

TERRITORIALITY IN ALASKAN SPRUCE GROUSE

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TERRITORIALITY among male Spruce Grouse (*Canachites canadensis*) was studied during three breeding seasons in south-central Alaska as part of an investigation of the species' population ecology. Almost no published data exist on territoriality in Spruce Grouse. MacDonald (1968) refers to a study by Stoneberg (1967) who obtained evidence from five banded males that suggested they were territorial in spring.

STUDY AREA

The study area was located on the Kenai National Moose Range, Kenai Peninsula, Alaska, within the forested lowlands where glaciation was important in shaping current topography. Lakes from 1 to 25 acres in surface area cover about 10 per cent of the region. Relief ranges from 100 to 350 feet above sea level. The low rounded hills support open stands of white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), and occasionally aspen (*Populus tremuloides*) or poplar (*P. balsamifera*), all attaining heights of 100 feet. Characteristic understory plants on these hills are menziesia (*Menziesia ferruginea*), devil's club (*Echinopanax horridum*), mountain alder (*Alnus crispa*), and bluejoint grass (*Calamagrostis canadensis*). The slopes of hills grade into two general vegetation types, one being tall open stands of white spruce and birch with understories of grass, spiraea (*Spiraea beauverdiana*), blueberry (*Vaccinium uliginosum*), and lingonberry (*V. vitis idaea*), where broods and nests are commonly found (Figure 1A). Slopes also give way to moderately dense stands of mixed birch, white spruce, and black spruce (*P. mariana*) to 70 feet tall with understories of blueberry, lingonberry, and lichens growing in moss (*Sphagnum* spp.) (Figure 1B). Territories are usually associated with these moderately dense spruce stands. Around some lakes and bogs are dense stands of black spruce to 50 feet tall with a ground cover of mostly lichens and mosses where grouse are occasionally found.

METHODS

Mid-April to late October was spent in the field each year from 1965 to 1967 and the winter of 1969-70 was also spent on the study area. Dogs were helpful for locating grouse, even when snow was on the ground and the birds were arboreal. Most males were captured with a noosing pole similar to that used by Zwickel and Bendell (1967), but a few males too wild to noose were taken with an automatic bow-net trap (Tordoff, 1954) baited with a study skin of a female grouse. Males were aged by shape and color of the outer primaries (Ellison, 1968).



Figure 1. A, tall open white spruce and birch habitat commonly used by Spruce Grouse hens for nesting and rearing broods, and occupied by both sexes in winter. B, moderately dense stand of mixed black spruce and white spruce where cocks establish territories, hens sometimes nest, broods occur frequently, and where both sexes may be found in winter. (Photographs by Jerold Deppa.)

Radio-tracking equipment was similar to that used by Marshall et al. (1963) on studies of Ruffed Grouse (*Bonasa umbellus*). Range of reception of the 150-mc signal in Alaskan forests was $\frac{1}{4}$ to 2 miles, depending on topography, vegetation, weather, and size of receiving antenna. Usual range of a small hand-held antenna was $\frac{3}{4}$ mile. A single RM 401 mercury cell could be depended on to operate a transmitter for 60 to 80 days, though some cells functioned for 120 days. Each instrumented grouse was located by proceeding directly to the bird with a portable receiver. Locations were recorded by pacing to landmarks or to parallel lines marked out at 200-yard intervals over the study area. Though sometimes several fixes were made daily for each bird, the summaries in this paper represent only one fix per day, usually made in early morning. Areas of territories and home ranges were measured with a polar planimeter after drawing a convex polygon around the outer plotted locations.

DISPLAYS OF THE MALE SPRUCE GROUSE

The displays of males in Canada in the breeding season have been accurately described by Lumsden (1961) and MacDonald (1968), and the displays of Alaskan Spruce Grouse are essentially the same. Alaskan males commonly give three displays in spring. Strutting and the associated tail flicking are performed on the ground or in a tree, and may be given in the presence of another male, a female, or as a result of disturbance. Flutter jumping which, as Lumsden suggests, may be a form of territory advertisement, is usually performed as the male flies down from a tree to the ground. At a height of 6 to 8 feet above the ground, the male checks his flight and settles to the ground on "rapidly beating wings" producing a soft drumming audible up to 200 yards. I noted none of the soft hooting or loud wing clapping that MacDonald (1968) reports for *C. c. franklinii*.

Strutting and tail flicking occur in autumn and winter, though not with the frequency recorded in April and May. Flutter jump displays are occasionally seen in September and October. Fighting among males is more common among flocks in autumn than in spring, but it is not known if this means Spruce Grouse establish territories in fall, as demonstrated for Red Grouse (*Lagopus lagopus scoticus*) by Jenkins et al. (1963). Gullion (1967) indicates that some juvenile Ruffed Grouse established drumming logs in autumn.

SPRING MOVEMENTS OF MALES

To study movements during the breeding season 14 males were instrumented with radio transmitters in late April or early May. The period of territoriality among Spruce Grouse is arbitrarily designated as late April and the first 3 weeks of May, or that interval from the time males become localized and begin displaying (strutting, tail flicking, drumming) to the time displaying, but not necessarily localization, ends. End of the

TABLE 1
 SIZE OF TERRITORIES AND SIZE OF HOME RANGE AFTER PERIOD OF TERRITORIALITY AMONG NINE MALE SPRUCE GROUSE.

Band No.	Age	Area of territory (acres)	Period tracked for territory data	Area of home range after May 21 (acres)	Period tracked for home range data
38	Adult	4.6	21 April-21 May	29.6	21 May-22 July
38	Adult	4.6	19 April-21 May	—	—
93	Adult	6.2	3 May-21 May	18.5	21 May-18 June
92	Adult	8.9	1 May-21 May	4.5	21 May- 6 June
49	Adult	8.0	6 May-21 May	28.0	21 May- 8 July
78	Juvenile	20.6	30 April-21 May	31.4	21 May- 9 June
95	Juvenile	5.8	9 May-21 May	8.9	21 May-28 June
608	Juvenile	2.5	9 May-21 May	61.0	21 May-10 July
610	Juvenile	12.0	21 April-21 May	52.0	21 May-29 June

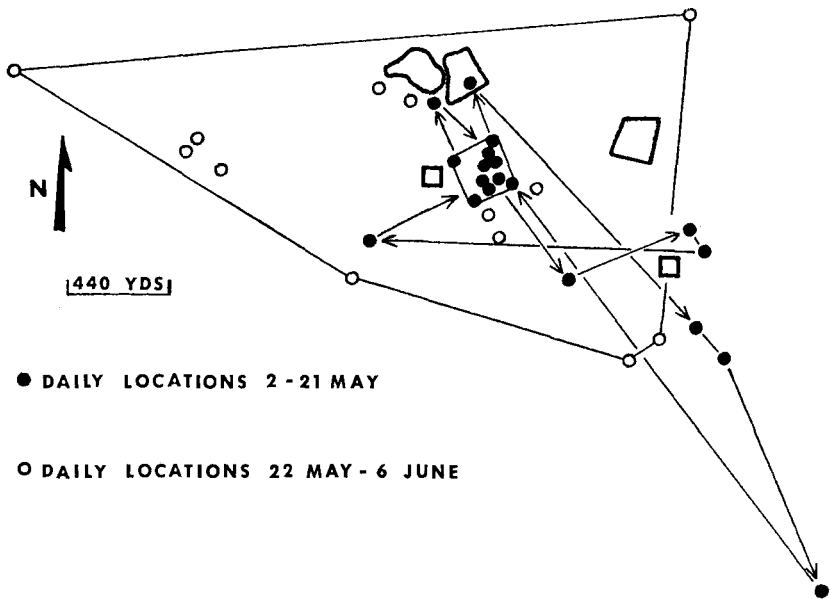


Figure 2. Movements of juvenile male 99 in relation to his activity center and territories of other males (heavy outlines). The bird made three lengthy excursions lasting 1 to 4 days off the activity center between 2 and 21 May before abandoning the center in late May.

display period coincides with the start of incubation by hens. My criteria for defining a territory were localization and "exclusive use" (Pitelka, 1959) without regard to whether or not the site was defended against other males. All adult males became territorial in spring but only a few of the juveniles did so. Classification of a male as territorial was arbitrary in some instances, but in general those birds termed territorial were localized on 3 to 21 acres of forest during late April and the first 3 weeks of May (Table 1). On three occasions males termed territorial were found off their territory. Maximum distance of these movements was 250 yards. In two of the instances the males had followed a hen, and in the third case the male had apparently pursued a wandering male that had invaded the territory. No correlation exists between size of territory and age of male. Bendell and Elliott (1967) found no correlation between age and territory size in Blue Grouse (*Dendragapus obscurus*).

The juvenile males classed as nonterritorial occupied "activity centers" 10 to 16 acres in size during late April and the first 3 weeks of May. In contrast to territorial males they often made lengthy excursions, by

TABLE 2
 SIZE OF ACTIVITY CENTERS OCCUPIED BY FIVE NONTERRITORIAL MALES DURING EARLY MAY, NUMBER AND EXTENT OF EXCURSIONS OFF THE ACTIVITY CENTER, AND SIZE OF HOME RANGE AFTER 21 MAY.

Band No.	Age	Area of activity center (acres)	Period tracked for activity center data	Extreme radius of each excursion off activity center (yards) ¹	Days off activity center during each excursion	Area of home range after 21 May (acres)	Period tracked for home range data
99	Juvenile	10.4	2-21 May	420	1	856	21 May-6 June
				1260	4		
				2200	4		
20	Juvenile	7.0	1-21 May	620	1	541	21 May-6 July
				950	2		
				950	3		
				970	2		
100	Juvenile	10.1	2-21 May	None ²	—	270	21 May-13 June
609	Juvenile	16.0	2-21 May	1050	5	42	21 May-6 July
700	Juvenile	9.6	9 May-6 June ³	550	2	—	—
				570	5		
				460	1		

¹ Measured from geometric center (Hayne, 1949) of the activity center.

² The apparent activity center included a portion of the territory of an adult male, and the juvenile was found on the territory on 6 different days.

³ Data into June used because radio tracking of bird began late in breeding season and daily locations were clustered, except for obvious excursions, until 6 June, when radio quit.

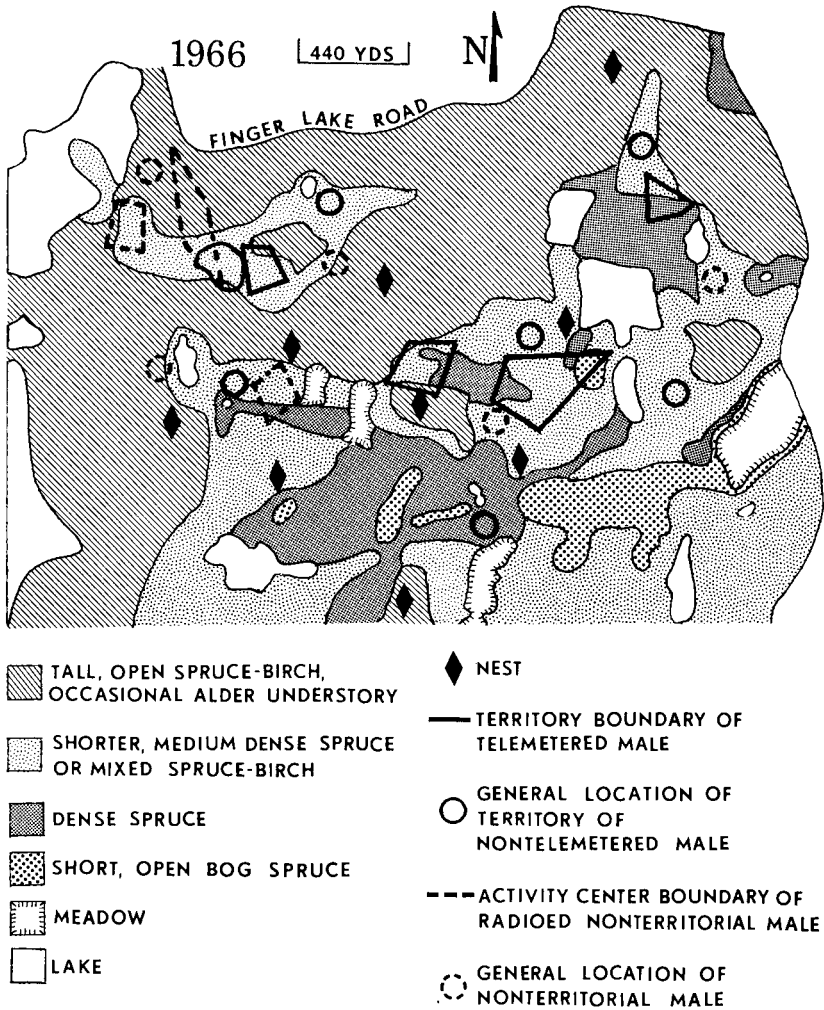


Figure 3. Two-square-mile study area searched in spring for male Spruce Grouse and nests in 1966. Boundaries of territories and activity centers determined by radio-telemetry.

short successive flights, of up to 1.25 miles from their activity centers (Table 2 and Figure 2). During these excursions the males were often found in the vicinity of other males. In 8 of 11 excursions they were at some time found on known territories or in the presence of another male, not always known to be territorial. Either or both males might be strutting, drumming, or inactive. Drumming was done by nonterritorial

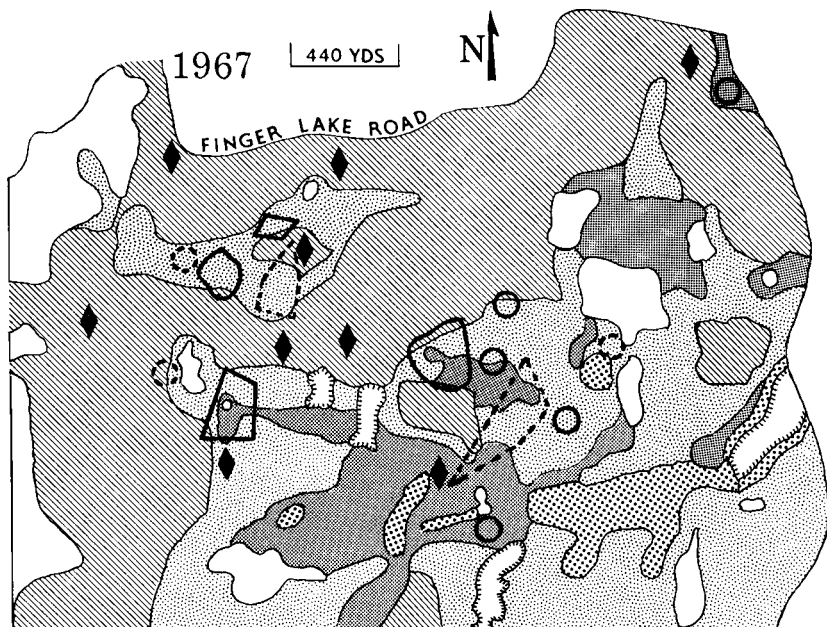


Figure 4. Study area in 1967. Symbols as in Figure 3.

males on and off their activity centers. One morning a wandering juvenile invaded an adult's territory and both males drummed on it for nearly an hour before the juvenile left, with no physical encounters occurring. Drumming by any male is known to stimulate territorial males to drum, and drumming probably also attracts wandering males to territories. Another possible characteristic of nonterritorial males was that they tended to wander quite widely in late May and early June, after abandoning their activity center and before settling on a molting range. Maximum size of the home ranges of eight territorial males in this period was less than 60 acres, whereas three of five nonterritorial males wandered over areas several hundred acres in extent (Tables 1 and 2).

As noted, classification of males as territorial was in some cases arbitrary. Juvenile male 78 was classified as territorial but had a relatively large territory (20.6 acres) and was found drumming only once. He was termed territorial because he made no long-distance excursions and he visited no other males. He possibly expanded his territory in early May when another territorial male adjacent to him was known to have been killed. Male 100 was classed as nonterritorial but made no excursions off his activity center. He was termed nonterritorial because his activity

center included a portion of the area occupied by a highly localized male who drummed nearly every morning. Male 100 was known to drum only once. In reality a continuum of behavioral types of males probably exists, and further study would lead to recognition of several categories similar to the "satellite" and "alternate" drummers Gullion (1967) discusses among Ruffed Grouse males. In any case, the presence of nonterritorial male Spruce Grouse in the spring population appears to resemble the situation in Ruffed Grouse (Marshall, 1965; Gullion, 1967), Red Grouse (Jenkins et al., 1963), and Blue Grouse (Bendell and Elliott, 1967).

PATTERN OF TERRITORIALITY AND HABITATS USED

The relative positions of territories, activity centers, and nests located in 1966 and 1967 are shown in Figures 3 and 4. The nine nests found each year were fewer than half those actually present. No nests were found on territories. Nests tended to be in the open spruce birch forest type whereas territories and activity centers were usually established in moderately dense spruce or spruce birch. A few territories were found in very dense lowland spruce. Males may prefer to display among the dense trees where they are safer from their principal predator, the Goshawk (*Accipiter gentilis*). A nesting hen is less conspicuous than a drumming male, so hens can nest in more open vegetation types that still have enough ground cover to conceal them on the nest. Sometimes nests are built in dry grass remaining from the previous growing season, and grass is rarely found in dense spruce stands. Nonterritorial males also often used the open spruce birch type during their excursions off activity centers.

Of five males tracked through the first week of July, all had by that time moved off their territory (3 males) or activity center (2 males) and had become localized on molting ranges 50 to 300 yards distant. Two moved into dense black spruce and three into open spruce birch with a partial alder understory. Molting males, who have difficulty flying, may seek alder for its cover value. Casual observations of marked birds indicated males were in the same general area in autumn and winter as in spring and summer. Three males occupied the same territory in successive years, and one moved his territory. Activity centers of one year did not become territories the next year.

DISPLAY ACTIVITY AND TERRITORY SIZE

Though wandering males perform all the displays of territorial males, it was obvious that birds with territories displayed more frequently. Among territorial males, birds displaying the most and considered to be

TABLE 3
DRUMMING RATES¹ AND TERRITORY SIZE FOR FOUR TELEMETERED TERRITORIAL MALE
SPRUCE GROUSE, 1967.

Band No.	Age	Number of 3-hour periods monitored	Number of 3-hour periods drumming occurred	Number of flights per hour ²	Size of territory (acres)
38	Adult	10	9	21	4.6
608	Juvenile	4	2	9	2.5
49	Adult	4	1	5	8.0
619	Juvenile	8	6	5	12.0

¹ Drumming data collected during 3-hour period at dawn.

² Mornings on which no drumming occurred not used in calculating average.

dominant were the most localized (Table 3). Watson (1964) found that among Red Grouse the dominant, more aggressive males had the largest territories. Similarly Robel (1966) reported that male Prairie Chickens (*Tympanuchus cupido*) performing the most copulations had the largest territories. Among Spruce Grouse males with small territories may perform most of the copulations, but data are lacking on this point. In all 3 years of the study a 4.6-acre territory was occupied by an adult, the same male (38) in 2 years, who drummed frequently. Each year this territory was the center of movements of several males. Juvenile males established one or two territories or activity centers near it, wandering males frequented it, and in early morning darkness hens could be heard calling nearby. Probably both the intense activity of the territorial male and the nature of the surrounding habitat attracted other birds to the general area. Gullion (1967) noted that in Ruffed Grouse hyperactive adults attracted other males to settle near them.

DENSITY AND AGE COMPOSITION OF MALES

The study area was censused for males during late April and May by searching the entire area systematically with the aid of a dog and by making repeated visits to habitats known to be preferred by males. The number of males found in 1965-67 was 19, 19, and 14. In the latter 2 years the territorial status and age of nearly all males were determined (Table 4). Each spring the population was composed of about 1/3 adults and 2/3 juveniles, with all adults and 30-50 per cent of the juveniles being territorial.

In 1966 and 1967 the accuracy of a once-over systematic census made between 9-26 May was checked by determining the proportion of birds found that were known by prior work to be present. For the 2 years together, 27 males had been found before the systematic census, and

TABLE 4
TERRITORIAL STATUS AND AGE OF MALE SPRUCE GROUSE ON 2-SQUARE-MILE PLOT,
KENAI PENINSULA, ALASKA, 1966 AND 1967.

Year	Total number of males	Number of territorial males	Age of territorial males	Number of nonterritorial males	Age of nonterritorial males
1966	19	11	5 adults 4 juvenile 2 unknown	8	7 juvenile 1 unknown
1967	14	9	4 adults 4 juvenile 1 unknown	5	5 juvenile

during the census 8 of these individuals were missed, including 2 territorial and 6 nonterritorial males. Thus repeated coverage probably revealed all territorial males but only roughly indicated the number of nonterritorial males with activity centers on the plot. Although nonterritorial males are harder to find, the count of them was biased upward by assuming that all wandering males encountered had activity centers on the plot. The accuracy of the final estimate of the proportion of nonterritorial males in the spring population is not known.

DISCUSSION

The general territoriality pattern in Spruce Grouse is occupancy of rather large, often widely spaced individual sites. Display grounds are not communal, though there is some suggestion that especially active adult males may attract other males, particularly juveniles, to settle near their territories, resulting in some grouping of displaying birds. Gullion (1967) speculated that a similar pattern in Ruffed Grouse might indicate males of that species "prefer to use a communal display ground." Possibly the same could be said of Spruce Grouse. Such groups might increase the probability of a female finding a male's territory, and once on a territory the female could be courted without transgression or interference by other males. Thus the function of territoriality in Spruce Grouse may be to increase mating success, a function Lack (1966) ascribes to most avian territorial systems.

Details of the mating habits of Spruce Grouse are not known, but presumably both sexes are promiscuous. There is no prolonged pair bond. The female comes to the territory only for mating. The female does not nest, feed, or rear her brood on a male's territory. Thus if a male will breed with more than one female and the female is not dependent on a

male territory for food or cover, then territoriality among males in spring cannot be a population regulating mechanism. A similar conclusion was reached for Blue Grouse by Boag (1966) and by Bendell and Elliott (1967). The only exceptions would be if breeding males were so few that females had difficulty finding them, or if females competed for a limited number of breeding males.

It is unlikely that territoriality in spring regulates the number of Spruce Grouse males in a population. Nothing suggested that wandering juveniles without territories suffered any higher mortality in spring and early summer than territory holders. Thus having a territory did not seem to confer any survival advantage, as it does among Red Grouse (Jenkins et al., 1963). Red Grouse establish territories in autumn and nonterritorial birds suffer considerable mortality before spring.

Whether territoriality among Spruce Grouse males regulates the number of them breeding is unknown. No experiments were done to determine if a wandering juvenile could breed or hold a territory should the death of a territory holder create a vacancy. All adult males held territories, and nothing suggested the presence of any surplus adult males. I do not understand why any juveniles should wander, as large areas of apparently suitable habitat seemed to be unoccupied. Possibly the function of wandering juveniles is to occupy territories of males that die, thus insuring mating success.

ACKNOWLEDGMENTS

This paper is a contribution from the Federal Aid in Wildlife Restoration Program, Alaska Projects W-6-R and W-13-R. Kenai National Moose Range personnel, particularly Will Troyer, provided help and facilities to set up the field station. Robert Weeden, Alaska Department of Fish and Game, contributed many ideas essential to planning the study. Fish and Game employees assisting in field work were Gregory Bos, Jerold Deppa, Keith Koontz, and Robert LeResche.

SUMMARY

Studies of territoriality among male Spruce Grouse were made on the Kenai Peninsula, south-central Alaska, from 1965 to 1967. Data on movements and behavior were obtained during the breeding season by instrumenting 14 males with radio transmitters. During late April and the first 3 weeks of May, all adult males were localized on parcels of forest 5 to 9 acres in size. Some juvenile males (presumed to be territorial) remained on plots 3 to 21 acres in extent during the breeding season, but other juveniles were not localized and wandered extensively about an activity center, sometimes ranging out a mile from the activity center within a 24-hour period. During these excursions, the wandering

juveniles were often found drumming with other males. Presumed activity centers of juvenile males ranged in size from 7 to 16 acres.

Censuses on a 2-square-mile plot during the period males were localized in late April and May suggested a density of 10 males per square mile in 1965 and 1966, and 7 per square mile in 1967.

Territoriality among males in spring is probably not a population regulating mechanism. Territories apparently serve only as mating sites and hens do not nest, feed, or rear their broods on male territories.

LITERATURE CITED

- BENDELL, J. F., AND P. W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Canadian Wildl. Serv. Rept. Ser. No. 4: 1-76.
- BOAG, D. A. 1966. Population attributes of Blue Grouse in southwestern Alberta. Canadian J. Zool., 44: 799-814.
- ELLISON, L. N. 1968. Sexing and aging Alaskan Spruce Grouse by plumage. J. Wildl. Mgmt., 32: 12-16.
- GULLION, G. W. 1967. Selection and use of drumming sites by male Ruffed Grouse. Auk, 84: 87-112.
- HAYNE, D. W. 1949. Calculation of size of home range. J. Mammal., 30: 1-18.
- JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. J. Anim. Ecol., 32: 317-76.
- LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.
- LUMSDEN, H. G. 1961. Displays of the Spruce Grouse. Canadian Field-Naturalist, 75: 152-160.
- MACDONALD, S. D. 1968. The courtship and territorial behavior of Franklin's race of the Spruce Grouse. Living Bird, 7: 5-25.
- MARSHALL, W. H. 1965. Ruffed Grouse behavior. Bioscience, 15: 92-94.
- MARSHALL, W. H., R. B. BRANDER, G. W. GULLION, P. SCHLADWEILER, J. G. TILTON, AND J. R. MARCH. 1963. Studies of movements, behavior, and activities of Ruffed Grouse using radio telemetry techniques. Minneapolis, Minnesota, Univ. of Minnesota (30 pp., multilithed).
- PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor, 61: 233-264.
- ROBEL, R. J. 1966. Booming territory size and mating success of the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*). Anim. Behav., 14: 328-331.
- STONEBERG, R. P. 1967. A preliminary study of the breeding biology of the Spruce Grouse in northwestern Montana. Unpublished M. S. thesis, Missoula, Univ. Montana.
- TORDOFF, H. B. 1954. An automatic live-trap for raptorial birds. J. Wildl. Mgmt., 18: 281-284.
- WATSON, A. 1964. Aggression and population regulation in Red Grouse. Nature, 202: 506-507.
- ZWICKEL, F. C., AND J. F. BENDELL. 1967. A snare for capturing Blue Grouse. J. Wildl. Mgmt., 31: 202-204.

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