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TERRITORIALITY AND BREEDING BEHAVIOR OF A POPULATION OF BLUE GROUSE IN MONTANA

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Recent investigation of a forest-dwelling population of Blue Grouse (*Dendragapus obscurus*) in northwestern Montana has disclosed significant new facts concerning the life history of the species. Distinctive features of the nuptial display, wing notes, hooting habits, and territoriality of breeding males were observed. These features provide a definite basis for comparison with the characteristics and behavior of the coastal races. This study was begun when close-range encounter with a courting male revealed a display of unusual interest. Behavior patterns, previously unreported, were noted as investigations were continued through the season. As a result, it was possible to obtain a clear outline of the territorial relations and social structure of this breeding population.

ACKNOWLEDGMENTS

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AREA DESCRIPTION AND STUDY PERIOD

The study area in Montana (fig. 1) is a forested ravine and its enclosing slopes which lie on the upper, south-facing front of the Purcell Range. It is between Canoe Gulch to the west, and a high, flanking ridge descending to the southeast. The Kootenai River flows around the extended lower spur of this ridge to form the Big Bend of the Kootenai in central Lincoln County. This steeply ascending draw heads out at a saddle on the sharp shoulder of the mountain at about 4300 feet elevation. In its upper portion, two run-off channels, the wooded "west ravine" and the more rocky "east gully," separated by a low dividing ridge, form the narrow, descending floor of the depression to a point about midway in its course. Below, the west ravine continues down slope as the single, summer-dry drainage channel. It receives also the overflow rill from a seepage pool situated in mid-ravine close to the eastern hillside.

The lower ravine is marked by the widely parted walls of the draw and by its own broad, down-slanting floor. Half-way down the mountain front, at about the 3200-foot level, the ravine becomes shallow and is lost as a surface feature.

Mixed yellow pines (*Pinus ponderosa*) and Douglas firs (*Pseudotsuga taxifolia*) forest the floor and slopes of this little canyon. Grassy openings frequently break its arboreal cover. Aspen (*Populus tremuloides*), in scattered groves, mingles with the conifers in the deeper parts of the draw and is found on moister sites at the lower levels.

Thickets and scattered undershrubs, wild rose (*Rosa*), snowberry (*Symphoricarpos*), serviceberry (*Amelanchier*), and chokecherry (*Prunus*), together with balsam root (*Balsamorhiza*) and a wide variety of other forbs and grasses, carpet the area. Logging 12 years ago created minimum disturbance due to selective practices and limited cutting of trees and it has been followed by more than a decade of recovery.

In the spring of 1957, nine trips were made to the ravine, on April 16, 20, 22, 30, May 9, 15, 23, June 1, and 3. A total of 40 hours and 55 minutes was spent there, of which 21 hours, or 51.2 per cent, were occupied in close-up observation of displaying Blue Grouse. My earliest morning arrival on the area was at 8:30 a.m.; the earliest observation of a male bird was at 9:51 a.m. The latest evening observation was at 9:05 p.m.

IDENTITY AND TERRITORIAL LOCATION

Three breeding males occupied the ravine. At first my attention was centered on courtship display, but I soon became aware of individual identity and territoriality in these grouse. The displaying birds were designated males A, B, and C, and they occupied territories 1, 2, and 3, respectively. From May 9 on they were sought and successfully located entirely on the basis of this classification. No male was seen at any time on the territory of another except on April 22, 1957, when apparently the entire population was gathered in communal display on the lower west slope. Except for this occasion, each male was found and observed only on his own limited territory. Attendant female grouse were less approachable in the courtship period, and their number was not clearly determined. They were observed at intervals, but little attention was given them except in relation to the calling and courting of the males.

Male A, the first grouse seen, was a large grouse in rather light plumage. He displayed a perfect tail fan, a feature that at once distinguished him from other males in the area. This bird was notable for an uncommonly confiding nature and tolerance of close approach. At times he came voluntarily to within 6 or 7 feet of me, and, although often pressed closely, he never took wing except to fly into his roost tree at dusk. Male A was first encountered displaying among the open pines of territory 1. This plot, approximately 400×500 feet, included the eastern portion of a dense pine-fir stand on the floor of the lower ravine. From there, it extended up the semi-arid, pine-clad slope of the eastern ridge to rock slides and outcrops along the slanting summit. A game trail traversed the lower section, leading to the seepage pool and upper ravine. Male A was observed on territory 1 as follows:

April 16 (4:50–6:00 p.m.) 1 hour and 10 minutes; May 9 (3:37–4:30 p.m., 5:30–5:45 p.m.) 1 hour and 8 minutes; May 23 (8:12–8:51 p.m.) 39 minutes; June 1 (3:32–9:05 p.m.) 5 hours and 33 minutes; June 3 (3:40–7:00 p.m.) 3 hours and 20 minutes. Total observation time: 11 hours and 50 minutes. Male A was sought briefly but not found on April 20.

Male B, the occupant of territory 2, was a bird of medium size, somewhat darker than Male A. He was clearly marked by two short replacement tail feathers on the right side. These two adjacent feathers were about 1½ inches shorter than average. Male B was an energetic individual. When he was on the ground he was not tolerant of an approach closer than 30 to 40 feet. At that distance, he was indifferent to an observer and engaged in every normal activity. If approached too closely, he hurried away on foot. While flying, he made no effort to avoid me and occasionally came closer to me than he did while on the ground. Trailed on the ground for hours to all parts of his territory, he kept at a distance but he seldom took flight except to follow the hen. In only one instance did flight lead off his territory; on April 22, two birds from this territory were followed down the draw, where communal display was observed.

Territory 2, 400×600 feet, was a rather densely forested plot. It encompassed the

upper ravine, reaching from just above the seepage pool to a hundred paces below the high divide. At its upper limits the sloping walls of the draw converged, the ground there rising steeply to the saddle. Pine and fir, broken by grassy openings, ascended the ravine. Thickets of saplings partly filled its eastern gully; over the rounded dividing ridge on its slanted floor, taller firs were clumped in pure stands that became open near the summit of the mountain. Male B was observed on territory 2 as follows:

April 20 (4:23-4:33 p.m.) 10 minutes; April 30 (9:51 a.m.-3:05 p.m.) 5 hours and 14 minutes; May 15 (4:40-6:58 p.m.) 2 hours and 18 minutes. Total observation time: 7 hours and 42 minutes. On April 22 Male B was identified but was not on his territory.

Male C, a frequent drummer, appeared to be a darker, larger bird than Male B. He could be identified by one short tail feather on each side of the fan and several other tail feathers of irregular lengths on the left side of the fan. This male seemed rather wary but showed indifference to me at the height of courtship display when he was near the hen. His strutting ground was on the lower hillside of territory 3, a large irregular area estimated at 600×800 feet. Lying on the broad floor of the lower ravine, his territory extended up the western slope to include extensive open pine woods. It was not as well defined as the other two territories. This was due both to a wider separation of its vegetational components and to a briefer investigation of its occupant and his movements. The territory included the west portion of the pine-fir stand adjoining territory 1 and was separated from it by an old logging lane through the timber. From that point the territory spread across the floor of the draw, covered with low brush, to ascend the west hillside. On the southern or drainage side the apparent limits included an isolated stand of conifers. The edge of the heavier forest, descending from mid-ravine, bordered the plot on the north. From the west slope, there was a clear view across to the face of the east ridge opposite and the upper portion of territory 1, 250 yards away. Tall antelope brush (*Purshia tridentata*), serviceberry, and abundant balsam root gave portions of the slope increased cover, making the location of a displaying or even drumming bird difficult. Male C was observed on territory 3 as follows:

April 22 (5:10-5:25 p.m.) 15 minutes; May 9 (6:03-7:15 p.m.) 1 hour and 12 minutes. Total observation time: 1 hour and 27 minutes. Male C was sought on June 3 but not found although drumming could be heard. Drumming on three additional dates also indicated that a male Blue Grouse was stationed on the plot.

Investigation of territories 1, 2, and 3 always revealed one or more of the males on home ground. Failure, in a few instances, to locate an individual on his territory did not prove the absence of the bird. As hooting declined, the search for silent birds became a problem. Only a knowledge of the territorial behavior and individual habits of the three male grouse made later surveys of this well-wooded area successful. The three territories were seldom checked on the same day because a resident bird, when found, was usually followed for the remainder of the visit. Territorial borders were inferred from movements of individuals, the concentration and nature of their activities, and the distribution of vegetation. No territorial defense was observed. However, "territorial drumming" was noted throughout the course of the study.

TERRITORIALITY

Territoriality in breeding male Blue Grouse is an aspect of behavior that, with increasing information, is assuming greater significance. Study of territoriality facilitates comparison between the racial groups within the species and provides information on the habitat relations required for the solution of problems in wildlife management. Territoriality in the Pacific coastal Sooty Grouse, or *fuliginosus* group of *Dendragapus obscurus*, appears well authenticated (Bendell, 1955:369; Hoffmann, 1956:327). Studies

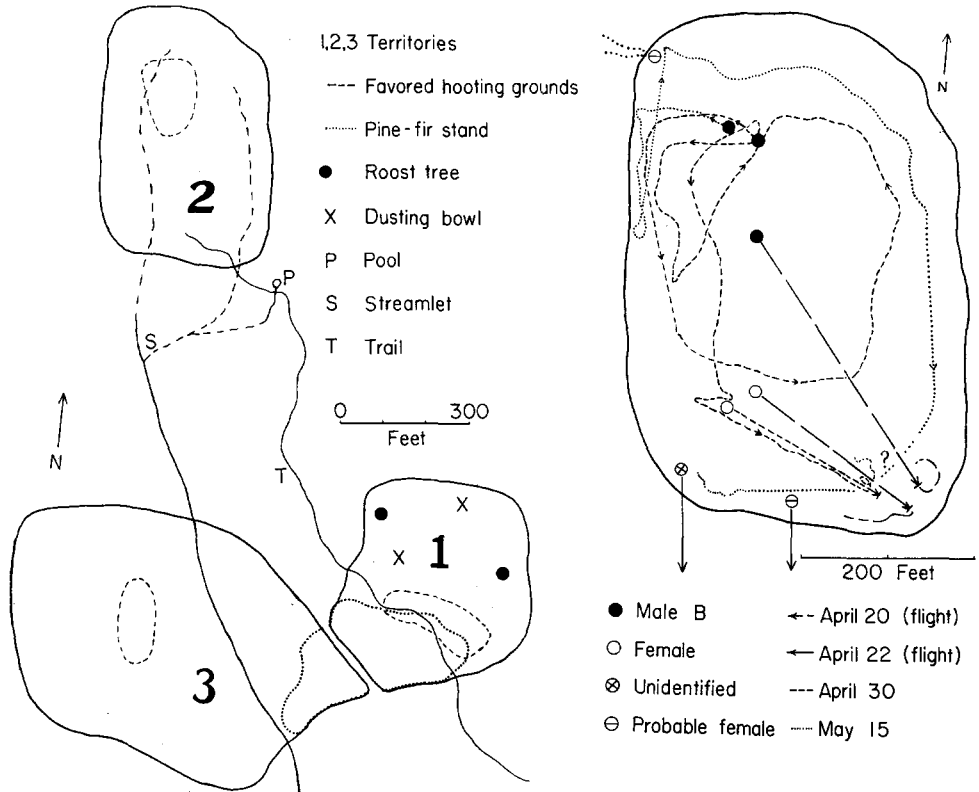


Fig. 1. Left: diagram of south front of Purcell Range, central Lincoln County, northwestern Montana, showing breeding season territories of male Blue Grouse in spring of 1957. Right: diagram showing movements of Male B on territory 2, April 20, 30, and May 15, 1957, and off-territory flight of two unidentified Blue Grouse on April 22.

of the interior Dusky Grouse, or *obscurus* group, occurring in the Rocky Mountain and Great Basin regions, have been less representative. Present reports deal only with breeding populations of the race *D. o. pallidus* occupying unforested sites. A tendency toward communal display, with no obvious territoriality, has been noted in Dusky Grouse on open summer range (Schottelius, MS; Caswell, MS). However, the vast montane coniferous forests of the interior, more open in character generally than those of the coastal areas, must be regarded as the metropolis of the Dusky Grouse. No major disparity is to be expected between the territorial habits of the two racial groups, both of which are essentially forest and forest-edge dwelling forms. Observations of the birds of the Purcell Range support this view. They show that, while the tendency toward communal display is indeed evident in this timber-dwelling population of Dusky Grouse, solitary display is more typical. In addition marked territoriality in both breeding behavior and daily activities is definitely indicated.

Routine daily activities.—Many routine activities of Blue Grouse were recorded in the course of this study. The everyday living pattern of each male was followed entirely on the bird's own territory. Male A may have sought water by short, off-territory flights to the seepage pool, but this is not definitely known. He was seen to take 14 identified food items, and many others, while foraging on his limited, yet apparently adequate

area. Feeding, resting, dusting, roosting, and other usual pursuits might all be observed on a single trip to the ravine.

With the warm days of late May and early June, there was a marked decline in nuptial activities. This was accompanied by increased feeding and lengthy intervals of leisure and rest. The cool shelter of two outlying evergreens on the north border of the lower wood, the scattered shade of groves on the pine slope, and an isolated, heavily branched fir on the higher rock slides were stations favored by Male A in late spring. At 4:10 p.m. on June 1, after 38 minutes of foraging in an area bordering the pine-fir stand, this male moved uphill on a northerly course. He progressed about 150 yards in three hours while foraging, preening, hooting, and displaying. In the evening, a rock slide and brush opening of the upper ridge, where the sunlight lingered, proved attractive. A rest period of 1 hour and 5 minutes there was followed by 43 minutes of occasional leaf-foraging and brief pursuit of insects. Time was spent in further preening, wing stretching, and "dozing." At 8:57 p.m. he had partly retraced his track along the slope and sought his roost. An immature yellow pine, standing at mid-slope near the eastern border of territory 1, was utilized by Male A as his roost on the evening of May 23. A fir, clumped with two yellow pines on the edge of a pine wood and slide rock opening along the western side of this plot, served as his shelter for the night of June 1.

By June 3, the bites of flies of the deer fly type and the bird's scratching for relief had made the base of Male A's upper mandible slightly bloody. Toward evening he hastened along the pine slope to a dusting bowl on an upper game trail and took a dust bath. Another such bowl was located beneath the low-spread boughs of the big evergreen on the upper slides.

Residence on territory, judging by observation and the facility with which this bird could be located, seems to have been continuous. Moreover, at the time he was first found on April 16, this male had already been in sufficiently lengthy possession of his territory to have attracted a hen. Similar routine activities of occupant males were observed on the other two territories.

BREEDING BEHAVIOR

Breeding behavior, together with related territorial organization, revealed the outlines of the social structure of this population of Blue Grouse. It was marked by disclosures of unusual interest concerning communication media, display characters, and the relations between the sexes.

Calls.—To appreciate breeding season activities in the ravine, it is advisable to clarify the terminology used to describe the vocal characteristics of Blue Grouse. "Hooting" commonly refers to the series of five or six notes of the calling male. This is low-toned in the Dusky Grouse and resonant and far-carrying in the Sooty Grouse. "Multiple hoot," the term employed by Caswell (MS), refers to this type of hooting specifically. Not all of the notes in a series may be audible in the case of the *obscurus* group, and there are some indications of individuality in rendition. The loud single note, *oop!* (as phoneticized by Brooks, 1926:281) is termed here the "display note," since it climaxes the full display of the courting male. Other calls heard were as follows: *Kut-kut-kut*, an alarm and warning note of two or more syllables, often extended to a series. This is given by both sexes. *K-r-r-r-r-r*, a low warning note which is voiced by a hen before flight. *Kutter-r-r-r-r*, a high, racketing, excitement call, long continued, wavering, and fluctuating greatly in pitch. This is given by the hen.

Wing notes.—No distinction appears to have been made among the wing notes of the Blue Grouse, and apparently only one—wing drumming—has been described. Three

very definite forms of this medium of communication and expression were utilized by the forest-dwelling birds at the Purcell Range site:

WING FLUTTER.—A brief flapping of loosely beating wings as the grouse rises 8 to 10 inches into the air. Although it lacks the power of display drumming, the sound still carries very well. Usually this is an arrival, location, or response signal. It is performed mostly by the hen but may be made by both sexes on the ground or in trees.

WING DRUMMING.—The usual drumming display flight. It is given as the male springs about three feet in the air, "hangs" momentarily on swiftly beating pinions and then descends. Variations, with the bird rotating before descent, have been described (Wing, 1946:154). This is performed as an individual display or enacted during communal courtship.

WING CLAP.—Similarly enacted by the male in an upward aerial leap. It is a single, sharp, very loud wing note. This was observed once; it was given from a log in excited response to the flight of a hen from a male's courting ground.

The volume and modulation of wing beat in take-off and flight, and sometimes in flight approach, also appear to function as means of communication.

Hooting stations.—Ground level hooting, accompanied by display, occurred at all points of a territory in the ravine. Nevertheless, a preferred strutting area of limited proportions seems to have been selected by each hooting bird, and from it the more intensive hooting was done. Similar vegetation distinguished all three strutting areas. They were in forest-edge situations that combined grassy, open, narrow forest border, and a dense conifer stand. Occasional rocky outcrops or ledges were found in the openings, and old logs were present on the deep-shaded forest floor. Any of these, or the openings themselves when the sun was not too strong, served for display. The principal variation was on territory 3 where the grassy, shrub-dotted, hillside floor of a tall pine grove provided the available "opening" farther from dense forest shelter.

Arboreal hooting.—For many years the reported behavioral differences between the racial groups of the Blue Grouse have influenced their taxonomic treatment (Hoffmann, 1956:321). Although morphological intergradation between them has now been described, and the taxonomy of the Blue Grouse rests on that fact, the differences in behavior between these groups are still important when comparing the coastal and interior forms on a broad biological basis. Consequently the validity or extent of these dissimilarities requires re-examination. Specifically, the belief expressed by Brooks (1926:282, 286), and presently held, that courting males of the *obscurus* group invariably hoot from the ground, is subject to correction.

It has long since been reported (Edson, 1925:228; Johnson, 1929:292) that the tree-hooting Sooty Grouse may occasionally digress from its usual behavior and hoot from ground level. Wing (1946:157) cast some doubt on the supposedly rigid adherence to terrestrial hooting in the Dusky Grouse, but no instance of departure from this habit was given.

Arboreal hooting by Dusky Grouse referable to the race *richardsonii* has been observed in the course of this study. My records show a marked tendency on the part of this representative of the *obscurus* group to vary from its supposedly typical behavior in the selection of a hooting site. On four occasions in the Purcell Range ravine, grouse were seen to hoot from trees. This activity was usually accompanied by, or alternated with, partial display, and two of the three males were involved. As the nature of these four occasions differed, and so that proper evaluation may be made, two instances are included as described in my field notes:

April 20, 1957. At 3:55 p.m., a female Blue Grouse flushed into a yellow pine. I kept her in sight from the low ridge on the floor of the upper ravine. After 20 minutes she flew down into mid-level

branches of a denser pine grove around the spring pool. I then climbed from the grassy opening of the ridge over toward the west "run" of the draw, and into immature Douglas firs. Had gone but 2 rods and only a few yards within the fir stand, when I heard hooting of a male grouse. No displaying bird was in sight on the ground, but the full-toned hooting seemed near at hand. Moving on a few paces, examining the trees, I turned east, up-slope toward the crest of the dividing ridge. The hooting was repeated, and I quickly saw a Blue Grouse [Male B] crouched on the fork of a limb, 12 feet up in an 8-inch (d.b.h.) fir. The performer was only 30 feet away and facing me. His wings were at sides, the tail but little fanned. With glasses, the combs showed a narrow, yellow curve over either eye, and the deep reddish-purple air sacs were moderately dilated. As he nodded, their white feather rosettes were half flared, while he continued hooting at frequent intervals.

I circled uphill for a side view, moving to within less than 25 feet. The grouse was perched about 2 feet from the treetrunk. Growing accustomed to my near presence, he resumed hooting; and fanned his tail to a quarter circle, tilting it a little forward over the back. The neck was considerably inflated. The eye wattles were now dull red, though but slightly distended.

The Blue Grouse faced the fir trunk, stepped to it along the branch; then out a similar distance on a lower bough. He hooted several times, and moved toward the branch tip. Near its limber end, he took off in swift downhill flight in the direction taken by the hen. At once, from above the spring, a high, racking *kutter-r-r-r*-ing call echoed at length through the timber. [This bird was under observation for ten minutes and the hooting was as loud as that heard at any time in the breeding season.]

May 23, 1957. At 8:27 p.m., when the big Blue Grouse of the eastern slope [Male A] reached the blackjack yellow pine, he flew with loud whirr of wings to a bough 12 feet up on the west side. I moved uphill from the pine, about on a level with and 25 feet from him. The grouse stepped out among the needled branchlets to feed on flower buds. He interrupted feeding to hoot—several series, some of them counted at 5 beats, and fairly audible, given with little display.

Returning along the bough, the Blue Grouse spiraled upward around the treetrunk, hopping from branch to branch. He paused at intervals to eat vigorously, cleaning out several clusters of the dark red cone flowers and pecking at staminate buds also. Continuing upward, the big, light-colored male often fanned his tail. To a quarter fan at times, lifted forward and tilted to one side. Further hooting was interspersed with feeding. Often it was barely heard, or else inaudible. Yet there was the usual pumping of air sacs, accompanied by partial display when the bird perched near the pine trunk; or muffled hooting with no display out among the limber side branches where he fed on cone flowers. Pulsation of the gular sacs was pronounced and plainly visible, the neck pockets being well exposed, although their feather rosettes were not broadly extended. At 8:37 p.m., 30 feet up in the pine, the grouse settled on a large limb facing me, and his own length from the treetrunk. There he hooted for a time—7 or 8 series of low notes, at 15- to 20-second intervals, not audible at 12 yards, or just barely so.

It was now early dusk. Male A went farther out on the same limb and was seen as a silhouette among the needle clusters. He flew to a spreading branch above, moved to a lateral fork among overhanging branchlets, and at dusk (8:51 p.m.) had gone to roost. [Much ground level hooting is likewise low in volume and sometimes inaudible at close range. It is similarly interspersed with display and other activity. Tempo increases, volume increases, and tone ranges higher when a male is calling to or courting a hen.]

The use of arboreal hooting sites by the Dusky Grouse appears to represent a continuation of normal terrestrial activity, rather than a definite seeking of trees as hooting stations. The ground level pattern of courtship display, while dominant in the *obscurus* group, seems to be in no way fixed or restrictive. The urge to hoot is persistent and is evidenced throughout the range of diurnal activities at this season. Even interruption by a potential enemy may not suppress it. If disturbed on the ground, at least limited display may again be indulged in after the bird has found safety at higher levels in trees. When the advent of the observer is not viewed with suspicion, or if his presence has been accepted, hooting and display, in a measure consistent with the elevated site, may readily coincide with other arboreal activity.

The different type of hooting site selected by the Sooty Grouse, together with its far-

carrying vocal efforts, would appear to have developed in conformity with a denser forest habitat, within the borders of which the *fuliginosus* group makes its home.

Territorial drumming.—Whether it was territorial or communal, drumming had social implications in this population. Through records of frequent performances, and by accompanying Male A, it became apparent that in the late afternoon this bird habitually moved up through the open pines of the eastern ridge and from its slope, toward evening, responded to the wing drumming of Male C from the western hillside opposite. Similar movement by the latter from the floor of the ravine was indicated. On May 9, Male A also gave instant response from his ridge front station to the flight of birds which I flushed across the draw on territory 3.

A wing drum from the hillside on that territory, heard by Male A at 6:48 p.m. on June 3, caused him to stand up on the alert in his dusting bowl. He faced in that direction for many minutes with primaries stiffened and extended to the ground, flicking them intermittently. My presence apparently inhibited a more demonstrative response.

When going to roost on May 23, Male A performed a wing flutter. Facing westward from the trunk of the pine along a heavy, lower bough, the big grouse sprang 10 inches into the air and executed this softer wing note with loosely beating pinions. Descending rapidly to the branch, he stepped out to feed on flower buds of the pine. After three or four minutes, there was a loud wing drum from the west slope. It was clear that responsive or rival drumming, from opposite slopes, between males on their respective territories, marked the usual course of events during the late afternoon and evening in the lower ravine. Perhaps this was also true in the early morning.

Display characters.—Nuptial displays of the Blue Grouse have long received attention since they rank among the most spectacular performances of the Tetraonidae. But certain aspects of the courtship routine, such as the eye-comb display and its accompanying color changes, have yet to be reported in detail. The distensible eye combs present in this genus are perhaps the largest and most highly developed in the New World tetraonids. When erected they become prominent, extending almost across the crown of the head. The color has been described by various writers as "yellow," "orange-yellow," "dusky-orange," and "fiery red." Only Wing (1946:156) has given a brief explanation for these seeming disparities: "In *Dendragapus*, the combs are normally yellow, but they change color under stress of sexual fervor and may become bright red."

On April 16, while descending the east ridge through the open pine of the ravine, I encountered Male A in full display. During the following hour and ten minutes, it was possible to observe the bird with 8×40 binoculars from distances of 11 to 30 feet. Occasionally the bird could be watched at a distance of 8 feet without field glasses. When first seen the grouse was engaged in the usual courtship performance with tail broadly fanned and tilted forward, wings trailing, air sacs dilated, and with the white feather rosettes encircling the air sacs widely flared. At this time another startling feature was visible. The eye combs were broadly erect and were bright orange to blood red. After some minutes this color subsided to orange-yellow. The orange tinge slowly disappeared; and the combs, still fully distended across the top of the head, turned to clear, deep yellow.

As I moved to within 12 feet of Male A and he resumed his display, it was apparent that the deeper coloration first appeared along the basal strip of the eye wattles, turning them orange-crimson for their full length. Above and around the basal area, the fringe of the comb still showed lemon yellow. Rather rapidly a blood-red flush spread throughout the comb, from the base into the fringe or dilated "spikes" adorning it, until both combs became brilliant orange and then crimson. Soon this crimson suffusion receded until, within four or five minutes, the eye combs, although fully erect, were clear bright

yellow once more. The suffusion might be renewed before it had completely vanished, obviously as his excitement increased. As the color receded, the base of the comb first turned yellow, just as it had initially turned red. Then the fringe of the comb cleared, the crimson subsiding to orange and the recession of color passing out toward the tips of the short spikes, where the brighter color disappeared last.

This occurred repeatedly; yet, in spite of the approach of a hen that flew up to a nearby perch in the pine-fir stand on the floor of the ravine, the color was not so brilliant as the grouse grew less wary. I circled the male to observe the other bird. When I returned to the male, he had ceased to strut. His plumage was in its usual form. Only the eye combs were half erect and were yellow in color. By close approach, I succeeded again in inducing display. But the Blue Grouse no longer attained the degree of excitement of his earlier efforts, nor did the eye combs assume the brilliance of their first coloring.

On each of seven subsequent trips to the ravine in the active breeding period, the foregoing observations were frequently confirmed. Close-up study of Male A and the two other males afforded numerous opportunities for noting the stages of erection, as well as the diffusion and recession of display coloration, in the eye combs of *Dendragapus obscurus*.

In repose, when contracted to a narrow curve above each eye, the combs of the male Blue Grouse are overlaid and concealed by compact skin folds and feathers of the head. A yellowish, terminal, circular spot may be visible in the loreal region directly in front of the eye. Raised in limited display, or observed in the process of contraction, they arch in lines of dull yellow over each eye. Dilated moderately, in response to mild stimulation, the combs appear as slightly expanded wattles of dusky red that brighten or fade again to ochre yellow. Such lesser manifestations may be preliminaries to strutting and full courtship display, or they may mark the usual appearance of the hooting bird in the absence of further excitation.

It is evident that the eye combs in this species are equipped with a specialized vascular system and nerve supply which react to the emotional stimuli experienced by the bird. Their physiology should prove of interest.

Courting.—Courtship activities provided the most certain proof of territoriality among breeding males in the study area. Such activities also revealed the more important social mechanisms that lead to the meeting and mating of members of this population.

On April 30, hooting was a chief occupation or an almost continuous adjunct to other male activities. Male B was located by his hooting at the edge of a fir clump high in the west ravine near the head of the dividing ridge. Between 9:51 a.m. and 12:30 p.m., while I followed him leisurely, he foraged, hooted, and displayed, taking a circular course about 100 yards in diameter that circumscribed this favorite area (fig. 1). After he had returned to the spot near the head of the ridge, where he had been found strutting 2½ hours earlier, I decided to press him more closely. He proceeded once more to the west slope, and then he hooted again within a dense fir stand where he had previously performed. However, when I retreated to a distance, the hooter hurriedly paraded past me on the slope below and returned directly to the starting point. At this time, from the edge of the upper fir stand, he settled down to steady, loud hooting, with little display, continuing for more than an hour. During one period of 10 minutes, Male B voiced his five-note series at least once every 15 seconds, with the exception of one 40-second interval. A little later during a 10-minute period, this male hooted 34 times, each time giving the full series. I moved to within 25 feet of him, and he edged upward across the open space to mount a log; his steady *umphs* continued.

At 2:00 p.m., I thought I heard a light wing flutter behind me from down the ravine. This impression was immediately confirmed by the calling male which went into striking display and dropped from the log. His eye combs flushed a bright crimson; they were fringed at the tips with orange-red and were distended broadly across his crown. His hooting stepped up to five of the five-beat series per minute.

With as much strut and display as the terrain and brush permitted, the hooter circled at 60 feet and hastened down the west ravine. Twenty-five yards away, I saw him go over a low rise in the floor of the draw, and hurrying forward I quickly relocated him in a little fir grove perhaps 100 yards below his upper station. The intensity of this male's display suggested the presence close by of the hen. Moving slowly, I flushed her from beneath a nearby evergreen. She hurried into some low briars in a little depression. Male B then crossed close in front of me, tail fanned to half circle, neck rosettes flared, and eye combs fiery red. Near the hen, he made an impetuous dash at her and emitted a single, very loud *oop*. She quickly flew 40 feet up into a tall fir which was 30 yards down slope. The cock strutted on into a conifer stand and continued hooting from an old log.

Presently the hen flew 85 yards down slope into the lower branches of some tall trees at the seepage pool. Instantly Male B responded to her departing flight by springing three feet into the air from the log and giving a sharp wing clap. The effect was much like the crack of a pistol shot and was apparently produced by one powerful downbeat of the incurved pinions. Male B then paraded after the silent female. Under the trees, he courted ardently and, as when he startled her into the fir tree, sounded another loud *oop*. As I was unable to locate the hen, and since it did not appear that she would come to the ground, I left after more than five hours observation of the male within the limits of territory 2.

On May 15, at 3:56 p.m., a male grouse, thought by reason of his territorial location and style of hooting to be Male B, was heard on the upper portion of this territory. For the first time the ventriloquism of a hooter introduced difficulties. After 44 minutes of intensive effort, Male B was found displaying on a mossy outcrop at the edge of dense conifers in the upper west ravine which was his favored hooting ground. In search I had completely encircled him and had passed within five yards of his station. Soon Male B climbed the west slope to feed in the foliage of the pine and fir trees. This was the same foraging ground that he had utilized on April 30. At 5:20 p.m. two wing flutters were heard nearby along the west hillside up the ravine. Male B did not react to this demonstration; this was the first indication of a more subdued attitude in the behavior of a breeding grouse on the study area.

Alternating feeding with resting periods, Male B flew 100 feet into a pine where he fed on the staminate flowers. At 6:03 p.m. he flew back and dropped into the top of a young fir just below me. At last he peered intently along the slope in the direction from which the two wing flutters had come an hour before. At 6:20 p.m., the grouse whirred toward the head of the ravine. Another wing flutter sounded there in instant response to his flight and approach. Trailing up slope, I saw Male B in full display beneath a fir in an open grove. Being chilled by inactivity, I did not await developments but proceeded to investigate the wing notes. Soon they were repeated from scattered pines 125 yards higher on the mountain side. Search again did not disclose the performer. The entire episode reflected the shy behavior of a hen. On this occasion the hen had come to the upper borders of territory 2, and it is clear that in signaling, and waiting for an hour, she had expected to find the male in this locality.

I returned to the displaying resident Male B. He strutted down into the west ravine, over the head of the dividing ridge, and into the dense fir thickets of the east gully. From

there he flew 100 yards down the ravine, where again a Blue Grouse rose in short flight, heading back west, and keeping within the limits of the territory which the bird was believed to occupy. It was 7:15 p.m., and since mid-afternoon, Male B had nearly completed an entire circuit close to the outer boundaries of this previously delineated area (fig. 1).

At 5:45 p.m., May 9, four loud display notes were heard at short intervals coming from the west slope of the lower ravine. Similar notes followed, and wing fluttering was heard in response. I crossed the ravine floor to the foot of the slope on territory 3. The birds there became silent. Then presently from my left came repeated *kut-kut-kut* notes of warning. From my right, there was further wing fluttering. At 6:03 p.m., at the point at which the warning notes had originated, a courting grouse (Male C) was located on the ground under open pines and fir. As before, he proved wary for a time. After a futile effort to discover the source of the wing fluttering from the pines 200 feet north along the slope, I followed Male C as he displayed and hooted. He led off down the ravine, repeating his six-note series, the second note being the unemphasized beat. But quickly, at 6:49 p.m., a series of *kut-kut* warnings came from behind me. Male C ruffed his plumage in full display and immediately reversed his direction. He strutted past me 20 feet down slope. A dozen paces beyond, nearer the "hen," he sprang three feet into the air and drummed; then he returned up slope to his original station.

Returning to the slope and pine grove 75 yards away, I detected the tail of a grouse 50 feet up in a yellow pine. This bird, which had been concealed behind the tree trunk, was readily identified as a hen. Aware of discovery, she raised her crest feathers and gave several series of alarm notes and then flew 160 yards across the lower ravine into the pine-fir wood. Male C promptly followed her flight, alighting on a log at the border of the wood. He was displaying there when I departed down the draw.

Observations through the season disclosed a number of visitations or occurrences of female grouse on male territories. A hen was seen on territory 1 on April 16, and on other occasions wing fluttering was heard twice, issuing from the pine-fir wood when Male A was displaying nearby. A hen appears to have been present on the plot every time I located Male B on territory 2. Male C was actively courting a hen on territory 3 on both observation dates, and wing fluttering may have indicated the arrival of a female on a third occasion. Thus it is apparent that females regularly responded to calling, territorial males.

Communal display.—Trailing two Blue Grouse that flushed from territory 2 in the upper ravine at about 5 p.m., April 22, I reached the broad floor of the lower draw. At the base of the west slope, a bird, thought to be the hen from up ravine, rose again and flew far over toward the crest of the west ridge, beyond the plot later defined as territory 3.

Standing near the center of that area (figs. 1, 2), a wing flutter was heard from among open pines on the slope above me. At once, another unseen bird, less than 100 yards to the northwest, uttered wavering notes of warning. A hidden grouse repeated the alert a similar distance along the slope to the south. Presently, from directly up slope, a drummer performed several times. When I entered an open stand of conifers to investigate the last alarm notes, a male in full display appeared from behind antelope brush and crossed the trail, and a hen hurtled into a pine. After half an hour these two courting birds flew into an isolated lower grove, and I circled back up hill to locate the wing drumming heard there. At that point, another strutting male flushed and flew 30 feet into a pine. He hooted tentatively and displayed. Soon he whirred away through the dense border forest toward the upper ravine. This was believed to have been Male B, and he was probably the second of the two grouse that had preceded me down the draw.

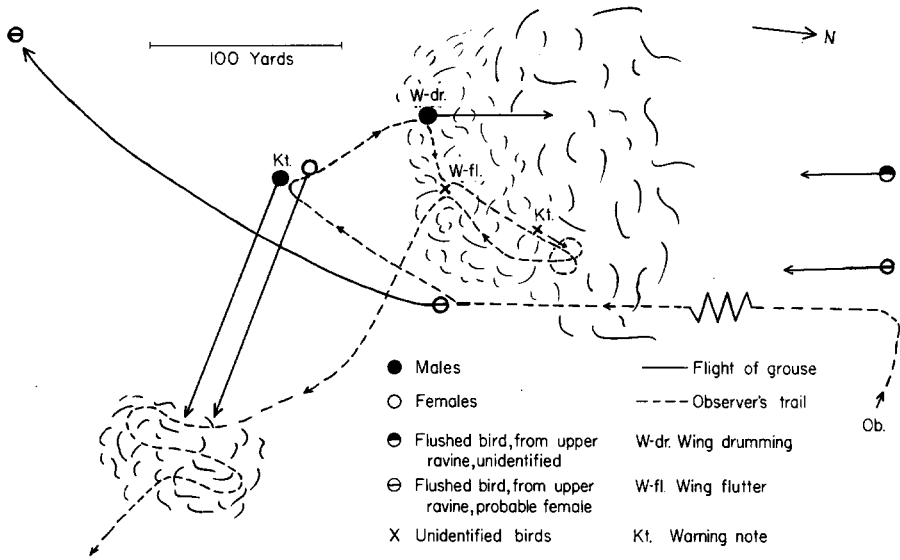


Fig. 2. Communal courtship of Blue Grouse, lower ravine, Purcell Range site, 5:10 to 6:15 p.m., April 22, 1957.

At once a wing flutter from the higher branches of tall, clustered pines down hill echoed his departure. Beyond in the undercover, where alert notes had first been heard, there was the sudden sound of a bird in short flight. Three Blue Grouse, two displaying males and a hen, had been seen on the slope. Another grouse, probably the hen from up ravine, had flown over to the crest of the west ridge. The final wing note from high in the pines, and the sudden burst of flight sound beyond it into denser timber, indicated the presence of two more grouse on the west slope. It seemed apparent that six courting birds had been located or observed within an area of about 125 yards diameter. It was now 6:15 p.m. and the grouse had dispersed.

On May 9, there was again much courtship activity in the lower ravine. A third performer, in addition to Male C and the hen, was briefly heard on the hillside just above territory 3. Male A drummed vigorously in response from the east slope, and he was observed there in full display. Before leaving at 7:15 p.m., I gained the impression that disruption of nuptial activities on the west slope, and my passage back and forth between these birds across the open floor of the draw, had likely inhibited another communal gathering like the one I had witnessed on April 22. Several authors (Schottelius, MS; Jewett, Taylor, Shaw, and Aldrich, 1953:194; Caswell, MS; Hoffmann, 1956:327, 332) have reported or recognized a tendency toward communal display (with no apparent territoriality) in the *obscurus* group of *Dendragapus*. These views are the result of observations of the race *D. o. pallidus* in open country.

The present study indicates that the timber-dwelling population of Dusky Grouse on the Big Bend of the Kootenai River, referable to the race *D. o. richardsonii*, is characterized by courtship habits of individual display, and by occasional, loosely-organized communal assemblage in the breeding season. As I have noted, displaying males of the *obscurus* group are basically territorial and, to a lesser degree, semi-communal, depending on that phase of diurnal, breeding season activity in which they are engaged.

It is not certainly known whether such gatherings, composed of scattered courting "pairs," assemble on common ground or on the territory of one of the male participants.

The widely drawn boundaries of territory 3, as tentatively outlined, include the site of the communal gathering described. This results from the fact that certain vegetational units, such as border forest and adjacent brushy pine slope, together with the movements of the occupant male, indicated that it was a natural inclusion. Further, when the courting group was interrupted, Male C was displaying at his usual station fairly close to the others.

There is reason to believe that the social organization of this group is typical of populations of the Dusky Grouse which live in similar environments in timbered country. It may be suggested that, since displaying male Sooty Grouse commonly descend to the ground at the climax of the breeding season (Haskin, *in* Bent, 1932:105), the possibility of loosely formed, small gatherings of courting pairs at forest edge or like situations should be investigated in the coastal races.

CONCLUSIONS

Observations of a population of forest dwelling Blue Grouse in northwestern Montana indicate that the breeding males are markedly territorial, participating to a lesser extent in communal courtship display, and further, that females seek calling males on the latter's territories. These females announce their presence at, or not far within, the territorial borders by wing signals to which the males react, and they are courted there by the occupant males. Open stands of timber, edge situations, or small openings in the timber, on the male's territory, seem favored as courting grounds.

Whether females initially seek males on their individual territories, or on communal courtship grounds, for fertilization is not known. It seems probable that display by the individual males, each on his chosen territory, precedes the gathering for group display. Furthermore, the loosely-organized communal activity seems to arise from such social stimuli as those generated by rival and responsive wing drumming. Early spring movements were not witnessed, and no evidence is available to support this supposition.

The use of one wing signal, namely, the wing flutter, by both sexes suggests that this is the basic form of wing signal in the species, and that its further development in the male gave rise to drumming. I did not actually see this wing note performed by the female, since I paid most of my attention to displaying males. However, investigation disclosed that the hen was at nearby locations when the wing flutter was heard. Finally, when the sound of the wing flutter, as given by both sexes, had become very familiar to me, Male A was observed performing it.

Some slight behavioral evidence of a rather strong pair bond was noted: (1) "pair" flights, (2) vocal danger-warnings to the male by the female, and (3) response of the male to warnings by the female.

Discussing a population of grouse at Sage Hen Creek, California, Hoffmann (1956: 329) states: "The validity of a census of displaying males rests upon the territorial behavior exhibited by adult male Sooty Grouse during the courtship period." Evidence of "strongly developed territoriality" has accumulated with respect to the *fuliginosus* group. No similar basis for a census of breeding males has been available for the study of Dusky Grouse populations. Even the casual location of hooting males of the *obscurus* group in forest environment has been complicated by the low-toned calling of these birds. With the recognition of territoriality, systematized studies become feasible. Such a procedure aids in wildlife management. The study of the breeding habits of the predominantly ground-displaying Dusky Grouse, supplemented by the establishment of territorial location, should inevitably prove more rewarding than field observations of the tree-hooting Sooty Grouse. Recent success in locating one or more of three individuals on each of nine trips to a forest area was largely due to acquiring such information.

SUMMARY

Three displaying Blue Grouse males were identified on individual territories. None was noted elsewhere between April 16 and June 3, 1957, in 21 hours of close-range observation, except during one evening of group display. Movements and daily routine of breeding males on their home grounds were recorded. Wing notes, hooting, hooting stations, drumming, and courtship are described in relation to territorial occupancy.

The behavioral characteristics of this population reinforce known affinities, and establish new relationships, between the racial groups of *Dendragapus obscurus*.

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