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12 Spruce Grouse

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Spruce Grouse

Dendragapus canadensis (Linnaeus) 1758
(*Canachites canadensis* in *A.O.U. Check-list*)

OTHER VERNACULAR NAMES

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

RANGE

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

SUBSPECIES (*ex A.O.U. Check-list*)

D. c. canadensis (Linnaeus): Hudsonian spruce grouse. Resident in east central British Columbia, central Alberta, central Saskatchewan, south-

western Keewatin, northern Manitoba, northern Ontario, northern Quebec, and Labrador south to central Manitoba, central Ontario, and central Quebec. Introduced into Newfoundland in 1964 (Tuck, 1968).

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

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

D. c. atratus (Grinnell): Valdez spruce grouse. Resident in the coast region of southern Alaska from Bristol Bay to Cook Inlet, Prince William Sound, and perhaps Kodiak Island (no recent records).

MEASUREMENTS

Folded wing: Males, 161–92 mm; females, 159–91 mm (males average 2 mm longer).

Tail: Males, 107–44 mm; females, 94–119 mm. (Adult males of all races average over 120 mm; females, under 110 mm.)

IDENTIFICATION

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

ochraceous buff in varying proportions; the sides are predominantly ochraceous and the underparts are mostly white.

FIELD MARKS

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

AGE AND SEX CRITERIA

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

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

Juveniles resemble adult females but have white or buffy markings at the tips of the upper wing coverts, as well as on their primaries and secondaries. Their tail feathers are dark brown, barred, speckled, and vermiculated with lighter markings (Ridgway and Friedmann, 1946).

Downy young are illustrated in color plate 61. The downy plumage of this species more closely resembles *Lagopus* than does that of the blue grouse and has a discrete chestnut brown crown patch that is margined with black. Downy spruce grouse lack the feathered toes of ptarmigan; however, they are also more generally rufous dorsally and have less definite patterning on the back.

DISTRIBUTION AND HABITAT

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

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

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

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

Finally, in southern Ontario, spruce grouse have nearly disappeared from the area south of Lake Nipissing (Hamerstrom and Hamerstrom, 1961).

Lumsden and Weeden (1963) pointed out that in the early 1960s spruce grouse had sufficiently high populations to be hunted in Maine, Montana, Washington, Idaho, Alaska, and all the Canadian provinces and territories except Nova Scotia (where it is protected) and Prince Albert Island (where it has been extirpated). In 1970, Minnesota allowed the hunting of spruce grouse as well, but it was still protected in Wisconsin, Michigan, New York, Vermont, and New Hampshire.

POPULATION DENSITY

Few estimates of population densities in spruce grouse are available. Robinson (1969) estimated a breeding density in northern Michigan of twenty to twenty-five birds (ten to twelve pairs) per square mile. Ellison (1968b) reported that a spring census of males in south central Alaska indicated a density of about ten males per square mile during two years and seven per square mile in a third year. He noted that this agrees with an estimate of seven males per square mile made by Stoneberg in Montana.

HABITAT REQUIREMENTS

A careful analysis of all the habitat needs of the spruce grouse remains to be done, but a recent study by Robinson (1969) provides a valuable analysis of summer habitat needs. By analyzing tree composition, as well as that of shrubs and low herbs, and comparing locations of spruce grouse sightings, a useful indication of habitat selection was obtained. Of 430 trees where spruce grouse were seen, 32 percent were spruces, although spruces (*Picea mariana* and *P. glauca*) made up only 3 percent of the tree cover. On the other hand, jack pines made up 91 percent of the tree composition but accounted for only 51 percent of the sightings. Pure stands of either jack pine or spruce were not used as much as mixed stands. In the shrub layer, young black spruces accounted for a larger proportion of spruce grouse sightings than would be expected from their relative abundance, while jack pines again provided a smaller proportion of sightings. Balsam firs at sighting points were more than seven times as abundant as at random sites. As to low vegetation, blueberry (*Vaccinium*), trailing arbutus (*Epigaea*), black spruce, and logs and stumps all were associated with higher than expected sightings of spruce grouse. In general, mature stands of either jack pine or spruce were not favored, apparently because of the lack of concealing cover at ground level. Robinson found that molting males used the same habitat in late summer as did females with broods and indeed were often seen accompanying broods. Robinson concluded that populations

of spruce grouse in Michigan were highest in areas of boreal forest and jack pine forest. In one such area, the grouse selected habitats that had a mixture of spruces and jack pine, had a prevalence of young spruces in the shrub layer, and had a varied ground cover that included blueberries, trailing arbutus, and scattered stumps and logs.

In a comparable study of Alaskan spruce grouse, Ellison (1968b) noted that hilltops covered with white spruce, birch (*Betula*), and species of *Populus* were not a preferred habitat, although where an understory of alder was present some brood use and use by molting adults occurred in late summer. Two upland cover types provided preferred habitat. These were a white spruce and birch community with understories of grasses, spiraea, blueberry, and cranberry, and a black spruce community with a blueberry, cranberry, and lichen understory. Grouse sometimes also used dense lowland stands of black spruce, and broods were often found in stunted black spruce borders at the edges of bogs.

MacDonald (1968) noted that the habitat of the Franklin race of spruce grouse in Alberta consisted of lodgepole pine forests, with some clumps of aspen and poplar. Somewhat open stands of pines, some twenty to thirty feet tall, were evidently preferred areas for display by territorial males.

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

FOOD AND FORAGING BEHAVIOR

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

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

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

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

MOBILITY AND MOVEMENTS

Spring Movements of Males.

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

6.9 acres. After May 21, these same males occupied larger home ranges of from 4.5 to 29.6 acres, averaging 20.1 acres. Considering four immature and territorial males as well, the maximum sizes of the home ranges of all eight males was 61 acres, while three of five nonterritorial males moved about over areas of 270 to 556 acres.

REPRODUCTIVE BEHAVIOR

Territorial Establishment

Ellison (1968b) reported that spruce grouse males established their territories and activity centers in stands of fairly dense spruce or stands of spruce and birch with trees some forty to sixty feet tall. Stands of trees up to eighty feet tall, with dense undercover, were sometimes used by non-territorial males but apparently were not suitable for territorial purposes. MacDonald (1968) indicated that pines from twenty to thirty feet tall which were not too closely spaced were preferred display sites. Stoneberg (1967) stated that of four males he studied, three displayed in small openings in dense forest, while one was in less dense forest. He estimated that the four marked males he studied had home ranges of ten to fifteen acres. Two remained in very localized sites during the display period, while one of the other two used several display sites within a twenty-five-yard radius, and the last moved about extensively and used no specific sites. However, this last bird was the only one that had no female on his territory at the time. MacDonald thought that males have favored display sites within their home ranges but that the latter are too large to have definite boundaries except in areas of contact with adjacent males.

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

Territorial Advertisement

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

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

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

When approaching a female in the strutting posture, the male may perform several displays that have been given different names by various writers. One is a vertical head-bobbing, which may grade into or alternate with ground-pecking (Harper, 1958; Lumsden, 1961a; Stoneberg, 1967; MacDonald, 1968). During the pecking movements the male faces the

*Michael Flieg, 1970: personal communication.

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

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

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

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

Squatting as described by MacDonald probably does not correspond to the typical head-jerk as described by Lumsden and Stoneberg, since MacDonald mentions no actual head-jerking movements and I likewise noted none during one observation of the squatting display. Lumsden mentions seeing repeated, sudden upward movements of the head, first to one side, then to the other, as well as occasional circular head movements. With each upward movement the tail was fanned open and again shut, producing the usual rustling sound. Stoneberg noted two types of head-jerking movements, one of which was a rapid tossing of the head from one side to the other for up to three seconds, pausing and repeating it, with the tail kept vertical and the head near the ground. A slower type of head-jerking was associated with strutting, when the bird would stop, facing the female, and jerk the head from one side to the other while fanning or flicking his tail.

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

Aerial Displays

In contrast to the terrestrial displays of spruce grouse, some population variation may occur in the aerial displays of males. Lumsden has summarized the observations of aerial display by the nominate subspecies, which apparently consists of several variations. One of these is a short, vertical flight from a few to about fourteen feet in the air, drumming on suspended wings, and fluttering back to the ground. This behavior is closest to the

typical flutter-jump of prairie grouse. More commonly, however, the male flies either vertically upward or horizontally toward a tree perch, checks its flight, and either lands on the perch or drops back to earth. If it lands on the elevated perch it may stay there varying lengths of time; Lumsden reports periods as short as ten seconds and as long as four minutes. The flight back down is always performed in the same manner, by dropping steeply downward until the bird is about four to six feet from the ground, then swinging the body into a nearly vertical position, and descending on strongly beating wings toward the ground. Although the drumming sound produced by the wing-beats can be heard as far as two hundred yards away, neither Lumsden nor Ellison (1968b) reported any wing-clapping sounds by males of this race, nor have other prior observers. Apparently no vocal calls are uttered during the flight.

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

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

According to MacDonald, the vertical flight to a perch may be followed by display on the perch prior to launching into the wing-clapping display. He reported that after alighting on a branch and prior to the wing-clapping flight, the male may perform either or both of two different displays. These include a short rush along the branch followed by a spreading of the wings

and tail, closing them, and again spreading the tail, apparently a variant of the tail-flicking display. A second display consists of three or four shallow wingstrokes, like the drumming of a ruffed grouse, producing a similar thumping sound.

Vocal Signals.

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

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

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

Nesting and Brooding Behavior

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

Nests of the spruce grouse are usually situated in a well-concealed loca-

tion, often under low branches, in brush, or in deep moss in or near spruce thickets. Ellison (Alaska Dept. of Fish and Game, *Game Bird Reports*, vols. 7-9, 1966-68) reported on nineteen nest locations, fourteen of which were in open, mature white spruce, birch, or spruce-birch-alder acotones, while two were in open black spruce, two were in moderately dense black spruce, and one was in a mixture of alder and grass. Of twenty-one nests he found, the clutches ranged from 4 to 9 eggs, and averaged 7.4. Tufts (1961) reported clutch sizes for thirty-nine nests, which ranged from 4 to 10 eggs and averaged 5.8. Robinson and Maxwell (1968) could find no authenticated record of a clutch of more than 10 eggs, and concluded that earlier estimates of larger clutches were in error. One instance of definite renesting has been found by Ellison (*Game Bird Reports*, vol. 9, 1968). Pendergast and Boag (1971) have reported the incubation period to be twenty-one days.

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

EVOLUTIONARY RELATIONSHIPS

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

It seems probable that the evolutionary origin of the spruce grouse was

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