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# HABITAT SELECTION IN BLUE GROUSE

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The objective of this report is to show the response of Blue Grouse, *Dendragapus obscurus fuliginosus*, to density of vegetation on a breeding range. The habitat used by breeding Blue Grouse (*D. obscurus*) has been described by a number of authors (Beer, 1943; Munro and Cowan, 1947; Jewett *et al.*, 1953; Bendell, 1954; Heebner, 1956; Hoffmann, 1956; Boag, 1958; Fowle, 1960; Aldrich, 1963; Mussehl, 1963; Zwickel, 1965; Bendell and Elliott, 1966; and others). We compared the numbers, locations, age, and sex of grouse in open and dense vegetation to provide a measure of habitat selection. We were interested in habitat selection because this may be related to the numbers of animals in an area and to processes of population regulation (Svardson, 1949; Kluyver and Tinbergen, 1953).

## STUDY AREA AND METHODS

Our study area was located on a portion of the breeding range of Blue Grouse near Middle Quinsam Lake, Vancouver Island. The location of the study area and plots and the general distribution of vegetation types are shown in figure 1. The figure shows the fire road, which separated open and dense cover, and the broken lines representing old logging roads. Figure 2a is a view from the juncture of the Argonaut Mine and fire roads across a reference plot to the removal area on the hill. Note on the hill, the separation of the cover by the fire road into open and dense types. We observed, banded, and shot grouse within the entire area, but detailed work was concentrated on the plots marked in single and double lines (fig. 1). Those enclosed in single lines were reference areas where grouse were observed repeatedly. The plots enclosed in double lines were removal areas where grouse were shot. Most of the data presented here were obtained from the removal area, which consisted of two pairs of plots. Each pair measured 1000 × 2000 feet or approximately 50 acres (fig. 1). In this report each pair of plots is considered as one area. One removal plot was located in Very Dense type of vegetation; the other was in Very Open cover (fig. 1). These were the habitats compared for grouse and will be described presently.

We attempted to shoot all grouse, except hens with brood, found on the removal plots. Hence we made a removal census of males except for those that were observed and escaped shooting. Males, especially those hooting, were found and shot with relative ease. Hens were more difficult to find and shoot, and since few were shot, the data on them are pooled with sightings of hens. Since most males on the plots in a year were shot, we could measure the response of new grouse in a subsequent year to the two types of cover independently of resident birds. When grouse were shot, or captured, banded and released, we recorded their weight, age, and reproductive condition.

The study plots were searched intensively for grouse from May through August of 1959 through 1962. In 1960 and 1962 work began in mid-March. Search con-

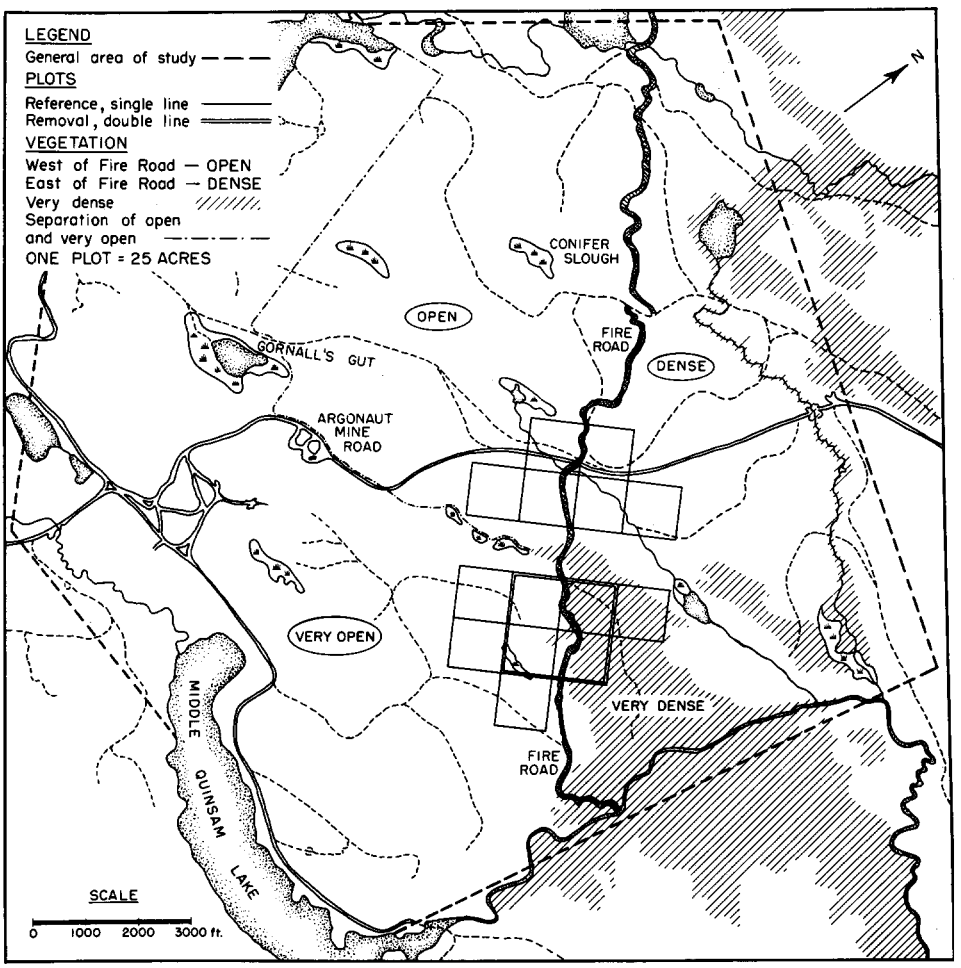


Figure 1. General area of study at Middle Quinsam Lake, reference and removal plots, and the distribution of types of vegetation.

sisted of one or two men patroling an area evenly, at times with pointing dogs. Search was concentrated in morning and evening hours when grouse are most conspicuous (Bendell, 1955). We believe that most of the grouse on the study plots were found, and, at least, all hooting males.

## TYPES OF HABITAT

The area at Middle Quinsam Lake may be placed within the ecotone between the Douglas fir Zone and the Western Hemlock Zone of the Pacific Coastal Mesothermal Forest (Krajina, 1965, and personal communication). The vegetation and soil of much of these zones have been changed by logging and repeated burning. Thousands of acres, once in coniferous forest, are now an open, prairie-like landscape dotted with charred logs and stumps. Plants grow in clumps interspersed with bare soil. As a result of time of logging and burning, edaphic features, planting of Douglas fir,

and kinds of plant succession, large areas are in a patchwork of vegetation from newly logged and burned to dense second growth. The contrast in vegetation provided an excellent opportunity to study the response of grouse to different kinds of cover within a short distance. The most obvious difference in cover was in its density or structure. We relate our observations on grouse primarily to the density of vegetation.

The removal plots were placed in Very Dense and Very Open cover. The Very Dense vegetation dated from logging and fire up to 1938. In an area east of the fire road of approximately two square miles, about 50 per cent was in this type (fig. 1). The Very Open cover was separated from the Very Dense by the fire road that more or less bisected the plots. The vegetation west of the fire road dated from logging and fire up to 1951. In an area of approximately three square miles, about 70 per cent was in Very Open type (fig. 1).

The main elements of each type of cover or habitat were sampled by 100-foot line-intercept transects and yard quadrats placed evenly on a study plot. Very Open and Very Dense types are shown in figures 2b and 2c, and as plant profiles in figure 2d. A profile was drawn from the line intercept that was most like the average of all lines put through a plot. The amount of ground covered by major elements of cover in Very Open and Very Dense types is presented in table 1. The photographs were taken and the lines and quadrats were run in 1962.

Clearly, there was a striking difference between the study plots in the density of vegetation. The species of plants were virtually the same in each plot. The coniferous trees, in order of importance, were: Western hemlock (*Tsuga heterophylla*), Western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga menziesii*). Most of the fir was planted. The deciduous trees were willow (*Salix sitkensis*) and red alder (*Alnus rubra*). Herbs that occurred most frequently and contributed most to the ground cover were: trailing blackberry (*Rubus vitifolius*), Oregon grape (*Mahonia nervosa*), pearly ever-lasting (*Anaphalis margaritacea*), white hawkweed (*Hieracium albiflorum*), hare's ear (*Hypochaeris radicata*), and lichens and mosses. In the Very Open type the vegetation was clustered around logs and stumps. This created clumps of cover separated by avenues of bare soil and duff.

A number of workers have correlated the local occurrence of Blue Grouse and height of land (Edson, 1925; Steinhoff, 1959; and others). The general study area was at an elevation of approximately 1000 feet on a flat to gently rolling plain. The removal plots included the crest of a gentle hill that ran across the north end of each (fig. 2a). This crest was approximately 150 feet above the surrounding lowlands.

## RESULTS

### The Numbers of Grouse in Open and Dense Habitats

The numbers of grouse shot and observed in dense and open cover on the removal area from 1959 through 1962 are presented in table 2. The data are classified by age, sex, and behavior of grouse when observed or shot. This information is relevant to an analysis of habitat selection and efficacy of census. In table 2, under "Grouse Observed," the category hooting males is a count of individuals where one or several observations were taken of a male on territory. Silent males, females, and females with brood are sightings and may include several observations of one grouse. The data for each year were too few to show differences between years and were, therefore, pooled.

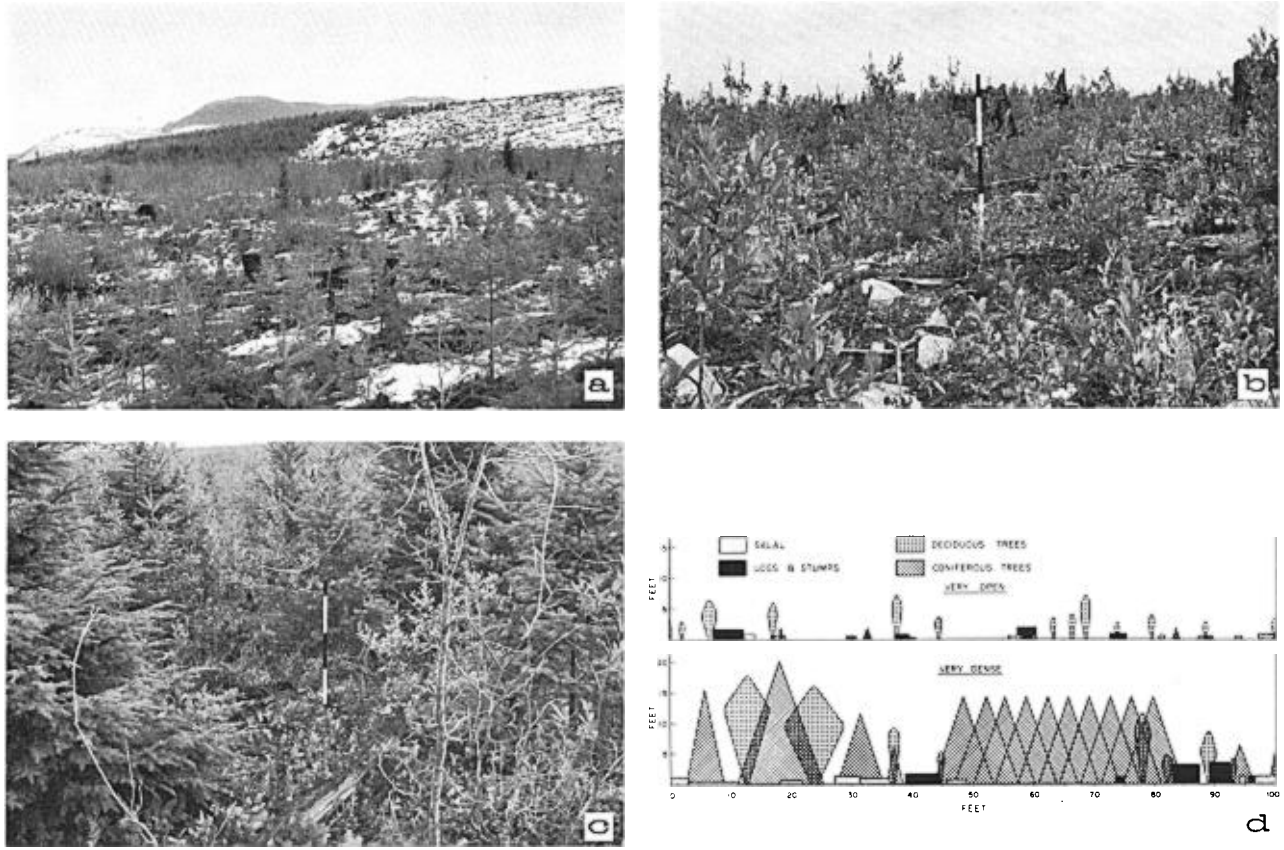


Figure 2. a. View across a reference plot to the removal area on the hill, March. b. Very Open type of vegetation. The rod is marked in sections of one foot. c. Very Dense type. d. Profiles of Very Open and Very Dense types.

TABLE 1

COMPARISON OF VERY OPEN AND VERY DENSE VEGETATION TYPES BY AVERAGE PERCENTAGE OF GROUND COVERED BY MAJOR ELEMENTS OF HABITAT

| Element of habitat | Very Open | Very Dense |
|---|---|---|
| Trees, salal, logs and stumps | 40 | 100 |
| Measured by lines[a] | | |
| Coniferous trees | 2 | 75 |
| Deciduous trees | 13 | 24 |
| Logs and stumps | 14 | 15 |
| Salal (*Gaultheria shallon*) | 11 | 31 |
| Bracken (*Pteridium aquilinum*) | 16 | 5 |
| Measured by quadrats[b] | | |
| Herbs | 21 | 44 |
| Duff | 68 | 83 |
| Bare soil and rock | 24 | 5 |

[a] For Very Open and Very Dense, 13 and 11 lines or
[b] 71 and 60 quadrats, respectively.

As measured by total grouse use, most birds of all classes occurred in the Very Open type of habitat. We conclude that grouse selected the Very Open in preference to the Very Dense type. We will now consider the classes of grouse separately to show their response to habitat.

*Adult males.* All adult males that were shot are pooled to give 16 from the open and 8 taken from the dense habitat (table 2). If hooting males observed are added to those shot, then 27 occurred in the open habitat and 10 in the dense. The difference between open and dense cover in numbers of hooting males is statistically significant. Most of the males simply observed hooting were probably adult.

In 1959, four adult males were shot on the open plot and five on the dense. Except for the adult males that were not shot in a year, all those taken after 1959 were probably two-year-old males establishing territory for the first time (Bendell and Elliott, 1966). In 1960, on the dense plot, three adult males were shot, and two were heard hooting. None was observed thereafter. Hooting adults and hooting males were taken or observed in all years on the open plot. Hence, new adult males selected the Very Open habitat and established territory. Moreover, since resident grouse had been removed from both habitats, new adult males were probably responding to the habitats independently of other males.

The presence of the adult males in Very Dense type can be explained by the faithfulness of Blue Grouse to their breeding site. From their first spring on the lowlands, males and females return each year to the same portion of the breeding range (Bendell and Elliott, 1966). The males probably established territories on the dense plot when it was more open. New males did not enter the thickening vegetation.

Kluyver and Tinbergen (1953) argue that territorial males may fill favored habitats and force other males into less favored places. In our study the numbers of territorial males taken from the open habitat fluctuated from year to year, but those in dense habitat declined to zero. If hooting males observed are added to the number of hooting males shot each year on the two plots, the counts in Very Open and Very

TABLE 2

GROUSE SHOT AND OBSERVED IN OPEN AND DENSE HABITAT AT MIDDLE QUINSAM LAKE, 1959 THROUGH 1962

| Category | Type of habitat | |
|---|---|---|
| | Very Open | Very Dense |
| Grouse shot | | |
| Hooting adults[a] | 15 | 8 |
| Silent adults | 1 | 0 |
| Hooting yearlings | 17 | 0[b] |
| Silent yearlings | 9 | 0[b] |
| Grouse observed | | |
| Hooting males | 12 | 2[b] |
| Silent males | 18 | 3[b] |
| Females | 25 | 5[b] |
| Females with brood | 18 | 1[b] |
| Total grouse use | 115 | 18[b] |

[a] Approximate ages: adult, 2 years; yearling, 1 year.
[b] Differences in the two habitats statistically significant ($P \leqslant 0.05$) by chi-square test.

Dense types were: 5 to 5; 9 to 5; 3 to 0; and 10 to 0. These data do not suggest that the territorial males settling on the one plot influenced those settling on the other. We conclude that the territorial behavior of males in the open habitat did not force males into the dense vegetation.

*Yearling males.* A striking feature of the removal experiment was the absence of hooting and silent yearling males from the Very Dense cover (table 2). Some yearlings may not hoot (Bendell and Elliott, 1966) and were possibly missed in the dense vegetation. We did find lone hens in the dense cover. Since they seem to be found as readily as silent males, we should have found some silent yearling males if they were present. Obviously yearling males selected the Very Open type of habitat and did not occur in dense cover with or without hooting adult males. Therefore, the yearling males, as the adults, were responding to the dense habitat rather than to hooting males.

Some yearling males establish territory in their first year, and others will do so if breeding males are removed (Bendell and Elliott, 1966). All yearlings, both hooting (or territorial) and silent, occurred in the open habitat. This is additional evidence that territorial behavior of adults or yearlings did not force other adults or yearlings from open to dense habitat.

Yearling males on the lowlands in spring are either on territory or move over what appears to be a relatively large home range (Bendell and Elliott, 1966). The results from the removal plots suggest that nonterritorial yearling males select the same kind of habitat when immature and when fully mature. As direct evidence for this, nine silent yearlings were banded and later relocated as hooting adults on the general study area. One was banded and checked as an adult in cover similar to Very Dense type. The rest were found as yearlings and adults in cover similar to

Very Open habitat. Hence, nonterritorial yearling males established territories in the kind of habitat they occupied as nonbreeding birds.

From time to time, on both study plots, hooting and silent males were observed and escaped being shot. These data are included in table 2. Generally, they support the conclusions reached from the analysis of shot males. Since silent males were probably observed unequally in the two types of cover, and hooting males may have been adults or yearlings, the data are of relatively low value and are not considered further.

*Females.* More females were observed in Very Open than in Very Dense habitat (table 2). These data may be somewhat biased because females were probably found more easily in open than in dense vegetation, and, since most were observed, the same hen may have been counted more than once. Hens move relatively widely on the breeding range and over the territories of a number of males (Bendell and Elliott, 1966). Hence, hens probably moved through the removal areas. Four banded hens were observed but once on the removal plots. These considerations suggest that counts were mainly of individual hens. We conclude that females selected the Very Open over the Very Dense type as did adult and yearling males.

The five lone females found in the Very Dense plot were shot or observed there in 1959. This suggests, as with the adult males, that they selected this habitat when it was more open.

After 1959 all lone hens were observed on the plot in the open despite the occurrence of hooting males in dense vegetation in 1960. Hens are not territorial and appear to be promiscuous breeders (Bendell and Elliott, 1966). These data suggest that, as with males, interaction between females or males and females was not important in the observed distribution of hens. A general impression from the few data on hens is that they responded to the two habitats in the same way as adult and yearling males. In support of this contention one should note that in both types of habitat hens made up approximately the same percentage of the population of hooting males and hens. In Very Open type this was 36 per cent (25/69) and in Very Dense type, 33 per cent (5/15).

*Hens with brood.* Virtually all sightings of females with brood were made in the Very Open habitat (table 2). These data are likely biased in the same way as the observations on lone hens. The one brood observed in Very Dense type was on an old road that ran across the corner of the plot, so it too was in an open area. Hens with brood move independently of each other and territorial males, and relatively widely over the breeding range (Bendell and Elliott, 1966). There were four banded hens with brood on the removal plot in the open. One hen was observed three times in the same year; the other three were not resighted on the removal plot. Hens with brood probably traveled through the plots and had the opportunity to select either type of habitat. We conclude that the hens with brood selected the Very Open habitat, and, since they move independently, this response was not related to other grouse.

The habitat selection of hens with young is important for it may determine the kind of cover selected by the young when they establish themselves on the breeding range. We banded chicks and relocated them as breeding birds on the general study area. Three chicks captured from two broods in habitat similar to Very Dense type were located as breeding birds in vegetation similar to Very Open type. A male and female chick from separate broods were banded in open cover. When located as breeding birds, both were in the same kind of habitat. Hence, some chicks that at

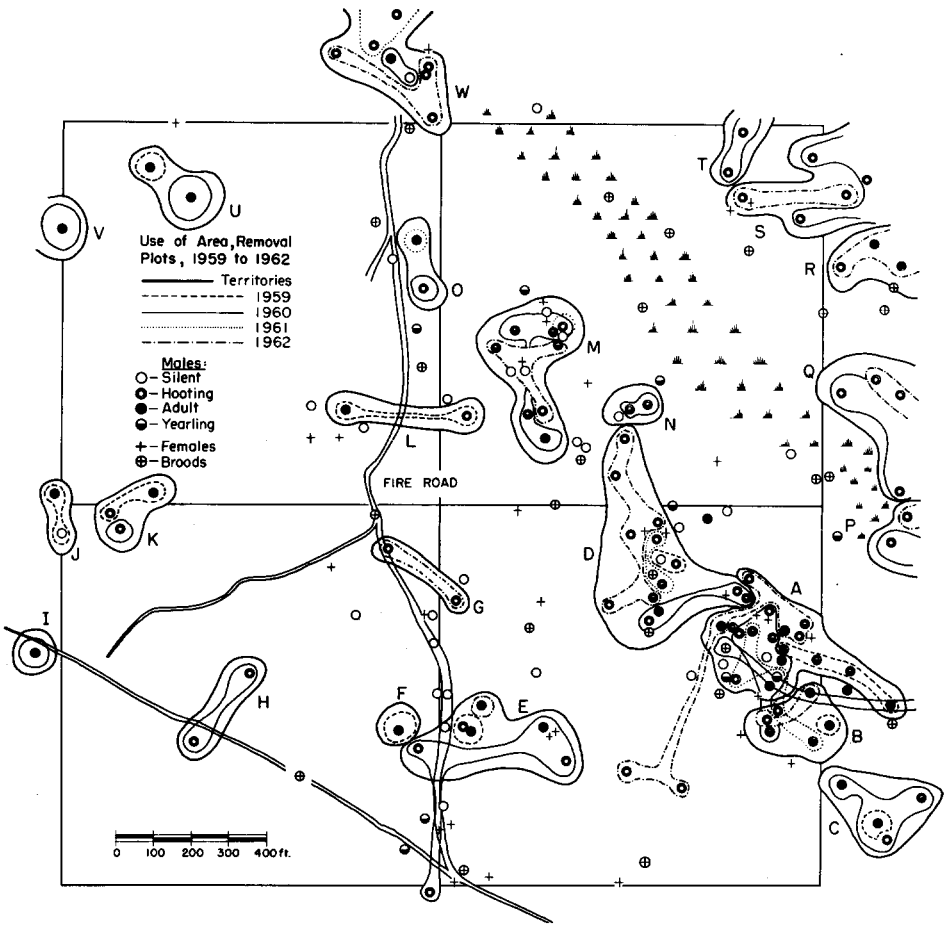


Figure 3. Locations of grouse and territories on the removal area, 1959 through 1962. North is to the bottom left corner of the illustration.

least traveled through dense cover selected more open habitat as breeding range. This suggests that the habitat selected by breeding grouse is not determined by the kind they used as chicks.

## The Locations of Grouse within Open and Dense Habitat

*Adult and yearling males.* We have examined the numbers of grouse shot or sighted in open and dense habitat. We will now consider the distribution of grouse within each type of cover. The points where grouse were shot or observed were plotted on maps. This procedure permitted an analysis of the positions of grouse and their relation to territories and topography. The places where grouse were observed on the two removal plots are shown in figure 3. This is an enlargement of the plots enclosed in double lines in figure 1. North is toward the bottom left corner of figure 3. Areas were considered as territories if they contained hooting males.

TABLE 3

NUMBER OF ADULT AND YEARLING MALES SHOT AND OBSERVED ON TERRITORIES IN VERY OPEN HABITAT, MIDDLE QUINSAM LAKE, 1959 THROUGH 1962 (adults/yearlings; x = Male heard or seen)

| | Highland | | | | | | | Lowland | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Territory | A | B | D | M | R | S | T | C | E | G | N | O | P | Q | W |
| 1959 | 2/6 | 1/0 | x | 0/0 | 0/0 | 0/0 | 0/0 | 1/0 | 1/0 | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| 1960 | 2/2 | 0/0 | 2/2 | 1/3 | 0/0 | x | x | 1/1 | 1/1 | x | 0/2 | 0/1 | x | x | 1/0 |
| 1961 | 0/0 | 1/1 | 0/1 | x | 0/0 | 0/0 | 0/0 | 0/0 | x | x | 0/1 | 1/0 | 0/0 | 0/0 | x |
| 1962 | 2/1 | 1/0 | 0/1 | 0/3 | 2/0 | x | 0/0 | 0/0 | 1/1 | x | 0/0 | 0/0 | 0/1 | x | x |

They are marked with a solid line and lettered from A to W. Silent males observed were referred to the nearest territory. The plot to the left of the fire road was in Very Dense cover, that to the right was in Very Open cover. In places, open and dense types extended short distances beyond the fire road (fig. 2a). Grouse in this region were placed in a cover type, but this cannot be shown in figure 3. With this exception the figure provides the data of tables 2 and 3. The places where hooting males were shot are only part of a territory. However, hooting males and their replacements tended to occur in areas that were similar to territories in extent and spacing between neighboring areas. This is evident in figure 3, and from comparison with natural territories beyond the removal area (Bendell and Elliott, 1966).

Previous work has shown that male Blue Grouse use elevated ground for display, and where the cover is a pattern of openings in dense vegetation, they locate their territories upon openings (Heebner, 1956; Bendell and Elliott, 1966). In the present study the locations of territories in the Very Dense type likewise may be explained by the positions of openings. These are territories: F, H, I, J, K, L, U, and V (fig. 3).

In considering the distribution and use of territories within the Very Open type of vegetation, one can see from figure 3 that territories B, A, D, and M were concentrated on a line running through the plot. These and territories R, S, and T were located on or close to heights of land. We divided the plot into squares each measuring 100 × 100 feet and noted within each square, over the four years of study, the presence or absence of hills and hooting males. These data were used to calculate Cole's measure of interspecific association (Cole, 1949). There is a strong and positive association between heights and hooting males ($C_7 = +0.29$, $\sigma_c = 0.04$). We conclude that breeding males selected heights of land for territories. Note, however, that not all locations of territories can be explained in relation to prominent elevations.

It is obvious from figure 3 that most adult and yearling males were associated on territories. When adult males were shot, hooting yearlings frequently took their place (Bendell and Elliott, 1966). Hence yearling males were attracted by adult males, yearlings and adults selected the same hills for territory, or both events occurred.

The use of territories was measured by frequency of occupancy and number of males shot on them. For this analysis, the data from the Very Open habitat in figure 3 are grouped by territories and year in table 3. A territory was occupied in a year if a male was recorded on it. Two territories were used in all four years (table 3): 5 in 3, 6 in 2, and 2 in 1 year only. Clearly, some territories were used more frequently than others.

The frequency of occupancy of territories cannot be related to height of land. The seven highland territories were used a total of 17 times in the four years. The eight lowland areas had males on them a total of 20 times. Hence, lowland territories were used about as frequently as those on the highland.

There were more males shot on the highland territories. The seven highland territories yielded 14 adult and 20 yearling males (table 3). The eight lowland territories yielded seven adult and only eight yearling males. The difference in total number of males shot on highland as compared with lowland territories is statistically significant. The data suggest that more adult and yearling males occurred on the highland territories. Hence, adult and yearling males selected the highland areas for territories. The relatively large number of yearling males taken on the highland and lowland areas may be explained by the behavior of adults and yearlings. Adult males remain on territories while nonterritorial yearling males move relatively widely over the breeding range. As males were shot from territories, they were replaced repeatedly by mobile yearlings.

Approximately the same ratio of adult to yearling males occurred on the highland and lowland areas. This is evidence for the attraction of yearlings to adults. There were 16 times when at least one adult male was shot on a territory (table 3), and on these areas 18 yearlings were shot, most shortly after the adult was removed. At least 30 times over the four years, territories were without territorial adult males. These areas yielded but 10 yearling males. The difference cannot be explained by the nature of the territories over the four years. The data suggest that yearling males were associated with hooting adults and not with their territories. We conclude that hooting males attracted yearling males to them. This same conclusion was reached by observing the locations of yearlings on the general study area (Bendell and Elliott, 1966).

The relationship between adults and yearlings suggests that once a male established a territory there would be a tendency to perpetuate it by the attraction of potential replacements. If a resident male established a tradition of use of an area, then territories should be occupied in sequence. The removal of yearling males would not help the demonstration of this relationship. Territories were classified as empty or occupied over the four years (table 3). The data were used in a one-sample runs test (Siegel, 1956) to distinguish between random and successive use of territories. There was a significant departure from random use. This appeared to be the case on both highland and lowland areas. The result supports the contention that there was a tendency for males to establish a tradition of use of a territory over successive years.

Territories were frequently adjacent, and resident males appeared to influence the activity of their neighbors. This finding suggested that a male on one territory might cause the occupancy of another. The data of figure 3 and table 3 were assembled to test this notion. Each territory was paired with its nearest neighbor, and the two were rated for each of four years as both occupied or one of the two occupied. As a comparison, each territory was paired with another selected at random. Occupancy of these pairs was rated as for neighboring territories. If there was a tendency for territorial males to influence the occupancy of adjacent areas, then we would expect a different pattern of occupancy on adjacent territories as compared with territories paired at random. In the test, neighboring territories were occupied in the same year 29 times and one of the two was occupied 21 times. In the pairs matched at random, both were occupied 24 times and only one of two, 26 times. The result

suggests that males occurred on neighboring territories as on areas related at random. Thus, the occupancy of adjacent territories was apparently independent. If so, then clumping of territories, as areas D, A, and B (fig. 3), is partly explained by the attractiveness of the habitat.

The edge between two types of cover is reputed to be important in the local distribution of animals. The two removal plots and comparable reference areas were almost evenly split by the edge between open and dense vegetation (fig. 1). As can be seen in figure 3, the locations of grouse do not show a concentration on edge, although territories did occur along the fire road.

On the reference plots we classified territories as: edge territories, with approximately equal portions in open and dense vegetation, and territories that were predominantly within a type. Over four years, four territories were located on the edge between types, while approximately 13 occurred within or mostly within the dense or open vegetation. If territories of the size observed were distributed evenly we would expect one edge territory to two to three in open and dense vegetation. Hence, there was no apparent concentration of territories on the edge between types of cover. Most observations on hooting males and other grouse were obtained away from the edge between types. Apparently, the edge between Very Dense and Very Open types did not influence the local distribution of grouse.

*Females and females with brood.* The distribution of females and females with brood on the removal area in open type was examined in relation to the territories of males. As with hooting males and hills, the association between lone hens and territories and hens with brood and territories was measured by Cole's coefficient of interspecific association (Cole, 1949). As might be expected, lone hens were strongly associated with territories of males ($C_7 = 0.75$, $\sigma_c = 0.053$). On the other hand, hens with brood occurred on territories as might be expected by chance alone ($C_7 = 0.14$, $\sigma_c = 0.076$). These results indicate that lone hens were attracted to territories of males while hens with brood moved independently of them. Similar conclusions were reached from the work on the reference area (Bendell and Elliott, 1966).

The occurrence of hens on territories on the removal area can be related to the presence of males. The data from each territory over a year were classified as: male and female observed, male only, female only, or nothing noted. Over four years, territories were occupied by males 38 times and empty 22 times. Hens were observed on territories 16 times and only when males were present. In comparison, hens with brood occurred five times on territory when males were present and three times when they were absent. This suggests that lone hens were attracted by males to their territories. Hens with young were found at times on areas used as territories but moved independently of them.

## DISCUSSION

Kluyver and Tinbergen (1953) note that rates of birth, death, and dispersal or habitat selection explain the numbers of a species on an area. Death rate of Blue Grouse beyond a year of age appears to be virtually the same in open and dense vegetation (Bendell and Elliott, 1966). Birth rate is likely the same. But we do not, as yet, have data on the death rate of young in or from dense vegetation. However, females with brood moved through open and dense vegetation and their range of movements was sufficient to take them into either kind of cover. Nonterritorial males, hens, and grouse that have dispersed also move widely on the breeding range

(Bendell and Elliott, 1966). We take the occurrence of grouse in a particular density of vegetation as indicative of habitat selection.

We can outline something of the response of grouse to Very Open and Very Dense cover. All yearling and adult males selected the open type when they first settled or established territory. This was apparently a reaction to an element or elements of habitat other than the presence of other males. In open habitat, hooting males tended to select elevations on the ground and established territories. The clumping of territories apparently results from the attractiveness of the habitat. However, territorial behavior acts to space breeding males (Bendell and Elliott, 1966). The edge between open and dense cover did not influence greatly the local distribution of grouse. Yearling males are attracted by territorial males. Territories in open habitat tended to be occupied in successive years even when residents were removed each year. Presumably adults attracted to the territories as yearlings continued the use of them. We could not show that a male on territory caused another male to settle nearby.

The hens were probably reacting to the open and dense vegetation in the same way as the males. Lone hens are attracted by territorial males. Finally, hens with brood moved over the open habitat independently of the breeding males and their territories.

The habitat selection of grouse may help determine population. Once grouse occupy a territory or home range on the lowlands, they apparently return each year until they die. This is done even though the cover around them grows from open to dense (Bendell and Elliott, 1966). New adults and yearlings, however, show habitat selection. Hence the population of an area may rise or fall depending upon the ingress or egress of young grouse selecting or avoiding habitat.

The decline of population on one of our study areas can be explained by the cover preference of new recruits. Two study plots, totaling 72 acres, at Lower Quinsam Lake, went from approximately 40 hooting males to zero in eight years. In the same time, the vegetation changed from open to dense. The decline of males was at the rate of approximately 30 per cent per year. This is virtually the same as the mean annual rate of death of grouse beyond a year of age (Bendell and Elliott, 1966). Hence, the decline of population may be explained by the avoidance of dense vegetation by new recruits.

The habitat preference of Blue Grouse helps explain their response to changes in dense forest. After logging and burning, Blue Grouse generally appear and may reach exceptionally high densities. Moreover, forest fires are probably a natural feature over the range of this grouse. Since grouse select open habitat, this may be part of the reason populations respond to new openings. In another way, the selection of open habitat by Blue Grouse may be viewed as an adaptation to make use quickly of new openings as breeding range.

It is evident from data in the literature that established birds may force others from preferred to less-preferred places. In our study all replacement by grouse on the removal plots was in open type. There was no evidence that interaction determined the numbers of grouse in each habitat. Territorial behavior spaced the breeding males in the open (Bendell and Elliott, 1966) but did not force males into the dense vegetation.

Wecker (1963) studied the role of early experience in habitat selection by the Prairie Deer Mouse, *Peromyscus maniculatus bairdii*. His mice showed an innate response to habitat; this could be reinforced but not reversed by early experience.

Our data fit this interpretation of habitat selection, for chicks captured in dense type, and presumably born there, selected open habitat when adult despite an early experience in dense vegetation.

Since chicks move through open and dense vegetation and leave the lowlands in the fall, habitat selection on the breeding range probably occurs in spring. Yearling and new adult grouse found on the breeding range appear committed to a territory or home range and a habitat. Hence, choice of habitat is probably made upon the arrival of yearling and new adult grouse on the breeding range.

The habitat selection and distribution of birds and mammals may be related to the structure of vegetation (Palmgren, 1932; Pitelka, 1941; Harris, 1952; and others). The main difference in our types of vegetation, as we observed it, was in density or structure. Blue Grouse apparently responded to the structure of what we have described as an open type. East of the Coast and Cascade mountains, Blue Grouse migrate from coniferous montane forests into lowland sagebrush grasslands that are used as breeding range. Our Very Open type of cover might be imagined as shrub and grasslands if logs and stumps are considered as shrubs. Moreover, in the summer, the burns that we have studied may have a prairie-like climate that is hot and dry. Thus, breeding range of Blue Grouse can be described as generally open and dry, with shrubs and herbs interspersed with bare ground. Winter ranges are in montane forests, apparently the parkland coniferous stands of the alpine-subalpine ecotone and open ridges in subalpine forest.

Within open vegetation on the breeding range, at least two other features affect the local distribution of grouse. The song posts of males and hence their territories are usually situated on heights of land. These may occur close to flat, open areas as are found naturally, and on old logging roads. Such situations probably give good visibility and provide an unobstructed area for the display of the male and female. They may also permit a male to hear and be heard better than if he were in a hollow where surrounding topography and vegetation might tend to muffle sound.

Data in the literature, and casual observations, reveal that the *fuliginosus* race breeds in old coniferous forest where there are natural openings among the trees (Brooks, 1926; Jewett *et al.*, 1953; Aldrich, 1963; and others). In this habitat hooting males may be observed over 100 feet up on branches of large Douglas firs and other conifers. It is remarkable that this grouse moves into, and breeds on, quite open and recently burned lowlands. Again, openings are a common factor in breeding habitat. On the burns there is little opportunity for males to hoot from trees. They were most frequently observed hooting on the ground or from a log or stump. Males did hoot from trees and most frequently in Douglas fir approximately 30 feet or more in height, and usually in dense vegetation. However, even where tall trees occurred on territories, males were observed most frequently hooting from the ground. This suggests that *fuliginosus* males prefer to hoot from the ground. In this respect and many others the mating behavior of the *fuliginosus* race is similar to that reported for *richardsonii* (Blackford, 1963).

The selection of prairie-like habitat as breeding range by Blue Grouse is partly explained by their possible evolution from prairie-dwelling precursors. Blue Grouse may be placed close to the Sage Grouse (*Centrocercus*), Prairie Chicken (*Tympanuchus*), and Sharp-tailed Grouse (*Pedioecetes*) on the basis of secondary sexual characters, breeding behavior, and other features of their biology. The use of prairie or prairie-like habitat as breeding range by the four genera adds to their similarity.

In addition to an historical explanation for the habitat selection of Blue Grouse,

there are a number of properties of the species that seem adaptations to an open habitat. Some of these became most apparent to us when we observed the distribution of Ruffed Grouse (*Bonasa umbellus brunnescens*) on our study areas and held Ruffed and Blue Grouse together in captivity.

In terms of behavior, the color, courting display, and dance of the male, Blue Grouse would appear to require an open space for best expression. We have already noted that males hoot from the ground and that their song posts are usually located close to open areas where they frequently display when hens are present. Male Ruffed Grouse, a forest species, may strut and display but show neither the color nor sweeping dance of the male Blue Grouse. Blue Grouse tend to "freeze" when disturbed, and when they fly, it is a heavy ponderous flight, usually in a straight line. They are expert at long, gliding flights down steep gullies and hills. In comparison, Ruffed Grouse usually flush when disturbed and veer sharply through the tangle of the forest. They land and climb easily in willowy trees that Blue Grouse of the same weight, because of their relatively poor agility and balance, would crash into, and fall from. When Blue Grouse do take to trees, these are usually robust conifers that provide large and firm branches.

Chicks of Blue and Ruffed Grouse of the same weight appear to differ in the size of body parts, particularly the legs and feet. A feature of the open habitat used as breeding range is the amount of bare ground interspersed among clumps of vegetation and other elements of cover. Mussehl (1964) points out that bare ground interspersed among grasses and herbs is important as an avenue of travel for Blue Grouse, particularly chicks. Hence, the apparent difference in body proportions between chicks of the two species may relate to their efficiency of operation in forest and open environment.

There is evidence that Blue Grouse are adapted physiologically to a dry habitat. The burns are usually hot and dry in July and August when broods are abroad. Over a burn, broods of Ruffed Grouse are found in the alder and willow thickets in wet areas as along the edges of streams. They rarely venture onto the dry burn, which is the brood range of Blue Grouse. This suggests that the one is less dependent upon water than the other.

In support of this contention we have a rough estimate of water consumption in juveniles of the two species held in captivity. In September approximately 60 Ruffed and 30 Blue Grouse were held in adjoining halves of a large, closed barn. The grouse were all birds of the year taken from the field. Their numbers made the total weight of each species about the same. The birds were fed dry, turkey-growing ration, lettuce, and water. Both food and water were in excess, and no interaction was observed over them. The grouse were held in this manner for approximately four months. In this time the Ruffed Grouse drank approximately twice the amount of water taken by the Blue Grouse (F. C. Zwickel, personal communication). We conclude that Blue Grouse require less water than Ruffed Grouse, and this difference may be related to the local distribution of the species.

## SUMMARY

Blue Grouse (*Dendragapus obscurus fuliginosus*) were shot and observed in Very Open and Very Dense cover to find their selection of habitat. This was done on a portion of a breeding range near Middle Quinsam Lake, Vancouver Island, from 1959 through 1962.

New adult and yearling grouse selected the open type of vegetation, and this was

apparently a response to part or parts of the habitat other than grouse. There was no evidence that grouse forced others from a preferred to a less-preferred type of vegetation.

Within open cover, hooting males selected heights of land and established territories. Yearling males were attracted by territorial males. The attraction of yearlings to hooting males probably perpetuates the use of a territory.

Lone hens were attracted by territorial males. Hens with brood moved over the breeding range independently of territorial males or their territories.

Blue Grouse apparently select their habitat on the breeding range in spring and respond to the structure of the vegetation. The breeding habitat of Blue Grouse may be defined as open and dry, with shrubs and herbs interspersed with bare ground. The winter range is in montane forest, apparently in the parkland coniferous stands of the alpine, subalpine ecotone, and open ridges in subalpine forest.

The cover preference of Blue Grouse may help determine population. New recruits are attracted to open areas and avoid dense vegetation. As a result, populations might increase or decrease partly because of the ingress or egress of grouse.

The habitat selection of Blue Grouse may be partly explained by an evolutionary origin from prairie-dwelling species of grouse. They seem adapted to dry, open habitat in a number of ways. These include an innate response to open habitat, and aspects of behavior, color, form, and the economical use of water.

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