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18 Sharp-tailed Grouse

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18

Sharp-tailed Grouse

Tympanuchus phasianellus (Linnaeus) 1858

(Pedioecetes phasianellus in *A.O.U. Check-list)*

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

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

T. p. columbianus (Ord): Columbian sharp-tailed grouse. Resident from north central British Columbia and western Montana south to eastern Washington, eastern Oregon (now nearly extirpated), northern Utah, and western Colorado. Formerly extended to Nevada and New Mexico.

T. p. 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. p. 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, 110–35 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 more buffy, 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 are illustrated in color plate 61. Downy sharp-tailed grouse 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.

DISTRIBUTION AND HABITAT

This species together with the pinnated grouse comprise the "prairie grouse" of North America. Such a designation for the sharp-tailed grouse

FIGURE 32. Current (shaded) and recent (dashed) distributions of the sharp-tailed grouse.

is not wholly accurate, for the original distribution of the species included not only grassland habitats but also sagebrush semidesert (*T. p. columbianus*), brushy mountain subclimax communites (*T. p. jamesi*), oak savannas and successional stages of deciduous and mixed 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 races have suffered considerably from habitat changes associated with man's activities. One of these is the Columbian sharp-tailed grouse, which has been reduced in a remnant distribution pattern to the point that it is wholly eliminated from California, virtually gone from New Mexico, rare in Utah, Nevada, and Oregon, uncommon to rare in Oregon and Washington, and generally uncommon in Colorado, Wyoming, and Montana (Hamerstrom and Hamerstrom, 1961).

The prairie race of sharp-tailed grouse has similarly been extirpated from Illinois, Iowa, and southern portions of Wisconsin and Minnesota and is in danger of extirpation in the northern parts of these states (Hamerstrom and Hamerstrom, 1961). In the Lower Peninsula of Michigan, introduced sharp-tails 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 sharp-tail population had decreased at least nine percent between 1956 and the early 1960s, primarily through habitat losses (Ammann, 1963a). In Minnesota the general population trend appears to be downward, as a result of improved farming practices as well as increased reforestation and tree-farming activities (Bremer, 1967). Hamerstrom and Hamerstrom (1961) report that the Wisconsin population is in greater danger than those in Minnesota and Michigan as a result of fire protection, forest succession, pine plantations, and modern farm practices. The Canadian populations of this race in Ontario, Manitoba, and eastern Saskatchewan appear to be in relatively good condition.

The plains sharp-tail, with its extensive range from northern Alberta to North Dakota and northern New Mexico, has apparently suffered the least of the United States races, and still supports legally hunted populations in three provinces and six states. However, it is gone from northwestern Oklahoma and western Kansas, and its range in eastern Colorado has shrunk appreciably (Johnsgard and Wood, 1968).

The remaining, predominantly Canadian, populations of sharp-tailed grouse are evidently in relatively satisfactory condition.

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 sharp-tail 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 tremuloides*), 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 semidesert 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) list a variety of grasses and herbs as important components of Columbian sharp-tail 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 independent 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 North Dakota sandhills (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 to total land surface is tolerable to sharp-tails in North Dakota.

Wintering Requirements

Grange (1948) reported that sharp-tails 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 and fairly coarse marshy vegetation.

Ammann's observations (1957) for Michigan sharp-tails 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, soy beans, 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 sharp-tails. 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 ninety-five sharp-tail dancing grounds in Michigan. Of these, twenty-seven were located on cultivated lands, and sixty-eight were on wild lands. Although the majority of these contained no woody cover, 35 percent had such cover present, but rarely did this cover exceed 30 percent of the surface area.

Favored sites for both sharp-tails and pinnated grouse appeared to be low, mottled 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 sixty-five pinnated grouse and ninety-five sharp-tail display grounds, 47 percent were in elevated situations and only four were located in depressions.

In Wisconsin, Grange (1948) found that wild hay meadows and marshes were frequent display locations for pinnated grouse and sharp-tails, with sharp-tails exhibiting an apparently greater preference than pinnated grouse 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 thirty-six display grounds studied by him, thirty-two were on open, dry, and elevated sites, three were on level ground, and one 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 twenty-six of thirty-six sharp-tail 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 Habitat Requirements

Ammann (1957) has provided a fairly detailed analysis of nesting requirements for sharp-tails in Michigan. He reported that they choose a wider variety of sites with respect to woody cover than do pinnated grouse, 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 twenty-nine nests found none was more than ten feet from brushy or woody cover. Of ten nests studied, six were in open aspen, three were in cut-over pines, and one was in an open marsh. These sites averaged 43 percent shrub cover, from three to six feet high, and 4 percent tree cover in excess of six feet tall. Associated shrubs were chokecherry, willow, and alder, and associated trees were aspen, spruce, and Juneberry. Of seven additional nests, four were located at the base of a small tree or bush, and there was one each in a hayfield, on an aspen-birch ridge, and in a heavy grass–sweet fern site.

Hamerstrom (1939) reported on cover sites for seventeen sharp-tail 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, two were in openings or edges of jack pine–scrub oak woods, two were in grass meadows, one was in a dry marsh, and one 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.

Since 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 sharp-tails 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 over-all shading by woody cover, with shrubs covering 43 percent of the area and trees covering an average of 70 percent in locations where fifteen broods were observed.

Hamerstrom's observations on about 190 broods confirm the importance of opening 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 fifty 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 sharp-tail survival.

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 percent 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. Considering only the occupied range in 1942, the average area per bird figure was calculated to be 138 acres. Ammann (cited by Edminster, 1954) reported spring densities on thirteen square miles of habitat on Dummond Island, Michigan, for a three-year period as averaging one bird per 45 acres, while the fall populations of sharp-tails on the island were approximately one bird per 18 acres of occupied range over a seven-year period. This island represents prime Michigan sharp-tail habitat, and these figures must be regarded as being unusually high densities which have not been maintained recently. Edminster (1954) summarizes 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 between twenty-five and forty birds per square mile (16 to 25.6 acres per bird) in the Sand Hills area, where an ideal combination of native grasses, shrubs, and small trees occur.

FOOD AND FORAGING BEHAVIOR

Dependable and nutritious winter food sources are critical to the survival of all grouse, and the sharp-tail 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 shrubs, 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, sharp-tails 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 pinnated grouse 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 it seeds and grass leaves were the leading food sources. Apparently the sharp-tail 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 sharp-tail closely resembles the ruffed grouse in its food cycle, and differences occur only because of the sharp-tail'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 sharp-tail and the pinnated grouse were that the pinnated uses a greater amount of grains and weeds and more generally depends on food sources associated with cultivation. Pinnated grouse may also feed to a somewhat larger extent on insects, especially grasshoppers, than do sharp-tails.

MOBILITY AND MOVEMENTS

Seasonal Movements

By far the most complete summary of sharp-tail 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 fifty to one hundred years ago, when most or all of the original sharp-tail 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 sharp-tails but also the availability of fall and winter grain sources has influenced their movements. However, the sharp-tail has not been so strongly influenced by this food source as has the pinnated grouse, and is less likely to leave its brushy winter habitat to obtain grain than is the pinnated grouse. Where sharp-tails 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, packing may occur in late winter during the reverse 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 twenty-one miles. Similarly, Aldous found that short-range movements were the rule, with the maximum distance for any return fifty-eight miles. Judging from comparable data on Wisconsin pinnated grouse, the relative over-all mobility of the two species would appear to be about the same. By transplanting sharp-tails and plotting their later recoveries, the transplanted birds were found in general to move farther than nontransplanted birds but to show no tendency to return to the point of banding. The maximum mobility of these transplanted birds

was found to be between twenty-six and twenty-seven miles from the point of release.

The relative distances of movements of sharp-tails 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 sharp-tails from winter feeding stations to spring dancing grounds ranged from 0.2 to 3.3 miles, 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 sharp-tails 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 in the fall sharp-tails had a rather large covey range that totaled about one hundred to two hundred acres in extent with from three to six such coveys usually to be found in an area of one thousand to fifteen hundred acres. They estimated that the usual winter daily cruising radius was about one mile.

Kobriger (1965) tracked a sharp-tail 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 sharp-tail 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 three of eighteen 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 which contained eighteen 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 five birds. When the ground was reduced to four participating males, no single bird was able to maintain a central dominant position. The clear result of his studies indicated that a strong centripetal 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 ten males that were marked one spring, five returned to the same dancing ground the following spring, while the other five disappeared and apparently had died. The areas defended by the five 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 10 different sharp-tail 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 sharp-tail and the pinnated grouse usually have an average of between 9 and 10 males (Johnsgard and Wood, 1968). Grange (1948) indicated that the average number of males on 14 sharp-tail grounds

in Wisconsin was 6, while 7 pinnated grouse 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 were 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 twelve-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 pinnated grouse and 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 (thirteen) 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) has classified the social displays of the sharp-tails 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. More recently, Hjorth (1970) has made an equally detailed analysis; his comparable terms will be noted and a few divergent observations briefly mentioned.

Signals which 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 sharp-tail 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 regards 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 notes 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 only uttered 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 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 pinnated grouse'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 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 reports 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 sharp-tails 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 underwing coverts in the region of the elbow. The shoulder-spot display is a conspicuous feature of several grouse species, such as the pinnated grouse and in several seems to indicate fear or submission. However, Hjorth (1970) did not observe this display in Montana sharp-tails and I have not seen it in Nebraska. Recently Lumsden (1970) has reviewed the occurrence of this display in various grouse species and has concluded that in some species (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 sharp-tails. Lumsden considers 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 undertail 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 (eighteen to nineteen 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) has recently 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 breaking his stamping rhythm momentarily.

Not only are the foot and tail movements of the male a highly coordinated series of activities, but males tend to perform the tail-rattling display in highly synchronized fashion. Two or more closely adjacent males will start and stop their dislay almost simultaneously, and sometimes all of 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 has 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 pinnated grouse, the male may perform several short and repeated bowing movements, while in the pinnated grouse 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 pre-copulatory display in only one of nineteen 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 of the eggs in a single clutch.

Vocal Signals

In addition to the calls already mentioned, Lumsden has 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 vocal signal 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 has suggested already, it is homologous to the loud *whoop* call of greater prairie chickens.

Other 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 twelve 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 twenty-three to twenty-four days.* 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 sharp-tails 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 foods

*W. Lemburg, 1970: personal communication.

(Grange, 1948). Chicks are able to fly to a very limited degree by the time they are ten days old, and from that time 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 relative of the sharp-tailed grouse is the pinnated grouse, and I agree with Short (1967) that they are obviously congeneric. 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). 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 sharp-tail's *pow* call no doubt is homologous to the *pwoik* of the pinnated grouse, and the whining and cackling calls of the two species are very similar. The sharp-tail's *lock-a-lock* aggressive call probably corresponds to the pinnated'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 sharp-tails is replaced in the pinnated by symmetrical tail-fanning movements, the forward "dancing" is represented by foot-stamping almost in place, and cooing in the sharp-tail appears to have much less visual and acoustical importance than the homologous booming of the pinnated grouse.

Short (1967) suggests that the sharp-tailed grouse is probably closer to the ancestral prairie grouse type than is the pinnated, 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 two species. I would suggest that both species have diverged equally from a common forest-dwelling ancestral type, the pinnated in a more easterly and southerly location (oak woodland or savanna habitat) and the sharp-tail 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).