SEASONAL SOCIAL ORGANIZATION AND MOVEMENTS OF SPRUCE GROUSE

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The results of a study of territoriality among male Spruce Grouse (*Canachites canadensis*) during the breeding season have already been summarized (Ellison 1971). The purpose of this paper is to report on some aspects of flock size, associations within sex and age classes, and minimum size of home ranges in all seasons. In comparison with other tetraonids, little published information exists on movements and social groupings in Spruce Grouse. Three unpublished M.S. theses (Stoneberg 1967; McCourt 1969; McLachlin 1970) discuss territoriality among males or summer movements of hens and broods. Lumsden (1961), MacDonald (1968), and Hjorth (1970) give excellent descriptions of displays and aggressive behavior between males in the spring. Robinson and Maxwell (1968) summarized some of their results obtained in a continuing study of population processes in Spruce Grouse.

STUDY AREA

The study was conducted on the Kenai Peninsula, Alaska, near the Finger Lakes in the Kenai National Moose Range. The study area lay within a forest some 2000 km^2 in extent, nearly all of which is occupied by Spruce Grouse. In the first 3 years of investigations, the forest on the study area was pristine except for two seismic trails bulldozed across it in search of oil. Most stands of trees were 60–200 years old, the variation being due to past fires. From 1965 through 1968, a 1040-ha study area existed, but in August 1969 a 36,000-ha fire burned across 70% of the study area, requiring a slight alteration of boundaries for subsequent studies. The fire left scattered parcels of forest up to 2 ha in extent on the burned part of the study area. The winter studies were conducted after the fire occurred, on the edge of the burn in a block of about 360 ha that was contiguous on two sides with unburned forest. Nearly all data for spring, summer, and fall were obtained in prefire years.

Most of the topographical features in the lowlands of the Kenai Peninsula are the result of past glaciation. On the study area, crystal clear lakes of 0.5–8-ha surface area are scattered among hills and ridges, usually the remnants of old moraines, rising to no more than 150 m above sea level. Mixed stands of white spruce (*Picea glauca*) and birch (*Betula papyrifera*) typify forests on hills and ridges, with pure stands of dense black spruce (*P. mariana*) being common on level areas. Common understory plants include alder (*Alnus crispa*), bilberry (*Vaccinium uliginosum*), and cranberry (*V. vitis-idaea*).

METHODS

Field work was conducted in the following periods: April through October 1965 and 1966, April through July 1967, and July 1969 through February 1971. Much information can be gained on social groupings from unbanded birds, but the data presented here are also based on 273 birds banded with four colored bands for individual recognition, 46 shot by the investigator in fall and winter, plus 55 instrumented with radio transmitters. Grouse were captured with a 6.5-m noosing pole similar to that described by Zwickel and Bendell (1967). For all banded or telemetered birds, home range sizes were measured after drawing a convex polygon around all plotted locations.

The telemetry equipment was similar to that employed by Marshall and Kupa (1963) on Ruffed Grouse (*Bonasa umbellus*). Telemetered birds were located by proceeding directly to them with a handheld antenna whose maximum range was 1.6 km. After a bird was instrumented, an attempt was usually made to locate it once each day, except that incubating hens were not tracked away from their nests. Table 1 lists by season the number of daily locations made of telemetered grouse. The transmitter, which weighed about 25 g, had no apparent effect on the behavior of adult birds. Four of five hens instrumented in May nested. The fifth hen who did not nest was found upon recapture to have both legs through the harness. Data for this hen were discarded. Two immature birds instrumented at about 8 weeks of age in mid-August appeared to immediately abandon their brood mates, suggesting instrumentation had affected behavior. Data for these two birds were also discarded. Instrumentation of immature birds in September did not obviously affect behavior. But in view of Boag's (1972) findings that instrumentation of immature Red Grouse (*Lagopus lagopus*) depressed food intake and activity of penned birds, the possibility must be acknowledged that data from telemetered birds introduce some bias into the data reported here on Spruce Grouse.

By 3 months of age, male and female Spruce Grouse can be distinguished at a distance, allowing determination of the sex composition of flocks. Juveniles (1–12 months old) can be recognized, at a distance, from older birds into early September. Juveniles captured from September onward were distinguished from older birds by shape and color of the outer two juvenal primaries (Ellison 1968). For the period September through May, I will refer to

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TABLE 1. Number of daily locations made of telemetered grouse each season, exclusive of incubating hens.

Sex and age of birds	Spring	Summer	Fall	Winter
Adult male	118(7)[a]	297(13)	150(3)	143(5)
Adult female	24(1)	156(5)	73(2)	107(3)
Juvenile male	242(10)	—	75(3)	116(4)
Juvenile female	52(4)	—	60(4)	411(10)

[a] Number of individual birds tracked each season.

only two age classes of grouse, juveniles and adults. For summer, unless a distinction is made, adults will include both yearlings (12–24 months old) and older grouse.

The term winter will include the 5 months November through March, or roughly that interval during which snow blankets the forest floor. Spring includes April and May; summer, June through August; and autumn or fall includes September and October.

RESULTS

GENERAL ACCOUNT OF LIFE HISTORY

Winter flocks break up in March, and by late April most males become localized on territories where they perform flutter-jump displays (Lumsden 1961) by settling to the ground on rapidly beating wings. Drumming produced during this display is similar to the drumming of Ruffed Grouse, but the sound does not carry so far. Apparently, all adult and some juvenile males become localized on territories in spring (Ellison 1971). Other juvenile males wander widely in spring and are therefore considered nonterritorial. Breeding is presumably promiscuous with both sexes, and no pair bonds are formed. Most hens apparently nest in the spaces between territories (Ellison 1971). Incubation begins in late May, and most eggs hatch around mid-June. A hen and her brood travel alone most of the time, and males do not assist in rearing broods. Most broods break up in late August and September, but a few lone juveniles may be seen as early as mid-August. In fall, Spruce Grouse are attracted to sources of grit found at the base of uprooted trees, on lakeshores and streambanks, and along graveled roads. Birds appearing on graveled roads become vulnerable to hunters, and probably over 90% of the Spruce Grouse harvested in Alaska are shot along roads. In winter the grouse are arboreal and live on a diet of spruce needles (Ellison 1966). Since grouse density could influence flocking behavior (Koskimies 1957), population densities during the study must be noted. Spring densities were roughly 7–11 birds/km^2. About 80–90% of hens seemed to rear broods, for a production of 3–5 broods/km^2. Broods averaged five to six chicks in early August. Autumn densities were about 20–36 birds/km^2.

TABLE 2. Frequency of single birds and flocks of Spruce Grouse encountered near Finger Lakes, Alaska. Summer data refer only to adult males.

Minimum number of grouse in flock	Spring (721)[a]	Summer (380)	Fall (460)	Winter (126)
1	93%	97%	55%	58%
2	6	3	18	18
3	1	0	9	11
4	0	0	6	5
5	0	0	3	6
6–15	0	0	8	4

[a] Number of grouse encounters made in given season. A single bird or flock was one grouse encounter.

SEASONAL FLOCK SIZE

Following Koskimies (1957) I shall consider two or more grouse to be a flock. Two birds were assumed to be in a flock if found within 18 m of each other, an arbitrarily chosen distance based on visibility in the forest. Since encounters with grouse were often brief, no minimum time was specified that two or more grouse had to remain together to be considered a flock. Flock-size frequencies are summarized by season in table 2. Sightings of hens on nests are excluded, and the data for summer refer only to adult males. Juveniles and hens are included in the fall, winter, and spring data. A potential source of bias in table 2 and several later tables results from an observer not always being able to see all birds in a flock. This bias would be most serious in winter when individuals in a group may be scattered high in the dense crowns of various spruce trees. Observations based on first finding a telemetered bird are not included in table 2 for fall and winter because in these seasons adult males tend to be more solitary than other sex and age classes of grouse. The fall and winter telemetry data could have been included in table 2 only if it had been known that the telemetry sightings reflected the true proportion of adult males in the population. In fall, the frequency distribution of grouse flock size was the same among birds seen on roads (56% of grouse encounters in fall) and in the forest (44% of encounters). Therefore, these two sets of data were combined in table 2.

The percentage of grouse encounters that were with lone birds was 55% in fall and 58% in winter, and the percentage of groups of two was 18% in fall and winter. Gullion (1970) reported that 70% of contacts with Ruffed Grouse in winter were with lone birds and 18% were with two birds. In spring and

summer, over 90% of contacts were with lone birds, a hen with brood being considered alone, indicating the very solitary nature of both cocks and hens in spring and summer. The transition from flocking to solitary behavior occurs sometime in late March or early April.

The mean size of 93 flocks of Spruce Grouse seen in autumn 1969 and 1970 was 3.8 birds. The mean size of 268 winter flocks, 3.0 birds, was significantly smaller ($P < 0.0001$). The larger autumn flock size is partially accounted for by the occurrence into September of hens with intact broods of up to six or seven juveniles. None of the above autumn flocks contained any telemetered birds, but about 80% of winter flocks were found by first locating a telemetered bird. Since there was no significant difference in size of winter flocks with and without a telemetered bird (mean of 2.9 and 3.2 grouse, respectively), the two sources of data were combined. Mean flock size did not vary significantly from month to month over the 5 winter months, the monthly range of means being 2.8–3.2 birds per flock.

The formation of winter flocks in Spruce Grouse was not correlated with unfavorable weather, as it is Red Grouse (Watson and Jenkins 1964), Rock Ptarmigan (*Lagopus mutus*) (Watson 1965), Black Grouse (*Lyrurus tetrix*), and Capercaillie (*Tetrao urogallus*) (Koskimies 1957). Neither do Spruce Grouse form such large flocks as the above species. Most winter flocks of Spruce Grouse are composed of only two to four birds, whereas Capercaillie flocks often contain five to ten birds and Black Grouse and Ptarmigan flocks may number a hundred individuals.

In late fall and winter, daily locations of telemetered grouse revealed that flocks rarely persisted more than 2 or 3 days. Even if flock size was the same on successive days, flock composition often changed. About a fourth of all winter flocks consisted of two birds, one or both telemetered, that separated within 1 day. The most stable group encountered in winter was three females, presumably the same three, who remained together for a maximum of 9 days. I do not think disturbance affected flock stability in winter because telemetered grouse were rarely flushed. Considering the temporary nature of winter flocks, I think they were rarely composed of siblings, as suggested for winter flocks of Black Grouse (Koskimies 1957).

SEX AND AGE COMPOSITION OF FLOCKS

In spring, two females were never found together (150 sightings of hens). Two males were together on 12 occasions, and both males and females were together on 15 occasions (569 sightings of males). In summer, five instances were recorded of two hens together, probably representing two broods, but these combined broods made up fewer than 2% of over 400 brood observations. About 10% of hens encountered in summer were broodless, and all were apparently solitary birds. Among nearly 400 observations made of cocks in summer, two cocks were found together on only eight occasions, seven of these occurring in July or August. No display was noted in any case where two males were together in summer, whereas cocks near broods were often displaying. A cock was found near a brood on nine occasions.

TABLE 3. Number of times birds of known sex and age were found together in winter.[a] Data based on a total of 122 sightings of 13 different adult males, 107 sightings of 14 adult females, 104 sightings of 16 juvenile males, and 313 sightings of 20 juvenile females.

	Ad. ♂	Ad. ♀	Juv. ♂	Juv. ♀
Ad. male	1	—	—	—
Ad. female	7	12	—	—
Juv. male	3	7	2	—
Juv. female	9	30	27	24

[a] For example, adult male(s) were found with juvenile female(s) on nine occasions.

In early fall, hens and juveniles are commonly together because some broods are intact. In fall, adult males continue to remain apart from one another (two adult males were seen together only once in 105 sightings of adult males). Among 86 fall sightings of adult hens, two were known to be together once and another time a flock of three birds shot in mid-October was found to consist of three adult hens. Since the age of a free-ranging grouse in fall and winter could be determined only if the bird was banded or telemetered, these data and the data in table 3 are greatly influenced by the percentage of marked birds in the population at any one time, which was less than 20% in this study during fall and winter. Table 3 summarizes the known associations between sex and age classes in winter. These data suggest, but do not prove, that adult males continue to avoid each other in winter, and that, in winter, hens commonly associate with each other and with juveniles of both sexes.

The percentage of times grouse of various sex and age classes were seen alone each season is given in table 4, except that hens and juveniles are excluded from the summer data. About 75% of this information for seasons except summer comes from telemetered

TABLE 4. Percentage of times grouse of each sex and age class were seen alone at Finger Lakes, Alaska, exclusive of incubating hens, and hens and juveniles in summer.

Sex and age class	Spring	Summer	Fall	Winter
Adult males	(196)[a] 95%	(391) 95%	(106) 74%	(122) 78%
Adult females	(18) 100%	—	(86) 45%	(107) 35%
Juvenile males	(239) 95%	—	(101) 37%	(104) 49%
Juvenile females	(48) 98%	—	(73) 40%	(313) 45%

[a] Total number of birds seen.

TABLE 5. Percentage of monosexual flocks among flocks seen in fall and winter at Finger Lakes, Alaska. All telemetry data excluded. Percentages for monosexual flocks are minimal because it was assumed that all birds in a flock were seen.

Season	No. of flocks	% all-male	% all-female	% mixed sex
Fall	139	14	24	62
Winter	41	7	29	64

birds, but I do not think telemetry introduces any bias here. Adult males showed an increase in association with other grouse from summer to fall (95% alone in summer vs. 74% alone in fall, Chi-square test, $P < 0.05$), and this difference may have been partly due to adult males meeting other birds at communal sources of grit. From fall to winter, adult males continued to associate with other grouse somewhat (78% alone in winter), but not significantly more so than in summer. In fall and winter, adult males were more solitary than the other sex and age classes ($P < 0.01$ for all six Chi-square tests). No significant changes were found in the degree of solitary behavior of any sex and age class from fall to winter.

For fall and winter, the percentage of monosexual flocks was calculated among flocks in which either the sex was known of all birds, or of enough to establish that both sexes were present (table 5). The low percentage of all-male flocks is due primarily to the solitary behavior of adult males, but the possibility of juvenile males avoiding each other is not excluded. The sex ratio of the population could also affect the percentages in table 5. Over five autumns, there was about a 50:50 sex ratio among hunter-shot birds in all years except one, when there were 61 males per 100 females. The winter sex ratio of 63 birds shot or captured at Finger Lakes was nearly 50:50 (30 males, 33 females). The data in tables 3–5 taken together suggest that fall and winter flocks consist primarily of adult hens and juveniles of both sexes.

SEASONAL FREQUENCY OF DISPLAY BY MALES

The seasonal frequency of display by males is outlined in table 6. A male was classed as displaying if he was performing any one or all of the following: strutting, tail flicking, or drumming. A grouse was said to be strutting if the neck and breast feathers were elevated, combs were enlarged, and the tail was spread. Strutting, as defined here, corresponds to the "upright" display of Hjorth (1970). Strutting, the most frequently observed display, may or may not be followed by a tail flick, performed by a rapid opening and closing of the vertically fanned rectrices. Flutter jumping, resulting in drumming, appears to require the highest level of motivation. Strutting and tail flicking were seen in all seasons, but flutter jumping was confined almost entirely to spring. Thus, the data of table 6 are misleading for spring because one encounter with a male giving all three displays in spring is given no more weight than an encounter with a strutting male in other seasons. Displaying declines from a peak in May to an annual low in June, increases slightly in late summer and fall, and continues intermittently through winter. In fall, significantly more adults than juveniles are displaying (Chi-square test, $P < 0.01$), but in winter, there is no difference in the proportion of the two age classes displaying.

No flutter jumping was seen in summer or winter, but in September two marked adult males were seen drumming. One was on his former spring territory. In both instances other birds were nearby, a juvenile male in one case, and a hen with brood in the other case. Of 43 males seen displaying in summer, fall, or winter, 6 were known to be displaying in summer or fall on or near their former spring territories, and the relationship of the other 37 to their territories, if they had one, was not known.

In summer, most displaying seemed to result from an investigator disturbing a hen with brood near a male, with the clucking of the hen and the flight of the young attracting the male. In fall and winter, average size of flocks containing a displaying male was 4.7 and 4.8, respectively. Thus, group stimulation may have played a role in eliciting fall and winter displays. Seven apparently lone males were seen displaying in seasons other than

TABLE 6. Seasonal frequency of display by male Spruce Grouse, Finger Lakes, Alaska. Data combined for juveniles and adults in spring, and for yearlings and adults in summer. Juveniles not considered in summer.

	Spring	Summer	Fall	Winter
Ad. males	—	(380)[a]	(106)	(122)
	—	2%	10%	2%
Juv. males	—	—	(101)	(104)
	—	—	1%	3%
All males	(569)	(380)	(389)	(389)
	21%	2%	7%	3%

[a] Number of males encountered.

spring, and disturbance by the investigator may have stimulated them to display.

Actual combat involving physical contact between males was seen only twice, in October, when two males were seen to rise into the air like sparring roosters. In spring, territorial males seemed to assert their ownership of territories by strutting, tail flicking, drumming, and by occasionally chasing other males in a "head and tail down" posture (Lumsden 1961). This kind of chasing was also seen occasionally in fall and winter when a male would chase another male or female. Once, in the fall, an adult male was chased by a female along a road. Only once was one female seen to act aggressively toward another, in winter when one hen appeared to chase another out of a feeding tree.

SPRING AND SUMMER MOVEMENTS OF HENS

Movements of three telemetered hens in the preincubation period covered 6–21 ha (table 7). The indicated size of these home ranges must be considered minimal because the terminal sightings were still resulting in increases in home-range size. The percentage increase in calculated home-range size due to the terminal five sightings was 22, 14, and 22%, respectively, for bird number 647, 614, and 18. During the egg-laying period, hen number 18 twice traveled 730 m from her nest to a male territory. All three hens were tracked in the same years that intensive efforts were made to locate territorial males, and it appeared that the hens spent 90% or more of their time outside the boundaries of male territories. It should be noted though that half the territorial boundaries were not accurately known because they were defined by fewer than 10 sightings of the territorial male.

An indication of minimal size of brood range is given by movement data from eight hens (table 8). During the entire summer, I would guess most broods utilize an area of about 50 ha. Among the two hens seen seven or

TABLE 7. Minimum home-range size of three telemetered hens in the preincubation period. The nest was included as a point in calculating the home-range size for all three hens, and no tracking was done during incubation.

Band no.	Age	Period tracked	No. of locations	Home-range size in ha
647	Juv.	9 May–1 June	19	13.0
614	Juv.	12–27 May	19	6.5
18	Ad.	8–26 May	18	21.0

eight times from June into September, the last sighting yielded no increase in size of home range for bird number 97, but it gave a 28% increase in home-range size for bird number 42. The brood range of telemetered hen number 614, who was seen 25 times from 20 June to 23 July, was still increasing by 34 and 37% on the last two sightings. But perhaps this hen was emigrating from the study area because, between 11–23 July, this yearling hen moved her brood 3.2 km from the nest site. Another yearling hen who had a brood on the study area in June 1966 was shot on 24 September 1966 8.0 km distant, also suggesting emigration. However, it is possible these two hens were migrating and would have returned to breed again, as did an adult hen who moved her brood 2 km one year but was back the next year in her original location with another brood. Movement data were also obtained on a broodless yearling hen whose nest was destroyed by a predator. During the 45 days after the nest was lost, she moved only 2.8 ha around the nest site (24 locations by telemetry).

As previously noted (Ellison 1971), most hens appear to nest outside of male territories, often in more open forest types than are used by males for territories. During summer, broods wander widely over areas several times

TABLE 8. Minimum size of brood ranges of Spruce Grouse, based on six or more sightings, at Finger Lakes, Alaska. Data from years 1965 to 1969, before fire.

Band no. of hen	Age of hen in summer	Period in which brood was seen	Number of sightings of brood	Size in ha of brood range
18[a]	Ad.	18 June–16 July	14	6.1[b]
1701	Ad.	3 July – 6 Aug.	6	17.9
42	Ad.	23 June–13 Sept.	8	26.4
97	Yr.	17 June– 1 Sept.	7	48.0
96	Yr.	17 June–26 July	6	27.5
679	Yr.	2 July – 5 Sept.	6	46.2
614[a]	Yr.	20 June–23 July	25	155.0[b]
647[a]	Yr.	22 June– 2 July	8	9.7[b]

[a] Telemetered hen.
[b] Nest site included in calculating size of brood range.

TABLE 9. Size of molting ranges of five males and the relationship of the molting ranges to the territory or activity center of the males.

Band no.	Status	Size (ha) of territory or activity center	Date abandoned	Date settled on molting range	Size (ha) of molting range	Distance (m) of molting range from activity center or territory	Dates telemetered
38	T[a]	1.9 (22)[b]	23 June	24 June	3.6 (22)	100	21 Apr.–23 Oct.
49	T	3.2 (12)	16 June	17 June	8.0 (17)	Adjacent	6 May– 8 July
608	T	1.0 (10)	14 June	22 June	4.0 (15)	270	9 May–10 July
609	NT[c]	6.5 (11)	30 May	1 June	6.5 (32)	230	2 May– 6 July
20	NT	2.8 (12)	19 May	13 June	20.0 (21)	200	1 May– 6 July

[a] Territorial.
[b] Number of sightings on which size of territory, activity center, or molting range was based.
[c] Nonterritorial.

larger than the size of spring territories of males. A brood may move across several territories in a few days. Thus, hens do not depend on the resources of a male territory to rear their broods. Brood ranges overlap spatially. Several different broods were often seen in a given summer within the mapped area of a particular brood range. Since two broods were rarely found together in summer, it appeared to me that the hens were avoiding each other temporally.

SPRING AND SUMMER MOVEMENTS OF MALES

Territory size in spring has already been reported for data from the years 1965–67 (Ellison 1971). In that study, nine telemetered males occupied territories of 1.2–8.5 ha in the last week of April and the first 3 weeks of May, these 4 weeks corresponding to the period of intense display. Five juveniles were also tracked that did not occupy territories, but wandered widely instead, sometimes covering 2 km in 1 day. During late April and May, the movements of these nonterritorial males occurred about an "activity center" of 3–7 ha (Ellison 1971), to which they tended to return after an excursion.

In 1966 or 1967, three territorial and two nonterritorial males were radio-tracked into July, by which time they had settled on "molting ranges" some distance from their territory or activity center (table 9). Mid-June to mid-July roughly coincides with the time males are molting their rectrices and inner six or seven primaries. All five males moved to dense cover (black spruce or alder) to molt, a characteristic also noted by McLachlin (1970). In late May and early June, the three territorial males and one nonterritorial male (609) made one to three round-trip excursions of 50–400 m away from their territory or activity center before settling on a molting range. The other nonterritorial male (20) abandoned his activity center in late May, wandered up to 1.6 km from it, then returned by 13 June to occupy a molting range 200 m from his activity center. Territorial male 38, who was tracked the longest, left his molting range and returned to his territory on 23 July, and from then until 23 October wandered over the territory, molting range, and other points within 200 m of them. About half of all locations from 23 July to 23 October fell within the spring territory. Three locations in his molting range fell within a stand of alder used by male 20 for 3–4 days during molting, resulting in a slight overlap of plotted molting ranges, but the two males were never seen together.

FALL MOVEMENTS OF ALL SEX AND AGE CLASSES

In September, broods break up and few chicks hatched on the study area remain there to breed the next spring. Of 74 juveniles (31 males, 43 females) banded in summer and early fall on the study area, only 9% (3 males, 4 females) were there the following spring. Overwinter survival of juveniles probably exceeded 20% (Ellison 1972). Of 148 banded adults (51 males, 97 females) known to be present in spring, summer, or fall, 36% (16 males, 37 females) were found the following spring. Overwinter survival of adults probably did not exceed 50% (Ellison 1972). Thus, adults showed a greater degree of philopatry than did juveniles. Band returns from birds shot by hunters confirmed that juveniles moved farther than adults from the study area. Thirteen birds banded as juveniles had traveled an average airline distance of 3.2 km (range 0.2–10.5 km) from the point of banding to where they were later shot in the fall; 27 birds banded as adults had moved an average of only 0.9 km (range 0.2–8 km) (means significantly different, $P < 0.01$). All but one of the movements of the adults were less than 1.6 km, with a yearling hen making the longest movement of 8 km. These data were

TABLE 10. Size of home ranges of seven telemetered Spruce Grouse in fall, with data on movements from home ranges to roads.

Band no.	Sex and age	Dates telemetered	Number of daily contacts	Area of home range (ha)	Distance from road to nearest part of home range (m)	Number of times seen on road	Maximum distance moved (m)[a]
626	Ad. hen	8 Sept.–23 Oct.	41	18.0 (30.8)[b]	230	1	1200
72	Ad. hen	15 Sept.–23 Oct.	39	105.0 (105.0)	overlapped	2	2300
640	Ad. male	14 Aug.–16 Oct.	48	18.8 (18.8)	50	0	1100
38	Ad. male	24 July –23 Oct.	80	5.7 (23.6)	450	3[c]	600
222	Ad. male	2 Sept.–23 Oct.	50	19.0 (27.0)	50	0[d]	700
634	Juv. male	26 Aug.–10 Oct.	46	72.0 (82.5)	100	3	1100
3	Juv. female	17 Sept.–18 Oct.	28	159.0 (177.0)	50	1[e]	2700

[a] Maximum distance separating plotted points.
[b] Area of home range if points involving movements to roads are included.
[c] Adjacent to road on two other occasions and thus may have visited it.
[d] Known to have crossed road twice.
[e] Known to have crossed road one other time.

from the years 1965–67. Data after the August 1969 fire could not be used because some adults were obviously displaced long distances after the fire. Three of nine birds banded as adults before or after the fire and shot in autumn 1969 or 1970 had moved 5–10 km. Too few returns were obtained for juveniles after the fire to determine if they were similarly affected.

Fall is also characterized by the appearance of grouse at sources of abundant grit, such as graveled roads and lakeshores. Dispersing young grouse probably encounter such sites by accident, but adults appear to make deliberate long-distance trips to these places. Both age classes apparently sometimes linger near sources of grit for several days, perhaps due as much to the social attraction generated by the presence of other grouse as to the availability of grit. The largest numbers of grouse are seen on roads in the first 2 or 3 hr after dawn. An undisturbed flock may stay on a road picking up grit and displaying for as long as 1.5 hr, but most undisturbed flocks or individuals remain only 30–40 min. As soon as snow covers the gravel, grouse cease coming to sources of grit. The urge for grouse to seek grit in the fall is probably related to its use in grinding the fibrous winter diet of spruce needles.

Since nearly all Spruce Grouse shot in Alaska are taken along roads, a knowledge of distances that grouse will move in the fall to reach these sources of grit is essential for evaluating hunting pressure. To date, only sketchy data are available on fall movements in relation to roads, but it is known that some juveniles show up on roads up to 10 km from their brood ranges, and that some adults appear on roads 2 km from their summer ranges. Seven grouse were telemetered in fall 1966 to study movements in relation to roads (table 10). The five adults listed were instrumented within an area of 250 ha, so the movements of all five relative to roads could be monitored simultaneously in the first 2–3 hr after dawn. The two juveniles tracked tended to be located later in the day. Most of the movements of adults to roads in early morning were probably detected, but some trips occurring later in the day were certainly missed. The small sample suggests that some adults living within 500 m of a road make five or more trips to it for grit in autumn. The five adults were still alive at the end of the study, but the two juveniles had settled near a road during their final movements and both were shot on the road. Size of home ranges of the adults, exclusive of trips to roads, varied from 6–105 ha, and those of juveniles from 72–159 ha (table 10). Calculation of the increase in home-range size contributed by each of the last 10 sightings for the data in table 10 suggested that telemetry had nearly defined the maximum home-range size for all birds except male 222 and female 3. For each of these birds, the last sighting yielded a 14–21% increase in home-range size.

WINTER MOVEMENTS

Observations of 38 adults marked in spring or summer and seen again in autumn suggested that adults who remained on the study area spent the autumn on or near their spring and summer ranges, with the exception of excursions for grit. The location of wintering sites of adults relative to their ranges in other seasons is not so well known because the winter studies were conducted after a 2-yr absence from the study area and after the August 1969 fire which burned most of the territories and brood ranges mapped by telemetry before the fire. Thus, when the winter telemetry studies were begun, I was unable

TABLE 11. Minimum home range size of 10 telemetered Spruce Grouse in winter, and percentage increase in home range size with each additional 10 daily sightings.

Sex and age	Juv. ♀ 7	Juv. ♀ 2M	Juv. ♀ 8	Juv. ♀ 4	Juv. ♂ 5	Juv. ♀ 2D[a]	Juv. ♂ 11[a]	Ad. ♂ 1[a]	Ad. ♂ 6[a]	Ad. ♀ 1[a]
Home range size (ha)	86.0	75.3	21.7	41.5	37.6	3.2	112.7	99.8	101.6	39.0
No. of daily locations	95	68	52	50	40	54	48	52	61	47
Dates telemetered	22 Nov–31 Mar	29 Oct–12 Jan	12 Dec–18 Feb	21 Nov–30 Jan	26 Jan–25 Mar	28 Oct–27 Dec	19 Oct–7 Dec	17 Jan–31 Mar	26 Oct–31 Dec	30 Oct–22 Dec
% increase in home range size from observation number 10–20th	123%	216%	117%	53%	198%	8%	430%	450%	5800%	800%
20–30th	28	137	19	230	213	0	17	390	34	3
30–40th	30	34	13	70	0	6	60	69	0	148
40–50th	5	0	1	0	—	16	13	11	21	—
50–60th	0	24	—	—	—	—	—	—	6	—
60–70th	4	—	—	—	—	—	—	—	—	—
70–80th	2	—	—	—	—	—	—	—	—	—
80–90th	2	—	—	—	—	—	—	—	—	—

[a] All or part of home range in burn.

to capture any adults whose spring, summer, or fall ranges had been mapped in detail in former studies. Nevertheless, based on sightings of nine adults banded before winter and seen again in winter, it appeared to me that cocks and hens wintered in the same general area which they had occupied the rest of the year. Also, two adult males who were radio-tracked from winter into spring established their territories within their winter ranges. One male occupied within the burn a winter range of 5.7 ha (29 sightings, 1 March–9 April), and established his territory of 1 ha (11 sightings, 6–16 May) inside the winter range. The other male wintered on 10.5 ha of mostly burned forest from 17 January to 14 February (26 sightings), then moved 1.3 km in 3 days to unburned forest where he took up a new winter range of 16.6 ha (31 sightings, 17 February–9 April). Ninety per cent of his 2-ha territory (11 sightings, 5–21 May) lay within the latter winter range.

During the winter telemetry study, seven juveniles were instrumented between 17 October and 7 November and were tracked for periods of 14–73 days. None of these young birds moved more than 1.3 km from their capture site, suggesting that these juveniles had by early November nearly completed their autumn dispersal and had settled in the general area of their winter range.

In winter, Spruce Grouse are dispersed throughout the forest on overlapping home ranges, and a given bird travels about and feeds in its range either singly or in temporary associations with other grouse. In the winter studies, 17 telemetered grouse were followed for periods of 14–138 days to obtain data on size of home ranges. However, since 40 sightings seemed to be the minimum number required to define home-range size in winter, data are presented on only the 10 birds who were located at least 40 times (table 11). These data suggest that the winter range of some individuals may encompass as much as 100 ha in unburned habitat. The three largest ranges listed in table 11 overlapped into the burn, which probably influenced their size. For example, juvenile male 11 occupied 66 ha within the edge of the burn from 29 October to 22 November, then in 1 day moved 500 m to take up a new range in unburned forest, enlarging his calculated home range to 113 ha. Similarly, adult male 1 moved 1.3 km in 3 days from a 10.5-ha range in the burn (17 January–14 February) to a new range of 17 ha outside the burn (17 February–9 April), making his calculated home-range size 100 ha, but he did not use most of those 100 ha. Adult male 6, who spent most of his time in the burn, did not shift his range, but made one 1.3-km excursion lasting 10 days out from it to unburned forest, which had the effect of enlarging his calculated home range from 12 to 102 ha. Grouse living in unburned forest made similar excursions or shifts in range, but these did not exceed 600 m. It should be noted that the smallest range (3.2 ha) was also in the burn, where a juvenile female remained 60 days in the same 3 ha of unburned trees that adult male 1 abandoned.

DISCUSSION

Territorial males probably make their most extensive movements in the fall when they travel to sources of grit. In this study, adult males also made long movements in winter, but these particular birds were living in

habitat disturbed by fire. On the average, hens may occupy larger annual home ranges than adult males, due to long-distance movements with broods. The size of home ranges on an annual basis, including movements to roads, may be as large as 100 ha for territorial males and 100–150 ha for hens who have nested. In spring, nonterritorial males wander over areas of up to 300 ha, and the time of year these males select a definitive home range or territory is not known. I would guess they have settled in the general area of their future territory by the second autumn of their lives. Neither do I know when those juvenile males who become territorial in their first spring chose the site for their spring territory. Field work was not intensive enough to determine if most juvenile males or juvenile females remain in spring near their winter range. Some juvenile male Ruffed Grouse apparently select territories in autumn (Gullion 1967), and young Red Grouse establish territories in autumn (Jenkins et al. 1963).

The largest flocks of Spruce Grouse of up to 15 birds were seen in early fall before all broods had disbanded. Probably if observations had been made of birds coming to undisturbed sources of grit, such as remote lake shores, larger flocks would have been recorded. I have received reliable reports of flocks of 20–30 birds in such undisturbed places. Flocks tended to be smaller in late fall and winter, and their size and composition was very unstable. Flocks in late fall and winter were believed to be composed mostly of adult hens and juveniles of both sexes. Some fall and winter flocks may have resulted from birds aggregating at sources of grit and preferred feeding trees, as well as accidental encounters elsewhere, but an element of social attraction cannot be ruled out in flock formation. Koskimies (1957) believed that social attraction was a basic property of flock formation in Black Grouse and Capercaillie.

In Spruce Grouse, there was no segregation of the sexes into different winter habitats, such as occurs among Capercaillie (Koskimies 1957) and Alaskan Rock and Willow Ptarmigan (*Lagopus lagopus*) (Weeden 1964). But adult male Spruce Grouse did tend to live alone in winter and during other seasons. In winter, hens and juveniles were sometimes found feeding with adult males, but two adult males were never identified feeding together. No particular hens were associated with the solitary adult males in fall or winter. Pair bonds that persist into spring are formed in autumn or winter in Hazel Grouse (*Tetrastes bonasia*) (Pynnönen 1954), Red Grouse (Jenkins et al. 1963), and Rock Ptarmigan (Watson 1965). Spruce Grouse apparently pair only momentarily, much as in Ruffed Grouse (Brander 1967).

Territoriality is usually defined in terms of defense of an area (Hinde 1956; Brown 1969), but Pitelka (1959) stresses exclusive use and the resulting ecological implications, such as partitioning of habitat. In spring, some male grouse can be said to be territorial because they are localized on sites they tend to use exclusively and apparently defend against other males. I did not observe territorial males attack intruding males in spring, but they did attack male study skins and attempted copulating with female skins. The strutting and drumming displays of territorial males seemed sufficient to drive away live intruders. Whether or not males are territorial during molting in June and early July is more difficult to define. Males are not displaying, so the criterion of defense cannot be applied. But males remain apart and are localized on molting ranges. In fact, even the formerly wandering nonterritorial males become localized and are no longer crossing territories or wandering over communal areas between territories. Thus, in terms of exclusive use, without any criterion of defense, males could be said to be more territorial during molting than during the breeding season. Rather than argue about whether males are territorial during molting, perhaps it is more important to simply note that the vulnerable molting birds are dispersed, they occupy dense cover, and they remain inconspicuous by refraining from displaying.

In late summer, fall, and winter, adult males displayed and seemed to remain apart from each other, but in fall and winter adult males sometimes associated with juvenile males. In summer and fall, some displaying was known to occur on or near the spring territory of the male involved, suggesting defense of it. Thus, it might be concluded that adult males, and perhaps some juvenile males seen displaying, showed signs of weak territoriality during August through March. But it must be noted that the entire extent of the large home ranges occupied in this period was not used exclusively relative to other males, and their entire extent could not conceivably be defended. The display activity and aggression shown in fall and winter by male Spruce Grouse is not so intense as that among Hazel Grouse (Pynnönen 1954), Red Grouse (Jenkins et al. 1963), and Rock Ptarmigan (Watson 1965), all of which are strongly territorial in winter. McLachlin (1970) reported Spruce Grouse defended ter-

ritories in all months of his study (May through September), though not so vigorously outside the breeding season. Robinson and Maxwell (1968) reported that male Spruce Grouse display in late summer and winter.

By the criterion of exclusive use, hen Spruce Grouse are not territorial in summer, fall, or winter. In summer, brood ranges are extensive and overlap. In fall and winter, ranges of adult hens overlap and adult hens are sometimes found together. The extent to which ranges are exclusively used in spring is not clear, but hens of all ages do remain apart from each other during April through the nesting season. Stirling (1968) has shown that Blue Grouse (*Dendragapus obscurus*) hens exhibit aggressive behavior from a few days before egg laying until the beginning of incubation, and he speculated that this behavior might space the nesting hens. MacDonald (1970) states that female Spruce Grouse attack other hens entering their home ranges during the period of egg laying. Thus, it is possible that hens defend and exclusively use territories in spring.

Lance (1970) has suggested that the number of Blue Grouse in spring breeding populations is determined by events occurring prior to the establishment of territories on the breeding grounds. A similar situation may exist in Spruce Grouse, with aggressive behavior or territoriality in spring merely spacing those birds present on the breeding range. Territoriality among male Spruce Grouse probably does not regulate numbers of males in the spring population because nonterritorial males apparently do not suffer higher mortality rates than territorial males, and territories occupy only a small fraction of habitat suitable for territories. Neither would territoriality among polygamous males seem capable of limiting mating success among hens in a population containing at least one territorial male for every two hens.

Hens are not dependent on the resources of a particular male territory at any time of year, nor are hens excluded from resources by territorial males at any time except perhaps during the preincubation period in spring. Thus, except for spring, territoriality among males would not determine any minimum or maximum number of hens surviving. During spring, no nonbreeding hens were evident, so I presume that, at the densities under study, territorial males were not limiting the amount of habitat available to hens during the preincubation period. The spacing of nests and broods did not appear to be population-regulating mechanisms either because in five summers of study more than 90% of hens nested and over 80% reared broods (Ellison 1972). Since I can detect no obvious means of population regulation in Spruce Grouse, I suggest that some subtle behavioral mechanism may be operating in late winter or early in the breeding season to determine the number of both males and females remaining on the study area during the breeding season. Emigration from breeding ranges in late winter has been reported in Red Grouse (Jenkins et al. 1963) and Rock Ptarmigan (Watson 1965). The studies of Bendell et al. (1972) and Zwickel (1972) also suggest that the spring breeding density of Blue Grouse is determined by behavioral interactions occurring before the breeding season. What might determine the size of the late-winter surplus in Spruce Grouse is not known.

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