

## FURTHER OBSERVATIONS ON THE BREEDING BEHAVIOR OF A BLUE GROUSE POPULATION IN MONTANA

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This paper presents observations made in 1958 and 1959 on the behavior of a forest-dwelling population of Blue Grouse (*Dendragapus obscurus richardsonii*) in north-western Montana. (See Blackford, 1958, for earlier observations.) New information was gathered on the following aspects of courtship and breeding biology: conduct of the sexes during the vernal altitudinal migration, arboreal hooting and display, wing notes and flight signals, pair formation, association of mated birds, and communal display.

### AREA AND STUDY PERIOD

The study area, a forested ravine on the south front of the Purcell Range in central Lincoln County, Montana, has been described previously (Blackford, 1958). Twenty-nine trips were made to this locality in the spring of 1958, starting on March 16, at which time no grouse or signs of them were seen. On 27 of the 28 subsequent trips to the ravine, from March 24 through June 21, during the period of arrival and active breeding, male Blue Grouse were located within boundaries that closely approximated the limits of two territories mapped in 1957. On six of these visits both resident males were located on their exclusive breeding territories. These two males were observed for a total of 118 hours and 57 minutes or 65 per cent of the 182 hours and 59 minutes which I spent on their territories. Other males were under observation on the area, during group display or migration, for 1 hour and 25 minutes. Females were observed on or adjacent to territories of males for 14 hours and 19 minutes.

In 1959, ten additional trips were made to the study site, from April 3 through May 19. Although the purpose of these visits was investigation of group display, male Blue Grouse, either territorial or apparently so, were located on each occasion. They were observed for 31 hours and 42 minutes; attendant females were observed for 7 hours and 23 minutes. In April a transient company of both sexes was studied for a total of 1 hour and 47 minutes. Throughout the seasons of 1958 and 1959, the presence of females, and their proximity to territorial males, was frequently indicated over much longer periods than they were seen.

### IDENTITY AND TERRITORIAL OCCUPANCY

*The population in 1958.*—In contrast to 1957, when three breeding males occupied the ravine, only two held territories there in 1958. However, at least two drumming and courting males were resident atop the long, sloping ridge that flanks the depression on the east. In the ravine, territories 2 and 3 were utilized in 1958. Their owners maintained boundaries similar to those of the preceding year, except that after the belated occupancy of plot 3, the male on territory 2 promptly extended his activities down ravine to within a more communicable distance. Boundaries have accordingly been redrawn to correspond with activities of the occupants in 1958 (fig. 1).

Bendell (1955:368-369) has shown that on Vancouver Island, British Columbia, males representative of the Pacific coastal races or *fuliginosus* group of the species are not only territorial but return to the same territories year after year. Evidence from the present study indicates that inland races in the Rocky Mountain region and Great Basin of the *obscurus* group do not differ in this respect. Judging by numerous traits of the individual birds, however, no residents of the population in 1957 returned to the

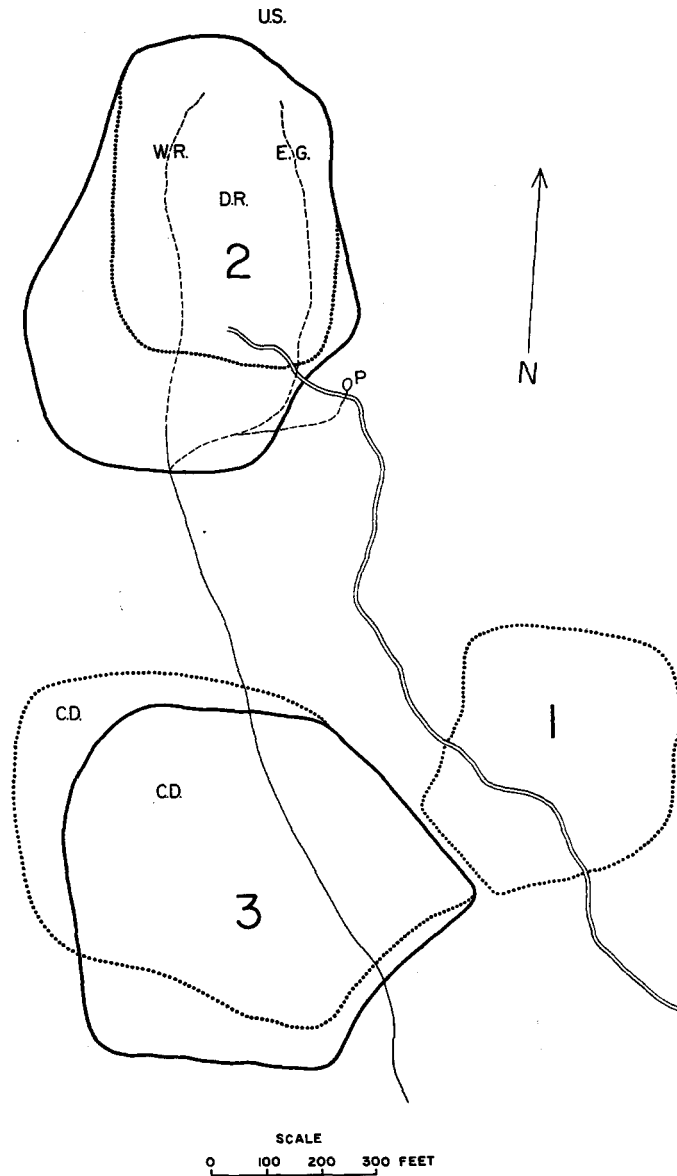


Fig. 1. Diagram showing outlines of breeding season territories (1, 2, 3) of male Blue Grouse in 1957 (dotted lines) and 1958 (solid lines), south front of Purcell Range, Lincoln County, Montana. Double line shows trail; narrow line, streamlet; P, pool; W. R., west ravine; E. G., east gully; D. R., dividing ridge; U. S., upper swale; C. D., communal display areas in 1957.

study area the following year. Either the previous occupants were casualties in the interval, or, as may be true also of the race *fuliginosus*, occasional shifting to nearby territories takes place.

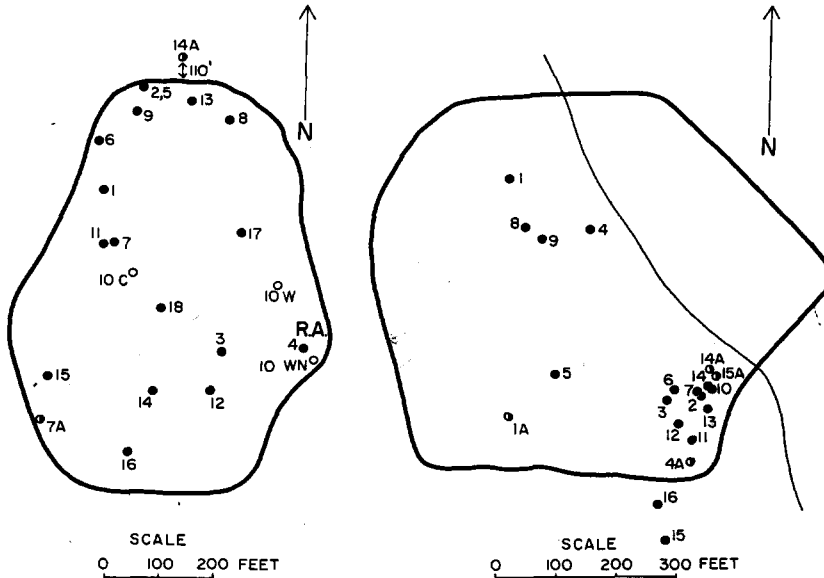


Fig. 2. Left, location sites of Male D on territory 2 in 1958; solid dots, locations where first seen; half dots, second location on same date; open circles, auditory locations; R. A., roost area. 1, Mar. 24, 1:46 p.m.; 2, Mar. 26, 1:06 p.m.; 3, Mar. 29, 3:52 p.m.; 4, Apr. 2, 10:52 a.m.; 5, Apr. 5, 11:46 p.m.; 6, Apr. 9, 12:22 p.m.; 7, Apr. 11, 11:50 a.m.; 7 A, Apr. 11, 5:25 p.m.; 8, Apr. 14, 9:10 a.m.; 9, Apr. 18, 1:26 p.m.; 10 C, Apr. 21, 5:28 p.m. (courting calls); 10 W, Apr. 21, 6:46 p.m. (wing note); 10 WN, Apr. 21, 7:16 p.m. (wing note); 11, Apr. 27, 11:09 a.m.; 12, Apr. 30, 8:01 a.m.; 13, May 3, 7:44 a.m.; 14, May 4, 7:40 a.m.; 14 A, May 4, 7:55 p.m. (during communal display); 15, May 7, 1:16 p.m.; 16, May 14, 7:23 a.m.; 17, May 17, 6:58 a.m.; 18, May 25, 7:20 a.m.

Right, location sites of Male E on territory 3 in 1958. 1, Apr. 30, 9:39 a.m.; 1 A, Apr. 30, 1:51 p.m.; 2, May 3, 9:58 a.m.; 3, May 4, 10:17 a.m.; 4, May 7, 4:19 p.m.; 4 A, May 7, 8:07 p.m.; 5, May 11, 11:04 a.m.; 6, May 14, 9:14 a.m.; 7, May 17, 11:39 a.m.; 8, May 19, 8:03 a.m.; 9, May 21, 5:52 p.m.; 10, May 22, 4:00 p.m.; 11, May 30, 3:51 p.m.; 12, June 1, 3:53 p.m.; 13, June 5, 2:31 p.m.; 14, June 14, 9:51 a.m.; 14 A, June 14, 11:47 a.m.; 15, June 16, 7:56 a.m.; 15 A, June 16, 2:57 p.m.; 16, June 21, 7:03 a.m.

The first male found in 1958 was located in an evergreen clump on March 24 on the northwest border of territory 2 (fig. 2). In nearly three hours of observation that followed, it was apparent that a compact band of two males and two females had recently arrived on, or were moving down into, the ravine breeding area. Apparently they were participants in the springtime, altitudinal migration of the species from higher forested summits to middle and lower levels of the mountain range. Male and female "pairs" appeared closely associated, males flying after the female, and vice versa. Males also followed females among the branches, and each "pair" rested together. There was no tendency either for the group to disperse or to leave the site where located.

Both males were in perfect and identical plumage. No certain identification could be made of either female. Whether this group remained as the ravine population during 1958 is not known, although four birds later constituted the resident population. In appearance, the two territorial males closely resembled these first arrivals; but the latter had not been seen in display, and no definite identification marks were established.

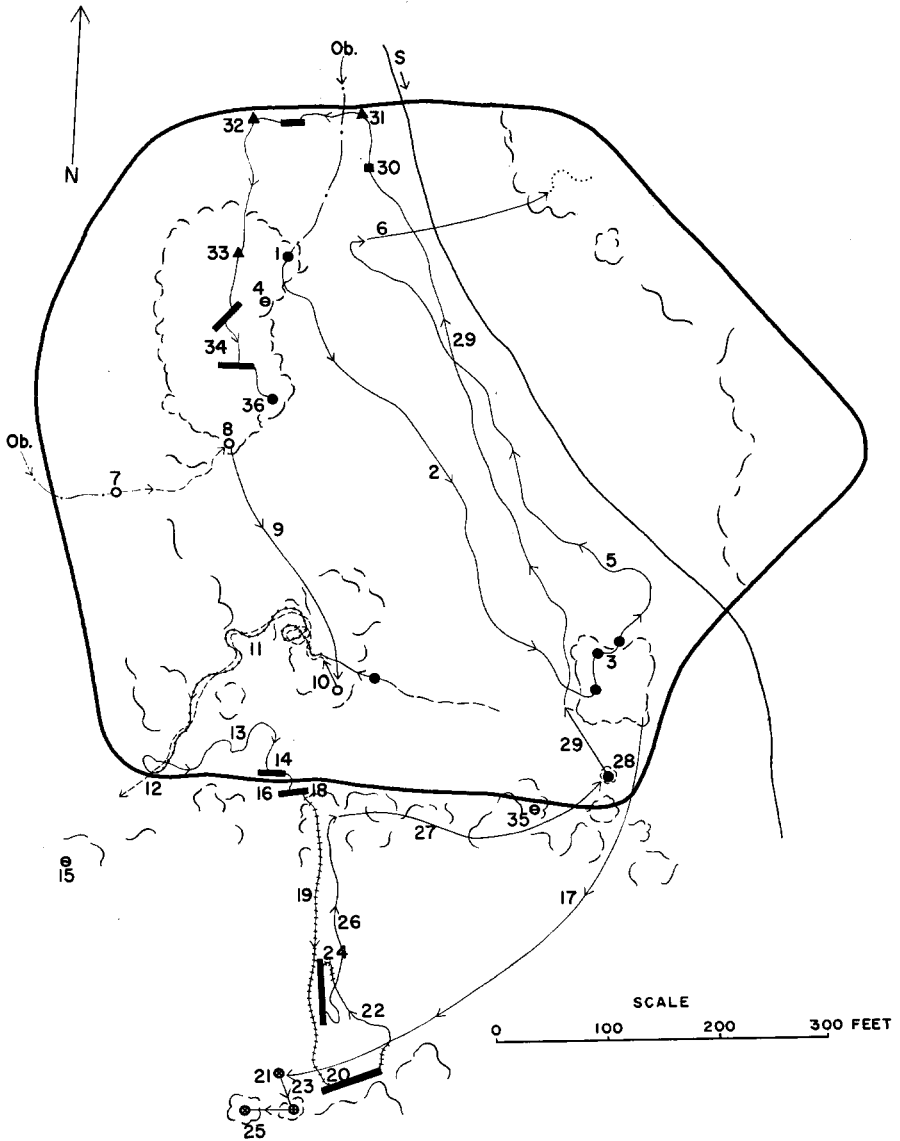


Fig. 3. Record of activities of Male E at territory 3 on April 30, 1958. 1, located, 9:39 a.m., on courting ground, drumming in response to occupant of territory 2, nuptial display; forages down to southeast fir grove. 3, calling, 10:15 a.m. 4, wing flutter of female, 10:43 a.m. 5, hurried return to west hillside, 11:05 a.m. 6, flight into east fir thicket, 11:10 a.m.; evades observer. 7, gray female located on upper slope, 1:26 p.m. 8, female's flight into pine and concealment; hooting heard down slope. 9, long flight of female to stunted pine, 1:47 p.m. 10, female's flight to ground in front of displaying male, 1:52 p.m. 11, Male E courts female; nine courting runs and calls, 1:52 to 2:04 p.m. 12, female leaves territory; Male E turns back near old border of territory 3. 13, hooting and display; forages; rests in shade. 14, calling on boundary log. 15, wing flutter uphill, 4:03 p.m. 16, renewed calling and nuptial display, 4:30 to 5:01 p.m.

17, flight of unidentified male from fir grove, 5:01 p.m. 18, instant territorial drumming by occupant Male E, 5:02 to 5:03 p.m. 19, running, off-territory "attack"; drumming and

Similarly, the females of this two-pair migrant band, observed in the trees in changing light, were not necessarily the same individuals as the "brown hen" and the "gray hen" that later ranged the upper and lower ravine, respectively.

Two days later a lone male was located on the northwest border of territory 2. He resembled the bird seen on March 24 and appeared resident in behavior. On each subsequent trip to the upper ravine during 1958, except on April 21, a male Blue Grouse was found within the limits of this territory (fig. 2). On two of these occasions, apparently the same male was located a second time on the plot 5½ and 11 hours after first contacts were broken. On April 21, a day of adverse wind and weather conditions, no grouse were seen; but courting calls and wing notes of a male were heard there in the occupant's favored haunts.

This perfectly plumaged and wary bird could not be identified by any physical feature until April 27, when it was seen that his fully fanned tail in display parted narrowly along the mid-line, showing slightly frayed inner rectrices. This character was noted again on May 3 and May 7. Otherwise evidence of a single, season-long occupant is based on the fact that a male of consistently similar behavior, habits, and appearance was observed on territory 2 on 17 of 18 trips to the upper ravine, from March 24 through May 25. These persistent behavioral characteristics were: (1) ranged more widely than the occupant of this territory in 1957, (2) showed wariness while on the ground, although rather indifferent to observer while in trees, (3) gave limited ground display in presence of observer, (4) hooted and displayed in trees, (5) drummed almost entirely on south border opposite territory 3, (6) appeared to roost regularly in the southeast section of territory north of the seepage pool and was localized on certain other areas of territory throughout the season, (7) gave alert note through early spring, (8) always uttered a 5-beat hoot, with notes of equal emphasis, (9) followed the same morning routines in calling and joining the female.

The occupant of territory 2 in 1958 was designated "Male D." No other male was seen there except on the initial date and briefly on May 4 preceding communal display. Seventy-five hours and 3 minutes were spent on territory 2, during which time Male D was observed for 26 hours and 17 minutes or 35 per cent of the time.

Male E (figs. 7, 8) which occupied territory 3 in the lower ravine could be recognized with certainty by the shape, position, and relative wear of the rectrices and tail coverts.

belligerent display. 20, hooting and aggressive strutting on canyon-side log; twenty minutes. 21, migrant Male F discovered by observer crouching on slope, 5:23 p.m.; no challenge offered to resident male; no conflict. 22, Male E starts back to territory. 23, observer flushes Male F into pine. 24, Male E mounts log to watch; returns along log; displays, forages. 25, Male F, up 20 feet in pine; continuous tree hooting and arboreal display, 5:57 to 6:21 p.m. 26, Male E leaves migrant; returns to territory, 6:21 p.m. 27, downhill flight into feeding tree. 28, courting calls from upper ravine, 7:14 p.m. 29, Male E flies to ground, 7:28 p.m.; running display toward north boundary. 30, drumming and full display. 31, 32, 33, territorial hooting and boundary display as courting calls continue up-ravine until 7:45 p.m. 34, courting ground calling by Male E at early dusk. 35, wing flutters in response from south border pines, 7:56 p.m. 36, continued calling through deep dusk; moonlight hooting 8:10 to 8:43 p.m. (nightfall at 8:40 p.m.). Observer leaves, 9:00 p.m.

Legend: solid dot indicates Male E; open circle, gray female; circle with bar, female, probably the gray hen; circle with cross, migrant Male F; Ob, indicates entry point of observer, followed by dash and dots to point of location of bird; thin, solid lines, route of Male E; dashed lines, route of gray hen; beaded line, courting of male; lines with cross-bars, territorial defense display; thick bars, logs; solid square, patrol drumming; triangles, boundary hooting and display.

The immediate and increasing tolerance shown by this bird to my presence, his deep-toned 6-beat hoot, powerful wing drum, localization about the southeast fir grove on territory 3, routine habits, and close association with the gray female gave additional proof of identity. Male E flew frequently but never clearly to escape me. At first he preferred to stay at 30 feet or more when on the ground but within three weeks permitted inspection at 8 to 10 feet. Occasionally, he displayed within four yards or, if in a tree, flew to the ground 15 feet from me. Although my presence could delay for hours the approach of the waiting female, who was then reluctantly responsive to his excited hooting and display, that fact caused no avoidance by the male and further demonstrated his individuality and previous experience with the observer. No other males were seen on this territory except one transient, momentarily, on April 30.

Male E was found on each of 16 trips to territory 3, from April 30 through June 21, 1958 (fig. 2). On four visits he was located on his territory a second time at intervals of  $1\frac{1}{4}$  to  $4\frac{1}{2}$  hours after first contact had been broken. He was observed on the plot (or close along its southeast border when the female appeared there with her chicks) for 92 hours and 40 minutes or for 85.8 per cent of the 107 hours and 56 minutes spent there.

*The population in 1959.*—A much altered situation was seen on the study area during 1959. A migrant flock of 10 Blue Grouse of both sexes was encountered in the ravine on April 3, 9, and 12. These birds ranged through the middle and upper draw, moving about as a fairly compact group or scattering over a small area; the flock had dispersed by April 19. Certain of its members remained in the ravine, contributing to the fluid and complex population pattern observed there during the latter half of the month. Male H, identifiable by reason of darker plumage, stereotyped behavior, and extreme localization, became resident early in the season on the west hillside in the middle of the ravine on territory 4 (fig. 9). A second member of the group settled higher on the slope to the northwest, and by April 12 a third grouse was resident on the steep river canyon front south of and bordering territory 3.

In addition, two males not associated with this roving band were already resident on the initial date. On April 3, upon entering territory 3 in the lower ravine, I encountered a displaying male on the old courting ground, recognizable because of distinctive plumage characteristics as Male E, the occupant of the territory in 1958. Male E was located on territory 3 on each of my first five trips to the ravine in 1959, and he was observed for approximately 20 hours. The only divergence in his behavior from the preceding year was a shift of his localization on the plot.

Also on April 3, another individual, the "ridge-front" male, flushed at the pool. He was resident near the spring and along the adjacent slope of the eastern ridge until the end of the month.

In summary, on 46 of 47 trips to the Purcell Range site, from April 16, 1957, through May 19, 1959, during three breeding seasons, one or more male Blue Grouse were repeatedly observed on territories in the study area, thus confirming my earlier report of definite territoriality in interior populations of this species (Blackford, 1958).

#### BEHAVIOR OF TRANSIENTS

The vernal movement of Blue Grouse from high mountain wintering ground to foothill or valley breeding range has been a little known phase of the life history. Activity of transients in the spring of 1959 provided new information on this topic.

Early on April 12 I encountered for the third time the large migrant company of

Blue Grouse then foraging on the study area. Three males and two females were grouped together on the rounded dividing ridge which rises between the east gully and west ravine in the upper draw (figs. 1, 4). Two other males were heard in drumming flights from adjoining slopes. One displaying male on the ridge was identified as an individual seen three days before; he again engaged in hooting, courting, and in drumming flight. Presently this central band trailed down the low ridge to the middle of the ravine where display notes boomed out every minute or two for the next 10 minutes from the valley floor. I found two males displaying there at the juncture of the streamlets. A courting call sounded from the drummer on the west slope.



Fig. 4. Looking up the rounded dividing ridge in the upper ravine from southern section of territory 2. East gully beyond at right; west ravine at left, June 16, 1958.

It was clear that the ten-member migrant company studied on April 3 and 9, was still in the ravine, moving about loosely together, the males hooting, displaying, and courting the females. An observer having met this sizeable band of grouse for the first time, and noting their nuptial activity, although unaware of their status as migrants, might readily have mistaken this assemblage of courting birds as a gathering for group display. Actually, individuals or pairs were courting within a roving migrant flock lingering in the ravine in the course of downward migration.

True communal display is performed by established territorial males and attendant females gathered on common ground at the height of the breeding season for social activity that plays an important role in the advancement of the sexual cycle. It is therefore highly significant that courting begins early in the season during the altitudinal migration and commonly among flocking birds. Thus it appears that mate selection is

then initiated and that pair formation may often be completed by the time migrants reach their breeding grounds at lower levels. Observation of the two-pair migrant band in 1958 had previously indicated this possibility.

Hooting is evidently correlated with the gonadal cycle and begins without relation to territorial occupancy.

#### TERRITORIALITY

Spring migration is followed by occupation of individual territories and establishment of social relationships among residents of an area throughout the season of reproduction.

*Early territorial behavior.*—Abundant evidence obtained in 1958 indicated that Male D was a season-long resident in the upper ravine. Occupancy began there on territory 2 soon after arrival of grouse on the breeding ground. This upper section, the most deeply wooded portion of the study site, is marked by dense clumps and thickets of Douglas fir (*Pseudotsuga menziesii*), interspersed with open stands of yellow pine (*Pinus ponderosa*), and by heavy mixed growth of the two species. It more closely approaches conditions of the high winter range than any other part of the study area.

From March 26, 1958, until late April, overcast skies, rain, sleet, frequent winds, and generally chilly temperatures prevailed. On that date the lone resident grouse was first located in a young fir on the upper border of territory 2. During one hour and forty-five minutes of observation, he hunched on his perch or foraged briefly in the same tree, finally flying into the dense evergreens where the small migrant band had been seen two days before. On March 29, apparently the same solitary male was observed for two and one-half hours at mid-level in a tall pine in the lower section of the plot. He was even more sedentary; moreover it was certain that he had been there for 3 hours and 24 minutes prior to discovery. On the following three days, similar behavior was noted in apparently the same male. Twice he was interrupted foraging on the ground. Thus it appears that the period of Male D's occupancy of territory 2, from March 26 through April 9, consisted of resting and feeding prior to the beginning of courtship activities. Judging from the long intervals spent in trees and the brief but increasing occurrences on the ground, it seems that the early period on the breeding range for territorial birds of this population is one of transition from largely arboreal winter habits to predominantly ground-level activities. It is also a time when a sparse growth of succulents on the forest floor offer some change from the winter diet.

*Early association of sexes.*—Arrival on the breeding range of males in company of females appears typical. Dispersal of migrant bands follows quickly, unless they delay enroute to lower levels. Males may become territorial at once. Associated females apparently remain in the same general area and are probably occupied in choosing the home ranges that they later frequent (Bendell, 1955:372-373). On April 11, 1958, two Blue Grouse were flushed together in the fir stands midway along the west border of territory 2. The male vanished swiftly in the direction of the southwest boundary, where a male grouse was located 5½ hours later. On being flushed a second time, he banked downhill in a complete half circle and flew back into the same heavy timber where the "pair" had been found that morning. The other bird had been quickly identified as a female. This was the earliest association noted in 1958 of a female with a territorial male. The first similar association in 1959 occurred on April 9, when Male E was observed on the ground courting a female 12 feet up in a boundary tree. Apparently the sexes are separated for only a short time during selection of territory.

*Late occupancy.*—In an effort to detect any resident grouse in the lower ravine in the spring of 1958, territory 3 was either searched or crossed on March 24, 26, April 5,



11, 18, and 27. I passed close by on all other occasions when going to or from the upper ravine. Territory 1 adjacent to it was similarly traversed. No grouse was seen or heard on either territory.

Twice on the afternoon of April 27 courting calls sounded from the top of the east ridge and from above the ravine to the north, providing the first intimation that Blue Grouse other than Male D had remained or lately arrived in the vicinity. On the following day, clear skies signaled reversal of weather conditions, and early on April 30, calls and wing drumming at the old south border of territory 2 indicated diversion of Male D's activities to that area in the middle of the ravine. This behavior contrasted with his usual pattern of meeting the brown female in the upper portion of his plot. When discovered, he flew 50 yards farther south, where his calling apparently induced the female to join him. Meanwhile Male E was drumming and displaying on territory 3 in the lower ravine.

An occupant of this forested, although more open plot, might readily have been overlooked for a time had its owner been "sitting it out" in the trees as Male D had done in the upper ravine until April 11. But this energetic and highly vocal bird could not have remained undetected throughout the last week of March and nearly all of April. Territory 1 remained vacant through the season. Other events also indicate that a late movement of Blue Grouse to middle and lower levels of the Purcell Range occurred, following the month of inclement weather already noted. Also on April 30, a third displaying male, evidently a migrant, crossed territory 3 to the river canyon beyond. The permanent extension down ravine of the territory of Male D to within 140 yards of the plot now held by Male E, and the continuing advertisement of boundaries by both birds which ensued, further emphasized the occupation of the latter territory in late April. No previous investigator has reported a second seasonal migration of Blue Grouse, but recognition of a second spring valleyward movement in 1958 seems unavoidable. Subsequently in 1959, some territories were occupied at a time when flocking migrants were present at the same elevation. Evidently, separate migratory waves occur, and the timing of territorial establishment in one area may be rather variable.

*Off-territory occurrence.*—Following selection of an area, male Blue Grouse exhibit strict territoriality throughout the breeding season. In 1958, Male D was seen beyond territorial limits on only two occasions: on May 4, a flight carried him 300 yards out of his territory, and on the evening of the same day, he moved to a high drumming rock 110 feet north of the plot in order to participate in group display.

Territorial defense by Male E on April 30, 1958, took him one hundred yards from territory 3. From April 3 through April 23, 1959, Male E restricted his movements to the territory. Male H was never seen to leave territory 4. Males are apparently absent from their territories only when attending communal displays, until late in the season.

*Duration of occupancy.*—A male grouse was last seen on territory 2 on May 25, 1958.

On June 21, 1958, when study for the season ended, Male E was still territorial. Moreover, he was fairly advanced in the postnuptial molt. Because new plumage growth places heavy physiological demands on the bird, it is probable that the return migration to the winter range would not have begun until the completion of the molt. In 1959, Male E disappeared from territory 3 after April 23.

#### TERRITORIAL DEFENSE

Established territorial boundaries of the Blue Grouse are advertised, patrolled, and defended by the male. A male Blue Grouse will even leave his territory to meet possible

challenge by a trespassing male lingering in the vicinity. On April 30, 1958, as Male E hooted from a south boundary log, evidently in an effort to recall the gray female, another grouse suddenly flew from the southeast fir grove of territory 3, 110 yards away, in curving flight around to the canyon slope below (fig. 3). Instantly Male E sprang into the air in loud drumming flight. Then, half running, half displaying, with eyecombs flushing to blood red, he hurried toward the intruder. After going a hundred feet, he leaped into the air to drum again, dashed forward another 60 yards, and commenced belligerent display from the top of a fallen pine trunk. After 20 minutes of hooting and



Fig. 5. Fir stands at head of the west ravine, from within north boundary of territory 2; slope of dividing ridge seen at left, June 16, 1958.

strutting he paused, then dropped from the log. Rising to follow, I found the other bird flattened on the grassy slope midway between. As Male E had now started back to his territory, I approached the crouching male to make certain that he had not been overlooked. He flushed into a conifer. Male E stopped to watch from a log. It was evident that he had been aware of the other's proximity. Unexcitedly he moved down closer to the tree, forging quietly. Male F, distinguished by his short lateral rectrices, flew to a pine beyond where he engaged in muffled hooting and continuous display. Male E made no response and after 24 minutes of this arboreal performance by the newcomer, the territorial male returned, hooting, to his defended area. It appeared that Male F, in crossing territory 3, was participating in the late, downward migration. Male E had been quick to anticipate further intrusion and reacted with "attack display." There was no challenge by the "submissive" transient for possession of the territory, and no conflict resulted. He was not seen again.

Breeding males of the Blue Grouse react to courting calls on nearby territories, but they have not been seen to leave their own ground under such circumstances. Following

his encounter with the migrant, Male E flew to a young evergreen south of the fir grove (fig. 3). He was still feeding in it at 7:14 p.m. when a display note sounded from the upper ravine. As other courting calls came from territory 2, Male E stopped foraging and flapped noisily to the ground. He then headed toward the upper draw, tail fanned and neck rosettes flared. The courting calls continued. Scraping through brush of the lower slope toward the old north boundary, the big grouse paused on a rock to give full display. Hearing another loud call, he rose high in a rotating wing drum and hurried on until close to the border of the plot set in 1957 where he displayed along the length of a rotten log, pausing to hoot excitedly. As shown by later patrols as well, this point was chosen as a hooting station along the 1958 boundary. Here, despite frequent courting calls from a short distance up ravine (30 or more during the entire episode), Male E turned and hastened uphill, along and not far from the old territorial boundary. Several times, regardless of the fading daylight, he mounted logs to emit his multiple hoot and to display. Finally he turned back into territory 3, as display notes from the upper ravine tapered off at 7:45 p.m. The close adherence of Male E to bounds observed by the resident in 1957 continued to astonish me; otherwise he differed markedly from that bird.

On numerous other occasions in 1958, activity on either territory aroused the neighboring male and brought him to the nearer border of his plot to demonstrate. Yet neither males D nor E were known to approach closer than 140 yards. Such situations imply "defensive belligerency"; but the resulting status quo at boundary lines introduces an accepted social relationship also.

Male Blue Grouse routinely hoot, drum, and display as notice of territorial occupancy at strategic points on established boundaries. For example, from 1:25 to 5:51 p.m. on April 12, 1959, Male E slowly quartered the south border zone up and down under the pines, seldom interrupting steady hooting and display on border logs. Finally he drummed and hurried south 90 yards beyond territory 3 to the river canyon, where he mounted a lookout log, uttering thumping hoots. Two courting calls came from just below on the steep slope. They were my first understanding of the afternoon's intensive patrol activity. Circling 70 feet farther, I flushed a male and a female there a foot apart. Their presence gave first evidence of the occupation of that adjoining area by the canyon male, a residency continuous throughout the remaining period of observation, and one that materially affected the behavior of neighboring Male E.

From the foregoing it is evident that in all major aspects, occupancy, boundary patrol, display, defense, and social relations, males of this species exhibit the same general characteristics that are typical of most territorial birds. Activity is thus adjusted to a limited area during the season of reproduction.

#### LOCALIZATION ON TERRITORY

Males of this forest-dwelling population are not only strongly territorial, but they are also markedly localized on certain portions of their territories. Extent of use of particular sections of the territory corresponds with various routine activities, nature of cover, topography, and relations with other grouse.

*Localization in 1958.*—Movements of Male D on territory 2 indicated that he roosted regularly in heavily foliated firs on the outer slope of the lower east gully (fig. 2). His first call notes, drumming, and my contacts of early morning traced his departures from that section. Furthermore, at dusk on April 21 a male was heard in that area. The head of the west ravine and adjoining slopes of the west hillside were preferred as residence and courting ground. Immediately after occupation of territory 3,



Fig. 6. Yellow pine forest of west hillside on south half of territory 3. Fir grove, residence area of Male E, at left; south border pines beyond. North outlier evergreens seen at center; edge of pine-fir stand at right, June 14, 1958.

however, these activities were transferred to the neighboring tall timber on the south border of territory 2. That area became the site of his territorial drumming. Open forest on the higher southwest slopes of the territory was often favored both for ground foraging and as a refuge, judging by long escape flights to it.

On territory 3, habits and movements of Male E also clearly demonstrated selective use of certain portions of the territory for different activities, as the following discussion will indicate.

*Southeast fir grove.*—This sharply defined 60 x 65-foot clump of immature firs (figs. 6, 9) embraced an open, log-strewn forest floor and a dense overstory. Scattered patches of tall pine grass and a dry needle carpet provided ground cover. Rock outcrops and fallen tree trunks were utilized as drumming and display platforms. On three sides, at short distances, outlying trees or conifer clusters broke the nearly complete isolation from the rest of the forest. Tall pines were found only to the south. Throughout the study in 1958 the movements of Male E radiated from this grove and he was located at or close by the grove on nine of 16 trips to the territory (fig. 2). Male E spent 59 hours and 29 minutes at the grove and its outlying evergreens (64.3 per cent of the observation time on this territory in 1958, table 1), and stayed in the fir grove itself for 31 hours and 53 minutes (34.4 per cent of observation time), yet he was very active afoot and frequently took to wing. Of four known roosting sites, two were in the grove, and two in his "feeding tree," 65 feet south. One of three probable roosting sites was in the fir stand. By mid-June a dusting bowl or bed had been established on each side

TABLE 1  
LOCALIZATION OF MALE E ON TERRITORY 3 IN 1958

Date	Hours at southeast fir grove and outlier evergreens		Hours in fir grove	
	Observation period	Duration	Observation period	Duration
April 30	10:10 -11:05 a.m. 6:25±- 7:28 p.m.	1 hr. 58 min.	10:10 -11:05 a.m.	55 min.
May 3	9:58 a.m.- 6:20 p.m.*	8 hr. 22 min.	9:58 a.m.- 4:05 p.m.	6 hr. 7 min.
May 4	10:17 a.m.- 4:10 p.m.	5 hr. 53 min.	10:17 a.m.-12:08 p.m. 2:03 - 2:08 p.m. 3:50 - 4:10 p.m.	2 hr. 16 min.
May 7	8:07 - 9:00 p.m.*	53 min.	8:10±- 9:00 p.m.*	50 min.
May 11	12:51 - 3:58 p.m. 7:25±- 8:45 p.m.*	4 hr. 27 min.	2:29 - 3:11 p.m. 7:25±- 7:40± p.m.	57 min.
May 14	9:14 a.m.-4:56 p.m. 6:25 - 7:50 p.m. 8:22 - 9:25 p.m.*	10 hr. 10 min.	9:14 a.m.-12:06 p.m. 6:25 - 7:02 p.m. 8:27 - 9:25 p.m.*	4 hr. 27 min.
May 17	11:39 a.m.-1:50 p.m.* 2:44 - 7:10 p.m.*	6 hr. 37 min.	11:39 -11:42± a.m. 11:50 a.m.- 1:50 p.m.* 2:44 - 7:10 p.m.*	6 hr. 29 min.
May 19	6:08 - 8:05 p.m.*	1 hr. 57 min.	6:08 - 7:30± p.m.	1 hr. 22 min.
May 21	6:40 - 6:44± p.m.	4 min.		
May 22	4:00 - 4:05± p.m.	5 min.	4:00 -4:02 p.m.	2 min.
May 30	3:51 - 8:58 p.m.*	5 hr. 7 min.	4:09 - 6:40± p.m.	2 hr. 31 min.
June 1	3:53 - 6:34 p.m. 7:47 - 8:29 p.m.	3 hr. 23 min.	3:53 - 4:01 p.m. 6:00 - 6:34 p.m. 7:47 - 7:54± p.m.	49 min.
June 5	2:31 - 3:07 p.m.* 3:56 - 9:15 p.m.*	5 hr. 55 min.	2:31 -3:07 p.m. 3:56 - 7:21 p.m.	4 hr. 1 min.
June 14	9:51 -10:36 a.m. 11:47 a.m.- 1:31 p.m.	2 hr. 29 min.	9:51 -10:36 a.m.	45 min.
June 16	9:15 - 9:40 a.m. 2:57 - 4:30 p.m.*	1 hr. 58 min.	3:14 - 3:32 p.m.	18 min.
June 21	7:26 - 7:37 a.m.	11 min.	7:30±- 7:34± a.m.	4 min.
Totals		59 hr. 29 min.		31 hr. 53 min.

\* Male E at same location when observer left.

of the grove. Only one well-used bowl was known elsewhere on the plot. In my absence the gray hen would come to the ground, and courting was heard several times at the fir stand.

*Feeding tree.*—Foraging in evergreens in the residence area was concentrated in the 40-foot fir south of the grove (fig. 9), and occasionally in fir and pine of the outlying conifer clusters. On the eight days that Male E was observed in 1958 in the feeding tree, he spent 10 hours and 32 minutes there, or 11.3 per cent of total observation time (table 2). Usually his tree hooting and arboreal display were performed in its branches. He visited the fir to linger beneath it on four other dates. This bird was not seen to forage in any tree in the fir grove itself, save on two occasions when he plucked a few needles. Such definite preference for one tree, and the fact that the previous year a male in the upper ravine would climb the hillside to forage in certain young Douglas firs, appears to indicate that the foliage of individual trees of this species is more palatable than that of others. Toward summer, some branchlets of the feeding tree were well stripped of needles.

Caswell (MS thesis) showed photographs of fir tops taken in winter that were



Fig. 7. Male E in partial display near feeding tree, May 19, 1958.

defoliated by Blue Grouse, while adjacent conifers were apparently untouched. Hoffmann (1956:325-326) and others noted that some winter roost sites are utilized to a much greater degree than others. He stated (p. 326) that at Sage Hen Creek, California, "only a small part of the total white fir on the areas was used for roosts. The factors influencing this selection on the part of the grouse are not known. No obvious correlation existed between size or dispersion of the trees and degree of winter use."

Male E foraged in his feeding tree on both evenings that he remained there to roost. It seems reasonable to suppose that foliage preference results in pronounced patronage by Blue Grouse of certain conifers, and that other factors being favorable, the foragers commonly stay in them over night. This would be especially true on winter range, and particularly during stormy periods, when Blue Grouse are less inclined to move about. In spring, grouse often seek growing buds and new needle tufts of young trees, but this type of selection would not occur in the forests in winter; hence no such correlation as to size and dispersal of trees would be noticeable then. Thus it is now clear that selection of many roosting sites may readily result from foliage preferences and feeding habits.

*Courting ground.*—The open floor of a yellow pine stand on the west hillslope marked the courting ground of the occupant of territory 3 in 1957. The same area (fig. 9) alternated with the fir grove as the strutting ground of Male E in 1958. Many fallen tree trunks and rocky ledges provided display platforms. Here, and about the broken-topped pine below, Male E spent 8 hours and 15 minutes, or 8.8 per cent of the total observation time that year (table 3).

TABLE 2  
LOCALIZATION OF MALE E ON TERRITORY 3 IN 1958

Date	Hours in feeding tree		
April 30	Foraging	6:25±-7:28 p.m.	1 hr. 3 min.
May 3	Foraging, resting	4:10±-6:20 p.m.*	2 hr. 10 min.
May 11	Foraging, hooting, full display	3:20 -3:58 p.m.	
	Foraging, hooting, roosting	8:00 -8:45 p.m.*	1 hr. 23 min.
May 19	Foraging	7:37±-7:55± p.m.	18 min.
May 30	Foraging	3:54±-4:05 p.m.	
		6:51 -8:55 p.m.	2 hr. 15 min.
June 1	Foraging	7:58 -8:29 p.m.	31 min.
June 5	Foraging, roosting	7:21 -9:15 p.m.*	1 hr. 54 min.
June 16	Foraging, hooting, display	9:20 -9:40 a.m.	
	Foraging, preening, resting	3:52 -4:30 p.m.*	58 min.
Total			10 hr. 32 min.
	Hours under feeding tree		
May 4	Hooting	2:08 -3:50 p.m.	1 hr. 42 min.
May 7	Hooting	8:07 -8:10± p.m.	3 min.
May 14	Calling, displaying	4:45 -4:56 p.m.	
	Calling, drumming	7:02 -7:50 p.m.	59 min.
June 16	Resting	3:32 -3:52 p.m.	20 min.
June 21	Foraging	7:26 -7:30± a.m.	4 min.
Total			3 hr. 8 min.

\* Male E still in tree when observer left.

*Aspen stand.*—At the east end of territory 3, aspens, grouped amid the pine-fir stand (fig. 9), offered foraging sites and high perches free of flies. On May 19, 1958, Male E was observed in the grove for 7 hours and 2 minutes, or 7.6 per cent of the time recorded on his territory. It was not an isolated visit, as indicated by his fondness for aspen leaves and the fact that I lost him in dense undercover apparently enroute to the aspen on June 21.

The vicinity of the fir grove, the courting ground, and the aspen stand were therefore three relatively small, widely separate areas where Male E spent 74 hours and 46 minutes (80.7 per cent of observation time) in 1958 on territory 3.

TABLE 3  
LOCALIZATION OF MALE E ON TERRITORY 3 IN 1958

Date	On courting ground and at broken-top pine		In aspen stand	
	Observation period	Duration	Observation period	Duration
April 30	9:39 -10:00± a.m.			
	7:50±-9:00 p.m.	1 hr. 31 min.		
May 4	5:10±-6:30 p.m.	1 hr. 20 min.		
May 11	4:56 -7:15 p.m.	2 hr. 19 min.		
May 14	8:05±-8:22 p.m.	17 min.		
May 19	8:03 - 8:04 a.m.		8:29-11:45 a.m.	
	5:15±-5:48 p.m.	34 min.	12:00- 3:46 p.m.	7 hr. 2 min.
May 21	5:52 -6:35 p.m.			
	7:06 -7:30 p.m.	1 hr. 7 min.		
May 22	4:12 -4:41 p.m.	29 min.		
June 1	6:36 -7:14 p.m.	38 min.		
Totals		8 hr. 15 min.		7 hr. 2 min.

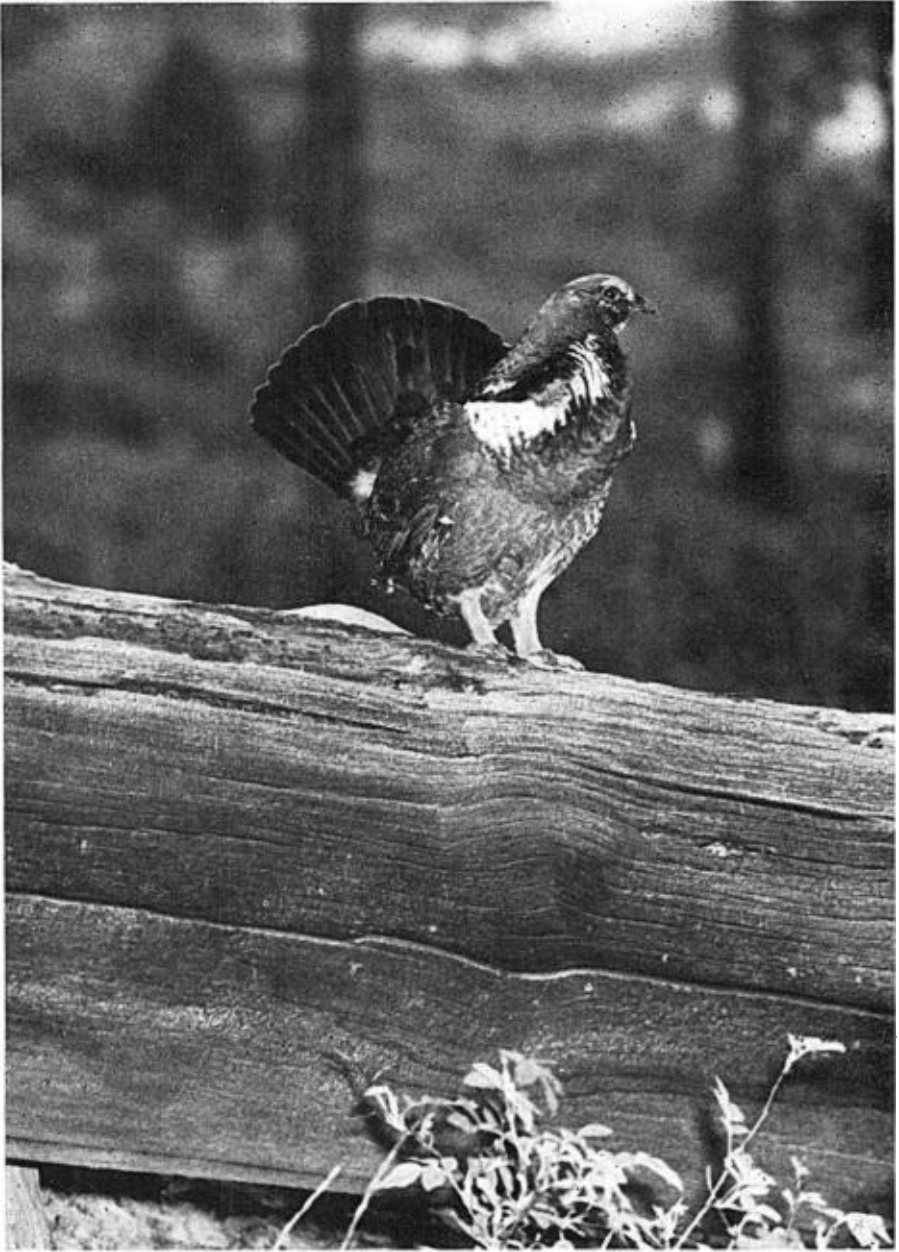


Fig. 8. Male E hooting on border log at fir grove, May 19, 1958. Note indistinct terminal tail band.

*Localization in 1959.*—In 20 hours and 34 minutes observation of Male E on territory 3 in 1959, a new activity pattern became evident. All five observations of this bird were made at the north boundary or on the nearby courting ground (fig. 9). Although he visited the southeast fir grove, and was seen to roost there, his activities



centered about the two points mentioned, apparently because the female was coming to territory 3 from the north. She appeared to range through the middle ravine floor and the eastern section of the pine-fir stand on former territory 1. This female could not utilize the canyon slope south of territory 3 as home range and brood area, as did the gray female in 1958, since that slope was now occupied by the canyon male and a light-faced hen (fig. 9). The male on the ridge-front held territory just across the ravine to the northeast, and Male H was resident on territory 4. To the west the hillside rose to an open ridge with scattered brush and pine, thus the hen had to resort to the remaining narrow area in mid-ravine. All observed contacts with her by Male E were made there along the north border of his territory. The presumably inadequate nesting and brood range for the hen, disturbing contacts with transient and roving migrants, general population pressure in the ravine, and human disturbance apparently accounted for the sudden abandonment by Male E of his territory and by the female of her limited plot by April 25. That date, as evidenced by the delayed downward movement of the preceding year, would not have been too late for continued migration and selection of another site. The male on the ridge-front and the associated female likewise deserted their station after April 30.

Localization was clearly evident on territory 4. Male H was found there on April 30, 1959. My records showed presence of a male grouse on the area on three previous occasions that spring; probably it was one of the migrant flock that favored this section and had become resident on the west slope. A male of distinctive appearance and behavior was located within 40 feet of the same site on May 6. It was within 20 feet of that lookout point on May 11 and was 70 feet from it on May 19. During more than five hours of observation, this male was seen to outline the boundaries of the territory yet seldom went beyond a small, irregular stand of mature fir and pine that delineated his headquarters area. An examination of his lookout point, a snowberry (*Symphoricarpos*) clump beside an outcrop of gray rocks at the lower edge of the conifer stand, showed heavy deposition of droppings near the shrub and among the rocks. Droppings were readily discernible, although more scattered, on the floor of the residence grove. A small brown female was usually found with Male H, or apparently sought him there while I was present. All evidence indicated unusual localization of the dark male at this conifer stand which was apparently indistinguishable from the surrounding forest, except that the trees were grouped more closely and contained a greater proportion of heavily foliated firs among the tall pines.

The male Blue Grouse thus utilizes his territory in a systematic manner which permits diversified activity during the breeding season. Essentially the same territories are commonly chosen for successive years by the same or by different tenants. This repeated use indicates that special needs must be met and that certain areas are most suitable. Likewise, adjacent or nearby areas must satisfy the requirements of the female and young. It is therefore inferred that whenever such appropriate conditions are materially altered or destroyed the indigenous grouse population is either displaced to less favorable habitat or permanently eliminated.

Considering that intensive use is made of special areas on territories, over-utilization during years of population abundance may occur. Without occasional seasons of non-occupancy, as is normally the case, inadequate natural disinfection and disinfestation may result, particularly in the vicinity of residence areas on male territories and on brood range of the young. Depletion of required food sources also may bring nutritional loss, resulting likely in an increased incidence of disease and parasitism. The restriction of total range and decrease in size of individual plots under conditions of crowding,

together with year-around occupation of some areas, could contribute to population reduction.

Many investigators have reported the population cycles and "crash" declines of

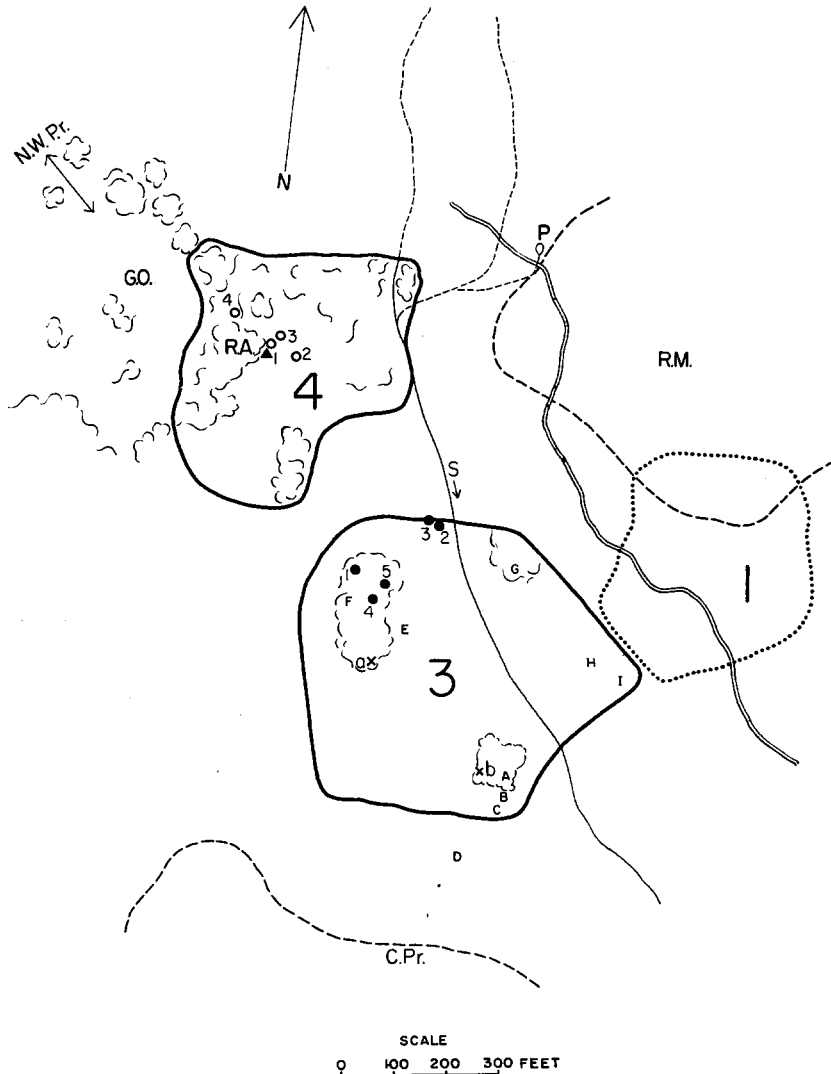


Fig. 9. Territories occupied (3, 4) in breeding season of 1959; previous territory (1) of 1957 also outlined (dotted lines).

Locations of Male E on territory 3: 1, Apr. 3, 1:41 p.m.; 2, Apr. 9, 8:58 a.m.; 3, Apr. 12, 10:29 a.m.; 4, Apr. 19, 10:14 a.m.; 5, Apr. 23, 5:06 p.m.

Features in territory 3: A, southeast fir grove; B, trail to feeding tree; C, feeding tree; D, south border pines; E, broken-top pine; F, old courting ground; G, fir thicket; H, pine-fir stand; I, aspens; a x roosting, Apr. 3; b x, roosting, Apr. 12.

Locations of Male H on territory 4: 1, Apr. 30, 4:16 p.m.; 2, May 6, 3:59 p.m.; 3, May 11, 4:16 p.m.; 4, May 19, 3:15 p.m.

Legend: G. O., grassy opening; R. A., residence area of Male H; NW. Pr., north-west pair; C. Pr., canyon pair; R. M., ridge-front male; triangle, lookout point of Male H; dashed lines, probable boundaries of other territories.

North American grouse. Hoffmann (1956:327-331, 334-337) has summarized findings on cycles in the Blue Grouse. The marked territorialism and localized habits of Blue Grouse may have application to this problem. One seeming or possible early response to local population pressure, that of territorial abandonment, has been described here.

#### ROOSTING HABITS

Roosting sites of male Blue Grouse noted from 1957 through 1959, were either at the edge of a dense forest grove or in a lone tree of an open stand. The common advantage of these sites appears to be ease of escape. If a bird were alerted to the presence of an aerial predator, retreat into evergreen cover would be possible. Escape from tree-climbing predators by flight into the open could occur without risk of colliding with branches in the dark.

Data on time of roosting obtained for Male E suggest that light intensity is an important regulating factor (table 4); the grouse tend to roost later in the day as the photoperiod lengthens in the spring. Occasionally overcast or cold weather may cause the birds to roost early.

#### VOCALIZATIONS

*Calls.*—In addition to notes previously reported (Blackford, 1958), grouse of the ravine voiced the following: *Arrival notes*, low, guttural, throaty notes uttered by a female alighting near the male; *cackle*, the loud outburst of the female resembling that of domestic fowl; *cac-rrrr-cac-rrrr-cac-rrrr*, a weird complaint and alarm note, given apparently by a female on interruption of courting that preceded communal display; *t-oot*, a light, ventriloquistic call of the male that may serve as a preliminary or invitatory display note; *kut-kut-kut*, formerly mentioned, is uttered as a call, or as a low warning note, with mandibles opening and shutting rapidly. Under excitement this latter call is rendered loudly, for two or three minutes, almost without interruption, and it is sometimes given in flight.

*Alert note.*—The alert note of the male was of major importance in enabling early season location of individuals on territories. Usually the utterance consists of two or three barely audible, ventriloquistic grunts of extremely low pitch and volume. An alert of one to a few such grunts, usually close together, is voiced as an intruder approaches. It is usually not repeated later in the day should the observer again come near when the male, early in the season, is solitary on his territory. However, when the male is joined by the female, the alert note serves as his customary warning. It may then be

TABLE 4  
TIME OF ROOSTING OF MALE E ON TERRITORY 3

Date	Male at roost	Male near roost	Remarks
May 7, 1958	8:26 p.m.		
May 11, 1958	8:14 p.m.		Heavy overcast after evening shower.
May 14, 1958	8:36 p.m.		
May 22, 1958		8:39 p.m.	Flight to roost in south border pines; identity not confirmed.
May 30, 1958		8:58 p.m.	Flight into fir grove at late dusk.
June 1, 1958		8:29 p.m.	Flight to pine-fir stand at dusk. Heavy, broken clouds; cool.
June 5, 1958	8:56 p.m.		Retired into dense branch cluster of feeding tree.
April 3, 1959	6:37 p.m.		Clear; chilly.
April 12, 1959	7:29 p.m.		

repeated at indefinite intervals if the intruder remains in the vicinity. As the season advances, these notes merge into very low and muffled hoots in keeping with the performer's full-toned voice at that time. Alert notes were first heard at 1:35 p.m. on March 24, 1958.

In early spring when males are inactive prior to overt territoriality and do not call, drum, or display, the alert note proved to be the only means of detecting a recently resident male. Before May, only two successful locations were achieved otherwise.

*Hooting.*—The usual vocalizing of male Blue Grouse has been described as "hooting" or "grunting," according to impressions of different observers and apparently without intent to make distinction between the two. Grunting is a vocalization of harsh tonal quality, rendered in lowest register with limited volume. Such notes may be the only ones uttered in early spring. Soon hooting is initiated with a single note or two, barely perceptible, followed by other low, grunting hoots. Neck pockets are then unopened and the tail flips but slightly. Gradually thereafter the white of the feather bases of the neck rosettes is disclosed as covering feathers part and the tail is flipped regularly with the low steady beat. With continuation of the multiple hoot, at two or three series per minute, the throat swells, the neck bulges rhythmically, and the white of the neck pockets flashes with each pulsation, while rose-red neck sacs show and the first, rather harsh, although often muffled, hooting of the year is heard. As territorial hooting, calling, and courtship and display begin, the quality of hooting rises to the true, hollow-toned, full-timed multiple beat. At this time either muffled tones or high, hollow tones of varying volume characterize the typical hoot. Grunting is seldom heard. This tonal transition likely coincides with the seasonal recrudescence of the vocal structures.

The usual performance is initiated with a slight gape as though the bird were taking a small gulp of air before pulsation of the cervical sacs begins. The intake of air is probably negligible because the bill is quickly closed and generally remains so throughout the multiple hoot. Any subsequent minor parting of the mandibles is apparently a result of attendant vibrations.

Muffled hooting apparently results when the neck pockets are but partly opened. Full, hollow-toned hooting is heard when feather rosettes are more widely flared and the neck sacs are filled to greater degree. The deceptive effect is accentuated by muffled hooting, and ventriloquistic qualities are most pronounced when the hooter is within 100 feet. Distant hooting is more directional and more readily placed. Ground-level hooting was first observed on April 11, 1958, and on April 3, 1959.

Tree hooting is common behavior in grouse of the race *obscurus*. It serves as territorial song as does ground-level hooting. Display may not accompany early season vocalizing, but partial display is usually given by tree-hooting males once courtship has begun. Full arboreal display was occasionally observed. Proximity or arrival of the female is the stimulus that usually evokes full display, irrespective of whether the male is in a tree or on the ground.

All three males seen in trees during 1958 hooted and displayed there. Male D engaged in tree hooting for 25.9 per cent of the observed time on territory 2; Male E during 1.2 per cent of the time on territory 3; and migrant Male F for 44.4 per cent of the time during the single contact made with him.

Several males, both migrant and territorial, were seen to hoot in trees during 1959.

It is now evident that tree-hooting by males serves to call females; wing signals by arriving hens are given in response. The following excerpt from my field notes serves to illustrate this point.

From the pine where he displayed, Male D whirred south 100 yards along the hill-

side. At length he flew voluntarily into a fir when I was at 35 yards and foraged up through its boughs. By 1:37 p.m., he commenced muffled hooting that changed to steady calling. At 2:04 he turned and faced northward, at a height of 35 feet. Rosettes were flared, tail fan tilted forward, and tempo of hooting increased. Within 2 minutes a wing flutter rustled north along the hill. Male D gave a moment of full display and continued calling. Another soft flutter was heard. The male hooted louder. A third wing flutter emanated from the hillside forest, nearer, within 60 yards. Male D, vibrating all over, responded with higher, hollow-toned hooting, quickening the beat; but now the female held back. Through intervals of sunshine, spitting rain, and flurries of sleet the male grouse called from the fir throughout the afternoon. Above a stirring, 20 mile-per-hour wind that brought loud soughing in the timber, his notes could be heard at 100 feet. Steady hooting subsided when he perched close to the trunk through chill blasts but continued in the fir top at 5:15 p.m. as I scouted northward for the female in a slanting sleet shower.

On May 11, 1958, after calling for 38 minutes in the feeding tree, Male E suddenly burst into striking display. Moving out on a nine-foot bough, he leaped to the ground, paraded uphill, paused to face me in full display at three yards, and continued excitedly up the slope. There, rosettes flashing, he faced the gray female on the grassy hillside.

No basic behavioral difference in use of terrestrial and arboreal sites for calling and display is indicated between males of the racial groups of *Dendragapus*. Preference of inland forms for ground-level hooting as compared with the usual choice of tree level by coastal birds is a difference in degree only. Both groups employ either type of hooting station.

Hooting on the roost at dusk is an habitual mode of communication. A male Blue Grouse will hoot from his roost in response to a wing flutter, evidently given by the roosting female nearby. Or the hen may respond with a wing note to initial hooting by the male.

At 8:26 p.m., on May 7, 1958, Male E flew into an evergreen on the eastern edge of the fir grove (figs. 6, 9). He settled 15 feet up on a bough. Within four minutes, a wing flutter sounded from pines 100 yards uphill on the south border of territory 3. At once Male E responded from his roost with low hooting. The low hoots continued for eight minutes (table 5) from his roost.

Communication between members of a pair from their roosts at dusk evidently serves for purposes of "reassurance" and location.

From the evidence now available, I am unable to agree with Wing (1946:157) when he said of the race *obscurus* that it "probably can be considered as on the way towards losing the well-developed throat sac and progressing in the direction of *Lagopus*." There seems to be no perceptible disuse of this structure. Migrant, territorial, and nuptial hooting extend over a period of several months. Except during intervals of foraging and rest, hooting is a constant activity of males of the race *obscurus* during the height of the breeding season. It is a chief means of calling and other communication. It is performed at lower forest levels, in trees, and on the roost. Hooting is heard at length, in usual volume, during the molt. Thus there appears to be no behavioral basis on which to postulate the regression of hooting in the inland group. Rather it would seem that the race *obscurus* represents the norm for the species, and that the coastal races have responded to occupancy of the heavier coastal forests with increased specialization of their vocal equipment. In more open forests of the interior, the display signal (see beyond) and drumming evidently provide the inland races with adequate means of distance communication and territorial advertisement. The display

TABLE 5  
DURATION OF ARBOREAL HOOTING IN 1958

Male D		
Date	Observation period	Duration
April 5	4:07- 5:18 p.m.*	1 hr. 11 min.
April 27	11:12-11:20 a.m. 1:37- 5:15 p.m.*	3 hr. 46 min.
April 30	8:10- 9:15 a.m.*	1 hr. 5 min.
May 4	7:59- 8:44 a.m.	45 min.
Male E		
May 7	8:30- 8:38 p.m.**	8 min.
May 11	3:20- 3:58 p.m. 8:12- 8:16± p.m.**	42 min.
May 14	8:25- 8:27 p.m. 8:36- 8:38 p.m.**	
	8:40- 8:46± p.m.**	
	8:53- 8:54± p.m.**	11 min.
May 22	8:53- 8:55± p.m.**	2 min. (identity not confirmed)
June 16	9:37- 9:40 a.m.	3 min.
Male F		
April 30	5:57- 6:21 p.m.*	24 min.

\* Observer left before conclusion of performance.

\*\* On roost.

signal results from the pulsating neck-feather rosettes that are exposed during active hooting. These flashing white rosettes can be seen much farther than the soft hooting is heard. Far beyond range of hearing, one can quickly count with field glasses the beats of each multiple hoot. In open forest types, that is, in such environment as is generally occupied by breeding grouse of the race *obscurus*, erected rosettes could inform distant males and females of the presence of a territorial and calling male. Such effective, eye-catching signals have apparently made it unnecessary for the *obscurus* group of the interior to develop the more specialized vocal structures possessed by coastal races which inhabit denser cover. It is interesting in this connection that Male E, who occupied open yellow pine forest of the lower ravine, spent a relatively small amount of time in hooting from trees.

#### WING SIGNALS

Additional data on communication signals was gathered in 1958 and 1959 that supplement earlier information presented on "wing notes" (Blackford, 1958:149-150).

*Double wing flutter.*—The single wing flutter (Blackford, 1958) is repeated in quick succession; it is given by an excited hen.

*Perching signal.*—A fairly sharp whipping of the wings at the termination of flight as the bird is about to alight in a tree. The loud sound produced is not the usual accompaniment of perching. It is performed by either sex as a location, arrival or approach signal.

*Explosive flush.*—The loud whirring takeoff flight of the Blue Grouse. It apparently serves as a danger, warning, or departure signal to other individuals hidden nearby. When grouse took wing silently, it appeared that the flushed bird was either alone or visible during takeoff to other grouse in the vicinity.

Accentuation of the usual fluttering involved in short tree-to-tree flight appeared at times to indicate location or approach. Unlike the perching signal this fluttering only occasionally evoked immediate response, such as a wing flutter or renewed hooting, from the other member of a pair.

*Aerial signal.*—An unusual type of flight signal was observed on May 6, 1959. Upon entering territory 4, I watched a female leave Male H and fly south to the courting ground on territory 3 (fig. 9). The male hurried uphill to his residence area and flew into a conifer at 35 feet from the ground. After lengthy silence, he commenced low, thumping hoots, given while facing down toward the courting ground. Apparently in response to his efforts, there suddenly erupted a series of rattling *kut-kut-kut* notes from that direction. Instantly, the grouse shot out from a perch near the trunk, hung in mid-air on whirring wings, banked in a nearly vertical drop, leveled out, and glided 70 feet south. He alighted on the ground among evergreens close to the northwest boundary of the other territory. Calls of the female precipitated sharp drumming and vigorous display. The maneuver might be viewed as a momentary checking of flight and subsequent change of course; yet there was no need for such behavior because the way was directly open from the perch to landing site. Evidently the performance was a flight signal, serving both as a location notice and as an instant, excited response to calls of the female. She was soon located a few yards beyond the displaying male.

*Drumming.*—In true drumming flight, in contrast to rotational drumming described by Wing (1946:154), the male springs from the slope, ledge, or log on which he displays and flies with powerfully beating wings to the same or much greater height reached in rotational drumming. After turning in a brief, horseshoe-shaped course, he alights near the takeoff point. His nearly circular flight track averages from 10 to 12 feet in diameter. There is nothing about the performance that resembles the whirling half spin and glide of rotational drumming. In the latter, the drummer slides to an apparent, off-balance, crouching position, involving no such control as that shown in drumming flight. Male E was seen to return from drumming flight to the log itself, although he usually landed alongside, whence he clambered back upon the log or outcrop to perform again. Male E frequently drummed once or twice shortly before seeking his roost.

Wing drumming re-enforces territorial hooting and display, belligerently announces reaction to trespass, is involved in communal courtship, and serves as a signal between the members of a pair.

*Drumming hours.*—Wing (1946:154) remarks: "Although the birds hoot throughout the day in varying degrees, I have so far not observed drumming flight except in the morning or evening." On May 7, 1958, Male D drummed loudly on the southwest slope of territory 2 at 1:24 p.m., then moved downhill into heavy timber where he joined the female in a tall fir. At 4:46 p.m. on May 7, Male E drummed on his north boundary; an immediate response echoed from a drummer on the east ridge. He also drummed under the outlying firs at 2:06 p.m. on May 11. Drumming was the prelude to steady calling and tree hooting that brought the female to the slope above at 3:58 p.m. Drumming usually occurred before 9:45 a.m. and after 5:00 p.m., during peak hours of social activity among the grouse.

The existence and frequent use of a broad spectrum of wing signals and vocalizations among Blue Grouse is beyond doubt. These apparently serve to transmit routine messages concerning arrival, location, summons, warning, and territorial occupancy. The development of an elaborate communication system is undoubtedly of survival value to such a large, gregarious, migratory, prey species. During the reproductive

season this system facilitates the meeting and association of the sexes, the advertisement and maintenance of territories, and the periodic gathering of local populations.

#### BREEDING BEHAVIOR

*Moonlight activity.*—Moonlight courtship by breeding Blue Grouse is a distinct possibility. On the evening of April 30, 1958, Male E returned from boundary display into the courting ground on territory 3. There his attention was diverted by two loud wing flutters from the pines at the southeast border. At once he hastened toward the southern end of the strutting ground and continued deep hooting. By 7:56 p.m. it was becoming difficult to follow him in the fading light under the pines. At 8:35 his calling became louder, then ceased a few minutes later. The only light was that of the overcast moon—barely enough to throw a discernible shadow. From eight yards one could perceive the outline of the bird with glasses. He remained alert on the same spot, apparently with no intention of going to roost. I left him at 9:00 p.m., a late hour in comparison with the usual time, even during longer periods of daylight at later dates, for seeking his roost (table 4).

*Courtship.*—A paired female Blue Grouse makes almost daily visits to the territory after association with the male has begun. During the active breeding period the female spends long hours there, or lingers on the borders near the residence area of the male. She forages, rests, and ranges freely on the territory of her mate. She also roosts in the vicinity, possibly at times upon the territory itself. Association of the pair commonly begins in the early morning; courtship may ensue and activities decline toward midday. From early afternoon to late afternoon the male recalls the female; she may have remained on his territory or ranged elsewhere. Courting is frequent during both morning and afternoon hours but attains its peak at evening. This activity pattern is prevalent for some time before and during deposition of the eggs. Nevertheless a female Blue Grouse will seek the male on any part of the territory at any time of day.

*Association of the sexes during incubation and breeding.*—There is no indication that incubation interrupts the association between members of a Blue Grouse pair other than for required duties of the female at her nest. Although participation in courtship by the nesting female terminates with the onset of incubation, barring failure of the clutch, continued company of the male is sought at familiar locations on the territory.

For example, as Male E foraged in the feeding tree on May 30, 1958, the gray female flew in at 4:05 p.m. to perch 23 feet from me. The male climbed through the branches and began hopping back and forth beneath her, looking up while opening and shutting his bill. The female fluttered to a nearby pine, and the male followed, repeating his antics. When she flew to the fir grove, he pursued her there. Presently she continued on alone to the pine-fir stand to the northeast. At 4:44 a perching signal was heard from the border pines just above the feeding tree. In the evening, wing flutters were heard in the fir grove behind me as the male again foraged in the young fir. This date was midway in the indicated incubation period. The lingering of the female near Male E for four or five hours on this occasion suggested that the nest had been lost, although the female may have voluntarily remained off her nest because the afternoon and evening were warm. The male made no courtship display during this time.

The appearance of the gray female with her brood near the southeast boundary of the territory on June 16 provided evidence that she had successfully nested in that area. On May 30, a hot day, she disregarded my presence to join Male E in the feeding tree, flew to the pine-fir stand, the next heavy cover farther up-ravine, and later returned to linger near the male until nightfall. On the cool evening of June 1, she made only



one rapid passage across the hillside, again going north, and was not heard from again. On the first occasion she remained off her nest, perhaps because of the heat. On the latter occasion, she crossed the territory without delay, avoiding the residence area of the male. The weather may have made her return to the eggs, yet on the way she twice signaled to the interested male when he climbed the slope to intercept her. Evidently, in each instance, the gray female had gone north to the pool for water. Both events disclosed her close association with the territorial male during incubation, when conditions permitted. Such relations appear to be the normal, routine behavior of mated pairs.

The pair bond is maintained for an undetermined period after the young hatch.

Early on June 16, 1958, after hearing three display notes, I located Male E approximately 125 feet beyond the southeast boundary of territory 3 (fig. 2). He was hooting and strutting in full display, 35 feet from the gray female. Postnuptial molt showed unmistakably on his head and neck. Close to the croaking and clucking female, I started a yellowish, downy chick. When pursued, it took wing and flew a dozen yards down the steep canyon slope, rising to a height of four to five feet. From appearance and flight performance, the chick was eight or nine days old.

According to the observation on June 16 of a male Blue Grouse closely associated with a hen and chicks, the male still voices the display note in company of the female at that season and after he has begun the molt. Age determination of the brood indicated the eggs had hatched about June 8. An incubation period of 21 to 24 days would set commencement of the period at sometime between May 16 to 19. In summary, the gray female was with, or sought the company of, Male E on several occasions between May 17 and June 16 and thus was closely associated with him throughout incubation and the early phases of brood care.

The displays and/or "courting call" of the male given late in the season are no indication in themselves that a female has lost her young and that courtship has resumed as has been stated (Brooks, 1926:283-285). As shown by various writers (Wing, Beer, and Tidyman, 1944:435ff.; Bendell, 1955:377), chicks of several family groups may be cared for by from one to a few females, leaving some females temporarily free. Consequently, postbreeding, productive females, unaccompanied by young, may be occasionally expected in the company of displaying males; the latter may then voice the display note, regardless of the negative response of females.

Apparently male territoriality is maintained throughout early rearing of the brood. Because the male is then fairly advanced in the molt, he would likely remain on familiar territorial ground until molt is accomplished. Territorialism, moreover, would appear advantageous if it enabled renewed courtship by the male, either of a paired female or of an unattached, late-breeding female. Male E probably did not complete the molt until mid-July or later in 1958.

*Pair bond.*—Bendell (1955:373) stated that on Vancouver Island males of the race *fuliginosus* were seen to court from two to six females as the females appeared on individual territories of the males; he considered this as evidence that males are polygamous. There is no reason at present to think that the race *obscurus* differs in this respect. Yet where population numbers, spatial distribution, or topography favor situations where single females are attendant on males, a remarkably close pair bond develops. Considerable evidence of a season-long pair bond was obtained during 1958 and 1959: (1) early association of female with territorial male, (2) response to signals between members of a pair, (3) familiarity of female with territory of male, (4) constant use by female of border area adjacent to residence area of male on territory, (5) lengthy courtship and nuptial activities, (6) close association of sexes through incubation and

early brood rearing, and (7) season-long occurrence of female on territory. The strong territoriality of only the male of the pair, however, suggests that polygamous behavior may occur under certain circumstances.

*Communal display in 1958.*—Conclusive evidence of group display by forest-dwelling grouse of the race *obscurus* was obtained during the study in 1958. At evening on May 4, a gathering of both sexes was witnessed in the upper swale, a shallow, partly wooded and sloping depression, 90 feet in diameter, situated just above the east gully, 50 feet north of territory 2 (fig. 1). Four males were identified about this circular area; hooting indicated that a greater number was present. One or two females were present, as demonstrated by vocal and wing notes. Other, silent females were probably also in attendance.

Responsive drumming preceded the occurrence. Male E in the lower draw and Male D high on the northwest border of territory 2, together with a third male that appeared at mid-ravine on the shoulder of the east ridge above the pool, staged these preliminaries. Their drumming flights were accentuated by booming display notes from Male D. Presently the birds converged on the swale, with the exception of Male E, who remained on his recently acquired territory.

I left Male E on his hooting ground at 6:30 p.m. and moved up the ravine to take cover. Twenty minutes later he began the first round of drumming. As I entered territory 2, a second round commenced. Silence ensued when I arrived in the upper draw. At 7:43, when near Male D, a wing drum suddenly sounded behind me over the low, rounded dividing ridge in the upper ravine, and a male grouse was seen to drop in the spin of rotational drumming. Within seconds he climbed out of the east gully, came over the hump, and again drummed excitedly. He had appeared fully 75 feet within the north boundary of the territory, having crossed or ascended the eastern drainage channel. There was no challenge from Male D at the fir borders of the northwest boundary although this was the favorite haunt of that individual. Instead, cackling alarm notes, *cac-rrrr-cac-rrrr-cac-rrrr*, came from that corner of the territory as the bird moved up toward the middle of the slope at the head of the ravine. Evidently the alarmist was a female, judging from the notes emitted. The newcomer displayed in response to this weird racket and ran uphill as though to intercept her. By his ragged tail fan he could be distinctly recognized and was designated "Male G." On the steepening slope, he paused excitedly to drum. At once, two other drummers performed, one 200 feet down the east ridge (probably the bird from above the pool), the other on the rocky rise above the upper swale on the far side. Running rapidly, Male G turned back that way into the half-wooded depression.

Soon a drummer displayed on a rocky prominence 110 feet north of territory 2. Indications were that, upon the break-up of the courting pair, Male D had also crossed above me to mid-slope, but at a much higher angle on the hill front than the female.

As the light faded, two wing drums reverberated across the shallow depression. I moved into the clump of young evergreens where Male G had disappeared. The wailing "hen" had preceded him. Then, in an opening a few yards upslope, the warning *cac-rrrr-cac-rrrr* broke out again, followed by an outburst of rotational drumming and wing fluttering given together. Instantly, the "lookout" males on the western promontory rock and on the rocky rise to the east responded with thunderous drumming flights. In the deepening dusk, such a confusion of drumming and hooting arose throughout the area that it was not possible to keep account of it. Cackling alarm notes sounded again, this time below me in the dim woods.

Silence followed, save for occasional drumming flights from the two outlying par-

ticipants. Then occasional wing notes and hooting revealed that the performers had dispersed. A single wing drum then came from the high promontory rock. As I left in darkness at 8:35 p.m., a drumming flight from the promontory again emphasized that Male D remained alone. One other drummer responded distantly from along the east ridge.

This assemblage of breeding Blue Grouse that was apparently interrupted before some members arrived and which failed to follow its customary course as a result of my intrusion still gives abundant proof of group display. The instant response of the lookout drummers to activities in the swale shows that such display in grouse of the race *obscurus* is not limited to courtship between scattered pairs on common ground but becomes truly communal, involving all participants in related activity. Thus there is group organization and at times joint participation in some phase of the event.

It was evident that a high pitch of excitement is attained at these gatherings; indeed it was exhibited by individuals as they arrived and rapidly increased during group activity. This excitement, built up and sustained by the group, may have a definite function in the reproductive behavior of the species by stimulation and synchronization of the gonadal cycle in both sexes.

What signal alerts members of a population of Blue Grouse and brings them to communal display? A concerted movement toward the upper swale on the evening of May 4 was observed. Wing drumming, the loudest audible performance of the interior races, was a major feature of the gathering on this occasion, but before it began the movement was underway. A favorable change in the weather during the height of courtship activity may likely elicit the formation of such an assemblage. Yet there seems to have been some previous anticipation of the event, because the participants converged rapidly toward one site without any perceivable signal prior to the preliminary drumming in the ravine.

Group performance does not appear to last long; the birds disperse at late dusk. There remains the possibility that communal display may occasionally continue through a brief period of evening darkness until light is provided by the early rising of the moon. In this instance the moon was full on the previous night.

A male enroute to group display will readily cross the territory of another male that borders a communal court. He will unhesitatingly drum on occupied territory, apparently in announcement of his imminent arrival at the gathering. No challenge resulted from the "trespass" by Male G that ordinarily would have invited immediate and hostile retaliation. Close approach or drumming at the borders of a territory, unless by a neighboring resident, is usually not tolerated once the season is well advanced.

Communal courting grounds appear to lie adjacent to established territories. In the instance described, the upper swale bordered territory 2 on the north. The area on the west hillside where group display began in 1957, except where the occupant male courted on his neighboring plot, has been shown by subsequent occupation not to be a part of territory 3. Evidently the communal display grounds of both 1957 and 1958 bordered but did not include occupied territory.

*Communal display in 1959.*—Toward evening on May 11, Male H on territory 4 was alerted by arrival of two Blue Grouse, a female from the timber to the northwest where a pair was known to court and a male in a fir at the boundary of his territory. No hostility showed between them, although Male H momentarily joined the female after she arrived, and then the male.

The newcomers presently retired to a wide grassy opening on the upper border of the plot (fig. 9), where active courting began. However, they refused to continue under

observation. The approach flight and alighting flutter then notified me of the arrival of a fourth grouse which may have been the small brown female that came regularly to Male H.

One hour and 47 minutes after their arrival, the visiting pair flew southward along the hillside 140 yards beyond territory 4, above and beyond the old courting ground on territory 3 (now vacant). As I followed, a wing drum was heard behind me, apparently a signal from Male H to the brown female or to the departing pair.

Drumming, courting calls, and low hooting directed my search on the brush-scattered slope. The pair was found in close company of a third displaying male and a small, very light-colored female. Quickly one male, followed by the other, whirred back north to the old courting ground. A wing note came from the pine stand there. Instantly both hens rose together and in curving flight rejoined the males. Two calls from the old display ground at dusk revealed their renewed activity.

Five birds, 2 males, 2 females, and 1 unidentified, had thus converged on the territory of Male H, who also participated. My presence forestalled group activities at the grassy opening. The quick contact made by the two courting pairs, and their return north together, disclosed that these birds were well aware of one another's presence and had gathered for group display. As in previous years the communal court bordered on the territory of a male.

#### CONCLUSIONS AND SUMMARY

No basic difference has been observed between the behavior of individual grouse of the race *obscurus* and that reported for grouse of the coastal race *fuliginosus*. Considering that the breeding habits of the coastal races are still little known, it is much too early to say that any significant divergence exists in the social behavior of the *fuliginosus* and *obscurus* groups. Specifically, no available evidence indicates that group display is, or is not, present in the *fuliginosus* group.

Certain features of local topography and flora seem to favor the location of communal courts. But apparently among Blue Grouse the site is not fixed. In each of the years that group display occurred, a different place in the ravine was used.

Whether the common display ground is a site for actual mating is not known. However, if social assembly of both sexes during the breeding season defines a lek species, then the Blue Grouse is a true lek form. It follows that lek behavior is not limited on this continent to those grouse that inhabit open country and its borderlands, for example the Sage Grouse (*Centrocercus urophasianus*), Prairie Chicken (*Tympanuchus cupido*), and Sharp-tailed Grouse (*Pedioecetes phasianellus*), nor to nonterritorial galliforms, but that it may also occur in the forest-dwelling, territorial Blue Grouse.

Territorialism of breeding males of an inland race of the Blue Grouse has been confirmed. Behavior indicating mate selection and pair formation during spring migration was observed. The arrival, occupancy, early season behavior, territorial defense, boundary display, localization, and other territorial habits and activities of resident males are described.

New information concerning means of communication employed by this species was obtained.

The calling of males and response of females, courtship, movements of females on male territories, their association with males during incubation and brood care, and the close pair bond existing between members of a Blue Grouse population are reported.

Because the behavioral characteristics of this inland population studied evidently do not differ materially from those of the coastal races of *Dendragapus obscurus*, the two racial groups are more closely allied than has been formerly implied.

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