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10 Sage Grouse

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Part II

Accounts of Individual Species
Sage Grouse

Centrocercus urophasianus (Bonaparte) 1827

OTHER VERNACULAR NAMES

SAGE hen, spiny-tailed pheasant, sage cock, sage chicken.

RANGE

From central Washington, southern Idaho, Montana, southeastern Alberta, southern Saskatchewan, and western North Dakota south to eastern California, Nevada, Utah, western Colorado, and southeastern Wyoming (modified from A.O.U. Check-list).

SUBSPECIES

C. u. urophasianus (Bonaparte): Eastern 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. u. phaios Aldrich: Western sage grouse. Resident from central and eastern Washington south to southeastern Oregon.
MEASUREMENTS

Folded wing: Males, 282-323 mm; females, 248-79 mm. Using flattened wings, females range from 240 to 285 mm and males from 288 to 334 mm, with 290 mm a calculated best division point (Crunden, 1963).
Tail: Males, 297-332 mm; females, 188-213 mm.

IDENTIFICATION

Adults, 19-23 inches long (females), 26-30 inches long (males). The large size and sagebrush habitat of this species 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, which grade into longer and softer white feathers and finally into a number of long, black hair-like 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.

FIELD MARKS

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

AGE AND SEX CRITERIA

Females may readily be separated from adult males by their weights and measurements (see above), by the absence of black on the upper throat, and by the fact that the white tips of the under tail coverts extend part
way down 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, the outer primaries are more pointed and mottled than the others, the outer wing coverts are narrowly pointed instead of being unmottled dark gray and are marked with brown and white and have 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 are 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 bursa 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 (illustrated in color plate 61) 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 definiteloral 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 HABITAT

At one time this species 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 which lasted nine years. The species became completely extirpated from British Columbia and New Mexico, although New Mexico has recently successfully reestablished the bird, and British Columbia has been attempting to do the same (Hamerstrom and Hamerstrom, 1961). There are no recent specimen records from Nebraska, although a few birds may occasionally stray across the Wyoming state line. There are 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 (1944 and 1945), 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.

In the past decade the sage grouse has recovered sufficiently to be a major game species again in about five states. 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 for the country as a whole.

The most recently available hunter-kill estimates would indicate that the sage grouse is at least maintaining its population sufficiently to be a major game species in five states and of secondary importance in six more states and one province. The estimated 1969 kill in Idaho was 81,729 birds, and in 1968 total state-wide harvests were 55,361 in Wyoming and 53,462 in Montana. Colorado biologists estimated that 21,922 sage grouse were shot there in 1969. Kill estimates for Nevada and Utah were 11,765 (1968) and 11,109 (1969), respectively. Considerably smaller numbers are harvested annually in California (3,200 in 1969), Washington (2,300 in 1969), Oregon (4,760 in 1969), and South Dakota (about 2,000 in 1967). Currently Alberta and North Dakota each have kills of only a few hundred per year. The overall yearly harvest is thus currently about 250,000 birds. This harvest does not reflect so much a recent increase in grouse populations as increased
hunting pressure and a recognition that limited harvests are not a controlling factor in protecting the security of the sage grouse.

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 current distributional patterns. The range map that I have prepared is based largely on Patterson's map, but has been modified to take into account information such as that appearing in recent sage grouse status questionnaires. Patterson estimated that some 90 million acres of preferred sagebrush-grassland habitat existed in the early 1950s and that an additional 40 million acres of desert scrub habitat was also available to sage grouse. If the 90-million-acre figure is assumed to be currently representative, this would total about 140,000 square miles of preferred habitat. If an average population density of 10 birds per square mile might be assumed, the total sage grouse population might be roughly estimated at 1,500,000 birds. The present yearly harvest of 250,000 would then represent 17 percent of the total, which would not seem exorbitant.

In spite of this seemingly comfortable number of birds, it is difficult to be optimistic about the long-term future of the sage grouse in North America. The continued clearing of extensive areas of sage for irrigated farming, as has occurred widely in central Washington, and the expanded use of herbicides to improve grazing conditions are likely to further reduce sage grouse habitat and populations in future years. Schneegas (1967) estimated that five to six million acres of sagebrush have been removed in the last thirty years, a portent of things to come.

**POPULATION DENSITY**

Patterson (1952) estimated sage grouse densities by determining strutting ground sizes and numbers 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, of course, excluded all females and probably some immature males from consideration. Edminster (1954) thus calculated that the total spring population of sage grouse might be from 30 to 50 birds per square mile, or thirteen to twenty-one acres per individual. Rogers (1964) likewise reported that certain counties of Colorado support 10 to 30 birds per square mile in some sections, while the remaining habitat supports 1 to 10 birds per square mile.
FIGURE 22. Current distribution of the sage grouse.
HABITAT REQUIREMENTS

Wintering Requirements

During winter, sagebrush provides not only nearly 100 percent of the food which is utilized by sage grouse but 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 thirty to fifty miles from the habitats used during fall and spring. Black sage (Artemisia nova) is the preferred winter food in eastern Idaho but is often covered by snow.

Spring Habitat Requirements

In late winter, male sage grouse begin to leave their wintering areas and return to their traditional strutting grounds. Based on a total of forty-five strutting grounds classified by type of land area, Patterson (1952) found that eleven were on wind-swept ridges and exposed knolls, ten were on flat sagebrush areas with no openings, seven were on bare openings on relatively level lands, and the remaining seventeen 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 one-fourth to one-half acre in dense stands of sage.

Nesting and Brooding Requirements

Patterson (1952) reported that 92 percent of the nests he found were under sagebrush plants, usually in cover from ten to twenty inches tall, and in drier sites where the shrub cover was less than 50 percent. In Utah, Rasmussen and Griner (1938) found that a related species, silver sage (A. cana), provided preferred nest cover, with plants of this species from fourteen to twenty-five 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). In nesting habitats he noted that the sagebrush averaged only eight inches tall but that taller plants were preferred for nest sites. No nests occurred 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 sage grouse 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 ninety-eight 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 of Martin (1970) in Montana indicated that in 158 locations, young broods used areas having less plant density and lower crown cover (nine to fifteen inches high) than did older broods or adults (seven to twenty-five inches high). Rogers (1964) also reports that low sage (seven to fifteen 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 sage grouse, apparently by altering vegetational composition, particularly of favored food plants (Martin, 1970). Similarly, Peterson (1970) concluded that components of brood habitat for sage grouse include a diversity of forms and a density of sage ranging from 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 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 sage comprised 77 percent (of a total of 95.7 percent plant material) of foods found in 49 samples from adult sage grouse
in Wyoming and 47 percent (of a total of 89 percent plant material) from 45 juvenile sage grouse 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 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 comprised 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 sage grouse. He found that, in a sample of 35 sage grouse collected from July to September, sagebrush totaled 34 percent of the food, while dandelion (Taraxacum) comprised 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 indicate that weedy forbs such as prickly lettuce (Lactuca) and cultivated herbaceous broad-leaved 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 the recent study of Peterson who analyzed the food of 127 birds up to twelve weeks of age. During that period, forbs comprised a total of 75 percent of the diet, and two 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 eleven weeks.

**MOBILITY AND MOVEMENTS**

*Seasonal Movements*

The most complete study on seasonal movements of 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 eight-thousand-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 seventy-five air miles from its point of banding.

In mountainous country, wintering grounds of 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 from fifty to one hundred miles along established routes before reaching their strutting grounds. Adult females evidently reach the strutting grounds about the same time as adult males or somewhat later. Patterson (1952) noted that males 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 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 birds 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 subordinant males to establish territories in various locations. Earlier, Dalke et al. (1960) had reported that 70 percent of banded 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 the females 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 three or four miles from a display ground to a nest site and may travel as far as seven miles.*

Following nesting, females 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 or twelve weeks, when they have completed their molt into juvenile plumage.

Spring dissolution of the strutting grounds by males 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 down into alfalfa fields near irrigated valleys. Schlatterer (1960) reported that the sequence of arrival of birds on the summering areas in Idaho was males, unproductive females, and productive females. In southern Idaho the summer brood range may be from thirteen to twenty-seven miles from the nesting grounds, a considerable movement for these recently fledged birds.

Fall movements toward wintering areas is likewise a gradual process, and the rates probably vary according to weather conditions. Pyrah (1954) reported that immature females 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 twenty degrees Fahrenheit. Birds usually remained in a single place for several days then moved out in groups. By the time the first snows fell, flocks were usually composed of between fifty and three hundred birds in loose associations. During severe weather, flocks of up to one thousand birds could be seen, but in midwinter they normally consisted of less than fifty individuals, with old males often in groups of less than twelve.

Daily Movements

Daily movements and activity patterns of sage grouse have yet to be carefully documented, but some work with banded birds is of interest.

*Terry May, 1970: personal communication.
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 fifty-five meters from Lumsden's blind, six males left their usual territories and moved toward the hens, apparently maintaining their positions relative to one another. Of twenty-seven 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 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 which may be within a half mile of the strutting grounds (Pyrah, 1954). Hens rarely return to the strutting grounds in the afternoon.

Observations on nesting 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 between fifteen and twenty-five minutes, according to Nelson.

In late summer, 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 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 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 pinnated grouse 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 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 separate fully 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-male social dominance) and relative individual reproductive success (fertilization of females) provides a basic key to 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 which 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 develop-
ment 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 squatting display with wings partially spread, which is virtually identical in all grouse so far studied. In the 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.

MaleTerritorialAdvertisementBehavior

Although strutting 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 ten to twenty 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 eight to twelve 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, male grouse draw up the skin on the sides of the neck, thus erecting the filoplumes and increasing the exposed areas of white

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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.

When on territory and between strutting sequences, the male 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 upwards and utter a soft snoring note that is apparently associated with the inhaling of air (Hjorth, 1970).

The strutting display ("ventro-forward" of Hjorth, 1970) is a complex sequence of stereotyped movements (figure 23) 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 forty-five-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 upwards ("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
Figure 23. Sequence of the ventro-forward display of the sage grouse, from Hjorth, 1970. (Numbering represents cine frames exposed at the rate of twenty-four per second. Enlarged views illustrate the three forward thrusts from two angles.)
head is quickly withdrawn into the neck feathers so that it becomes completely concealed, compressing the esophageal 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 upwards 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, swishing" noise (Lumsden, 1968) that is followed by two plopping sounds. However, a call is also uttered, which Lumsden described as sounding like wa-um-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 sage grouse lacks much of the pivoting action of the pinnated grouse'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 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 fifty to seventy hens have been seen in single clusters in large leks. Lumsden noted that, although hens clustered at twenty 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 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 sage grouse because of the large number of males usually present and the conspicuous nature of individual birds. Lumsden also believes 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 underwing coverts 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 regards this display as an expression of conflict, with fear as one of the components.

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

**Nesting Behavior**

Once fertilization has been accomplished, the hen apparently leaves the strutting ground for nesting. There 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 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 10½ days would be required to lay an average clutch of eight eggs, and that 26½ days more would be required for incubation, for a total elapsed time of 37 days between mating and hatching.

Estimates of average clutch size usually range from 7 to 8 eggs. Patterson (1952) reported an average clutch size of 7.26 eggs in eighty nests during one year, and 7.53 eggs in seventy-four 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 twenty-five-to-twenty-seven-day incubation period for 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 twenty-to-twenty-four-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 the sharp-tailed grouse. Not until the analysis by Hudson and Lanzillotti (1964) was it proposed that the 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 sage grouse. Lumsden’s analysis of behavior (1968) also presented this view, and he pointed out that the male sage grouse shares with the blue 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 sage grouse and blue 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 (Dendragapus 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 blue grouse have many features in common. The evolution of lek behavior by the 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.