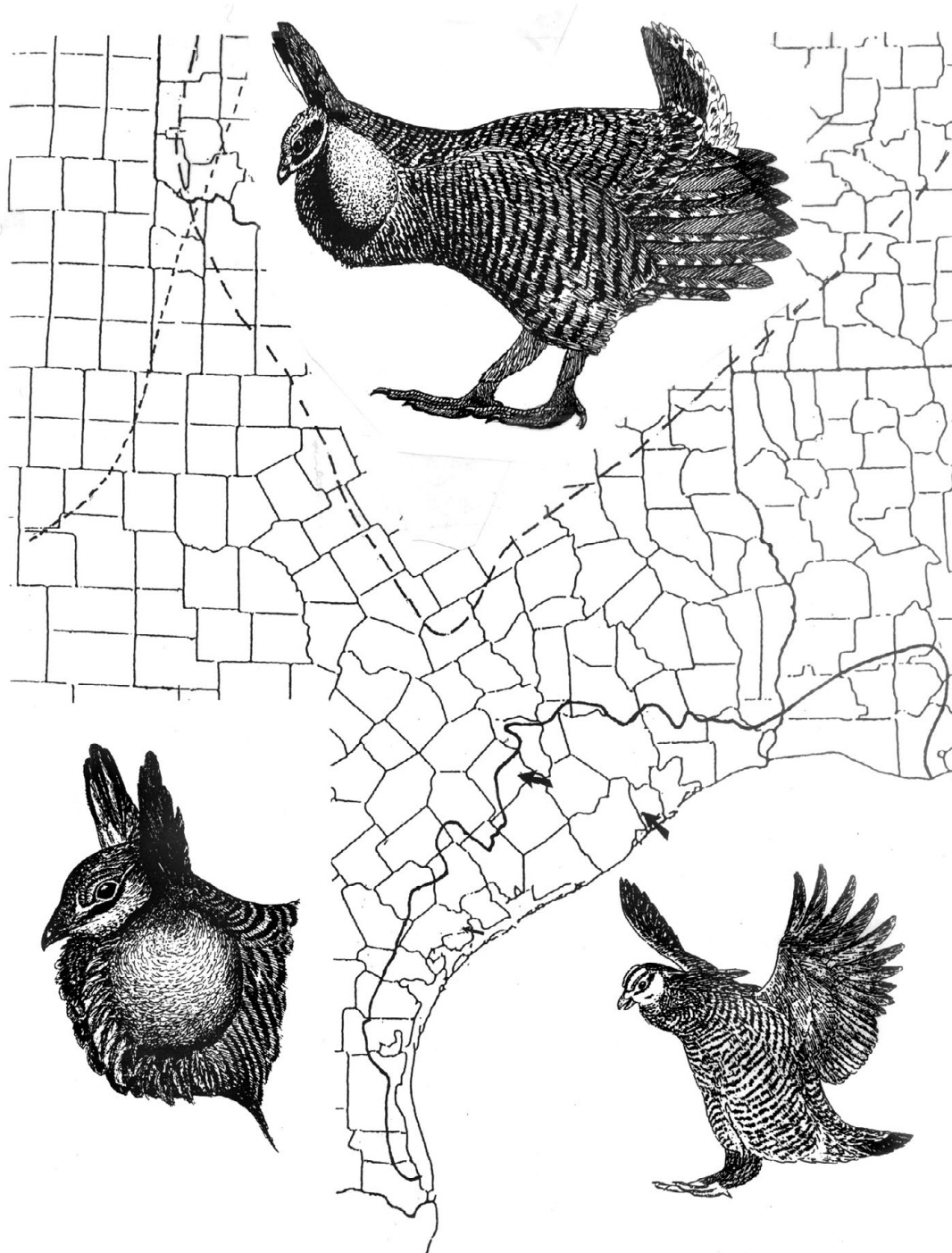
*Map 10. Historic distribution (inked line) and surviving population locations (large arrows) of the Attwater's prairie-chicken. The small arrow indicates a recently extirpated population.*

Kansas, northeastern Colorado, and extreme southwestern Nebraska, where it may have been geographically sympatric for a few years with the greater prairie-chicken (Sharpe, 1968). However, their habitat requirements are quite different (R. Jones, 1963), and very few natural hybrids between these forms have been reported from Kansas, where lesser prairie-chickens have expanded north and encountered greaters.

During several decades the greater prairie-chicken survived extremely well in these interior grasslands, where remaining native vegetation provided the spring and summer habitat requirements and the availability of cultivated grains allowed for winter survival. Eventually, however, the percentage of land in native grassland cover was reduced to the point that these habitat needs could no longer be provided, and the species began to recede from much of its acquired
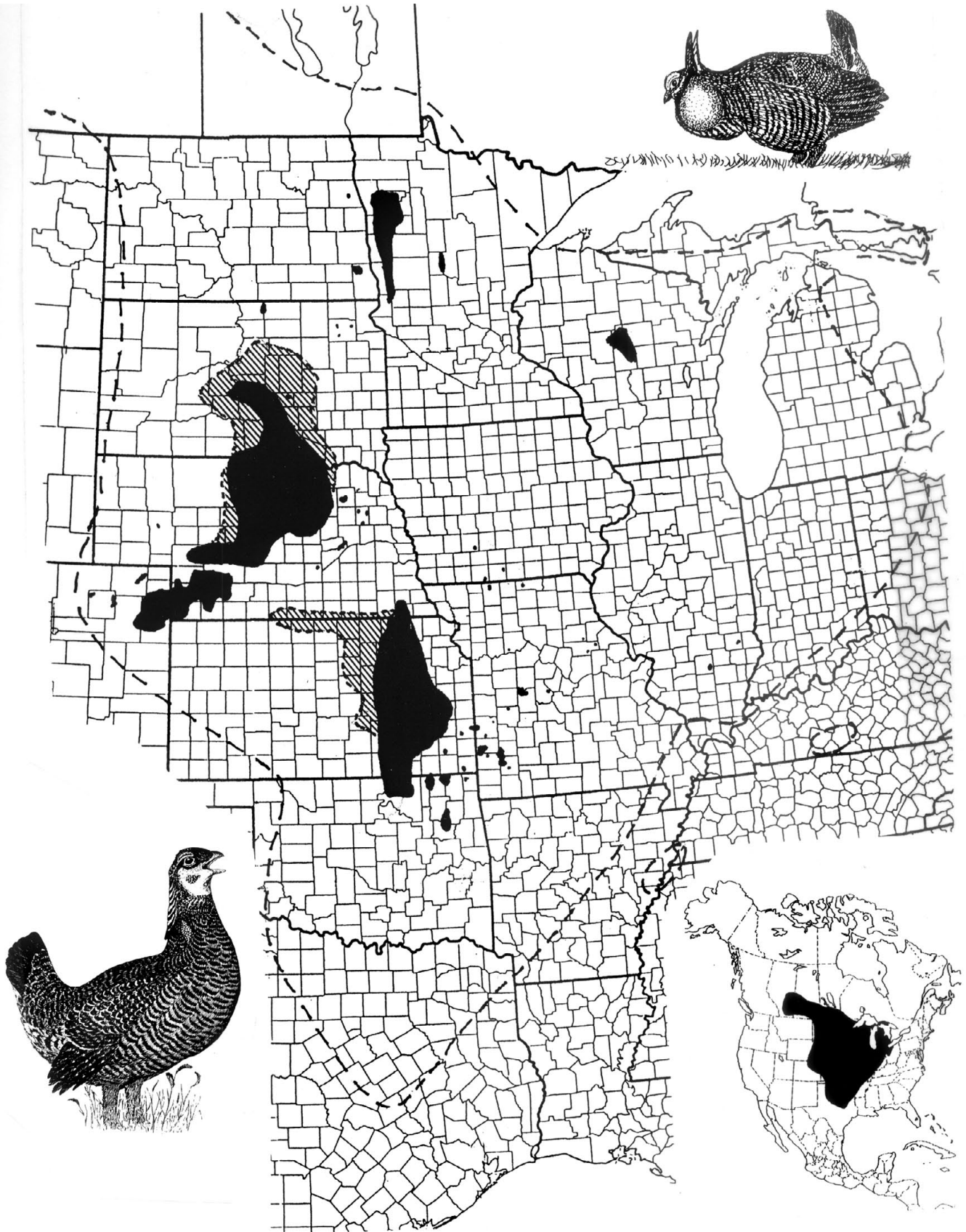
*Map 11. Historic (dashed line) and current (inked) distributions of the interior greater prairie-chicken. Marginal populations are indicated by hatching. The race's maximum historic distribution is shown on the inset map.*
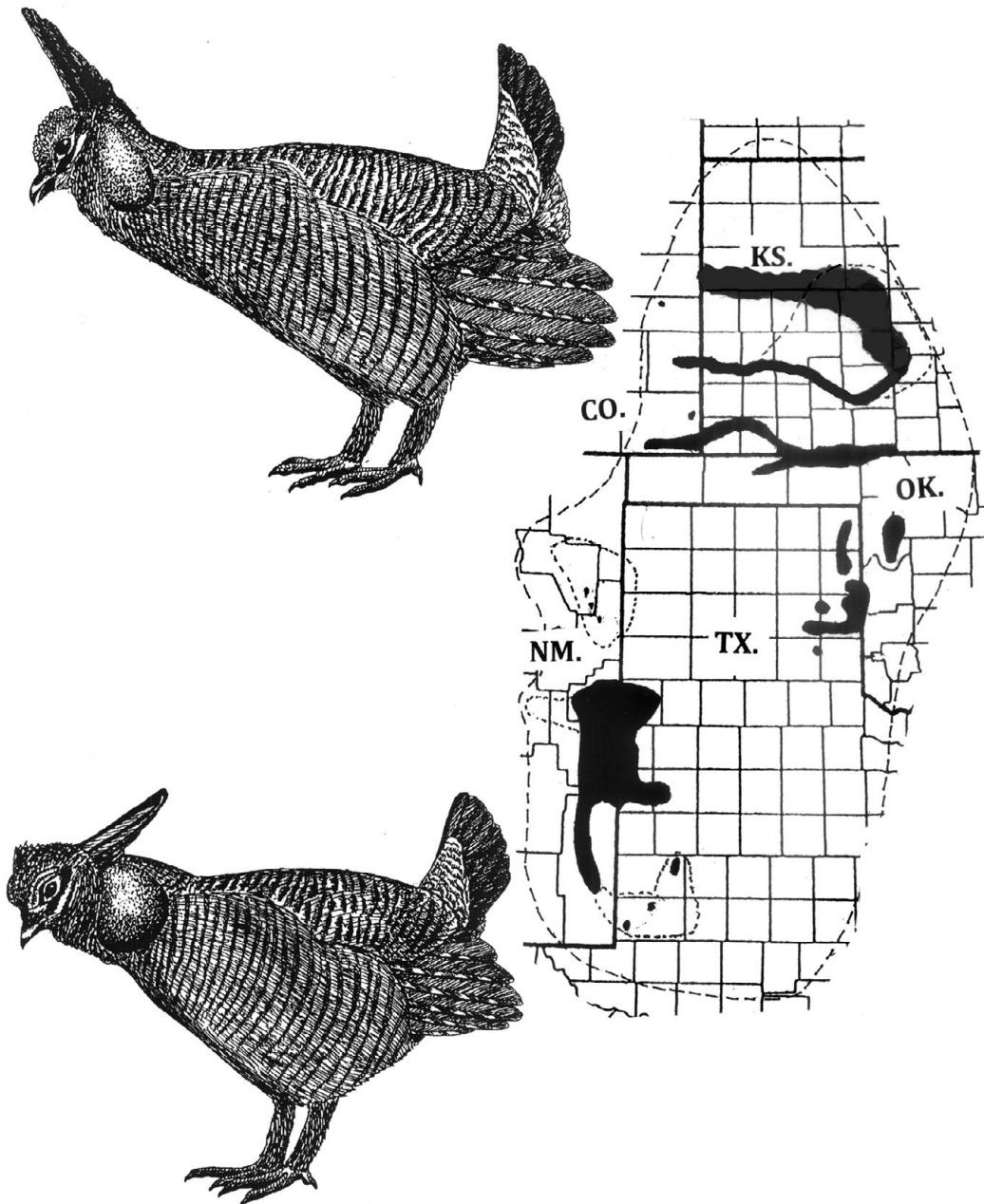
*Map 12. Historic (dashed line) and current (inked) distributions of the lesser prairie-chicken. Short dashes indicate a few recent extirpated or nearly extirpated populations. Drawings on left indicate yodeling (above) and bubbling (below) postures.*

range and to seriously decline or become eliminated from virtually all of its original range. The sad history of this range restriction and population diminution has been recounted in various places (Johnsgard and Wood, 1968; Johnsgard, 2002). Space does not allow a detailed review of these changes, and all that will be attempted here is a statement of the current range and status of the still-extant forms.

The status of the interior greater prairie-chicken is alarming. By 1960 it had been nearly extirpated from all of the four of the Canadian provinces it had earlier colonized (Hamerstrom and Hamerstrom, 1961). Christisen (1969) provided

a useful summary of the bird's status in the United States during the 1960s. Considering the form's probable original range, it has been extirpated as a breeding species from Iowa, Ohio, Kentucky, Texas, and Arkansas by 1960. The birds were gone from Ohio before 1930, and from Kentucky, Texas, and Arkansas at even earlier dates.

The last nesting prairie-chickens in Iowa were reported in 1952, and stray birds were seen as late as 1960 (Stempel and Rogers, 1961). Reintroduction attempts since then have apparently been unsuccessful. Virtually no birds were present in the state until the early 1980s when transloca-

tions were begun. In 1980 and 1982 101 birds were released near Onawa, but this effort failed. Later efforts were made in southern Iowa. A total of 549 birds were released between 1987 and 1994 at four different sites, mostly in Ringgold County, where prairie-chickens had last nested in the early 1950s. Between 1995 and 1998 there were from 17 to 42 males seen on booming grounds in the general area of these releases (Moe, 1999).

The estimated native population in Indiana diminished from more than 400 males occupying 33 booming grounds in 1942 to four males on a single booming ground by 1966. Christisen (1969) indicated a current estimated total Indiana population in the late 1960s of only ten birds. The Indiana population is now extirpated.

In Illinois the situation is only slightly better. Although protected since 1932, the population trend has been downward, and an estimated 300 birds remained in the state by the late 1960s (Christisen, 1969). In 1994 only 46 native birds were found on the state's booming grounds, and these birds were showing declines in fertility and nest success. Translocations were made during the 1990s from Minnesota, Kansas, and Nebraska sources. Spring population estimates in 1998 totaled 256 birds (Westemeier and Gough, 1999).

The birds were gone from their original ranges in southern Wisconsin and Michigan by the 1960s and persisted in small pockets farther to the north, where their total 1960s populations were estimated at 1,000 and 200 birds, respectively. From the 1950s to the 1990s surveys of central Wisconsin booming grounds (especially in Portage County) have fluctuated greatly, often reflecting land use changes, but also somewhat conforming to a ten-year population cycle long reported for upland game birds from the Great Lakes region (Anderson and Toepfer, 1999).

In Minnesota the species was by then also gone from most of its acquired range by the 1960s. It was last hunted in 1942, when an estimated 58,300 birds were taken. During its population peak in 1925, an estimated 411,900 birds were killed; by comparison the statewide population was estimated at 5,000 in the late 1960s (Christisen, 1969). Lek counts in Minnesota from 1974 through 1998 have also shown marked fluctuations but have trended upward, the number of males on booming grounds totaling more than 1,600 in 1998, and the total number of booming grounds about 140, with a long-term (25-year) average of 10.1 males present per ground (Svedarsky, Wolfe, and Toefer, 1999). In 2007 3,294 males were counted on 263 booming grounds in western Minnesota, and limited hunting seasons have been held since 2003.

Virtually all of Missouri might be considered as original greater prairie-chicken range (Johnsgard and Wood, 1968), but between the early 1940s and the mid-1960s the species' range diminished from 2,500 square miles to 900 square miles, and from nearly 15,000 to about 7,000 birds (Christisen, 1967). The birds were last hunted in 1906, with an estimated 10,000 birds present in the late 1960s (Christisen,

1969). State population surveys for the region south of the Missouri River (nearly all of the state's population) averaged about 1.3 birds per 247 acres (100 hectares) in 1945 but rose to 2.2 birds in the 1960s, then underwent a prolonged decline from 1970 to the late 1990s with about 0.4 bird per 247 acres in 1997. The remaining populations were by then concentrated in Pettis, Benton, Barton, Jasper, and Dade counties. During the 1990s translocations were made into Sullivan, Mercer, and Putnam counties of north-central Missouri, with uncertain long-term success (Mechlin, Cannon, and Christisen, 1999).

Colorado, Wyoming, and North Dakota all represent regions of acquired range for the greater prairie-chicken. Only northeastern Colorado and easternmost Wyoming were ever colonized by the birds. In Wyoming it was limited to Goshen County, but it once also occurred in Laramie County. The last occurrence record for the state was for 1952.

In Colorado, the best populations have long occurred in Yuma and Washington counties (Evans and Gilbert, 1969). A statewide 1960s population estimate was of 7,600 birds (Christisen, 1969). Reintroduction efforts in Yuma County began in 1984 and continued in 1990. By 1997–98, 18 booming grounds were located in the reintroduction area, and an estimated 300 to 400 birds were present. Later releases (1991–92) in Washington County were also made, and 8 booming grounds were found in 1996–97, with an overall estimated population of 100 to 200 birds. By 1999 there were an estimated 8,000 to 10,000 prairie-chickens in northeastern Colorado's core population (Yuma, Washington, and Phillips counties). Others were present in Logan, Sedgwick, Morgan, and Weld counties (Giesen and Schroder, 1999). The population is currently hunted regionally, with a three-month season in 2015–16, and a bag limit of two birds per season.

In North Dakota prairie-chickens have been protected since 1945. Prairie-chickens arrived in the state during the homesteading days of the 1880s, peaked in the early 1900s, and began to decline in the 1930s. Between 1938 and 1942 the estimated total population ranged from 300,000 to 450,000 (Johnson, 1964). The 1960s state population was approximately 1,800 birds (Christisen, 1969). Lek surveys of prairie-chickens were begun on the Sheyenne National Grasslands of southeastern North Dakota in 1961, when 20 males were found. Numbers peaked in 1980 (410 males), but by 1997 the number was back down to 69, although the long-term population trend was then upward.

By 1999 there were still a few greater prairie-chickens in North Dakota's southwestern Sargent County, along the South Dakota border, with as many as 8 males being seen. Prairie-chickens had already been present in Grand Forks County in 1968 when the first land purchases were made to establish the Prairie Chicken Wildlife Management Area. By 1999 that site had expanded to about 11,000 acres. From 1992 to 1998 over 300 prairie-chickens were transplanted into the site, and in 1997 a total of 53 were found in 11 locations. In 1997 the estimated state population was 300 birds (Hier, 1999).

South Dakota's prairie-chicken distribution largely represents acquired range, since the species probably originally extended not much farther than the location of the present city of Yankton. No harvest figures are available for the early years of this century, but the populations were probably comparable to those of North Dakota during the same era. In both states the drought of the 1930s brought about a severe decline in the number of prairie-chickens that probably lasted for much of that decade. Since 1942, prairie-chickens and sharp-tails have been hunted every year, with an average combined harvest through 1960 of about 40,000 birds but sometimes in excess of 100,000. By the 1960s they were largely limited to relatively few counties (Janson, 1953; Henderson, 1964). The highest populations occurred in Jones County, where the native grasslands then occupied about 70 percent of the land area and cultivated lands abut 30 percent (Janson, 1953). The 1967 harvest of prairie-chickens was about 10,000 birds, and the estimated state population was approximately 100,000 birds (Christisen, 1969).

Prairie-chicken surveys in South Dakota began in 1956 and were conducted yearly at least to 1997. The 42-year mean number of males seen per lek was 7.02 birds, with a maximum of 10.58 in 1973, and a minimum of 4.19 in 1993 (Fredrickson, Crouch, and Heismeyer, 1999). In 1999 the estimated state population was 65,000 birds, with a hunter-kill of 8,000 (Hier, 1999).

In Nebraska the species probably originally occurred in the eastern part of the state, but it is now largely limited to the central portion, where it occurs along the eastern and southern edges of the Sandhills, where native grasses and grain crops are in close proximity and provide both summer and winter habitat needs (Johnsgard and Wood, 1968). The state's population is relatively static, and this species as well as the more common sharp-tailed grouse have been regularly hunted, except in the case of the small and isolated population in southeastern Nebraska, which is an extension of the large Flint Hills population of eastern Kansas. In 1967 the estimated Nebraska harvest was 15,000 birds, and the state's total population was estimated at 100,000 birds (Christisen, 1969). In 1989 the hunter-kill estimate was 35,000 birds, or well above the 1960s estimates (Westemeier and Gough, 1999). Surveys from 1982 to 1997 in the Sandhills region resulted in mean annual male counts of 10.3 to 12.2 males per site; in 1997 109 sites had 1,087 males present, but no consistent population trend is evident. Between 1986 and 1997 the estimated total population in the state ranged from about 220,000 in 1987 to about 100,000 in 1995. Over the period 1982 to 1997 prairie-chickens composed 36 to 55 percent of the total prairie grouse (including sharp-tailed grouse) killed by hunters in the Sandhills, with no clear trend in numbers or relative species percentages evident (Vodehnal, 1999). A Sandhills-only population estimate for 1997 was 131,000 birds (Hier, 1999).

The heart of the interior greater prairie-chicken's remaining range has long been in eastern Kansas, amid the bluestem (*Andropogon*) prairies that extend from the Oklahoma border in Chautauqua and Cowley counties to near the Nebraska border in Marshall County (Baker, 1953). This area includes an easternmost zone of interspersed natural grassland and croplands; a zone of sandy soils associated with natural grasslands and wooded hilltops; a zone of flinty, calcareous hills and associated native grasslands; and a transition zone between these hills and the cultivated lands to the west. In the best areas for prairie-chickens, the ratio of natural grasslands to cultivated feed crops is roughly two to one (Baker, 1953). Greater prairie-chickens have been given protection in Kansas periodically since 1903. Their population apparently underwent a marked decline in the early 1940s, followed by an increase to the end of that decade, when 50,000 birds were conservatively estimated to be present in the state (Baker, 1953). In 1967 some 46,000 birds were harvested, and an estimated 750,000 were believed present during the late 1960s (Christisen, 1969).

Population surveys for greater prairie-chickens in Kansas have involved booming ground counts, rural mail carrier surveys, and hunter-kill surveys. The booming ground surveys over four regions from 1960 to 1998 all indicated peak numbers occurring in the late 1960s and early 1980s, with sharp declines thereafter. The lowest numbers occurred in the 1990s. Rural mail carrier surveys over the same period indicated similar downward trends, but with greater population fluctuations. Hunter-kill estimates from 1957 to 1996 ranged from a high of 109,000 in 1982 to 13,000 in 1972 and 16,000 in 1996. Long-term comparison of that data shows no obvious trends (Applegate and Horack, 1999).

The only remaining state still supporting interior greater prairie-chickens is Oklahoma. They probably once inhabited all of eastern Oklahoma, but they became largely restricted to the northeastern corner of the state north of the Arkansas River. Besides occurring in eight of the northeastern counties, restocking efforts were made in four more southerly and westerly counties (Sutton, 1967). In contrast to all other states, the 1960s population trend in Oklahoma for prairie-chickens was upward (Christisen, 1969), and in each of the 1967 and 1968 hunting seasons 13,000 to 14,000 grouse were killed. Although Oklahoma did not invest in prairie-chicken refuges, its restocking program combined with a policy of converting marginal timberlands and agricultural lands to natural grasslands was evidently the major reason for the improvements in greater prairie-chicken populations during that period.

By 1999 the remaining greater prairie-chickens in Oklahoma were mostly limited to the Tallgrass Prairie Preserve (37,000 acres) of Osage and Kay counties, the northern parts of Nowata and Craig counties, and extreme northwestern Nowata County. There were also a few birds in Noble, Pawnee, and Ottawa counties, and around the common boundary areas of Rogers, Wagoner, and Mayes counties. From 1979 to 1998 there was a population decline of at least tenfold in Oklahoma, especially after 1990, based on an index

calculated from the numbers of booming grounds found and the average number of males seen per booming ground. Hunting seasons for both greater and lesser prairie-chickens in the state were terminated after the 1997 season (Horton and Wolfe, 1999).

## Population Density

### *Lesser Prairie-chicken*

The lesser prairie-chicken once occupied a large area of arid grasslands in the central and southern Great Plains, with interspersed dwarf oak and shrubs or half-shrub vegetation (Aldrich, 1963; R. Jones, 1963). These birds occurred over an extensive area from eastern New Mexico and the panhandle of Texas northward across western Oklahoma, southwestern Kansas, and southeastern Colorado. Over this area they were found on two major habitat and soil types, the sand sage–bluestem (*Artemisia filifolia–Andropogon*) shrub grasslands of sandy areas and the similarly sand-associated shin oak–bluestem (*Quercus havardi–Andropogon*) community (R. Jones, 1963; Sharpe, 1968).

The present range of the lesser prairie-chicken centers in the panhandle of northern Texas but also includes parts of New Mexico, Oklahoma, Kansas, and southeastern Colorado (Copelin, 1963). In Oklahoma the occupied range by 1960 consisted of about 2,400 square miles. Copelin estimated the 1960 population in Oklahoma to be 15,000 and 30,000 in spring and fall, respectively.

In Texas lesser prairie-chickens declined seriously as a result of overgrazing, pesticide spraying, and altered farming practices (Jackson and DeArment, 1963). The estimated Texas population in 1963 was no more than 3,000 birds. After thirty years of protection, limited hunting of lesser prairie-chickens was again established in 1967, and seasons were also held in 1968 and 1969. The 1967 Texas population was approximately 10,000 birds.

In contrast, the very small Colorado population of lesser prairie-chickens may have increased; Hoffman (1963) reported an increase of from 6 to 104 males on censused display grounds between 1959 and 1962.

In Kansas, Baker (1952, 1953) reported that the drought of the 1930s nearly eliminated the bird from the state. He found that the birds were then limited to sandy lands in fourteen counties south of the Arkansas and Cimarron rivers but did not estimate total population size. A 1963 population estimate for Kansas was10,000 to 15,000 birds (Sands, 1968) In 1970 the lesser prairie-chicken was legally hunted over most of its Kansas range on a three-day hunting season, the first that Kansas had allowed since 1935.

The late 1960s range of the lesser prairie-chicken in New Mexico was limited to about five counties and centered on Roosevelt County. The total yearly kill averaged 1,153 from 1958 to 1968. The New Mexico population in the late 1960s was thought to be 8,000 to 10,000 birds (Sands, 1968).

The total 1960–70 population of the lesser prairie-chicken may thus be estimated as a few hundred in Colorado, pos-

sibly 3,000 in Texas, perhaps 15,000 in Oklahoma, 10,000 to 15,000 in Kansas, and 8,000 to 10,000 in New Mexico. These estimates would suggest a 1960s population of about 35,000 to 43,000 over the species' entire range.

Now-outdated data on male spring densities for the lesser prairie-chicken are available from Oklahoma (Copelin, 1963). Over a six-year period on four different study areas having display grounds, the densities of males per square mile varied from 1.5 to 18.31 and averaged 7.4 males. Earlier figures available from one of these study areas for the 1930s indicated densities of from about 15 to nearly 40 males per square mile. Hoffman (1963) reported that male densities on three areas in Colorado increased from 0.8 to 5.8 males per square mile over a four-year period in this marginal part of the species' range. In Texas, Jackson and DeArment (1963) noted that numbers of males on a 100,000-acre area reached as high as 600 birds in 1942 (about four birds per square mile) but more recently have averaged about 200 males. These data would collectively indicate that spring densities of males in favorable habitats once exceeded 30 per square mile, but probably averaged less than ten.

An estimated reduction of 97 percent of lesser prairie-chicken numbers has occurred since the 1800s, and between 1963 and the 1980s there was an estimated 92 percent reduction in the overall range of the lesser prairie-chicken. Droughts in the early 1990s continued the decline; drought has perhaps been the most important factor in causing the species sad population decline (Giesen, 1998).

By nearly the turn of the century, after a major drought in the early 1990s, the lesser prairie-chicken became a candidate for listing under the Endangered Species Act, and limited hunting was then allowed only in Kansas and Texas. Attempted transplants into New Mexico have been failures (Giesen, 1998).

By 2013 the lesser prairie-chicken's total population was believed to be only about 17,600 birds. It had been classified as "threatened" in Colorado since 1973, and for many years had been a candidate for national listing as a threatened species. In March of 2014 the U.S. Fish and Wildlife Service finally classified the lesser prairie chicken as threatened under the Endangered Species Act (ESA). Immediately after the listing was announced, it was attacked by the Republican-led Congress. An all-out effort was begun to delist the species by attaching its delisting to any available, if irrelevant, legislation (such as the Republicans' favorite boondoggle, the Keystone pipeline project), and thus preventing any federal funding for its conservation. Led by Republican senator Jerry Moran (Kansas), every voting Republican (plus one Democrat) opted for delisting, but the effort fell short of passage. However, in September 2015 a U.S. district judge from Texas (Robert Junell) vacated the threatened listing, based on lawsuits filed by Oklahoma and New Mexico agencies representing the oil and gas industry and other regional interests. At about the same time, the long-proposed ESA listing of the greater sage-grouse as a threatened species was also derailed.

*Greater Prairie-chicken*

Population density estimates for greater prairie-chickens vary greatly for different areas. In general these variations probably reflect the deteriorating status of the species, with declining populations being studied more intensively than the relatively few healthy or increasing populations. Grange (1948) estimated a spring prairie-chicken population in Wisconsin of one bird per 110 acres in 194, and one per 138 acres in 1942, or 4 to 6 birds per square mile. In 1943, the prairie-chicken range in Missouri likewise averaged 4.8 birds per square mile. In South Dakota's best remaining prairie-chicken habitat of six counties, spring population densities of from 2 to 4 birds per square mile occurred in the early 1950s (Janson, 1953).

In contrast, Baker (1953) studied several flocks of greater prairie-chickens in high-quality Kansas range on a study area covering about 3.5 square miles. Two flocks used this area exclusively, and two other flocks used it in part. Spring numbers of one flock varied over a three-year period from 15 to 104 birds, while a second flock varied from 15 to 43 birds during this period. Using conservative figures, an average spring population of at least 50 birds must have been dependent on the area, or at least 14 birds per square mile. During population "highs," the spring density may have reached about 50 birds per square mile for the study area as a whole, and even more if only the composite home range areas are considered.

The estimated total state populations in 1997 were Kansas, 178,000; Nebraska 131,000 (estimate the Sandhills region only; other smaller population centers exist); South Dakota, 65,000; Colorado, 10,000; Minnesota, 1,868; Oklahoma, 1,500; Wisconsin, 1,222; Missouri, 1,000; North Dakota, 300; and Iowa, 200 (Westemeier and Gough, 1999). By the start of the twenty-first century, the greater prairie-chickens could still be legally hunted in Kansas (estimated 1997 kill, 16,000 birds), South Dakota (8,000), and Oklahoma (under 200). No estimates of hunter kill were available for Nebraska.

In summary, it would seem that at the start of the twenty-first century the total collective populations for the three extant prairie-chicken forms would have been less than 100 for the Attwater's, under 20,000 for the lesser, and perhaps close to 400,000 for greater prairie-chickens, with about half of the greater's total population confined to Kansas. Only in Kansas, Oklahoma, Nebraska, Colorado, and South Dakota are the greater prairie-chicken populations not in substantial danger of extirpation. A 2004 estimate of the greater prairie-chicken's continental population was 690,000, while that of the lesser was 32,000 (Rich et al., 2004). By 2016 greater prairie-chickens could be legally hunted only in South Dakota, Nebraska, Kansas, Minnesota (two birds per season), and Colorado (two birds per season). Hunting for lesser prairie-chickens in Kansas, the last state to allow it, was terminated in 2014, and grouse hunting within the lesser's range has remained closed.

## Habitat Requirements

### Wintering Requirements

The winter requirements for prairie-chickens seem to center on the availability of a staple source of winter food, rather than protective cover or shelter from the elements. Lehmann (1941) reported that Attwater's prairie-chickens moved into lightly grazed natural grassland pastures by mid-November and remained there until spring. In Oklahoma, Copelin (1963) found that the lesser prairie-chickens used cultivated grains, especially sorghum, extensively during two winters. In the following winter, when production in the shin oak grassland pastures was apparently high, the birds remained in this pastureland area. During the following two winters there was an increased use of cultivated grains, particularly in late winter when snow was nearly a foot deep for a week or longer, and shocked grain sorghum was then extensively utilized.

Edminster (1954) concluded that grain fields represent an important part of present-day greater prairie-chicken habitat, with corn providing the best winter habitat, provided that it is either shocked or left uncut. Sorghum, like corn, stands above snow during the winter and thus is almost as valuable. Robel et al. (1970) confirmed the importance of sorghum in winter for Kansas prairie-chickens. Other small grains such as wheat and rye are also utilized whenever they can be reached by the birds during winter.

In contrast to the sharp-tailed grouse and nonprairie grouse, greater prairie-chickens provide little evidence that they ever resort to buds as a primary source of food during winter. Martin, Zim, and Nelson (1951) list the buds and flowers of birch as a minor source of winter food for these grouse in the northern prairies, but they found them of far less importance than cultivated grains or wild rose (presumably rose hips). Edminster (1954) listed the buds of birches, aspens, elm, and hazelnut among items used in the northern range during winter, but so long as grain or other seed sources are available this would not appear to be critical to winter survival. Mohler (1963) reported that the best winter habitats for prairie-chickens in the Nebraska Sandhills were areas where cornfields were located near the extensive and lightly grazed grasslands of the larger cattle ranches, which together provide a combination of available food and grassy roosting cover.

### Spring Habitat Requirements

The habitat requirements of the lesser prairie-chicken for display ground locations have been summarized by Copelin (1963). He reported that the males always selected areas with fairly short grass for display grounds and that the grounds were usually located on ridges or other elevations. In sand sagebrush habitat, on the other hand, display grounds were located in valleys on short-grass meadows if the sagebrush on adjacent ridges was tall and dense. Lehmann (1941) noted that of several hundred Attwater's prairie-chicken booming grounds studied, most were on level ground or slightly below the adjacent land surface, but they typically consisted

of a short-grass flat, about an acre in extent, surrounded by heavier grassy cover.

Ammann (1957) provided similar observations for the greater prairie-chicken in Michigan. He noted that of 65 greater prairie-chicken and 95 sharp-tail display grounds that he observed, 47 percent were located on elevated sites and only four were in depressions.

In a comparison of spring display requirements of greater and lesser prairie-chickens, R. Jones (1963) found that both species preferred level or elevated sites associated with short grasses. Plant cover differences were not significant, but greater prairie-chickens tolerated somewhat taller vegetation than did the lesser (a mean of 15.1 cm versus 10.4 cm). Anderson (1969b) reported that greater prairie-chickens preferred grass cover less than six inches tall for their booming grounds, the combination of short cover and wide horizons apparently being far more important than the specific cover type present on the land.

Robel et al. (1970) found that greater prairie-chicken booming grounds in Kansas were associated with clay pan soil types, and the birds remained on these sites for some time after display activities ceased, feeding on succulent green vegetation, especially forbs. With the coming of hot summer weather, the steep limestone hillsides received greater use, probably because of the availability of shade for loafing. Lehmann (1941) likewise reported that heavy shrub cover provides shade for hot summer days, protection against predators and severe weather, and a source of fall food.

### Nesting and Brooding Requirements

Ammann (1957) indicated that of 13 greater prairie-chicken nests found in Michigan, 8 were in hayfields, 1 was in sweet clover, 3 were in wildland openings, and 1 was located at an airport. All of the nests were in fairly open situations. Hamerstrom (1939) has similarly reported on 23 greater prairie-chicken nests in Wisconsin. Eleven of these were in grass meadows near drainage ditches; 3 were in dry marshes or marsh edges; 3 were in openings or edges of jack pine–scrub oak woods; 3 were in scattered mixtures of brush, small trees, and grass; 2 were in small openings in light stands of brushy aspen or willow; and 1 was in rather dense mixed hardwoods. Both of these studies indicate the importance of grassy, open habitats for greater prairie-chicken nests. Hamerstrom, Mattson, and Hamerstrom (1957) and Yeatter (1963) both emphasized the importance of mixed natural grasslands or substitutes in the form of redtop (*Agrostis alba*) plantings as nesting and rearing cover types for greater prairie-chickens. Yeatter (1963) correlated a decline in redtop production and prairie-chicken populations in Illinois, and found that birds nesting in redtop had a nesting success as high as or higher than those using pastures, idle fields, or waste grasslands.

Schwartz (1945) also provided information on nest site preferences in greater prairie-chickens and noted that of 57 nest locations 56 percent were in ungrazed meadows. Half the remainder were in lightly grazed pastures, while the others were in sweet clover, fencerows, sumac, old cornfields, or barnyard grass. The usual proximity of nests to booming grounds led Schwartz, Hamerstrom (1939), and R. Jones (1963) to comment on this relationship. However, Robel et al. (1970) found considerable movements between booming grounds by female greaters and questioned whether the location of booming ground has any major influence on female nesting behavior. He found that 19 nest sites averaged 0.68 mile from display grounds and ranged up to 1.13 miles away. R. Jones (1963) noted that all of the 9 greater prairie-chicken nests he found were located near pastures or old fields that had a large number of forbs into which the broods were taken following hatching.

Lehmann (1941) reported that of 19 Attwater's prairie-chicken nests found, 17 were in tall-grass prairie, one was in a hay meadow, and one was in a fallow field. All of them were located in the previous year's grass growth, and 15 were in well-drained situations, often on or near mounds or ridges. Twelve were located near well-marked trails, such as those made by cattle. All of the nests were roofed over with grassy vegetation, and most had good to excellent concealment characteristics.

Copelin (1963) reported on 9 lesser prairie-chicken nests in Oklahoma and Kansas. None of these occurred among shrubs more than 15 inches high, and 7 were located between grass clumps, particularly little bluestem (*Andropogon scoparius*). Two were under bunches of sage, and 1 was under tumbleweed. Shin oak shrubs from 12 to 15 inches tall were associated with 5 of the nests.

Following hatching, females with broods typically moved to somewhat heavier cover than was utilized for nesting. Copelin (1963) noted that only one brood of lesser prairie-chickens was found in the low oak shinneries, but 27 were seen in oak motts (clumps of oaks 4 to 20 feet tall, growing in stands up to 100 feet in diameter). Oak motts provide better shade than do oak shinneries. In the absence of oak, the broods moved into cover provided by sagebrush or other bushy plants. Lehmann (1941) likewise found movements of both young and old Attwater's prairie-chickens toward cover types that provided a combination of shade and water. The need for free water for prairie grouse broods has been questioned (Ammann, 1957), but certainly in moister habitats the availability of succulent plants, insects, and shade all contribute to the value of the area as rearing cover.

Yeatter's (1943, 1963) studies in Illinois indicated that greater females with newly hatched young feed mainly in redtop fields, and to some extent in small grain or grassy fallow fields. They also move along ditch banks and field borders, where there is heavier cover. In Missouri, females take their young to swales that provide cover in the form of slough grass, where a combination of shade, protection, and easy movement is present. As the birds grow older, they gradually move to higher feeding grounds such as grain fields or stubble but still return in the heat of the day to rest in the shade provided by shrubs, large herbs, or trees.

## Food and Foraging Behavior

Winter foods of prairie-chickens are virtually all from plant sources (Judd, 1905b; Schwartz, 1945). Judd indicated that prairie-chickens consume only about half as much mast as does the ruffed grouse, consisting mostly of the buds of poplar, elm, pine, apple, and birches. They also consume some hazelnuts (*Corylus*) and acorns, which are swallowed whole. In most parts of the bird's present range, however, grain is much more important than buds as winter food. As noted earlier, corn and sorghum represent major winter foods for the species, with corn more important in northern areas and sorghum of increasing importance farther south.

Korschgen (1962) found that in Missouri corn kernels and sorghum seeds are the primary winter foods for greaters, with corn remaining important well into spring. In late spring, soybeans (*Glycine*) exceed corn in importance, with the leaves being consumed first and later the seeds and seed pods. Sedge (*Carex*) flower heads are also important in the spring diet, as are grass leaves. Two cultivated grasses, oats and wheat, are heavily depended on in summer, first for their leaves and later for their grains. Korean lespedeza (*Lespedeza*) foliage is used almost throughout the year, but especially from July through September. In September ragweed (*Ambrosia*) seeds begin to appear in the diet and are used to a limited extent until February.

On a year-round basis, Judd (1905b) reported that animal foods (mostly grasshoppers) constitute about 14 percent, and plant foods 86 percent of prairie-chicken diets. Martin, Zim, and Nelson (1951) stated that during summer the animal component may reach 30 percent, but in winter and spring is as little as 1 to 3 percent.

Lehmann (1941) found that adults of the Attwater's prairie-chicken consume about 88 percent plant material and 12 percent insect food, with seeds and seed pods alone composing
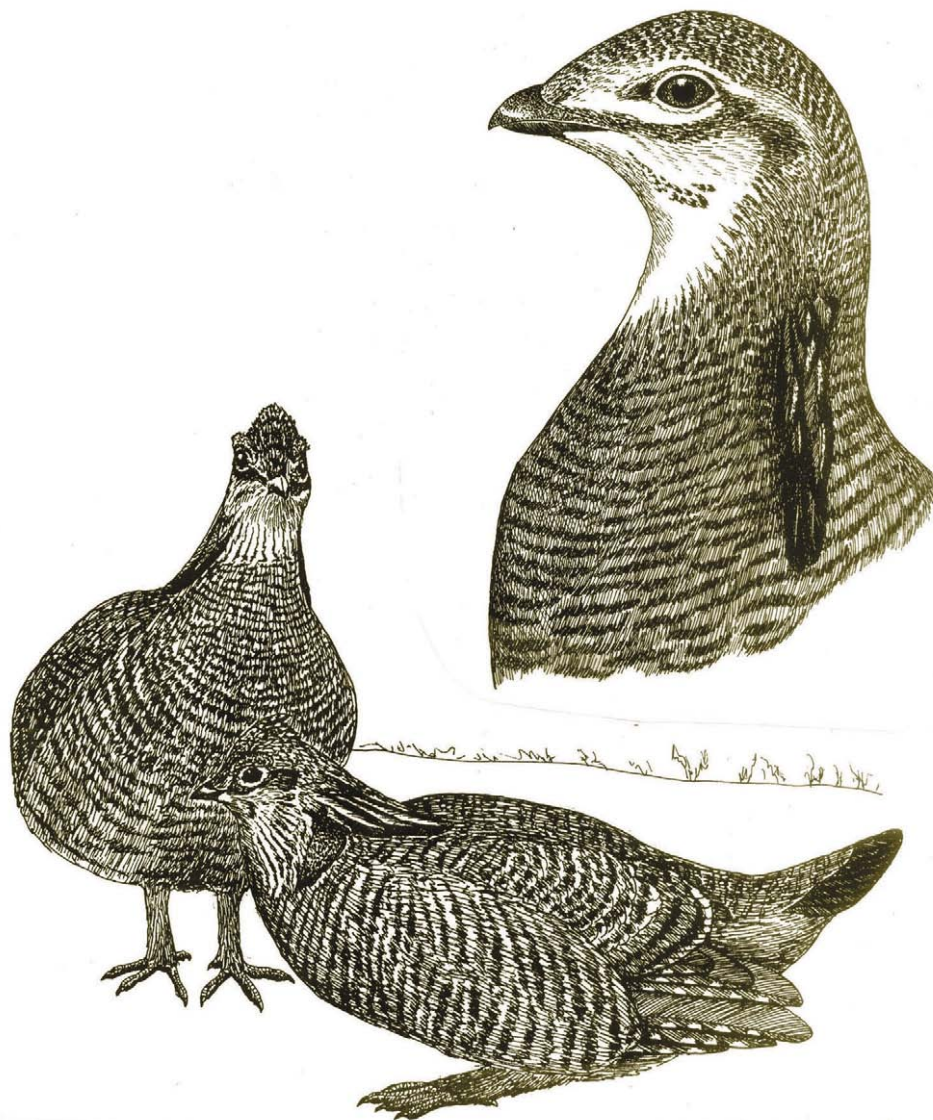


*Fig. 27. Attwater's greater prairie-chicken: detail of male head (above), and two males in territorial dispute (below).*

more than 50 percent of the materials eaten. In contrast to the high percentage of cultivated grains found in most studies of the greater prairie-chicken, native plants found in lightly grazed pastures provided the major food items listed by Lehmann. These included ruellia (*Ruellia*), stargrass (*Hypoxis*), bedstraw (*Galium*), doveweed (*Croton*), and perennial ragweed (*Ambrosia*) as well as many other less important species.

R. Jones's study (1963) of the greater and lesser prairie-chickens in Oklahoma brought out some striking differences in foods taken in study areas about 250 miles apart. The percentage of insects consumed was much higher in the case of the lesser prairie-chicken (41.8 and 48.6 percent of average yearly volumes in two habitats) than was true of the greater prairie-chicken (8.2 and 20.8 percent average volumes in two habitats). The remainder of the food of both species consisted of seeds and green vegetation, with the latter usually composing more volume than the former. Both species fed in grassy cover, but whereas lesser prairie-chickens preferred mid-length grasses for foraging, the greater was found feeding more frequently in short grasses. Jones also reported (1964b) that during the six-month period when plants were important food items, the half-shrub cover type (associated with sandy soils) was used for foraging for five months, and the short-grass cover type (associated with clay soils and used for display purposes) was heavily used only during April. Copelin (1963) reported that the relative use of sorghum in winter was closely related to the amount of snow cover, with large flocks moving to grain fields when snow was about a foot deep for a week or more. When such snow is present, lesser prairie-chickens regularly make snow roosts (R. Jones, 1963), suggesting a fairly recent climatic adaptation to the warmer climates typical of the bird's present range.

## Mobility and Movements

An early analysis of greater prairie-chicken seasonal movements was made by Hamerstrom and Hamerstrom (1949) for the Wisconsin population. They suspected that little movement occurred during summer, especially during the brood-rearing period. However, during autumn considerable movement does occur, and some slight migratory movements may exist. Autumn movements of up to 29 miles were established using banded birds, which perhaps correspond to the "fall shuffle" of quail, or the general fall dispersion of young birds known for other grouse. Most of the longer movements found were those of females; 6 of the 8 females recovered had moved at least 3 miles, while 18 of 30 males had moved less than 3 miles.

During winter, prairie-chickens typically occur in large packs formed by mergers of the fall packs. In Wisconsin these consist of 100 to 200 birds, which become progressively less mobile in the most severe weather. During very bad weather the birds move very little and may scarcely leave their winter roosts. Roosting sites in the Hamerstroms's study area were often from 0.25 to 0.5 mile from feeding fields and were seldom more than 1.25 miles away.

By February, the winter packs begin to break up and the males start returning to their booming grounds. The Hamerstroms found that 50 of 56 banded males usually moved less than 2 miles from their winter feeding grounds to their booming grounds, while the remaining 6 males moved 2 to 8 miles. Apparently many males winter at feeding sites that are the nearest available to their booming grounds, and in late winter some daily movements between these locations occurred. During spring there was little movement on the part of males; the birds roosted on their territories or within a few hundred yards of it. Sources of water, shade, dusting places, and loafing sites were often within 0.5 mile. Following the termination of display activities, the males often remained close to their booming grounds for much of the summer.

Later studies of movements of greater prairie-chickens have been made by Robel et al. (1970) in Kansas, using radio telemetry. These biologists established monthly ranges for 39 adult males, 27 adult females, and 31 juveniles. Movements of adult males were greatest in February, when the birds began to visit their booming grounds and also had to search somewhat harder for food. Flights of a mile or more between feeding areas and display grounds were sometimes seen, and there was also some movement between display grounds. Immature males, however, exhibited their greatest movements in late February and March, with the later flights undertaken largely between display grounds as the birds unsuccessfully attempted to establish territories at various grounds.

During April and May both adults and immatures exhibited reduced movements, with the birds remaining closely associated with specific booming grounds. Maximum movements of females occurred in April, during the time of peak male display. Females often visited several different booming grounds, with movements of up to 4.8 miles being recorded. One female that attempted to nest three times was fertilized at a different booming ground prior to each nesting attempt. Summer movements by both sexes were minimal, as the birds molted and females were rearing broods. However, during fall, longer movements again became typical, especially among juveniles. Three juvenile males moved distances of from 2.7 to 6.7 miles during October and November, but comparable data for females are not available. However, daily movements of females during that time averaged farther than those of males (808 yards versus 660 yards).

Monthly movements of greater prairie-chickens studied by Robel et al. (1970) reflect this seasonal behavior pattern. Summer monthly ranges of adult males were greatest in June (262 acres), fairly small in July (132 acres), and smallest in August (79 acres). In fall and winter the monthly ranges increased from 700 to almost 900 acres from November to February and reached 1,247 acres in March, then decreased sharply and were at a minimum of 91 acres in May. Data for juvenile males indicated a similar monthly mobility pattern for the year. On a daily basis, adult males were most highly

mobile in February (with an average daily movement of 1,121 yards), and they decreased their daily mobility through August (320 yards per day). The movements increased again in fall and through the winter averaged from 600 to 700 yards per day until February. During the period of February through September, adult females had average daily movements of from 332 to 928 yards. Juveniles of both sexes had daily movements rather similar to those of adult males, being least extensive in August and increasing to a peak in March.

Comparable data for the lesser prairie-chicken are not available, but Copelin (1963) does provide some observations on mobility. He also found that movements were most limited in summer and most extensive in winter. The summer range of a female and her brood was estimated to be from 160 to 256 acres, or somewhat less than the estimates of monthly summer mobility in greater prairie-chicken females. On the basis of observations of 114 banded birds, 79 percent were found within 2 miles of their point of capture, and 97.4 percent were within 4 miles. The maximum known distance of movement was 10 miles. In common with the Hamerstroms' study, Copelin found that juveniles often moved considerable distances between their brood ranges and display grounds the following spring, with all of 14 birds moving at least 0.5 mile, and 2 moving nearly 3 miles. Considering birds captured in fall and winter and observed the following spring on display grounds, he found that juvenile birds tended to move farther than adults during this time, and that juvenile hens moved farther than juvenile males. Forty juvenile males moved an average distance of 0.93 mile, and 20 adult males moved an average of 0.46 mile. Six juvenile hens moved an average distance of 2.12 miles and 1 adult hen moved 3.75 miles.

Lehmann (1941) provided some observations on seasonal movements in the Attwater's prairie-chicken, which in general support the studies already discussed. He noted a summer movement of adult and fairly well-grown young from nesting areas into heavier summer cover that provided shade and water, followed by a sedentary state until fall. At this time, from September onward, the birds moved out of some pasturelands and into others that provided winter food and cover conditions. During this time, large concentrations of up to 250 to 300 individuals were sometimes seen, in addition to many smaller flocks of 8 birds or fewer. These winter packs break up late in January, when males begin to display.

## Reproductive Behavior

### Territorial Establishment

As in the sharp-tailed grouse, fall establishment of territories and associated fall display occurs regularly in prairie-chickens. Copelin (1963) noted that during the fall old male lesser prairie-chickens reestablish territories that they held during the spring, and although young males visit the booming grounds, they are apparently not territorial. In the greater prairie-chicken an active period of fall display is likewise a regular phenomenon, at least in Missouri (Schwartz, 1945), Michigan (Ammann, 1957), and various other states, al-

though Hamerstrom and Hamerstrom (1949) did not regard it as typical in Wisconsin. Whether or not the females regularly visit the grounds during fall is not so important as the fact that territorial boundaries are reestablished by mature and experienced males, and young males learn the locations of these display grounds. During the following spring some shifting about may occur as deaths among the males during the winter remove some territory holders, but the basic structure of the booming ground is probably formed during fall display.

The average size of the lek, in terms of participating males, is similar to that of sharp-tailed grouse. Lehmann (1941) indicated that for five Attwater's prairie-chicken grounds studied over a three-year period, the average yearly numbers of participating males ranged from 7.2 to 8.4. Grange (1948) indicated that on 17 display grounds in Wisconsin in 1942, an average of 6.9 males were present. In Nebraska, an average of about 9 male greater prairie-chickens is typical of booming grounds (Johnsgard and Wood, 1968). Generally similar figures have been indicated for Missouri (Schwartz, 1945) and Illinois (Yeatter, 1943). The largest reported booming grounds for greaters were those noted by Baker (1953) in Kansas; he observed one ground containing approximately 100 males.

Copelin (1963) summarized numbers of male lesser prairie-chickens on display grounds in Oklahoma from 1932 to 1951. For a total of 64 grounds studied over varying periods of years, the average number of males present was 13.7, and was as high as 43. These grounds occurred on a study area of 16 square miles, and in different years from 8 to 40 display grounds were found on this study area. The average figure of 24 display grounds would indicate that good lesser prairie-chicken habitat might support about 1.5 active display grounds per square mile. Baker (1953) indicated that six greater prairie-chicken booming grounds were present on a study area of about 3.5 square miles of excellent range in Kansas, or 1.7 grounds per square mile. Most other studies indicate a greater scattering of display grounds for the greater prairie-chicken than for lessers, which may be in part a reflection of the effective acoustical distances associated with the male vocal displays. The lower-pitched booming calls of the greater prairie-chicken presumably are effective over greater distances than are the homologous "gobbling" calls of the lesser prairie-chicken, and this might affect spacing characteristics of display grounds.

### Male Display Behavior

Since the basic sexual and agonistic behavioral patterns of the greater, lesser, and Attwater's prairie-chickens are shared, a single description of motor patterns will be given, with comments on any differences that might occur, based on Sharpe's comparative analysis of the three (1968).

Booming is the collective term given to the sequence of vocalizations and posturing of greater prairie-chicken males that serve both to announce territorial residence to other

*Fig. 28. Interior greater prairie-chicken, calling by territorial male.*

males and to attract females. During booming, the tail is elevated, the pinnae are variably raised to a point that may be almost parallel with the ground, the wings are lowered while held close to the body, and the primaries are spread somewhat. The bird then begins a series of foot-stamping movements (about 20 per second according to Hjorth, 1970), during which he moves forward a relatively short distance, followed by a multiple snapping of the tail in three rapid fanning movements.

At the same time as the tail is initially clicked open and shut, a three-syllable vocalization ("yodelling" of Hjorth, 1970; also often called "tooting") begins, lasting almost two seconds and sounding like *whoom-ah-oom*, with the middle note of reduced amplitude. During the second note a rapid

and partial tail-fanning ("tail-widening" of Hjorth) also occurs and the "air sacs" are partially deflated. During the third note the esophageal tube is again inflated and the lateral apteria or "air sacs" are maximally exposed. Simultaneously, the tail is rather slowly fanned open and again closed. Sharpe (1968) indicated that in the lesser prairie-chicken a single, exaggerated tail-spreading movement occurs during the first phase of booming and the latter tail-spreading elements are lacking.

Sharpe estimated that the maximum amplitude of the fundamental harmonic during booming (yodelling) is about 300 cycles per second (Hz) in the greater and Attwater's prairie-chickens, and about 750 Hz in the lesser prairie-chicken. In addition, the vocalization phase of the lesser lasts about 0.6
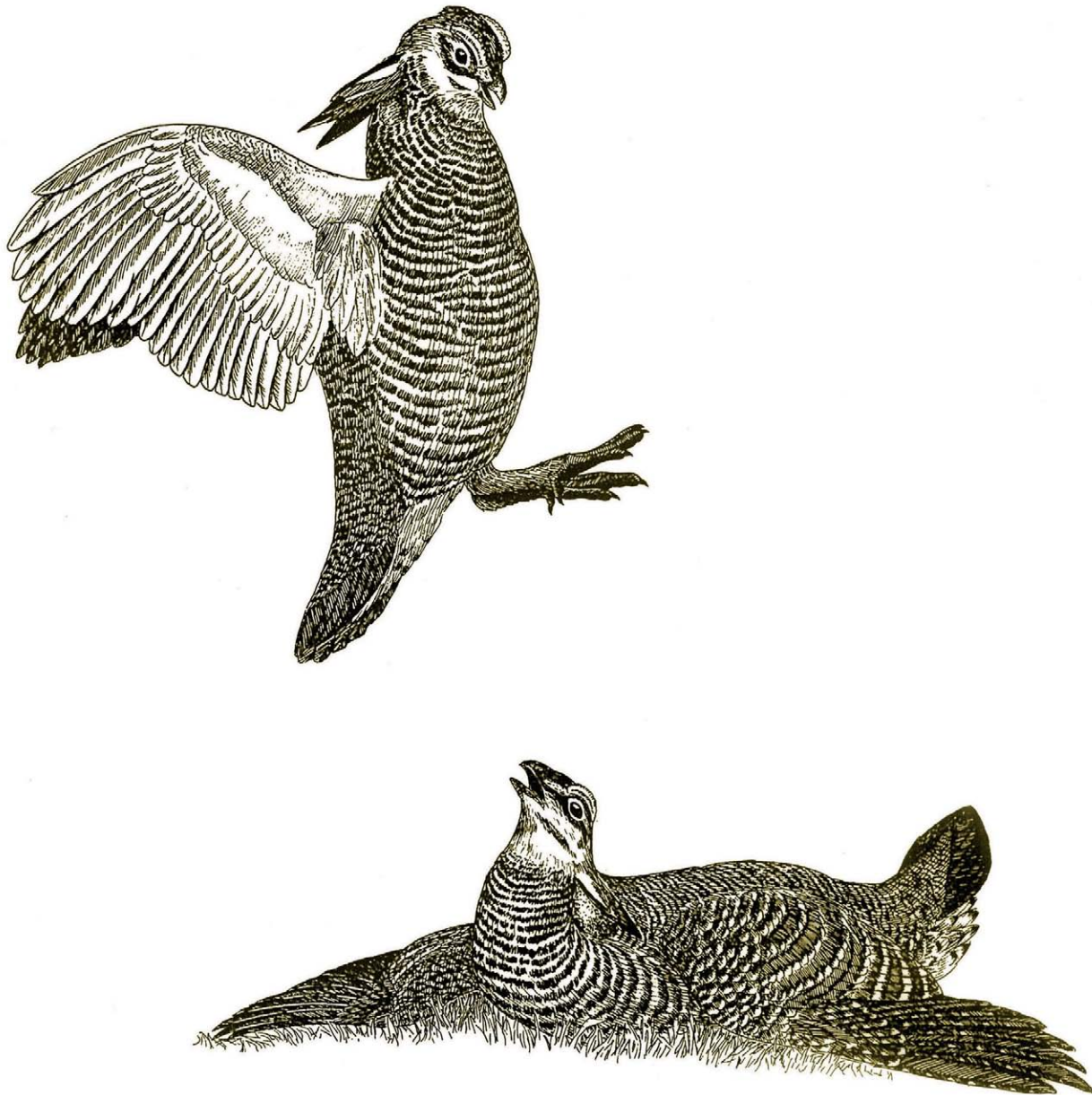
*Fig. 29. Interior greater prairie-chicken, territorial males fighting.*

second, as opposed to nearly 2 seconds in the greater. The associated call sounds more like a "gobble" and has two definite syllables, plus a terminal humming sound.

Hjorth (1970) has distinguished a variant of the lesser prairie-chicken's gobbling call that he called "bubbling" ("sounding like air bubbles emerging from water"), containing 5 to 6 notes and containing a mixture of yodeling posture elements, and may precede or follow a series of yodels. It appears to be an incomplete and less stereotyped version of the more typical call and posture, and may corresponds to Sharpe's "low intensity booming." In contrast to the greater prairie-chicken, male lesser prairie-chickens in close proximity to each other frequently utter their booming/yodeling displays in an antiphonal fashion ("duetting" of Hjorth, 1970),

with up to ten displays being performed in fairly rapid sequence. An additional visual difference between the displays of the lesser and greater species is that the exposed gular sac of the lesser is mostly red, whereas those of the greater and Attwater's greater prairie-chickens are yellow to orange (Jones, 1964a; Lehmann, 1941).

A second major display of all prairie-chickens is flutter-jumping. It is performed in the same fashion by this group as by sharp-tailed grouse and no doubt serves a similar advertisement function. Unlike that of the sharp-tail, however, most prairie-chicken flutter-jumps have associated cackling calls ("jump-cackle" of Hjorth, 1970). Sharpe (1968) found that calls occurred during 27 of 30 flutter-jumps in Attwater's prairie-chickens, 16 of 20 in lesser prairie-chickens, and 17 of
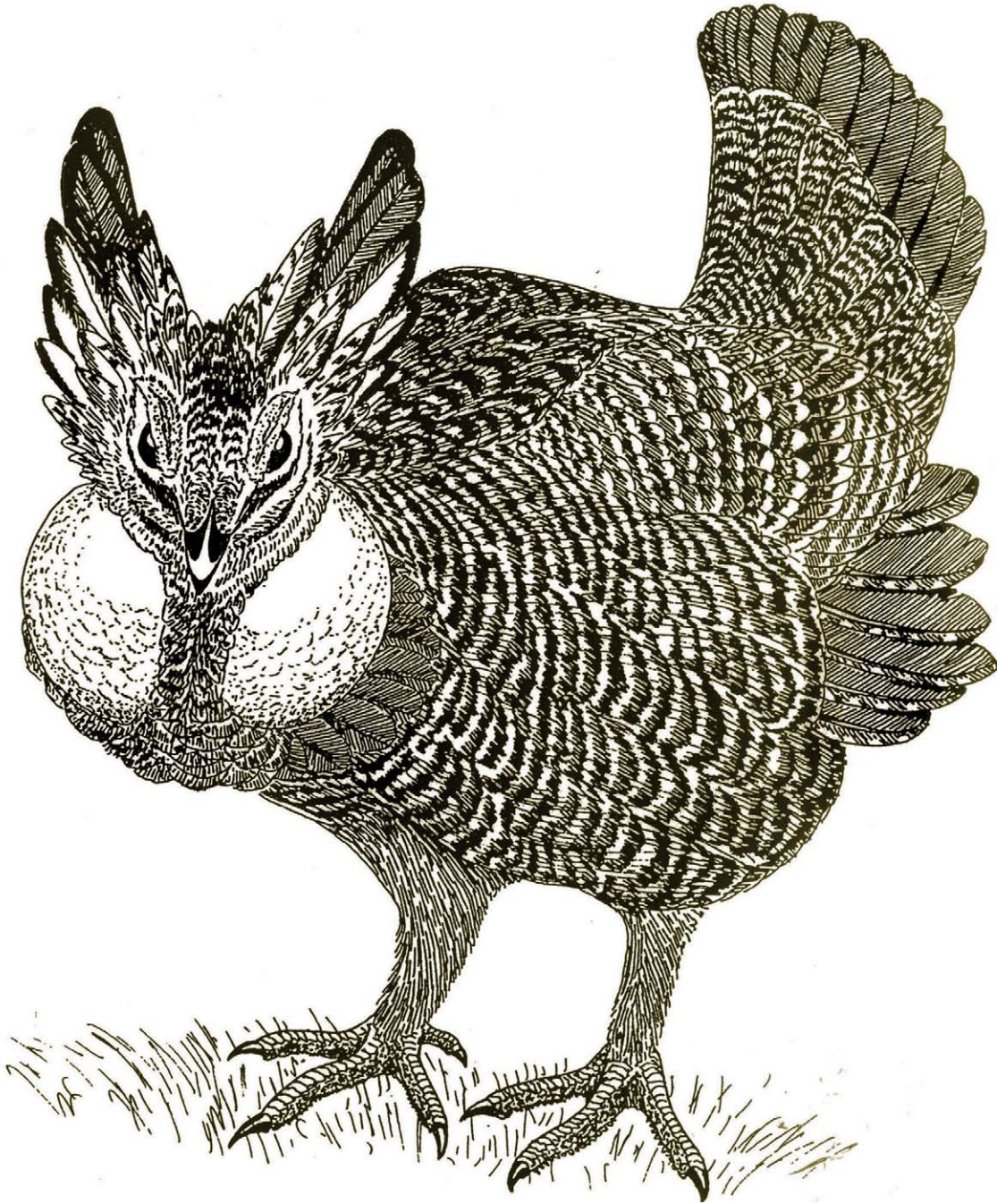
*Fig. 30. Interior greater prairie-chicken, side view of male booming.*

20 in greater prairie-chickens. He noted that flutter-jumping is especially typical of peripheral males when hens are present near the middle of the display ground.

When defending territories against other males, several display postures and calls are typically seen and heard. Ritualized and actual fighting, similar to that described by Lumsden (1965) for the sharp-tailed grouse, is commonly seen, often with short jumps into the air and striking with the feet, beak, and wings. Between active fights, the males will commonly "face off," lying prone a foot or two apart and call-

ing aggressively. Associated calls during facing off include a whining call much like that of sharp-tails', and a similar more nasal "quarreling" note (Sharpe, 1968) that sounds like *nyah-ah-ah-ah*. Grange (1948) describes the "fight call" as a very loud, raucous *hoo'wuk*. So-called "displacement" sleeping, "displacement" feeding, and "running parallel" displays have also been noted by Sharpe at territorial boundaries. A white shoulder spot is often evident in such situations, and Hjorth (1970) noted that in both sexes of lesser prairie-chickens this may frequently be observed.

*Fig. 31. Interior greater prairie-chicken: male flutter-jump and landing sequence (above), and two males fighting (below).*
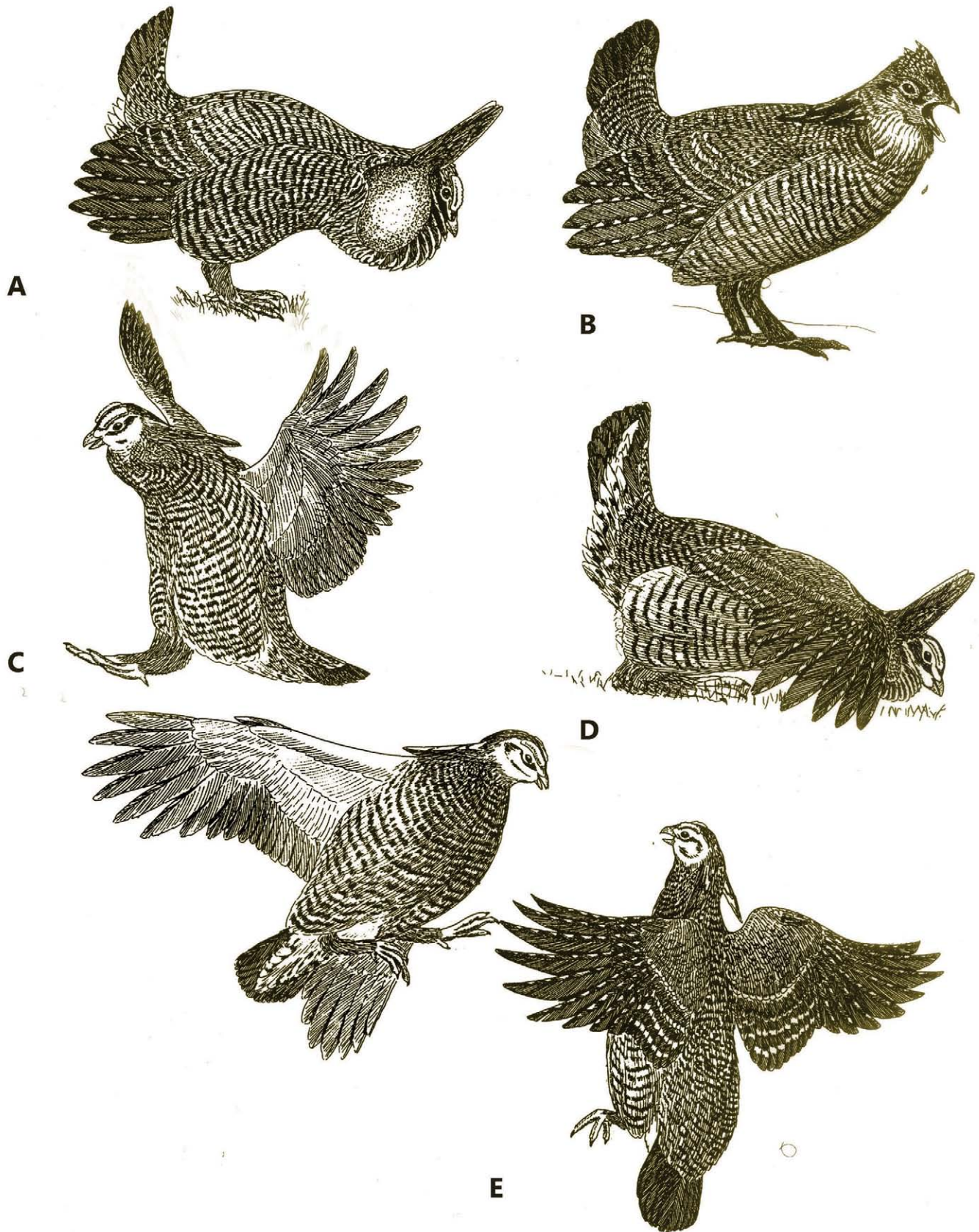
*Fig. 32. Male interior greater prairie-chicken displays, including (A) booming, (B) cackling,
(C) landing, (D) bowing, and (E) fighting.*
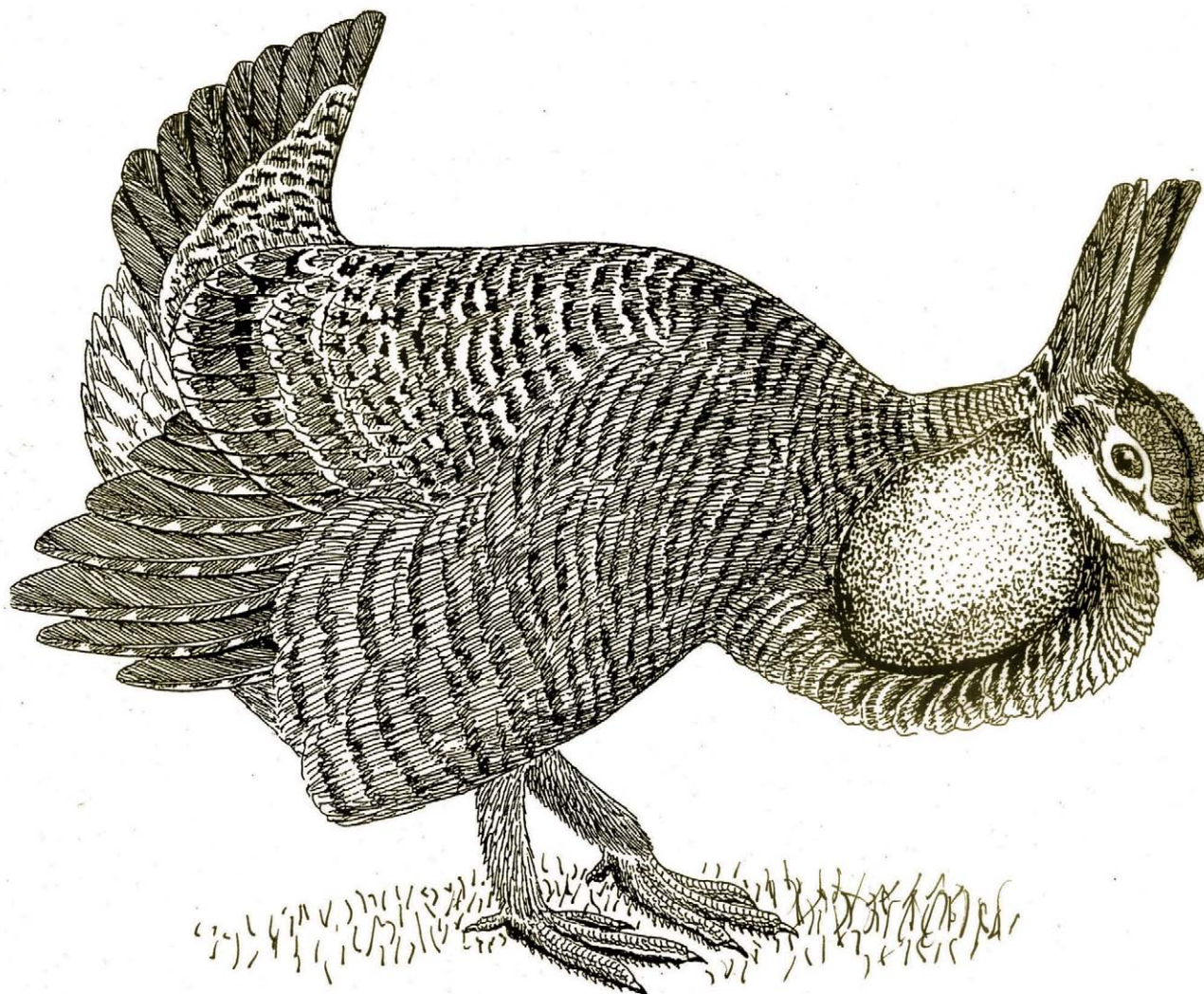
*Fig. 33. Male lesser prairie-chicken yodeling.*

When a female enters a male's territory, his behavior changes greatly. Booming ("tooting" in lessers) is performed with high frequency and extreme posturing, particularly as to pinnae erection and eye-comb enlargement. The eye-combs of all three forms are a bright yellow, but those of the lesser prairie-chicken are relatively larger than those of either the greater or Attwater's prairie-chicken. Between booming displays the male will sometimes stop and "pose" before the female while facing her, but most booming displays are not oriented specifically toward the hen. Rather, the male circles about her and all aspects of his plumage are visible to her.

In the presence of females, when they are either nearby or at some distance, a characteristic *pwoik* call ("whoop" of Hjorth, 1970) is frequently uttered by males (Lehmann, 1941). Sharpe reports that this call is very similar in both the greater and Attwater's prairie-chickens, but in the lesser it is higher pitched and sounds like *pike* ("squeak" of Hjorth, 1970). It lasts for a shorter duration (0.23 seconds compared to about 0.4 seconds in the larger forms) and the greatest sound am-

plitude occurs at about 1,000 Hz, rather than 550 to 600 Hz.

All three forms of prairie-chickens perform the "nuptial bow" ("prostrate" of Hjorth, 1970), which Hamerstrom and Hamerstrom (1960) originally described for the greater prairie-chicken. They regarded it as a sexual display that often precedes copulation but is not a prerequisite for it. Sharpe (1968) found that the same applies to the Attwater's and lesser prairie-chickens, and in all three the display has the same form. The male, while actively booming and circling about a nearby female, suddenly stops, spreads his wings, and lowers his bill almost to the ground while keeping his pinnae in an erect posture. He may remain in this posture for several seconds as he faces the female.

When female prairie-chickens are ready for copulation they squat in the typical galliform manner, with wings slightly spread, head raised, and neck outstretched. When mounting, males grasp the female's nape, lower their wings on both sides of her, and quickly complete copulation. After copulation, females usually quickly run forward a few
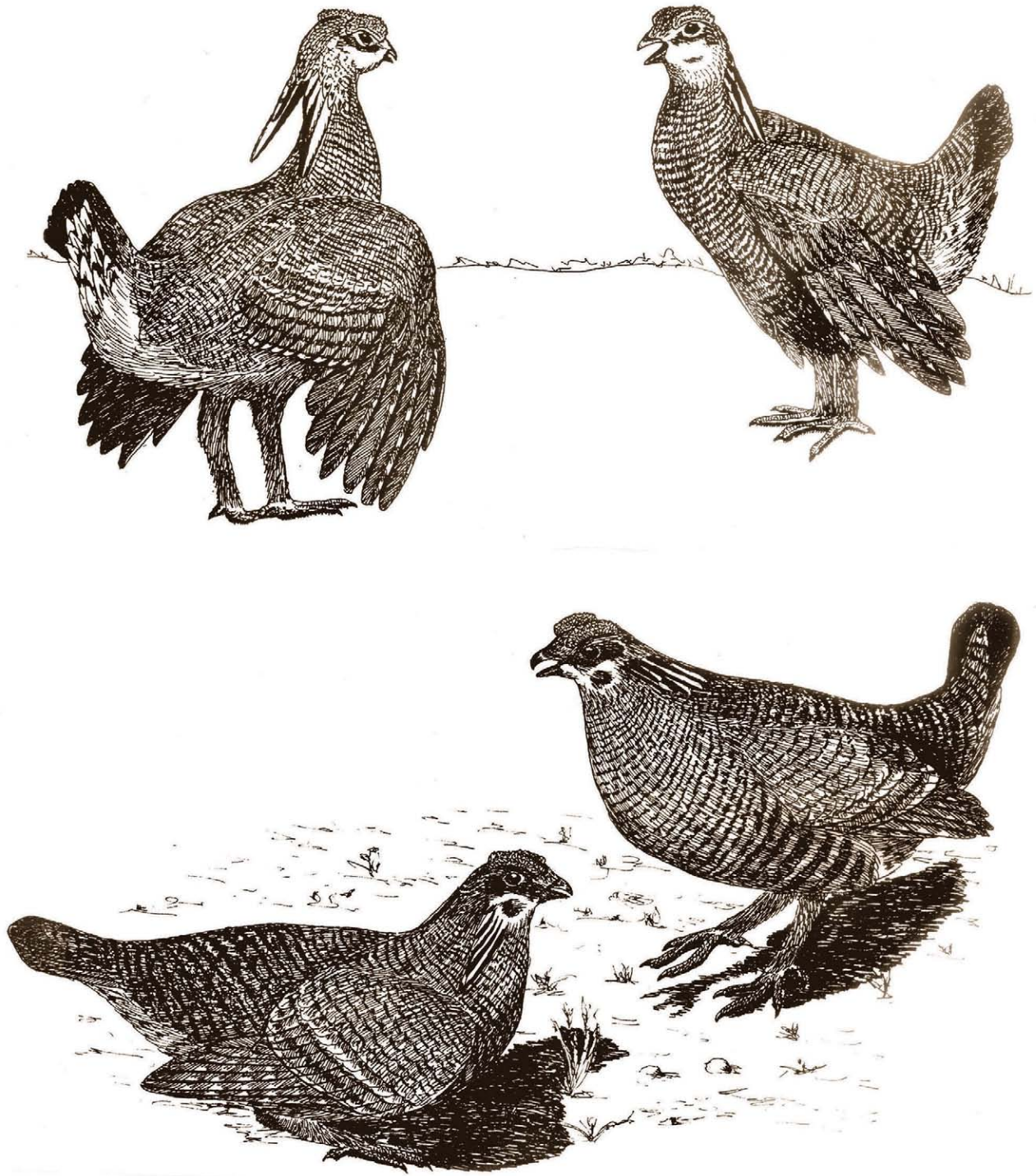
*Fig. 34. Male lesser prairie-chicken displays, including standing (above) and crouching (below) territorial disputes.*

feet and then stop to shake. Males lack any specific post-copulatory displays and often begin booming again within a few seconds.

### Vocal Signals
In addition to the booming, whining, quarreling, and *pwoik* calls already mentioned, pinnated grouse have several other vocal signals. Many different cackling sounds are also uttered. Sharpe (1968) recognized a "long cackle" that consists of several individual notes spaced about 0.2 seconds apart and sometimes lasting several seconds. The notes uttered during flutter-jumping are essentially the same as these individual long-cackle sounds. Lehmann (1941) has listed

*Fig. 35. Booming/cooing display postures by greater prairie-chicken (top), greater prairie-chicken × sharp-tailed grouse hybrid (middle), and sharp-tailed grouse (bottom).*

several variants of these cackling calls and combinations of *pwoik* and cackling notes, and he also mentions several other notes. These include calls sounding like *kwiee*, *kwerr*, *kliee*, *kwoo*, and *kwah*. In the absence of comparative study and sonographic analysis, their possible functions cannot be guessed. Hjorth (1970) has noted that between flutter-jumping or booming greater males often utter an indefinite

staccato cackle, and during territorial confrontations may produce cackling sounds that range from whinnies to whining cackles and explosive cackling sounds.

### Nesting and Brooding Behavior
Following mating, the female begins to lay a clutch almost immediately; indeed, it is probable that she has already es-

tablished a nest scrape prior to successful copulation. She may move a considerable distance away from the ground to her nest site and may actually nest nearer to another booming ground than to that at which copulation occurred (Robel et al., 1970). Robel et al. found that females had to visit a ground for an average of three consecutive days before copulation occurred but did not return thereafter except perhaps for renesting attempts. Lehmann (1941) and Robel both found that renesting birds laid progressively smaller clutches, and sometimes up to two such attempts were made. The average clutch size of first clutches is about 12 to 14 eggs for the lesser (Copelin, 1963), Attwater's (Lehmann, 1941), and greater prairie-chickens (Hamerstrom, 1939; Robel et al., 1970). Later clutches, probably the result of renesting, often have only 7 to 10 eggs.

Eggs are laid at the approximate rate of one per day, with occasional lapses of a day, so that it may take about two weeks to complete a clutch of 12 eggs (Lehmann, 1941). Incubation may begin the day before the laying of the last eggs or several days after the last egg is laid, according to Lehmann. Apart from two feeding and resting periods in early morning and late afternoon, the female incubates constantly. The incubation period is probably 23 to 26 days in all three forms (Lehmann, 1941; Schwartz, 1945; Coats, 1955; W. W. Lemburg, pers. comm.).

The process of egg-pipping may require up to 48 hours, during which the female appears highly nervous and the nest is apparently extremely vulnerable because of the noises made by the chicks and the odors of the nest (Lehmann, 1941). Normally, the nest is deserted within 24 hours after the last chick is out of its shell. Females with young chicks typically perform decoying behavior with heads held low and wings drooping and nearly touching the ground, uttering a low *kwerr*, *kwerr*, *kwerr* (Lehmann, 1941). After the young are able to fly well, both the hen and brood typically flush when disturbed.

Chicks less than a week old may be brooded much of the time, possibly up to half the daylight hours (Lehmann, 1941). However, older chicks are brooded only at night, during early morning hours, and in inclement weather. Broods typically remain with females for six to eight weeks, when families gradually disintegrate. There is also considerable brood mixing, as when separated chicks join the broods of other females, even if the young are of different ages.

### Evolutionary Relationships

The close and clearly congeneric relationships of prairie-chickens to the sharp-tailed grouse have already been mentioned in the account of that species. Thus, comments here will be restricted to the relationships among the several forms of prairie-chickens. Short (1967) dealt extensively with the morphological criteria advanced by Jones (1964a) for considering the lesser prairie-chicken as specifically distinct from the greater prairie-chicken. Since then, Sharpe (1968) has found some male behavioral differences between the

lesser prairie-chicken and the two surviving races of *cupido*. These differences consist of acoustic differences (higher frequencies in the lesser), time differences (more rapid and shorter displays in the lesser), and some motor differences (one versus two tail movements during booming in the lesser). A few other contextual and orientational differences were also found, but Sharpe admitted that these differences may be attributed largely to size differences in the birds and possible selection related to aggressive behavior patterns rather than being the result of reinforcement for species differences during some past period of sympatry. He concluded that the lesser should be considered an "allospecies" to emphasize its greater difference from *T. c. pinnatus* than that exhibited by *T. c. attwateri*. The American Ornithologist's Union currently (2016) considers them to be distinct species.

It would seem that the living forms of prairie-chickens and those which have recently become extinct were all derived from some ancestral grouse associated with deciduous forest or its edge, since the original ranges of the lesser and greater prairie-chickens as well as the extinct heath hen all had affinities with oak woodlands or oak-grassland combinations. The Attwater's prairie-chicken, on the other hand, is apparently associated with pure grassland vegetation.

The separation of the ancestral stock of the lesser prairie-chicken probably occurred during an early glacial period, and subsequent adaptation during postglacial times to an unusually warm and dry grassland habitat in the southwestern states accounts for its smaller size and generally lighter coloration. More recent separation of gene pools no doubt brought about the separation of the Atlantic coast (heath hen) and Gulf coast (Attwater's) populations from the interior greater population, but the behavioral and morphological differences among these appear to be minimal. Genetic evidence indicates a fairly recent separation of the greater and lesser gene pools, resulting from sexual selection and/or adaptation to different environments (Geisen, 1998).

*Suggested reading:* Gross, 1928 (heath hen); Lehmann, 1941 (Attwater's prairie-chicken); Copelin, 1963; Giesen, 2005; Haukos and Boal, 2016 (lesser prairie-chicken); Grange, 1948; Schroeder and Ross, 1993; Svedarsky, Hier, and Vilvy, 1999 (greater prairie-chicken); Johnsgard, 2002; Paothong, 2012 (prairie-chickens)

Plate 24. Lesser prairie-chicken, male yodeling; April.



Plate 25. Lesser prairie-chicken, two males yodeling (duetting); April.

*Plate 26. Lesser prairie-chicken, male perching; April*

*Plate 27. Interior greater prairie-chicken, male displaying before females; April.*



*Plate 28. Interior greater prairie-chicken, male booming; April.*

Plate 29. Interior greater prairie-chicken, male cackling; April.

*Plate 30. Interior greater prairie-chicken, males fighting; April.*

# Sharp-tailed Grouse

*Tympanuchus phasianellus* (Linnaeus) 1758

## Other Vernacular Names

Brush grouse, pintail grouse, prairie grouse, prairie pheasant, sharptail, speckle-belly, spike-tail, spring-tail, white-belly, white-breasted grouse

## Range

Currently from north-central Alaska, Yukon, northern Mackenzie, northern Manitoba, northern Ontario, and central Quebec south to eastern Washington, extreme eastern Oregon, Idaho, northeastern Utah, Wyoming, and Colorado, and in the Great Plains from eastern Colorado and eastern Wyoming across Nebraska, the Dakotas, northern Minnesota, northern Wisconsin, and northern Michigan.

## Subspecies

*T. p. phasianellus* (Linnaeus): Northern sharp-tailed grouse. Breeds in northern Manitoba, northern Ontario, and central Quebec. Partially migratory.

*T. phasianellus kennicotti* (Suckley): Northwestern sharp-tailed grouse. Resident in Mackenzie from the Mackenzie River to Great Slave Lake.

*T. phasianellus caurus* (Friedmann): Alaska sharp-tailed grouse. Resident in south-central Alaska east to the southern Yukon, northern British Columbia, and northern Alberta.

*T. phasianellus columbianus* (Ord): Columbian sharp-tailed grouse. Rare to local resident in central British Columbia (declining), northern Washington (very rare), eastern Oregon (now nearly extirpated), southern Idaho, northern Utah, and western Colorado. Formerly extended to Montana, Nevada, and New Mexico.

*T. phasianellus campestris* (Ridgway): Prairie sharp-tailed grouse. Resident from southeastern Manitoba, southwestern Ontario, and the Upper Peninsula of Michigan to northern Minnesota and northern Wisconsin. Formerly extended to northern Illinois.

*T. phasianellus jamesi* (Lincoln): Plains sharp-tailed grouse. Resident from north-central Alberta and central Saskatchewan south to Montana (except the extreme west), northeastern Wyoming, northeastern Colorado, and western portions of Nebraska, South Dakota, and North Dakota. Formerly extended to Kansas and Oklahoma.

## Measurements

*Folded wing:* Adult males, 194–223 mm; adult females, 186–221 mm (males of all races average 202 mm or more; females, 201 mm or less).

*Tail:* Adult males, 110–135 mm; adult females 92–126 mm (males average 4 mm longer than females).

## Identification

Adults, 16.4–18.5 inches long. The sexes are nearly identical in plumage. The tail is strongly graduated in both sexes, with the central pair of feathers extending far beyond the others, but the tips are not pointed. Both sexes are feathered to the base of the toes, and males have an inconspicuous yellow comb (somewhat enlarged during display) and pinkish to pale violet areas of bare neck skin that are also expanded during display, though not to the degree found in prairie-chickens. Both sexes have inconspicuous crests, and the head and upperparts are extensively patterned with barring and spotting of white, buffy, tawny brown, and blackish. White spotting is conspicuous on the wings, and the relative amount of white increases toward the breast and abdomen, which are immaculate. The middle pair of tail feathers is elaborately patterned with brown and black, but the others are mostly white. The breast and flanks are intricately marked with V-shaped brown markings on a white or buffy background.

## Field Marks

The grassland, edge, or scrub forest habitat of this species varies considerably throughout its range, but the bird is basically to be found in fairly open country, where its pale, mottled plumage blends well with the surroundings. In flight the white underparts are conspicuous, as is the whitish and elongated tail. On the ground, the birds have a much more "frosty" appearance than do prairie-chickens, which are generally darker and lack definite white spotting.

## Age and Sex Criteria

*Females* may be identified with about 90 percent reliability by a transverse barring pattern on the central tail feathers, compared with the more linear markings of males. Also, the crown feathers of males have alternating buff and dark brown cross-bars, whereas the male crown feathers are dark with buffy edging (Henderson et al., 1967).

*Immatures* are identified by the usual character of pointed outer primaries. Ammann (1944) suggested that a comparison of the eighth and ninth primaries as to relative amounts of wear (equal or little wear on either in adults, greater wear on the ninth in immatures) is the most suitable method of judging age in prairie grouse.

*Juveniles* have white rather than buffy throats and have shorter median tail feathers than do adults. The lateral tail feathers of juveniles are buffier, mottled, and speckled with brown, while the median two pairs have broad, buffy central stripes (Ridgway and Friedmann, 1946). White shaft-streaks are conspicuous on the upperparts as well.

*Downy young* have a clearer and paler mustard yellow color overall than do prairie-chickens of the same age and lack the rusty tints of that species. There is the trace of a median black crown line and a few small crown spots, but only one or two black spots between the eyes and the ear region are present in this species.

*Map 13. Recent distributions of the Alaska (A), Columbian (C), northern (N), northwestern (NW), plains (Pl), and prairie (P) races of the sharp-tailed grouse. The known historic range is indicated by stippling.*

## Distribution and Habitat

This species, together with the prairie-chickens, compose the "prairie grouse" of North America. Such a designation for the sharp-tailed grouse is not wholly accurate, for the origi-

nal distribution of the species included not only grassland habitats but also sagebrush semidesert (*T. p. columbianus*), brushy mountain subclimax communities (*T. p. jamesi*), oak savannas and successional stages of deciduous and mixed
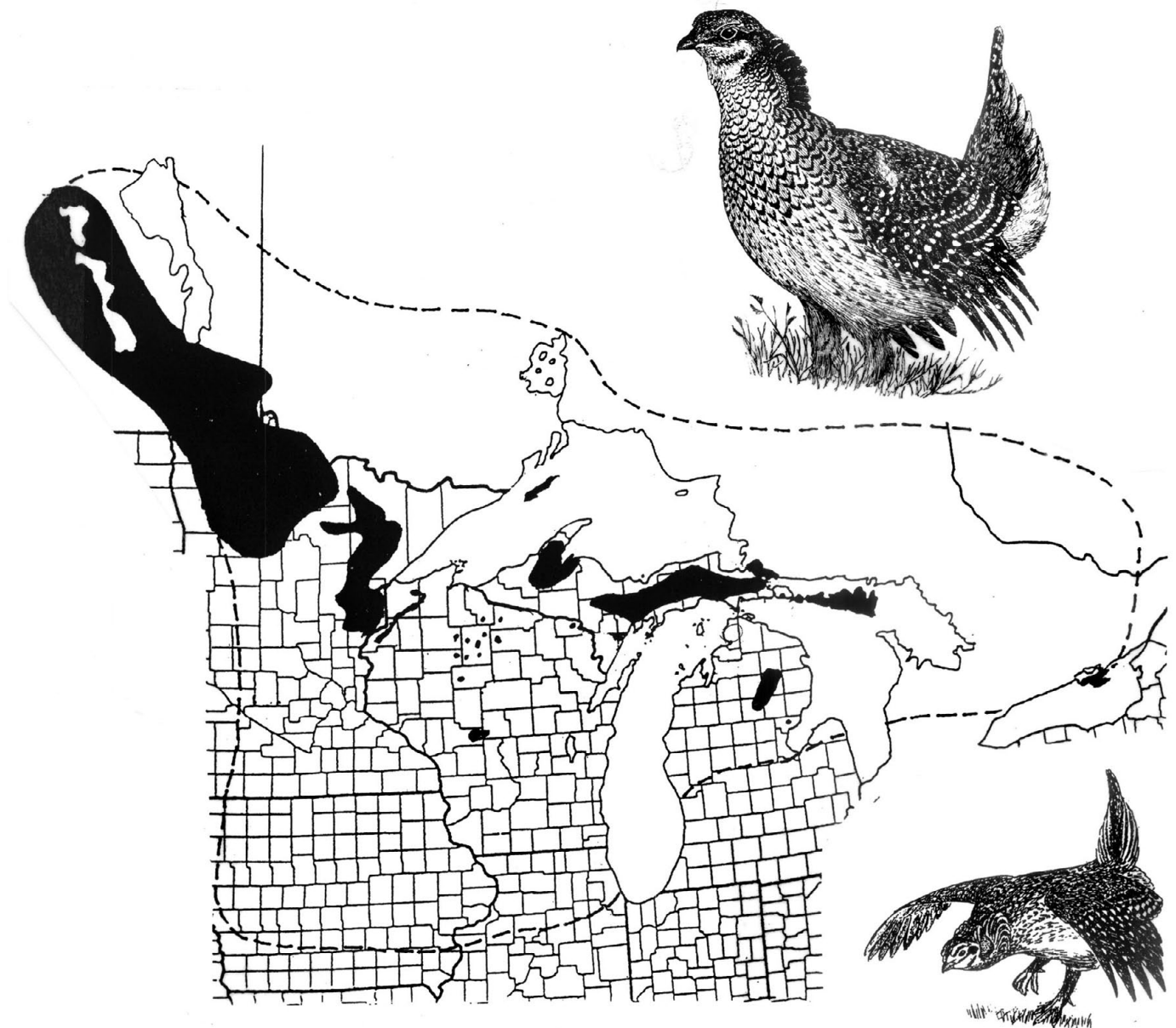
*Map 14. Historic (dashed line) and current (inked) distributions of the prairie sharp-tailed grouse.*

deciduous–coniferous forests of the eastern states (*T. p. campestris*), and brushy habitats of boreal forests from Canada through Alaska (*phasianellus*, *caurus*, and *kennicotti*), as summarized by Aldrich (1963).

Two of the sharp-tailed's races have suffered greatly from habitat changes associated with human activities. One of these is the Columbian sharp-tailed grouse, which has been reduced in a remnant distribution pattern to the point that it has been extirpated from California, Montana, Nevada, Oregon, and New Mexico; is rare in Utah and Washington; and is local in Colorado and Wyoming. In 2015 it was still considered common enough in Idaho to allow a hunting season, with a limit of two birds per day. In California there was an eight-day season, with a single bird allowed per season. In Utah the five-week 2015 season allowed only two birds per season, and Colorado had a 20-day season with a limit of two birds per day. Wyoming has not allowed sharptail hunting within the Columbian's range recently, and the sharptail is listed as state threatened in Washington. There it persists in seven scattered populations in Lincoln, Douglas, and Colville counties, plus the Colville Indian Reservation. Last hunted in 1987, the Washington population dropped to an estimated low of 472 birds in 2001, but by 2011 had rebounded to 902. In British Columba this race is blue-listed (of "special concern"), generally declining, and regionally extirpated from southern parts of the province.
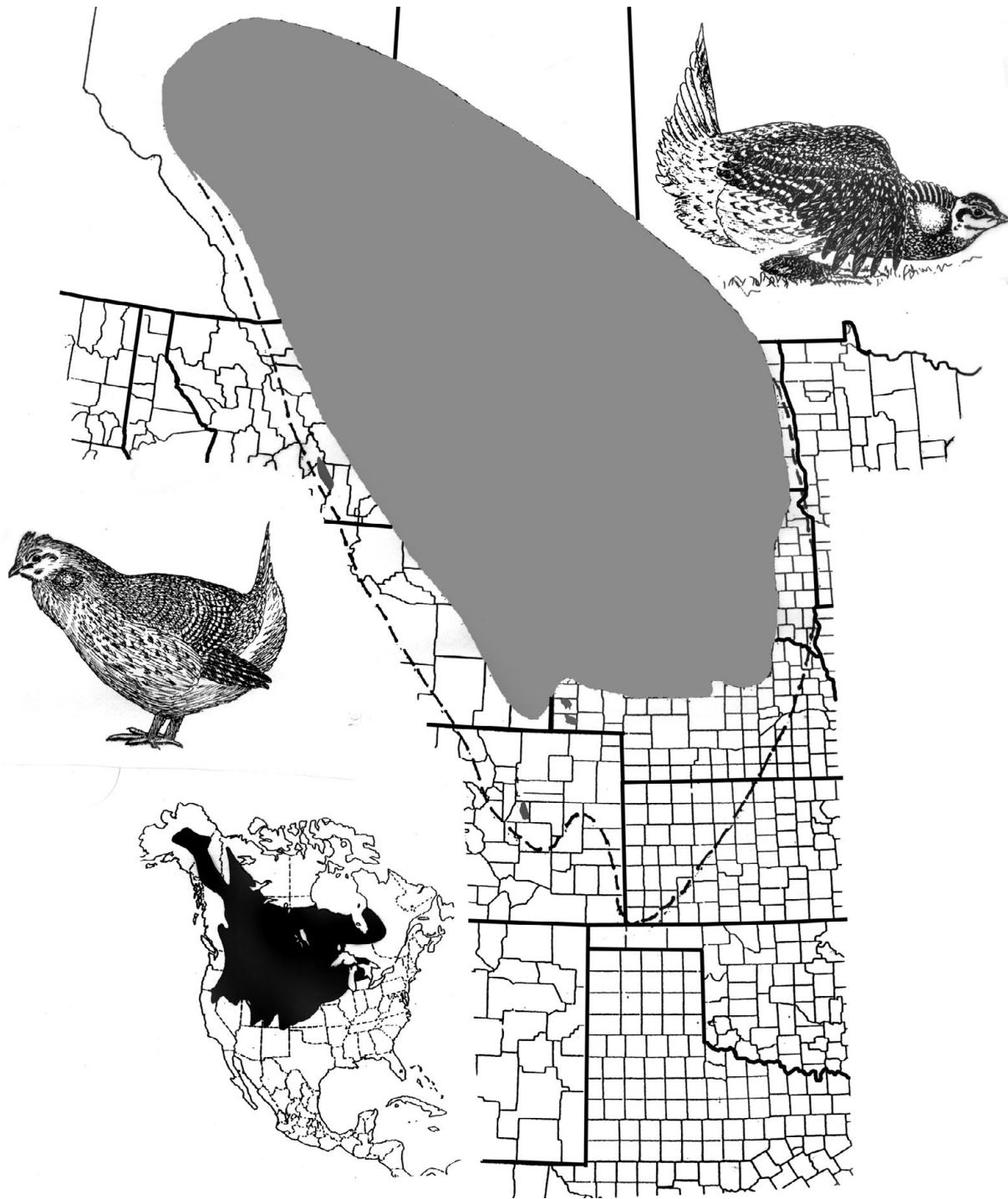
*Map 15. Historic (dashed line) and recent (inked) distributions of the plains sharp-tailed grouse.
The inset map shows the species' overall historic distribution.*

The prairie race of sharp-tailed grouse was similarly extirpated by the mid-1900s from Illinois, Iowa, and southern portions of Wisconsin and Minnesota, and by 1960 was in danger of extirpation in the northern parts of these states (Hamerstrom and Hamerstrom, 1961). In the Lower Peninsula of Michigan, introduced sharptails probably reached their greatest distribution by 1950 (Ammann, 1957), and by the early 1960s only a few hundred birds could be counted on display grounds (Ammann, 1963a). On the Upper Peninsula, the sharptail population had decreased at least 9 percent between 1956 and the early 1960s, primarily through habitat losses (Ammann, 1963a). Dancing-ground studies since
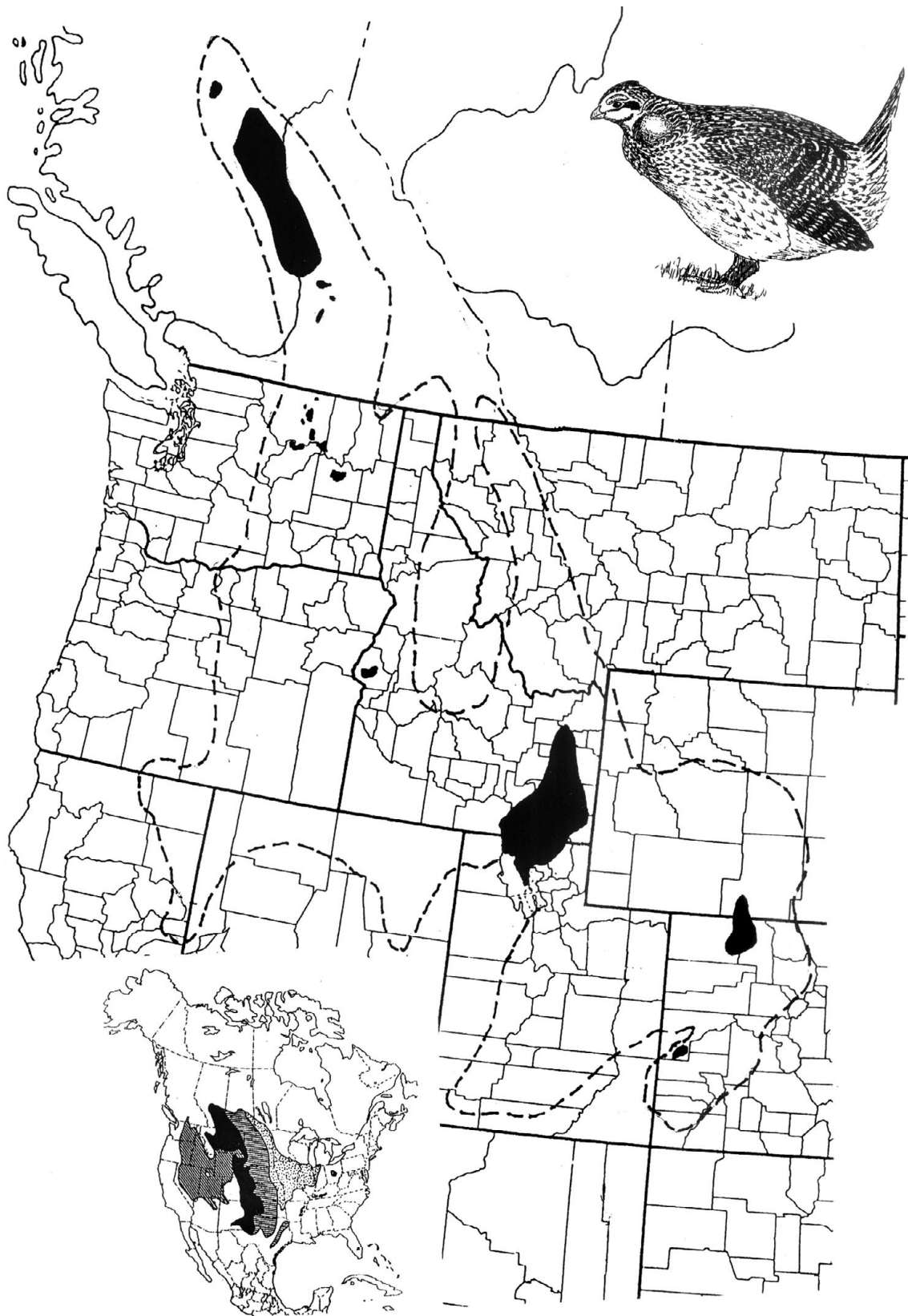
*Map 16. Historic (dashed line) and current (inked) distributions of the Columbian sharp-tailed grouse. The inset map shows the approximate distributions of tallgrass prairie and Texas coastal prairie (stippled), mid-grass prairie (horizontal hatching), shortgrass prairie (inked), and sage grasslands (diagonal hatching).*

then have indicated continued long-term population de-clines (Drummer, Corace, and Sjogren, 2008). In 2016 a 21-day hunting season was allowed in Chippewa and Mackinac counties, with a two-bird daily kill limit.

In Minnesota the twentieth-century population trend also appears to have been downward, as a result of improved farming practices as well as increased reforestation and tree-farming activities (Bremer, 1967). Range-wide dancing-ground studies were begun in 1975, and have indicated a long-term downward trend that was first documented in the 1950s (Berg, 1997). Hunters in each of the two years 2012 and 2013 killed an estimated 12,000 sharp-tailed grouse.

Hamerstrom and Hamerstrom (1961) reported that the Wisconsin population was then in greater danger than those in Minnesota and Michigan as a result of fire protection, for-est succession, pine plantations, and modern farm practices. Lek counts of males from 1991 to 2014 in Wisconsin have in-dicated a slow rate of population decline, and populations on all state-managed areas have been in decline since 1998. No permits for hunting sharp-tailed grouse in Wisconsin were granted in 2014, after hunting was suspended for review in 2013. In contrast, the populations of the prairie race of sharptails in Ontario, Manitoba, and eastern Saskatchewan appear to be in relatively good condition (Johnsgard, 2002).

The plains sharptail, with its extensive range from northern Alberta to North Dakota and south (historically) to northern New Mexico, has apparently suffered the least of the United States races and still supports legally hunted populations in several provinces and states, including Montana, Wyoming, the Dakotas, and Nebraska. However, it is gone from New Mexico, northwestern Oklahoma and western Kansas, and its range in eastern Colorado has shrunk appreciably (Johnsgard and Wood, 1968; Johnsgard, 2002).

The remaining Canadian and Alaskan populations of sharp-tailed grouse are evidently in relatively satisfactory condition, although little population data exists.

## Population Density

Some of the best figures as to spring population densities for sharp-tailed grouse come from the work of Grange (1948). Using spring dancing ground counts and assuming a 55 per-cent ratio of males in the total populations, he calculated an estimate for 1941 of 235.2 acres per bird on 130,560 acres, and 186.7 acres per bird on the same area in 1942. Consid-ering only the occupied range, the average area per bird figure was calculated to be 138 acres in 1942. Ammann (cited by Edminster, 1954) reported spring densities on 13 square miles of habitat on Dummond Island, Michigan, over a three-year period as averaging one bird per 45 acres, while the fall populations of sharptails on the island were approximately one bird per 18 acres of occupied range, over a seven-year period. This island represents prime Michigan sharptail habi-tat, and these figures were unusually high densities that were not later maintained. Edminster (1954) summarized a variety of other fall density estimates from various states that in

general indicate that from 27 to 125 acres per bird in summer or fall are probably typical. One other high density figure has been reported for Saskatchewan, with Symington and Harper (1957) estimating late summer populations of 25 to 40 birds per square mile (16–25.6 acres per bird) in the Great Sandhills area, where an ideal combination of native grasses, shrubs, and small trees occur.

## Habitat Requirements

General habitat characteristics of the prairie race of sharp-tailed grouse have been analyzed by Grange (1948) for Wisconsin and by Amman (1957) for Michigan. Grange concluded that sharp-tailed grouse are abundant in areas covered from 25 to 50 percent by wooded vegetation, and Ammann indicated that from 20 to 40 percent woody cover is ideal, preferably with the trees in scattered clumps rather than widely scattered. Sparse or bare patches in the ground cover should not exceed half of the total, and the area of suitable open habitat in wooded vegetation should not be less than a square mile, in the opinion of Ammann. According to him, ideal summer sharptail habitat on a square mile unit should include an open portion of about 6 percent of the total area that would be a display site, loafing and foraging habitat for adult males and broods, and roosting sites for displaying males. About half of the area should consist of scattered large shrubs and trees, especially aspens. Heavy ground cover is needed for roosting, nesting, and feeding, while lighter ground cover serves for resting, dusting, and feeding, especially by broods.

The remaining 44 percent of the cover should consist of an alternating series of small (ten-acre) brushy clearings and heavier second-growth timber stands of mixed hardwoods and conifers, which serves as a source of winter browse and protection from severe weather as well as escape cover. The scattered small clearing provides additional nesting and brood-rearing habitat and winter roosting opportunities. Paper birch (*Betula papyrifera*) and aspen (*Populus tremu-loides*), especially the former, represent major winter food sources when snow cover prevents foraging on grains or other similar foods.

Although these habitat needs may apply to the prairie sharp-tailed grouse, they are clearly not strongly applicable to the Columbian and plains races, which occur in semides-ert scrub and relatively dry grasslands, respectively. For the Columbian race at least, shrubs and small trees are important habitat components only during the late fall and winter, while during the rest of the year weed-grass cover types as well as cultivated crops such as wheat and alfalfa provide important food and cover requirements (Marshall and Jensen, 1937). Likewise, Hart, Lee, and Low (1952) listed a variety of grasses and herbs as important components of Columbian sharptail habitat in Utah.

Similarly, the plains sharp-tailed grouse inhabiting the Sandhills of central Nebraska and the comparable sand dune areas of north-central North Dakota are relatively indepen-

dent of extensive tree cover (Aldous, 1943; Kobriger, 1965). In the late fall and winter these birds resort to foraging on rose hips and willow buds in the sand hills (Aldous, 1943), while in Utah the buds of maples and chokecherries are major sources of winter foods (Marshall and Jensen, 1937). According to Edminster (1954), a minimum of 5 percent brush cover relative to total land surface is tolerable to sharptails in North Dakota.

### Wintering Habitat Requirements

Grange (1948) reported that sharptails do not roost in trees overnight during winter; instead they utilize snow burrows, which they scratch out in fairly dense marsh or swamp vegetation, or sometimes in open stands of tamarack or spruce in northern Wisconsin. During snowless periods, roosting usually occurs in dense, fairly coarse marshy vegetation.

Ammann's observations (1957) for Michigan sharptails are similar. During fall, the birds concentrate in "packs" on grain plantings near their summer habitat and may continue to use grain as long as it remains available. When the snow is deep and grain becomes unavailable, the catkins, twigs, and buds of trees such as paper birch, aspen, juneberry, hazel, and bog birch are preferred, as well as the fruit of mountain ash, sumac, common juniper, rose, and black chokecherry. Of all these, the buds and catkins of birch and aspen are especially important, particularly birch. A wide variety of grains is taken if they are available, including wheat, buckwheat, field peas, corn, barley, soybeans, millet, and rye. Thus the availability of grain or native food sources in the form of fruiting shrubs or deciduous trees is an important component of winter habitat.

The presence of adequate snow during unusually severe weather conditions may be important to sharptails. Marshall and Jensen (1937) found that movement to maple-chokecherry cover in Utah was related to snow depth; there the birds could feed on buds and roost under the snow unless it crusted heavily, when they preferred to roost above the snow in brushy cover. Some deaths by freezing have been reported when strong winds were associated with low winter temperatures and no snow was available for roosting (Edminster, 1954).

### Spring Habitat Requirements

Ammann (1957) reported on the general cover characteristics of 95 sharptail dancing grounds in Michigan. Of these, 27 were located on cultivated lands and 68 were on wild lands. Although the majority of these contained no woody cover, 35 percent had woody cover present, but rarely did this exceed 30 percent of the ground's surface area.

Favored Michigan sites for both sharptails and prairie-chickens appeared to be low or sparse vegetation with good visibility, allowing for good footing and unrestricted movements. Elevated, rather than level or depressed sites, were preferred for both species; of 65 prairie-chicken and 95 sharptail display grounds, 47 percent were in elevated situations and only 4 were located in depressions.

In Wisconsin, Grange (1948) found that wild hay meadows and marshes were frequent display locations for prairie-chickens and sharptails, with sharptails exhibiting an apparently greater preference than prairie-chickens for wet marshes. A variety of other cover types was also found to be used by both species, including abandoned fields, cultivated fields and, less commonly, upland grassland, peat burns, and clover fields.

In Alberta, Rippin (1970) noted that of 36 display grounds studied by him, 32 were on open, dry, and elevated sites, 3 were on level ground, and 1 was on an elevation with heavy shrub cover. In the Nebraska Sandhills, Kobriger (1965) found that three-fourths of all prairie grouse display grounds studied were on wet, mowed sites. Similarly, Sisson (1970) reported that 26 of 36 sharptail dancing grounds in the Nebraska Sandhills were within one-eighth mile of a windmill, where the vegetation was fairly low as a result of grazing and trampling of vegetation by cattle, and where visibility was good in all directions.

### Nesting and Brooding Requirements

Ammann (1957) has provided a fairly detailed analysis of nesting requirements for sharptails in Michigan. He reported that they choose a wider variety of sites with respect to woody cover than do prairie-chickens, with site conditions varying from open to 75 percent shaded. Most nests were either protected by overhead cover or were within a few feet of such cover. Of 29 nests found, none was more than ten feet from brushy or woody cover. Of 10 nests studied, 6 were in open aspen, 3 were in cutover pines, and 1 was in an open marsh. These sites averaged 43 percent shrub cover, 3 to 6 feet high, and 4 percent tree cover above six feet. Associated shrubs were chokecherry, willow, and alder, and associated trees were aspen, spruce, and juneberry. Of 7 additional nests, 4 were located at the base of a small tree or bush, and there was 1 each in a hayfield, on an aspen-birch ridge, and in a heavy grass–sweet fern site.

Hamerstrom (1939) reported on cover sites for 17 sharptail nests in Wisconsin. Of these, eight were at the edges of marshes, brush, or woods in brushy or woody (aspen, willow, etc.) cover. Three were in small openings of dense brush such as aspen or willow, 2 were in openings or edges of jack pine–scrub oak woods, 2 were in grass meadows, 1 was in a dry marsh, and 1 was in a mixture of scattered brush, trees, and grass. In this study as well as Ammann's, an apparent avoidance of cultivated areas for nest sites would seem to be present.

Because the males do not participate in nesting, they gradually move away from their display grounds to foraging and daytime resting sites that usually include brushy cover, aspen or willow thickets, or young conifer stands. In Utah, summer daytime resting places gradually change from weeds and grass during June and early July to shrubs and bushes in late July and August (Hart, Lee, and Low, 1952). For night roosting, fairly open and upland cover with good ground cover is preferred by sharptails over marsh and bog vegetation (Ammann, 1957).

Brooding habitat requirements have been analyzed by Hamerstrom (1963) in the Wisconsin pine barrens and by Ammann (1957) for Michigan. Ammann concluded that the birds tend to favor somewhat more woody cover than that chosen for nest sites but in general remain in areas that do not exceed 50 percent shading by woody cover. Peterle (cited by Ammann) estimated a higher (70 percent) average overall shading by woody cover, with shrub cover present in 43 percent of the area, and trees an average of 70 percent in locations where 15 broods were observed.

Hamerstrom's observations of about 190 broods confirm the importance of openings in forested areas as brood habitat. Of his brood habitat records, about 80 percent were in open situations, 14 percent were in edge situations, and only 5 percent were more than 50 yards inside woody habitats. He concluded that brood cover should be basically grassland, with some shrubs and trees, but the taller the woody species present, the fewer there should be. Shrubs are more important than trees, since they provide not only cover but also food sources for chicks. Thus, berry-producing species such as blueberries, cherries, and juneberries are valuable, as are catkin-bearing shrubs that can be used as a source of winter foods. Aspens and willows, although valuable as sources of winter buds, are most useful in small thickets and young trees. Hamerstrom stressed the importance of distinguishing the open, predominantly herbaceous brooding habitat from the fall and winter woody cover that is also critical to sharptail survival.

## Food and Foraging Behavior

Dependable and nutritious winter food sources are critical to the survival of all grouse, and the sharptail appears to be somewhat flexible in its winter diet in comparison with other grouse species. In central Wisconsin, paper birch (*Betula papyrifera*) buds and catkins are the primary winter diet, with aspen (*Populus tremuloides*) of secondary importance. Among other woody plants, rose (*Rosa*) hips and hazel (*Corylus*) buds and catkins are important foods (Grange, 1948). In Ontario, the paper birch is also the primary winter food, supplemented by browse of willow, aspen, blueberry, and mountain ash (Snyder, 1935). In North Dakota, willow buds provide the most important single source of winter foods, but chokecherry, poplar, and rose hips are also major supplementary species (Aldous, 1943). During winter in Utah, sharptails move during periods of heavy snow into thickets of maple, chokecherry, and serviceberry, where they feed on the buds of these species. In the Nebraska Sandhills the sharp-tailed grouse appears to be more efficient than the greater prairie-chicken in finding winter foods and surviving the severe weather conditions, and is much more common and more extensively distributed through that region (Kobriger, 1965; Johnsgard and Wood, 1968).

Throughout the range of the species, the percentage of woody mast foods sharply decreases in spring as herbaceous plants become available after periods of thawing. Such plants include cultivated grain species, clover, alfalfa, and native annuals and perennials. Jones (1966) found that during the spring and summer months, green materials comprised the bulk of the diet in Washington, with grass blades alone (especially *Poa secunda*) totaling half of the spring foods and three-fourths of the summer diet. Flower parts were the rest of the spring and summer foods, particularly those of dandelion (*Taraxacum*) and buttercup (*Ranunculus*). The importance of dandelion continued on into fall, when its seeds and grass leaves were the leading food sources. Apparently the sharptail relies to a lesser extent on animal sources of food during the summer than does the pinnated grouse (Jones, 1966), although Grange (1948) reported that grasshoppers are a major summer food, and Edminster (1954) estimated that from 10 to 20 percent of the adult summer food is of insect origin. Kobriger (1965) found that the juveniles had increased the amount of vegetable food in their diets to more than 90 percent; he reported that in Nebraska such important food plants included clovers, roses, cherry, and dandelion, the most important of which were favored by wetland mowing practices.

During fall, a diverse array of seeds and cultivated grains are taken in the diet, especially in agricultural areas. Otherwise the fruits of shrubs such as roses, snowberry, wolfberry, bearberry, blueberry, mountain ash, and poison ivy are taken, as well as seeds and green leaves of herbs, shrubs, and trees. Probably a superabundance of suitable foods is normally available during this time, and much local or yearly variation in foods taken might be expected to occur.

Grange (1948) has pointed out that in general the sharptail closely resembles the ruffed grouse in its food cycle, and that differences occur only because of the sharptail's stronger preference for more open habitats. Differences in foods taken are most pronounced in late summer and fall, but from late fall through spring they may be nearly identical. The primary differences noted between the sharptail and the prairie-chicken were that the prairie-chicken uses a greater amount of grains and weeds, and more generally depends on food sources associated with cultivation. Prairie-chickens may also feed to a somewhat larger extent on insects, especially grasshoppers, than do sharptails.

## Mobility and Movements

### Seasonal Movements

By far the most complete summary of sharptail movements is that of the Hamerstrom and Hamerstrom (1951), and the following account is based on their analysis of seasonal movements in this species. Evidence for a definite seasonal migration dates from a century or more ago, when most or all of the original sharptail range was occupied. At that time, marked seasonal movements evidently did occur, but there is no clear evidence indicating migratory distances or even the directions involved. In areas of mountains or hills where woody cover occurred, an upward altitudinal migration apparently occurred, but few if any cases of a downward movement have been reported.

Much of what has been interpreted as migration has consisted simply of movements to woody cover for the winter period, with distances of such movements gradually being reduced as the birds were driven out of their grassland habitats to woody edges, ravines, and similar brushy or woody situations. Thus, long-distance movements from prairies to wooded wintering habitats have in recent years been completely eliminated, although seasonal changes in habitat preferences still persist in local areas.

With the advent of agriculture, not only were the prairies made relatively unsuited for breeding grounds for sharptails but also the availability of fall and winter grain sources has influenced their movements. However, the sharptail has not been so strongly influenced by this food source as has the prairie-chicken, and is less likely to leave its brushy winter habitat to obtain grain than is the prairie-chicken. Where sharptails have simply incorporated grain into their winter diets they have thus altered their winter behavior very little, but in some areas the availability of grain throughout the winter has enabled the birds to winter in relatively open situations.

During the period of habitat shift from open to relatively brushy habitats, fall "packing" occurs, as coveys or broods gather into small flocks, which in turn form packs of up to several hundred birds. To a smaller extent, clustering may occur in late winter during the return movement to breeding grounds.

The Hamerstroms presented banding data related to mobility for 167 sharp-tailed grouse banded in Wisconsin. Of the 162 birds for which the point of return was known, 81 percent were retaken within two miles of the point of banding. Only 12 percent had moved more than three miles, and only 10 percent were retaken more than five miles away. The longest distance away from the point of banding was 21 miles. Similarly, Aldous found that short-range movements were the rule, with the maximum distance for any return 58 miles. Judging from comparable data on Wisconsin prairie-chickens, the relative overall mobility of the two species would appear to be about the same. By transplanting sharptails and plotting their later recoveries, the transplanted birds were found in general to move farther than nontransplanted birds but showed no tendency to return to the point of banding. The maximum mobility of these transplanted birds was found to be 26 to 27 miles from the point of release.

The relative distances of movements of sharptails from their wintering quarters to spring display grounds doubtless vary greatly in different areas. Kobriger (1965) found that in the Nebraska Sandhills the dispersal of 35 male sharptails from winter feeding stations to spring dancing grounds ranged from 0.2 to 3.3 mile, and averaged 0.9 mile. The majority of these birds moved from their wintering areas to the nearest dancing ground. However, this probably implies that the birds picked the suitable wintering area nearest their dancing ground rather than vice versa, since Evans (1969) found a high degree of fidelity of male sharptails to specific leks between successive years. Similarly, most nests are located within a mile of the nearest dancing ground (Hamerstrom, 1939; Hamerstrom and Hamerstrom, 1951).

### Daily Movements and Home Ranges

The Hamerstroms (1951) reported that during fall, sharptails had a rather large covey range that totaled about 100 to 200 acres in extent with from three to six such coveys usually to be found in an area of 1,000 to 1,500 acres. They estimated that the usual winter daily cruising radius was about one mile.

Kobriger (1965) tracked a sharptail male by radio telemetry through the summer months, during which it moved about 2.5 miles from its dancing ground. Similarly, a female was tracked from a dancing ground to a nest site 2 miles away. In the Nebraska Sandhills sharptail display grounds average less than 1 mile apart, and it is thus probable that females may move considerably greater distances than this between a dancing ground and their selected nest sites.

## Reproductive Behavior

### Territorial Establishment

Territorial establishment by sharp-tailed grouse probably occurs as early as the first fall of life. The Hamerstroms (1951) found that at least 3 of 18 males seen on a dancing ground in North Dakota during late September were young birds. Likewise, Rippin (1970) found that, although only adult males were among those trapped or shot on a display ground in late August, by late September and early October, several juvenile males were also present. This regular fall period of display, which is also typical of pinnated grouse but not the sage-grouse, may provide an important basis for the learning of traditional display sites by young birds.

Rippin found that when he killed all of the males using a dancing ground during the spring, there was no usage of that display site the following fall, but on another area where he killed all but one of the displaying males, the lone bird formed a nucleus for display behavior with several other juvenile birds that following fall. Young probably begin trying to establish peripheral territorial areas their first fall of life, and these territories are then held again the following spring. Rippin reported that on two control dancing grounds (on which he did not experimentally remove any males), the percentage of immature males was 43 percent in 1968 and 37 percent in 1969. On his experimental grounds, he first mapped the relative territorial positions of the participating males; in each he recognized one or more centrally located males and approximately three outer rings of less dominant males defending peripheral territories. On one display ground that contained 18 males, a marginal male originally defending a peripheral territory gradually established itself as a centrally located bird as Rippin progressively reduced the number of males on the dancing ground to 5 birds. When the ground was reduced to 4 participating males, no single bird was able to maintain a central dominant position. The clear result of his studies indicated that a strong centripetal
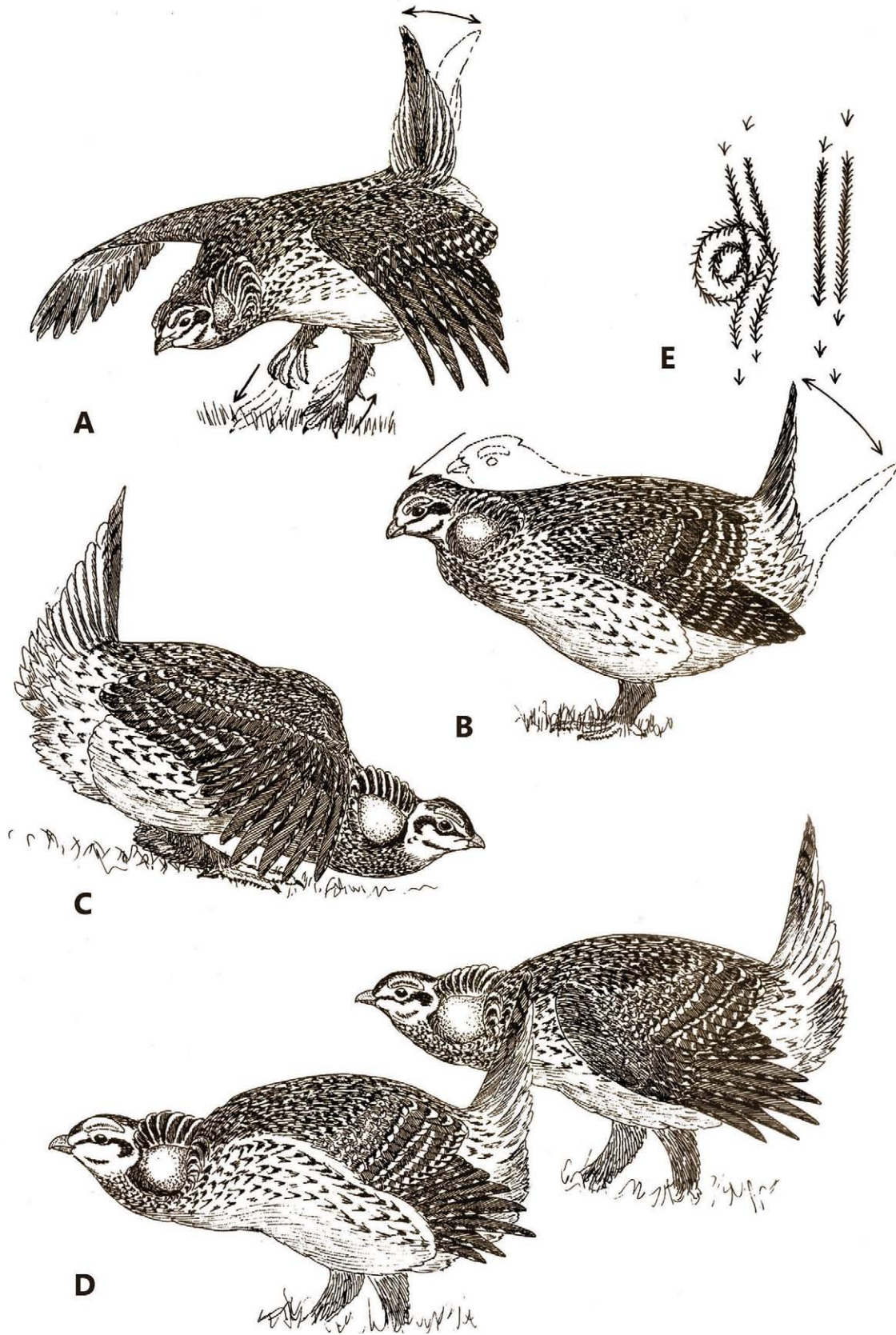
Fig. 36. Male sharp-tailed grouse displays, including (A) dancing, (B) cooing, (C) prostrate posture following dancing, (D) running-parallel by males at common territorial boundary, and (E) examples of footprints made while dancing. After Hjorth (1970).

tendency was present in all the males, with each attempting to attain and defend a relatively central territory.

When such display ground social structures are not disrupted by the death or removal of males, they exhibit a high degree of stability. Evans (1969) found that of 10 males that were marked one spring, 5 returned to the same dancing ground the following spring, while the other 5 disappeared and apparently had died. The areas defended by the 5 returning males were virtually the same as those they had defended the previous spring, with a single minor exception. Hjorth (1970) analyzed Evans's data and concluded that on two grounds the average territorial size was about 90 square meters, ranging from 14 square meters in the central area to 170 square meters on the periphery. He also determined that the average territorial size for a Montana display ground was about 50 square meters, with the four central territories averaging 25 square meters.

The average sizes of display grounds, in terms of numbers of territorial males present, probably vary with population density. Ammann (1957) provides average numbers of birds of both sexes present on ten different sharptail dancing grounds, which averaged 12.4 but ranged from 3 to 29 birds in different years and on different grounds. In the Nebraska Sandhills, display grounds of both the sharptail and the prairie-chicken typically have an average of between 9 and 10 males (Johnsgard and Wood, 1968). Grange (1948) indicated that the average number of males on 14 sharptail grounds in Wisconsin was 6, while 7 prairie-chicken grounds averaged 7 males in attendance. In Utah, Hart, Lee, and Low (1952) reported the average number of birds present on 29 dancing grounds as 12, although as many as 50 had been seen. Lumsden (1965) summarized data from several areas in Ontario that indicated from 2 to 24 males present on dancing grounds. In North Dakota the 12-year average for 1,664 dancing grounds was 12.9 males (Johnson, 1964). It would seem that from 8 to 12 males represents a typical dancing ground for sharp-tailed grouse in most parts of their range.

Lumsden (1965) confirmed the observations of earlier persons working with prairie-chickens and greater sage-grouse as to the reproductive advantage of holding central territories in sharp-tailed grouse dancing grounds. He reported that such central positions were held by socially dominant birds that readily achieved superiority in disputes with neighbors. These central territories were often smaller than peripheral ones, and Lumsden thought that normally only fairly old males could successfully hold such territories. On one display ground Lumsden noted that the dominant male performed 76 percent (13) of the copulations or attempted copulations that were observed, which emphasizes the enormous selective value of occupying such central territories.

### Territorial Advertisement and Defense

Lumsden (1965) classified the social displays of the sharptails as those which serve aggressive functions, those which are concerned with courtship and mating, and those which are specifically associated with advertising the location of the display grounds. In addition, several signals serve as a predator warning system. Lumsden's account is unusually complete, and his terms and descriptions will be utilized here. Later, Hjorth (1970) made an equally detailed analysis; his comparable terms will be noted and a few divergent observations briefly mentioned.

Signals that serve primarily to advertise the location of the dancing ground and of specific males include the flutter-jump and cackling calls. Both sexes perform cackling calls. Cackling by females is usually performed as they approach the dancing ground, and this stimulates strong responses by the males, especially flutter-jumping. Flutter-jumping was first described for the pinnated grouse, and it is virtually identical in both species. The male jumps into the air a few feet, sometimes uttering a *chilk* note as it takes off, flies a few feet forward, and lands again. In so doing, the male clearly advertises its own presence as well as the location of the dancing ground as a whole. Cackling by males may occur between flutter-jumps, or may be uttered by males when others are flutter-jumping.

A large number of male sharptail displays are primarily aggressive and serve to establish and maintain territories. Secondary functions no doubt include the attraction of females to the male and allow for sexual recognition. These primarily aggressive signals include several calls and postures. The calls may be called the *lock-a-lock*, "cooing," the "cork" call, and the *chilk* and *cha* calls. Lumsden regarded the last two calls as being associated with courtship, since they are most often uttered when hens are present.

The *chilk* and *cha* notes are both loud, high-pitched vocalizations that carry great distances. They are often uttered before or after flutter-jumping, and often during the "tail-rattling" display, and both may be uttered with great rapidity. They evidently grade into one another and probably serve similar functions.

The "cork" note is a squeaking sound resembling that produced by pulling a cork from a bottle and is uttered only during the tail-rattling display. It is most often heard when a female is near but may be elicited by another displaying male. A similarly aggressive call is called "whining," which consists of drawn out and repeated sing-song *kaaa-kaaaaa* notes. Such notes are usually associated with territorial defense and are often uttered by birds when facing one another.

The *lock-a-lock* call is a gobbling note that is produced by males when they are standing at rest. With head lowered slightly, a male may utter this call as he approaches his territory before dawn. It is not uttered in the presence of females and apparently serves only an aggressive function.

The "cooing" display is a combination of posturing ("oblique" posture of Hjorth, 1970) and sound production that is clearly homologous with the "booming" of pinnated grouse. As in that display, the tail is partially cocked, the esophagus is inflated, and the head is distinctly lowered ("bowing" of Hjorth, 1970), as a low-pitched cooing sound
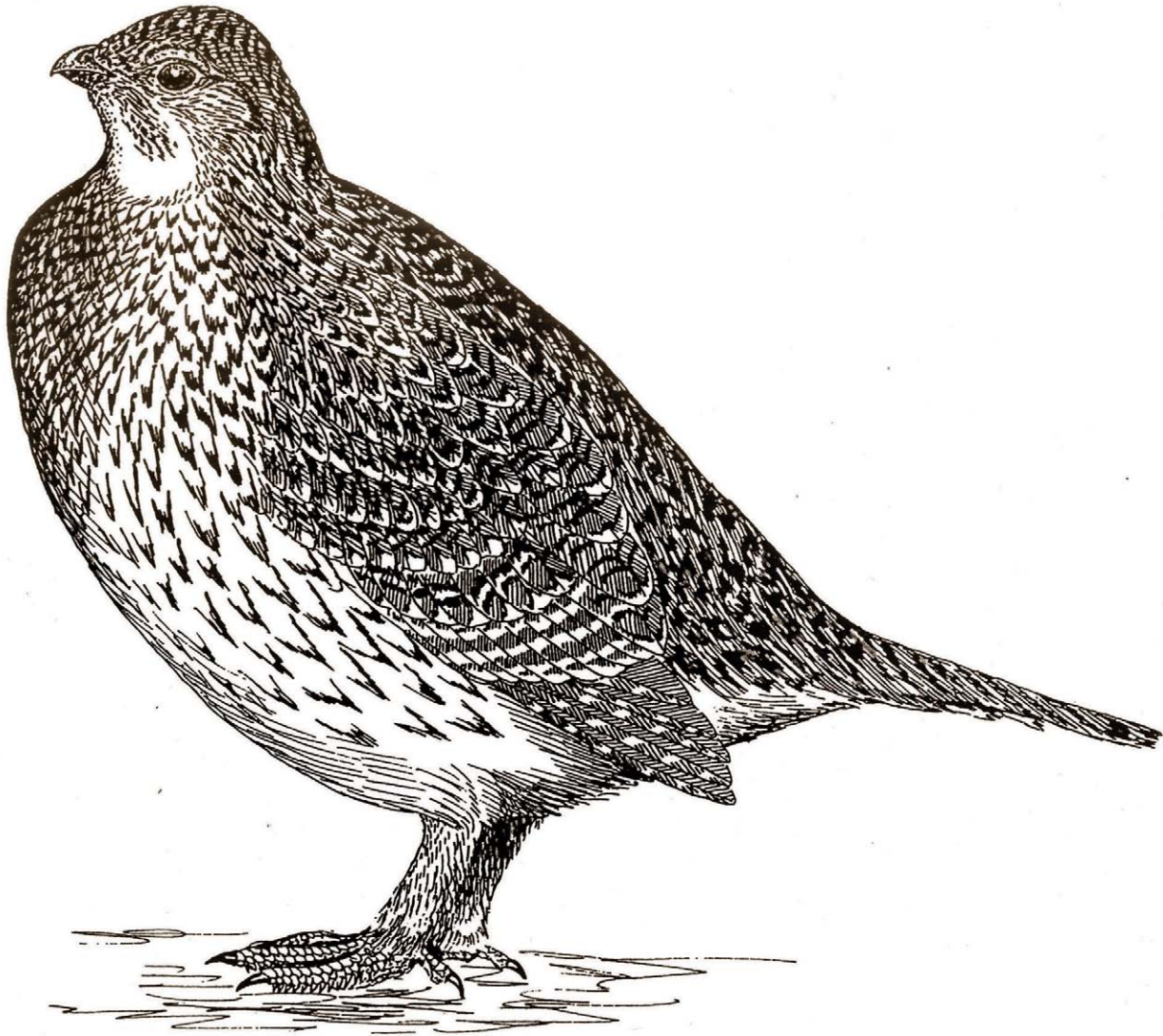
Fig. 37. Male sharp-tailed grouse, standing at rest.

of one or two notes is uttered. However, the folded wings are not strongly lowered, and the throat skin is not as strongly distended as the prairie-chicken's is during booming. The neck skin color is usually pink to purple and thus is also different from that of the greater prairie-chicken. Lumsden believes that cooing does not serve as a sexual signal but rather is evoked in aggressive situations, thus also differing functionally from the booming display.

Several postures or movements are also closely associated with territorial defense. These include an "upright advance" ("wide-necked upright" of Hjorth, 1970), which is an aggressive approach posture of a male during which the tail is cocked and the neck feathers are erected to expose the unfeathered apteria. "Walking or running parallel" consists of two males' moving along their territorial boundaries while threatening one another, often while uttering the *lock-a-lock* call. During this display the head is usually held low, the eye-

combs are enlarged, and the tail is cocked. During "ritual fighting" the birds face one another, often while squatting, and utter aggressive calls while periodically making short lunges toward the other bird. When not attacking, they usually hold their wings partly open and on the ground. During overt attacks the birds leap up into the air, flailing one another with their claws and beaks and sometimes striking with the wings.

Between such attacks the birds watch each other intently, and Lumsden reported that "displacement sleeping" may occur when the attack intensity wanes to a certain point. Should a male attempt to withdraw from such an encounter, it typically lowers its tail, covers its neck skin, withdraws its eye-combs, and sleeks its feathers. These submissive patterns give the bird the appearance of a female and tend to inhibit attack by males. Lumsden reported that the sharptails he observed in Montana, but not those in Ontario, performed

a shoulder-spot display when fighting and also just prior to copulation. This consists of exposing the white under wing-coverts in the region of the elbow. The shoulder-spot display is a conspicuous feature of several grouse species, such as the prairie-chickens, and in several seems to indicate fear or submission. However, Hjorth (1970) did not observe this display in Montana sharptails, and I have not seen it in Nebraska. Lumsden (1970) reviewed the occurrence of this display in various grouse species and has concluded that in some Eurasian grouse (such as black grouse and capercaillie), it serves as an aggressive signal function among males, while in females it indicates an expression of fear.

Much the most complex and interesting of the male displays is the "tail-rattling" or "dancing" display of sharptails. Lumsden considered this to be a courtship display, but it is also closely associated with territorial defense and proclamation. It consists of a highly ritualized series of rapid stepping movements, performed with the tail erect, wings outstretched, head held forward and rather low, and neck feathers erected to exhibit the bare purple skin. With the cocking of the tail, the white under tail-coverts become exposed and appear to be somewhat expanded for maximum visibility. In this rigid posture the male begins a series of very short and rapid stepping movements (18 to 19 per second according to Hjorth, 1970), causing him to move forward in a generally curving direction ("aeroplane display" of Hjorth, 1970).

In synchrony with the stepping movements, the male also performs a strong lateral vibration of his tail, producing a clicking or rattling frictional sound, which is a combination of these pattering sounds and the scraping noises of the overlapping tail feathers. Hjorth (1970) found that during tail-rattling not only are the lateral rectrices alternately spread and shut but the male also occasionally performs a rapid (0.08 second) symmetrical tail-spreading while momentarily breaking his stamping rhythm.

The foot and tail movements of the male are a highly coordinated series of activities, and further, the males together tend to perform the tail-rattling display in highly synchronized fashion. Two or more closely adjacent males will start and stop their display almost simultaneously, and sometimes all the males on a dancing ground will become silent simultaneously. At such times the birds appear to be highly attentive and sensitive to disturbance, whereas when they are all actively "dancing," they remain nearly oblivious to their surroundings.

When performing the tail-rattling display in the presence of a female, the male often alternates this display with a stationary posture Lumsden called "posing." During this posture the male usually faces or nearly faces a female, with wings slightly spread and drooped and the eye-combs greatly enlarged. Soft crooning notes may also be uttered. Typically the male moves from this posture into a crouching or "nuptial bow" position before the female, in which he lowers his body to the ground, fully spreads his wings to the

sides, and almost touches the ground with his bill ("prostrate" of Hjorth, 1970). The rear end of the bird is held high, so that the tail remains vertical, and in general the upper body surface and dorsal view of the tail appear to be presented to the female. In contrast to the comparable posture of the greater prairie-chicken, the male may perform several short and repeated bowing movements, while in the prairie-chicken the male typically remains prostrate and motionless before the female for several seconds. Although this display is normally performed by a male that is beside a female and not being bothered by rival males, Lumsden noted that he observed it as a precopulatory display in only 1 of 19 copulation sequences.

Most copulations by sharp-tailed grouse occur before or approximately at the time of sunrise. Preliminary postures may include the nuptial bow, posing, or tail-rattling displays. The female squats in the usual manner and is immediately mounted by the male. Usually the hen runs forward rapidly immediately after copulation, then vigorously shakes her body and wing feathers. Following a successful copulation the hen often leaves the display ground within a few minutes, and there is no evidence to date that more than one copulation is needed to fertilize all the eggs in a single clutch.

### Vocal Signals

In addition to the calls already mentioned, Lumsden described several other calls. In a situation of uneasiness or slight disturbance, a *yur* note with a downward inflection is uttered. In flight, a series of rapid calls *tuckle . . . tuckle . . . tuckle*, or *tuk . . . tuk . . . tuk*, are frequently uttered, and the same calls may be produced prior to flight.

One other vocalization that serves as a courtship signal, or at least is produced only when hens are on the display ground, is the "pow" call. When courting a hen, males will utter this call several times in rapid succession. Most probably, as Lumsden suggested, it is homologous to the loud *whoop* call of greater prairie-chickens.

### Other Social Signals

Lumsden has described several predator-response postures of sharp-tailed grouse, which include an "upright alert" posture, in which the bird stands upright to its fullest extent with its feathers sleeked and crest raised. A "prostrate alert" is performed in a similar situation, but with the bird in a crouched and "frozen" posture. "Alarm strutting" may be performed as the bird walks around or away from a source of possible danger, in a stiff gait and with occasional tail flicks, which reveal the white outer tail feathers.

### Nesting and Brooding Behavior

The female begins to make a nest scrape in a protected site at about the time she begins to visit the dancing grounds or possibly even before. Following successful mating, she leaves the dancing ground and probably will not return to it again, except in the event of renesting. The eggs are laid on an approximately daily basis until the total clutch of about 12

eggs is produced (Hamerstrom, 1939; Ammann, 1957). The female typically begins incubation at about the time the last egg is laid, and the incubation period is 23 to 24 days (W. W. Lemburg, pers. comm.). Renesting attempts by females evidently do sometimes occur but probably contribute no more than 10 percent of the offspring in an average season (Ammann, 1957).

Following hatching, the female leads the young away from the nest location fairly rapidly, and they particularly tend to move to fairly open areas where insects and green herbaceous foods are abundant (Hamerstrom, 1963). Although the young have been known to move as far as a quarter mile in a single day before fledging, it is probable that the summer brood territory is normally less than a half-mile in diameter (Edminster, 1954). Young sharptails feed to a large extent on insects during their first few weeks, with grasshoppers, spiders, ants, and weevils all contributing to their diet, while leaves and berries are also important sources of food (Grange, 1948). Chicks are able to fly to a very limited degree by the time they are ten days old, and from then have become increasingly independent of their mother. By the time they are six to eight weeks old, they are virtually fully independent, and broods begin to gradually break up and the young birds disperse, often fairly long distances.

## Evolutionary Relationships

There can be little doubt that the nearest living relatives of the sharp-tailed grouse are the prairie-chickens, and I agree with Short (1967) and more recent workers that they are obviously congeneric and quite closely related. Similarities in their downy young as well as in their adult plumage patterns bear this out as well as the frequency of hybridization under natural conditions (Johnsgard and Wood, 1968; Johnsgard, 2002). The two forms also share a number of common display patterns, such as booming and cooing, foot-stamping, the nuptial bow, and flutter-jumping. The sharptail's *pow* call no doubt is homologous to the *pwoik* of the greater prairie-chicken, and the whining and cackling calls of the two species are very similar. The sharptail's *lock-a-lock* aggressive call probably corresponds to the prairie-chicken's *hoo-wuk*; I have heard a hybrid male utter an intermediate call sounding like *wuk-a-wuk'*. However, the lateral tail-rattling of the sharptails is replaced in the prairie-chickens by symmetrical tail-fanning movements, the forward "dancing" is represented by foot-stamping almost in place, and cooing in the sharptail appears to have much less visual and acoustical importance than the homologous booming of the greater prairie-chicken.

Short (1967) suggested that the sharp-tailed grouse is probably closer to the ancestral prairie grouse type than are the prairie-chickens, on the basis of its less specialized neck feathers (rudimentary pinnae) and reduced esophageal sacs. However, its tail feather structure is specialized for the tail-rattling display (Lumsden, 1968), and these differences largely reflect the relative importance of booming and dancing in the species. I would suggest that these spe-

cies have diverged equally from a common forest-dwelling ancestral type, the greater prairie-chicken in a more easterly and southerly location (oak woodland or savanna habitat) and the sharptail in a more westerly and northerly location (grassland, coniferous forest edge habitat). There was probably little contact between these two forms until fairly recently, when human activities greatly altered the habitats of both species (Johnsgard and Wood, 1968). A 2004 estimate of the species' total population was 1,200,000 (Rich et al., 2004).

*Suggested reading:* Grange, 1948; Lumsden, 1995; Connelly, Gratson, and Reese, 1999; Johnsgard, 2002; Paothong, 2012

*Plate 31. Plains sharp-tailed grouse, male dancing; April.*



*Plate 32. Plains sharp-tailed grouse, male cooing; April.*

Plate 33. Plains sharp-tailed grouse, male posing; April.

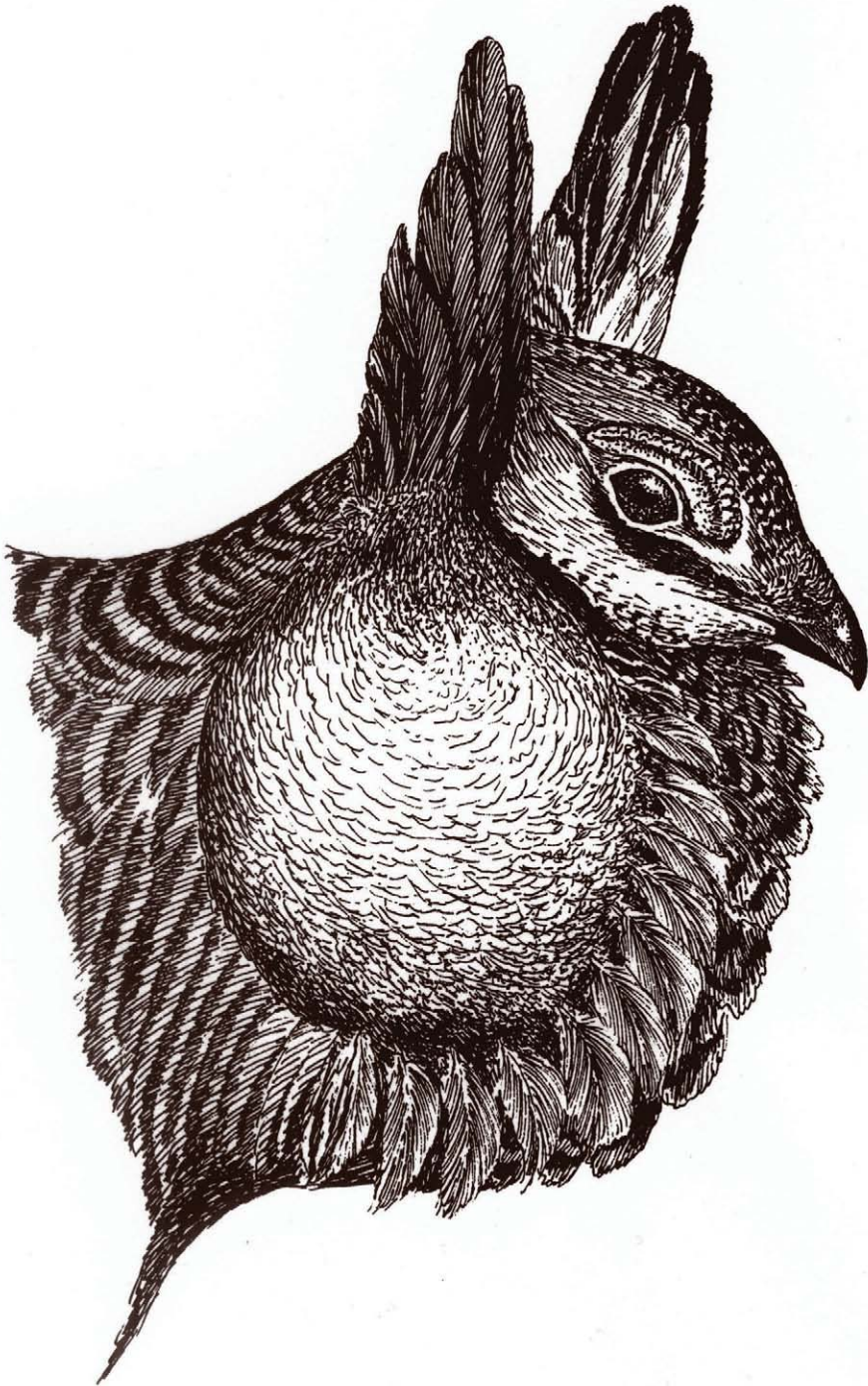*Plate 34. Plains sharp-tailed grouse, territorial confrontation; April.*



*Plate 35. Plains sharp-tailed grouse, female resting; April.*

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