



Structural characteristics and ecological relationships of male blue grouse (*Dendragapus obscurus* [Say]) territories in southwestern Montana
by Robert Rehm Martinka

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY in Fish and Wildlife Management
Montana State University
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Abstract:

Structural characteristics of male blue grouse (*Dendragccpus obsGurus*) territories and their relationship to land-use practices and forest succession were .studied from 1967-1969 on a 700-acre area of the Sapphire Mountains in southwestern Montana. A description of the physiography and vegetation was given. The area has been selectively logged periodically since 1948. During 130 observation trips, . 1,010 sightings of males on 40 territories were made. About 60 percent of the males were leg-banded for individual identification. Vegetative and physical characteristics were recorded for 27 territories where males were observed 14 or more times; Territory size averaged 1.99 acres. Thickets of-coniferous trees, which were the major vegetational component of territories, averaged .211 acres and provided about 675 feet of edge. . The density of thickets averaged about 1200 -trees per acre. Average thicket tree diameter was 4.9 inches. Most trees in thickets were from 10 to 60 years old Territory thickets composed mostly of Douglas-fir were generally of greater density and smaller total area than those composed mostly of ponderosa pine. The longevity of thickets used by males was apparently about 40 to 50 years. Territories that- were occupied intermittently during an eight-year known history averaged 2.33 acres while those occupied continuously averaged 1.79 acres. Discriminant function analysis indicated that territories could be distinguished from unused areas with a high degree of success (96 percent) when ten variables were used. As the. number of variables was reduced, the quality of the results decreased. Selective logging may be beneficial because it opens up the canopy which allows the regeneration of trees in the form of scattered thickets. Clear-cut- logging might also be beneficial if used on small blocks of timber (10 to 60 acres). - Silvicultural practices such as mistletoe control, terracing on clear-cut areas, and thinning were discouraged in multiple-use management where blue grouse breeding habitat is paramount. Breeding habitat was associated with a ponderosa pine fire successional stage in the Douglas-fir vegetational zone, or with immature climax stages in both the ponderosa pine and Douglas-fir vegetational zones. With the curtailment of uncontrolled fires, logging is probably necessary if blue grouse breeding habitat is to be maintained or created. Male territories tended to be evenly spaced which was possibly initially a result of habitat requirements and/or selection and secondarily of territorial behavior. Longevity of males did not seem to be related to habitat type.

STRUCTURAL CHARACTERISTICS AND ECOLOGICAL RELATIONSHIPS
OF MALE BLUE GROUSE (*DENDRAGAPUS OBSCURUS* [SAY])
TERRITORIES IN SOUTHWESTERN MONTANA

by

ROBERT REHM MARTINKA

A thesis submitted to the Graduate Faculty in partial
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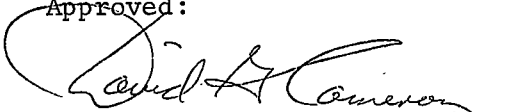
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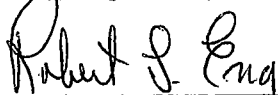
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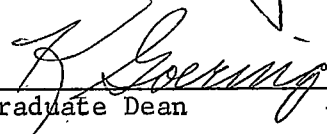
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ABSTRACT

Structural characteristics of male blue grouse (*Dendragapus obscurus*) territories and their relationship to land-use practices and forest succession were studied from 1967-1969 on a 700-acre area of the Sapphire Mountains in southwestern Montana. A description of the physiography and vegetation was given. The area has been selectively logged periodically since 1948. During 130 observation trips, 1,010 sightings of males on 40 territories were made. About 60 percent of the males were leg-banded for individual identification. Vegetative and physical characteristics were recorded for 27 territories where males were observed 14 or more times. Territory size averaged 1.99 acres. Thickets of coniferous trees, which were the major vegetational component of territories, averaged .211 acres and provided about 675 feet of edge. The density of thickets averaged about 1200 trees per acre. Average thicket tree diameter was 4.9 inches. Most trees in thickets were from 10 to 60 years old. Territory thickets composed mostly of Douglas-fir were generally of greater density and smaller total area than those composed mostly of ponderosa pine. The longevity of thickets used by males was apparently about 40 to 50 years. Territories that were occupied intermittantly during an eight-year known history averaged 2.33 acres while those occupied continuously averaged 1.79 acres. Discriminant function analysis indicated that territories could be distinguished from unused areas with a high degree of success (96 percent) when ten variables were used. As the number of variables was reduced, the quality of the results decreased. Selective logging may be beneficial because it opens up the canopy which allows the regeneration of trees in the form of scattered thickets. Clear-cut logging might also be beneficial if used on small blocks of timber (10 to 60 acres). Silvicultural practices such as mistletoe control, terracing on clear-cut areas, and thinning were discouraged in multiple-use management where blue grouse breeding habitat is paramount. Breeding habitat was associated with a ponderosa pine fire successional stage in the Douglas-fir vegetational zone, or with immature climax stages in both the ponderosa pine and Douglas-fir vegetational zones. With the curtailment of uncontrolled fires, logging is probably necessary if blue grouse breeding habitat is to be maintained or created. Male territories tended to be evenly spaced which was possibly initially a result of habitat requirements and/or selection and secondarily of territorial behavior. Longevity of males did not seem to be related to habitat type.

INTRODUCTION

Most blue grouse (*Dendragapus obscurus*) populations exhibit a seasonal, altitudinal migration. After spending fall and winter in coniferous forests on the higher mountain ridges, the males migrate in late March and early April to relatively open forests in lower mountain areas where they establish and defend breeding territories. Females arrive shortly after the males and nest in the same general areas (Bendell and Elliott 1967).

Structural characteristics of the vegetation found at male blue grouse territories have been discussed by several authors; however, no one has described them in a quantitative manner. Bendell and Elliott (1966 and 1967) noted that the position of territories in dense cover may depend on the location of openings, and other authors (Blackford 1958 and Mussehl 1962) have described territories in open areas as being associated with thickets of coniferous vegetation. Forest succession, following fire or logging activities, undoubtedly acts as a control on the density and positioning of territories (Bendell and Elliott 1966; Mussehl 1962). Breeding blue grouse accept a variety of different forest types, from moist forests in the Pacific Northwest to relatively dry forests of the interior Rocky Mountain region.

Personnel of the Montana Fish and Game Department have been conducting blue grouse population and pesticide studies (Mussehl and Finley 1967) since 1962 on a small area of the Sapphire Mountains in southwestern Montana. This area was chosen for a quantitative study of the vegetational characteristics of male blue grouse territories because of the known history of approximately 40 different territories. Also, a large proportion of the territorial males had been leg-banded for individual identification. Objectives of the study were to determine the structural makeup of male breeding territories and to evaluate the effects of forest succession in relation to silvicultural practices on blue grouse breeding habitat in ponderosa pine, (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) vegetation zones.

Full time field studies were conducted from late July to late August, 1967, from mid-April to mid-September, 1968, and from early April to early September, 1969. Approximately 130 trips to the study area were made for the purpose of locating male grouse, and about 200 were made for the purpose of vegetation analysis.

DESCRIPTION OF THE STUDY AREA

The study area (Figure 1), located 10 miles southeast of Hamilton, Montana, contains about 700 acres of Bitterroot National Forest land near Skalkaho Creek. According to Perry (1962), this area is composed of granitic rock of the late Cretaceous to early Tertiary periods. Elevations range from approximately 4550 to 5750 feet mean sea level.

Steep, open, south-facing slopes intermingled with heavily wooded draws characterize the area (Figure 2). Numerous logging roads traverse the hillsides providing excellent accessibility. Logging was begun in 1947 and has continued until the present.

Climatological data for Hamilton (elevation 3529 feet) show a mean annual temperature of 46.1 F. January is the coldest month and July is the warmest with average temperatures of 24.1 F and 67.9 F, respectively. Average annual precipitation is 12.74 inches. The only months with average precipitation exceeding 1.20 inches are May and June which average 1.67 and 2.04 inches, respectively. Because precipitation generally increases with elevation in this region, the study area undoubtedly receives more moisture than Hamilton. On April 1, 1969, portions of the study area had 18 inches of snow remaining on the ground while Hamilton had none.

In addition to the influence of logging operations on the area, heavy summer grazing pressure was exerted by domestic livestock,

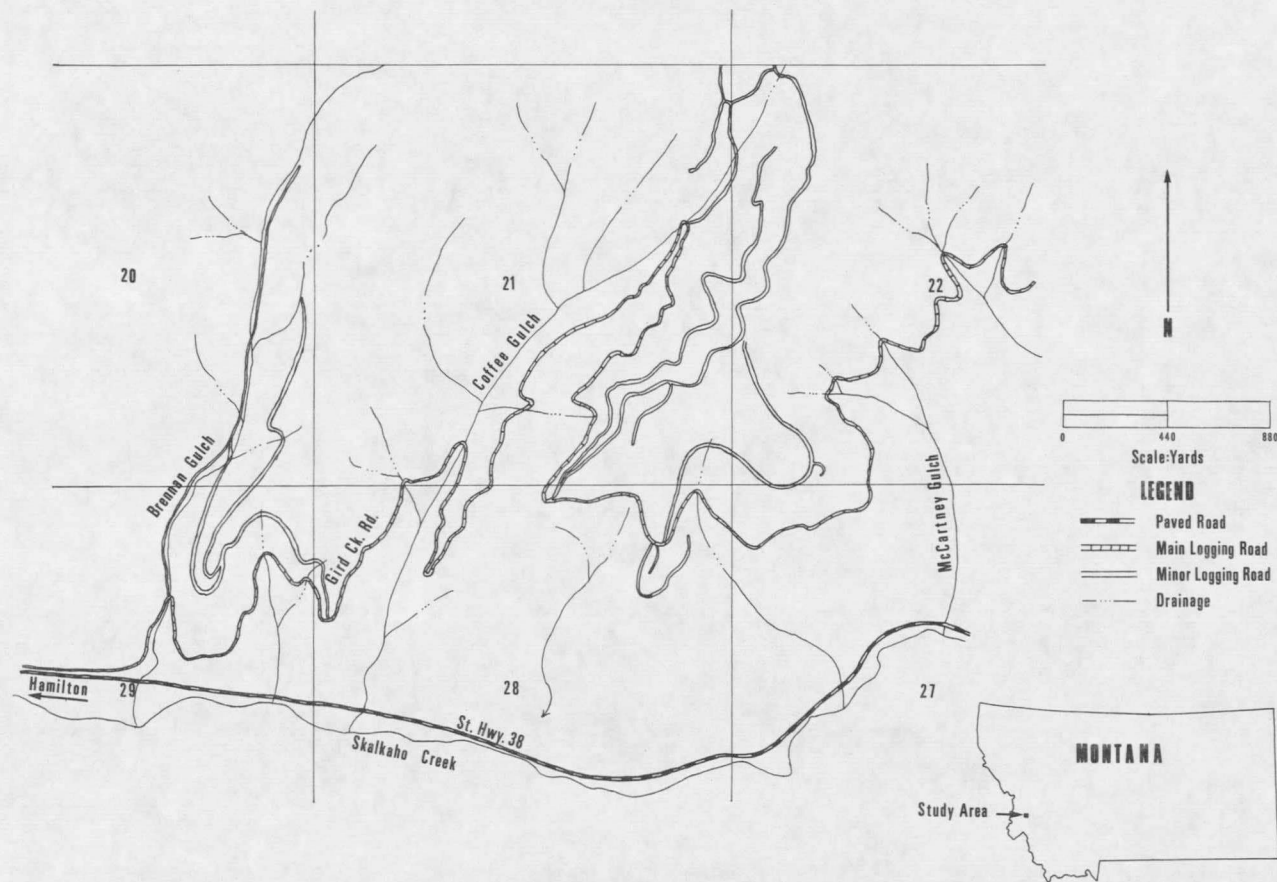


Figure 1. Map of the study area showing network of logging roads.



Figure 2. A view of the open slopes with heavily wooded draws.

particularly on creek bottoms and other moist sites. Mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) use the open, south-facing slopes as winter range.

The study area included portions of both the ponderosa pine and Douglas-fir zones as described by Daubenmire (1953). Semi-open stands of ponderosa pine dominated the lower elevations while stands of pine with Douglas-fir interspersed were found at higher elevations. The heavily wooded draws consisted mostly of Douglas-fir. The pine has been selectively cut on much of the area and is apparently being replaced by Douglas-fir at the higher elevations. Average crown cover of the study area as determined from aerial photographs was about 30 percent.

The unforested portions of the area consisted of three different vegetation types. Two herbaceous types were dominant while a shrubby type was of minor importance. Canopy coverage and frequency of occurrence of the principal plant species present in the two herbaceous types are presented in Table 1.

The dryer portions of the area supported a bunchgrass vegetation type in which bluebunch wheatgrass (*Agropyron spicatum*), Junegrass (*Koeleria cristata*), and Idaho fescue (*Festuca idahoensis*) were the major grasses and arrowleaf balsamroot (*Balsamorhiza sagittata*), silky lupine (*Lupinus sericeus*), yarrow (*Achillea millefolium*), and field chickweed (*Cerastium arvense*) were the major forbs.

TABLE 1. CANOPY COVERAGE AND FREQUENCY OF TAXA FOR THE TWO HERBACEOUS TYPES AS DETERMINED BY EXAMINATION OF TWENTY 2 X 5 DECIMETER PLOTS ON EACH OF 16 SITES.

Taxa ^{1/}	Vegetation Type			
	Bunchgrass (10 sites)		Pinegrass (6 sites)	
	Coverage	Frequency	Coverage	Frequency
GRASS AND GRASS-LIKE PLANTS	13	100	35	100
<i>Agropyron spicatum</i>	3.0	46	X ^{2/}	X
<i>Bromus tectorum</i>	1.4	35	X	X
<i>Calamagrostis purpurescens</i>	X	X	1.6	19
<i>Calamagrostis rubescens</i>	X	X	25.0	92
<i>Carex geyeri</i>	X	X	5.0	50
<i>Festuca idahoensis</i>	2.6	31	0.8	16
<i>Koeleria cristata</i>	3.3	58	-	-
<i>Poa</i> spp.	1.4	52	3.9	33
FORBS	16	99	19	100
<i>Achillea millefolium</i>	1.7	53	1.4	49
<i>Anaphalis margaritacea</i>	-	-	0.3	12
<i>Antennaria racemosa</i>	-	-	0.9	10
<i>Arenaria congesta</i>	0.4	14	-	-
<i>Arnica cordifolia</i>	-	-	1.5	43
<i>Balsamorhiza sagittata</i>	8.0	48	X	X
<i>Cerastium arvense</i>	1.2	36	X	X
<i>Erigeron</i> spp.	0.6	12	-	-
<i>Fragaria virginiana</i>	X	X	5.6	55
<i>Gayophytum nuttallii</i>	0.7	27	X	X
<i>Lupinus sericeus</i>	2.4	25	8.2	51
<i>Sedum stenopetalum</i>	X	X	0.5	14
<i>Silene noctiflora</i>	-	-	0.8	15
<i>Taraxicum officinale</i>	X	X	0.5	10
<i>Tragopogon dubius</i>	0.4	15	X	X
Unidentified forbs	0.8	25	X	X
SHRUBS				
<i>Symphoricarpus albus</i>	0.7	10	-	-

1/ Includes taxa with at least 10 percent frequency of occurrence or one percent canopy coverage in at least one vegetation type.

2/ Indicates taxon present but less than 10 percent frequency of occurrence or one percent canopy coverage.

The more moist portions of the area supported a pinegrass (*Calamagrostis rubescens*) vegetation type in which scattered pine and Douglas-fir were usually present. Pinegrass, elk sedge (*Carex geyeri*), and blue grass (*Poa* spp.) were the major grasses and grass-like species, and silky lupine, Virginia strawberry (*Fragaria virginiana*), yarrow, and heart-leaved arnica (*Arnica cordifolia*) were the major forbs.

A shrub vegetation type occurred on some of the more moist sites and in creek bottoms. The major shrub species present were common snowberry (*Symphoricarpus albus*), ninebark (*Physocarpus malvaceus*), mockorange (*Philadelphus lewisii*), chokecherry (*Prunus virginiana*), white spiraea (*Spiraea betulifolia*), and red dogwood (*Cornus stolonifera*).

A comprehensive listing of the plants occurring on the study area is presented in Table 2 in the appendix. Plant nomenclature is according to Booth (1950) and Booth and Wright (1966).

METHODS

Each year field work was divided into two major phases. From April through mid-June, a concerted effort was made to locate territorial males and plot their locations on aerial photographs. Mid-June to September was devoted to vegetation measurements. The severe decline in male breeding activity by mid-June created a natural division for the two phases.

Observational Procedures

A 4-wheel drive vehicle was used to travel an 8.8 mile route through the study area while conducting morning and evening observations. Morning observations were of three to four hours duration beginning about one-half hour before sunrise. Evening observations were begun about three hours before sunset and continued until visibility was impaired. These periods coincided with times of greatest breeding activity (Blackford 1963; Wing 1946; and Bendell 1954). During the seasonal breeding peak, the large number of observations prevented covering the entire area during a single morning or evening activity period. Some observations were made on foot. Observations from vehicles were probably more indicative of normal behavior because many males were more disturbed by persons on foot than they were of vehicles.

An attempt was made to capture and band all territorial males. They were captured with a plastic-covered wire noose attached to the end of a 24-foot telescoping fiberglass pole (Zwicker and Bendell 1967). Birds were marked for individual field identification with a combination of numbered, plastic and aluminum bands of various colors (Figure 3). Different color combinations were used each year.

When a banded territorial male was sighted, a 15x-60x spotting scope or a 7X50 binocular aided in checking the band number and/or color. If the bird was wary or too far away, a recorded female call (Stirling and Bendell 1966) was used to coax it closer. The call was also useful in locating males that were not readily observable. At least some gave multiple hoots in response or came out in the open.

Each male observation was plotted on colored aerial photographs taken during a low level flight in 1967. Territorial boundaries were then delimited from the plotted observation points.

The projected size of a territory varies with the number of observations until a point is reached where more observations will not add greatly to the size (Odum and Kuenzler, 1955). In order to determine this approximate point, the number of observations of each male was plotted against the size of its territory. Once this point was determined, emphasis could be placed on locating males which had been observed less than the desired number of times.



Figure 3. Leg band combination on a blue grouse for individual identification.

Territory Structure Analysis

Overall territory size was determined from aerial photos by measuring all the area included in boundaries formed by connecting the outermost observation points. To reduce the error in acreage determination caused by radial distortion in the photos, territorial boundaries were transferred to a sheet of paper using a method described by Meyer, et al. (1970). Area was then determined by using a dot grid. Most other measurements were made in the field with emphasis placed upon coniferous thickets in the territories. A thicket was defined as an area having a density of 300 or more trees per acre.

Among the variables measured were the number and total size of thicket(s) in use, tree species composition of thickets, average age of oldest trees, and the amount of edge formed by the perimeter of thickets and open areas. Tree age was determined with the use of an increment borer, and other quantitative measurements were made with the use of a 100-foot steel tape. Crown cover of each of the territories was determined from aerial photographs using a dot grid.

All trees in the thickets were measured with a diameter tape and placed in diameter categories of 1-3, 4-8, and greater than 8 inches. From these data, the number of trees per acre in each diameter category was determined. Where thickets were too large for all trees to be measured, ten randomly placed one-hundredth acre plots were used. Also measured was the height to the lowest live branches under 10 feet high.

The percent slope was measured with an Abney level, exposure was determined with a compass, and the average altitude with an altimeter. Other characteristics that were recorded were the amount of shrub cover, and the distance from the center of one territory to the center of the nearest neighbor territory. The activity center rather than the geometric center was used in determining this distance.

A vegetation density profile of each territory was determined using a technique modified from that proposed by Wight (1938). By this method, a board 6 feet in length with each foot marked off and numbered from one to six was used. The board was placed upright in the approximate center of the territory, and an observer standing 50 feet from it estimated and recorded the amount of cover obstruction at each one foot interval (Figure 4). Estimations of obstruction were made in categories of 0-5, 5-25, 25-50, 50-75, 75-95, and 95-100 percent. An average percent obstruction for each one foot interval was obtained by adding the midpoints of all obstruction estimates for that interval and dividing by the number of observations. Eight readings were made in each territory, one at each of eight major compass directions.

To permit a statistical analysis of the vegetational characteristics, a series of measurements similar to those described above were made on an equal number of areas designated as "non-territories". They were selected at random from portions of the study area that had coniferous vegetation present but no history of use by territorial male



Figure 4. Vegetation density board used to determine shrubby vegetation density profile.

blue grouse.

Discriminant function analysis (Snedecor and Cochran 1967) was used to determine if measurable differences existed between areas selected by male grouse for territories and areas not used by males. The variables which showed no significance in the analysis were eliminated and the remaining judged the most significant territorial characteristics.

In this method, all of the vegetation measurement data are used to formulate an equation, the discriminant function. The data from each territory and non-territory are then inserted into this equation separately. The magnitude of the resulting figure indicates whether the variables and interaction between variables for the particular area are more closely related to those determined overall for the territories, or those determined overall for the non-territories. Thus the area, whether it is actually a territory or a non-territory, is classified as one or the other through the use of the discriminant function. The probability that the area was classified correctly was also determined.

Overall Vegetational Analysis

Vegetational measurements in the open areas were made with a modification of the method described by Daubenmire (1959). Canopy coverage and frequency of occurrence of grasses, forbs, and shrubs were determined with the use of twenty 2 X 5 decimeter plots placed at

10 foot intervals along each of 16 paced transects through representative sites. The percent canopy coverage of each species, and percentages of bare ground and rock were recorded for each plot. Percentage classes were the same as those used in the vegetation density profile readings and the midpoint of each class was the value used in data tabulations.

RESULTS

Territory Occupancy

Observations of banded male blue grouse indicate that some may be present on territories as early as the last week in March. Others may not be situated on a territory until the second or third week in April even though they have been present in the general area since the beginning of that month. Initiation of breeding behavior occurred during the first week in April.

Forty-three territories have been occupied on the study area at one time or another since 1962 as indicated by the present and previous studies (Schladweiler and Mussehl 1968). In the springs of 1968 and 1969, 39 and 40, respectively, of these territories were occupied. At least two territorial males were killed by predators in 1968 and four in 1969. In a minimum of three of these cases, other males took up occupancy after variable periods of time.

A total of 1,010 sightings of individual adult male blue grouse was made. The number of sightings per male over the two-year period ranged from 1 to 72. All sightings were plotted on aerial photographs. The number of plotted observations of a given male may be greater than the number of individual sightings due to extensive movement during a single sighting.

A comparison of the number of observations of a male and the size of its territory indicates that the territory size increased with the

number of observations until a male was observed about 14 times (Figure 5). Therefore, fourteen observations of an individual male were considered sufficient to indicate the approximate size and extent of a territory. Measurements of vegetational characteristics were limited to the 27 territories where males had been observed 14 or more times. The number of observations and minimum age of males on these territories is presented in Table 3.

In 1968, 58 percent of 36 and in 1969, 70 percent of 36 territorial males closely observed were banded. For the years 1968 and 1969, 81 and 68 percent, respectively, of the males having bands the previous year returned to their respective territories. Over the two-year period, the return rate averaged 74 percent. Two males banded in 1962 were still occupying the same territories in 1969. One disappeared later that spring. Ten adult and seven yearling males were banded during this study.

Results of the daily observational periods are presented in Table 4. There was an indicated difference between 1968 and 1969 in the peak of breeding activity, based on the number of adult male observations per hour (Figure 6). The data from 1969 compare more favorably with other studies than those from 1968. The number of female sightings per hour, which also may be indicative of the relative degree of breeding activity, generally supports the data on males pertaining to activity peaks. About 11 percent of the male observations were made on foot rather than

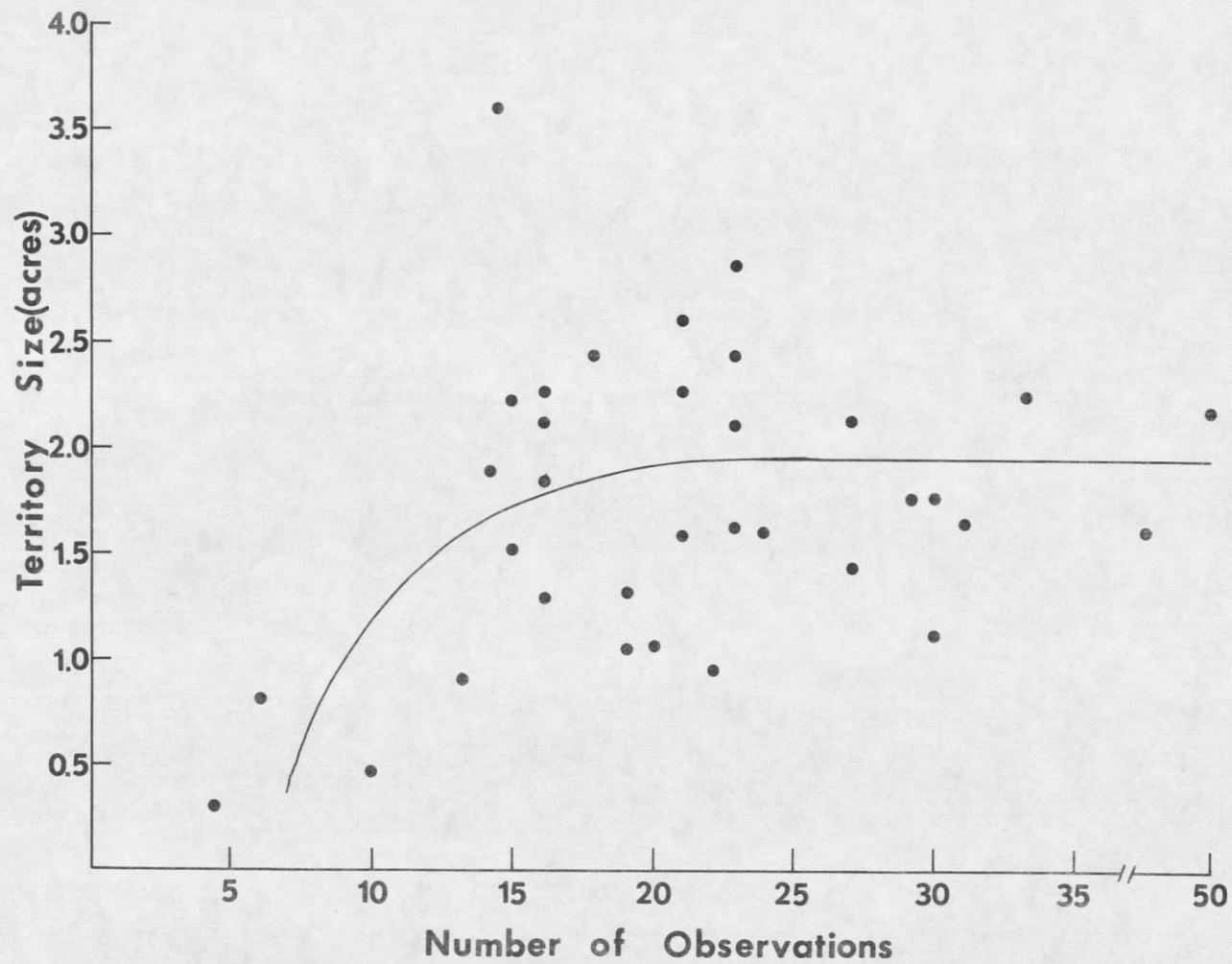


Figure 5. The relationship between the number of observations of males and territory size.

TABLE 3. THE NUMBER OF OBSERVATIONS AND MINIMUM AGE OF INDIVIDUAL MALES ON DIFFERENT TERRITORIES FOR 1968 and 1969.

Territory No.	Min. Age of Male (1969)	Number of Observations		
		1968	1969	Total
103A	5	22	43	65
104	5	5	23	28
105	4	9	30	39
42	unk. ^{1/}	4	16 (NB) ^{2/}	20
32A	8	7	27	34
32B	unk.	4	16 (NB)	20
30	3	3	14	17
30A	5	20	52	72
65	9	11	(21) ^{3/}	32
73A	2	7	(21)	28
54	9	9	19	28
94	4	9	23	32
94A	8	7	21	28
62	unk.	12	14 (NB)	26
38	2	15	(23)	38
38A	2	12	27 (NB)	39
72	2	19	(29)	48
27	unk.	6	16 (NB)	22
47	3	3	19	22
48	unk.	13	30 (NB)	43
51	unk.	6	(16)	22
53	4	22	31	53
52	2	7	(24)	31
82	2	6	(23)	29
115	2	12	15 (NB)	27
116	unk.	10	18 (NB)	28
78	unk.	20	(33)	53

^{1/} Age unknown

^{2/} Indicates that the male was not banded in 1968 so individual identification was not permitted for both years.

^{3/} Parentheses indicates that the territory was occupied by different males in 1968 and 1969.

TABLE 4. DAILY OBSERVATIONAL DATA FOR 1968 and 1969.

Period	Adult Males	Others	Total	Hours of Search	Miles of Search	Males/ Hour	Birds/ Hour
<u>1968</u>							
4-14	4	2	6	2.5	10.5	1.60	2.40
4-19 to 4-22	47	11	58	26.5	72.2	1.77	2.19
4-27 to 4-30	58	13	71	25.3	73.4	2.30	2.81
5- 3 to 5- 6	59	19	78	20.5	47.0	2.88	3.80
5-10 to 5-13	73	33	106	24.6	78.9	2.96	4.30
5-16 to 5-19	50	18	68	15.4	48.4	3.18	4.35
5-25 to 6-13	21	8	29	16.3	89.1	1.29	1.78
Sub-totals	312	104	416	131.1	419.5	2.38	3.17
<u>1969</u>							
3-29 to 5- 3	36	18	54	23.3	84.9	1.54	1.97
4- 6 to 4-12	127	72	199	40.4	167.2	3.14	4.93
4-17 to 4-19	52	36	88	15.2	72.2	3.41	5.77
4-20 to 4-26	140	84	224	38.1	167.0	3.68	5.88
4-27 to 5- 3	111	51	162	25.4	118.2	4.37	6.38
5- 4 to 5- 9	146	78	224	30.1	136.1	4.85	7.45
5-12 to 5-16	65	36	101	21.1	118.3	3.09	4.80
5-25 to 5-29	21	6	27	8.5	57.6	2.47	3.18
Sub-totals	698	381	1079	202.1	921.5	3.45	5.34
Totals	1010	485	1495	333.2	1341.0	3.03	4.49

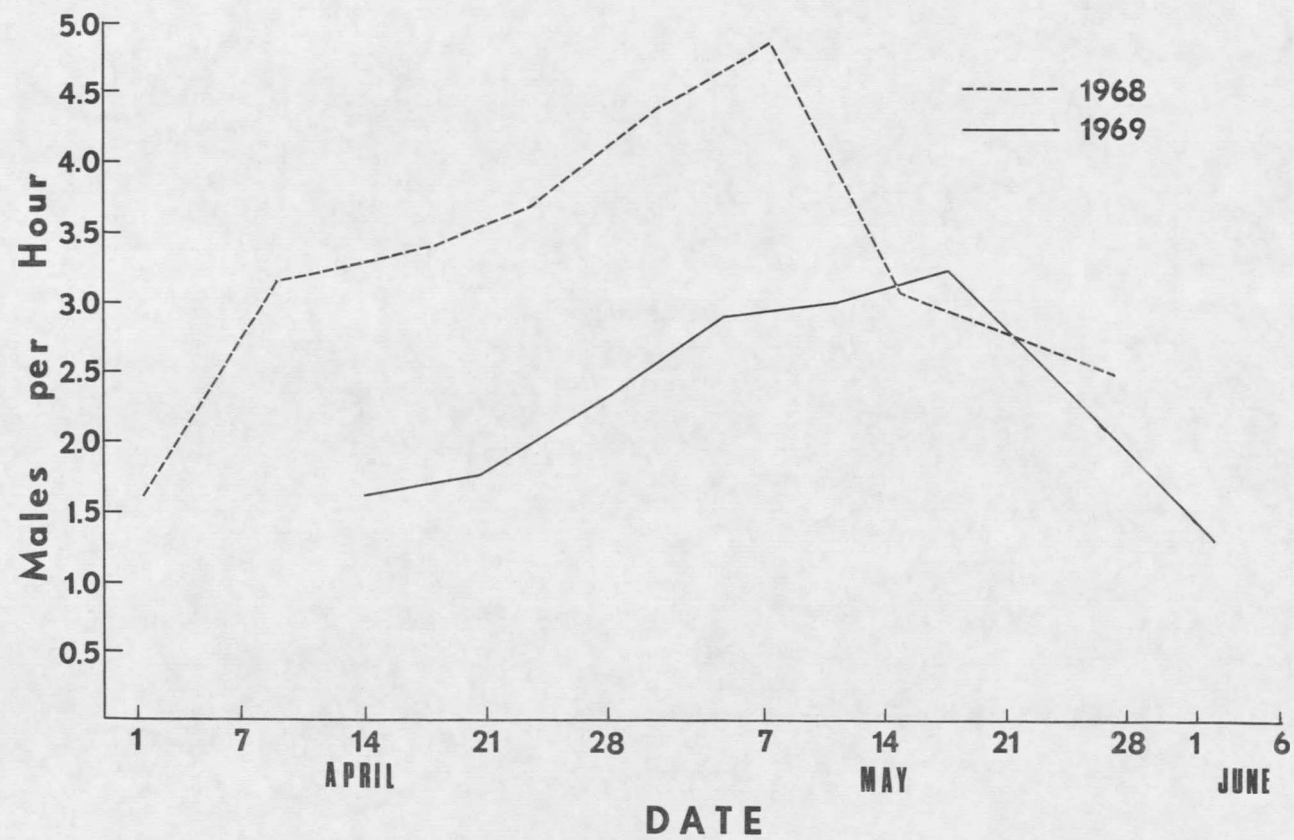


Figure 6. Seasonal distribution of the number of territorial male observations per hour in 1968 and 1969.

from a vehicle but have been included in the total.

Approximately 1.33 miles were driven for each adult male sighted and 0.90 for each blue grouse sighted. This latter figure is considerably better than the one grouse per 26.07 miles of travel recorded by Rodgers (1968) over a three-year period in Colorado. Bendell and Elliott (1967) recorded a high of .81 hooting males per hour of foot search during the peak of breeding activity (May 1 to 14) on Vancouver Island. During the present study, as many as 4.85 males per hour of vehicle search were recorded. Although differences in physiography and habitat types between the areas are considerable, the densities of territorial males were similar. Thus, it appears that search by vehicle, when feasible, may be more efficient than search on foot.

About 68 percent of all blue grouse observed were adult males. The high percentage of birds in this category is attributed to the fact that adult males are much more conspicuous, especially when displaying, than are females or yearling males. Also, the observer probably biased these results by concentrating the search mostly to known territories, where females and yearling males would not necessarily be found.

Eighty-six percent of the adult males observed were either "hooting" or displaying. Of these, 88 percent were in open areas. During rainy or windy weather, males were most often observed hooting in thickets or under trees (Figure 7). Twenty-eight percent of the males observed hooting in the open were on roads. These figures are undoubtedly



Figure 7. Blue grouse displaying under a ponderosa pine during rainy weather.

influenced by observational bias, but they probably reflect somewhat the tendency of males to display in open areas, particularly on roads (when available), where visibility is least restricted.

Vegetation Measurements

Thickets of coniferous trees which were probably used for resting and escape cover appeared to be a major vegetational component of each male blue grouse territory (Figure 8). Therefore, various measurements were made on the thickets and the trees of which they were comprised (Table 5). Similar measurements were made on 27 randomly selected areas designated as non-territories which corresponded in size to the territories (Table 6).

The least variable of all vegetational characteristics measured was the amount of edge provided by the thicket(s). The territories contained an average of .211 acres of thicket and an average of 677 feet of edge. Numerous small thickets often provided as much edge as one large one. For example, Territory 52 contained six thickets totaling .089 acres with 577 feet of edge, while Territory 105 had one thicket totaling .294 acres but only 570 feet of edge. In the non-territories, an average of .055 acres of thicket provided an average of 278 feet of edge, both of which were significantly different ($p < .01$) from the territories.



Figure 8. A thicket of ponderosa pine and Douglas-fir used by a territorial male blue grouse.

TABLE 5. CHARACTERISTICS OF CONIFEROUS THICKETS USED BY TERRITORIAL MALE BLUE GROUSE.

Terr. No.	Terr. Size ^{1/}	Thicket Area ^{1/}	Thicket Edge ^{2/}	Trees		%PP ^{4/}	%DF ^{5/}	Trees per Acre			
				Ave. DBH ^{3/}	Branch Ht. ^{2/}			All.	1-3"	4-8"	> 8"
103A	1.60	.254	599	5.4	4.9	93	7	1074	241	574	259
104	2.44	.366	897	8.7	5.3	88	12	434	46	153	235
105	1.14	.294	570	5.5	5.3	98	2	1123	395	633	95
42	1.82	.402	874	4.6	5.9	67	33	309	127	162	20
32A	1.42	.187	576	5.1	5.8	52	48	471	176	225	70
32B	2.26	.313	608	4.5	4.4	31	69	361	176	166	19
30	3.60	.152	573	4.7	5.4	17	83	1092	375	592	125
30A	2.16	.174	581	4.6	5.6	53	47	1288	437	730	121
65	1.58	.256	580	3.9	6.0	87	13	790	340	438	12
73A	2.61	.189	850	5.7	5.5	24	76	937	217	540	180
54	1.30	.148	584	4.0	4.6	2	98	1628	824	750	54
94	2.10	.156	665	3.7	4.4	4	96	1923	1064	814	45
94A	2.24	.174	697	4.4	5.0	5	95	1339	494	759	86
62	1.86	.235	787	2.7	5.1	8	92	1803	1244	513	46
38	1.60	.211	520	3.3	5.3	4	96	1341	744	597	0
38A	2.12	.276	795	4.3	5.3	9	91	1210	533	583	94
72	1.74	.197	697	3.7	5.3	1	99	1955	919	985	51
27	2.11	.123	625	4.6	4.5	9	91	1235	463	707	65
47	1.96	.143	660	4.9	4.8	11	89	1594	524	986	84
48	1.74	.196	598	5.2	5.0	10	90	918	291	490	138
51	1.29	.158	770	4.8	5.7	15	85	2323	842	1354	127
53	1.63	.208	923	4.2	6.7	18	82	1800	790	989	77
52	1.56	.089	577	6.5	6.3	99	1	1663	371	955	337
82	2.82	.117	614	9.3	6.3	100	0	778	60	410	308
115	2.27	.248	825	3.7	6.0	31	69	1298	802	468	28
116	2.43	.255	617	3.7	5.2	90	10	1263	710	510	43
78	2.22	.177	625	5.6	5.3	53	47	610	175	328	107
Average	1.99	.211	677	4.9	5.4	40	60	1205	496	608	105

^{1/} Territory size and thicket area are in acres.^{2/} Edge and Branch height are in feet.^{3/} DBH is in inches.^{4/} Ponderosa pine.^{5/} Douglas-fir.

TABLE 6. CHARACTERISTICS OF CONIFEROUS THICKETS NOT USED BY TERRITORIAL MALE BLUE GROUSE.

Non-terr. No.	Size ^{1/}	Thicket Area ^{1/}	Thicket Edge ^{2/}	Trees		%PP ^{4/}	%DF ^{5/}	Trees per Acre			
				Ave. DBH ^{3/}	Branch Ht. ^{2/}			All	1-3"	4-8"	> 8"
103A	1.60	.092	487	11.9	5.5	89	11	457	0	185	272
104	2.44	.052	266	5.8	7.5	89	11	635	19	481	135
105	1.14	.082	397	2.1	1.0	26	74	1549	1463	85	0
42	1.82	.039	350	3.4	4.2	0	100	2744	1641	1051	51
32A	1.42	.104	380	7.2	4.5	10	90	625	125	308	192
32B	2.26	.015	150	6.7	5.8	100	0	1000	67	800	133
30	3.60	.000	0	0.0	0.0	0	0	0	0	0	0
30A	2.16	.090	303	6.5	7.6	66	34	389	78	256	56
65	1.58	.039	240	7.1	5.8	98	2	1026	179	590	256
73A	2.61	.014	100	12.0	8.9	100	0	857	0	286	571
54	1.30	.032	220	9.6	5.5	100	0	688	0	250	438
94	2.10	.007	128	6.3	8.3	6	94	2430	290	1430	710
94A	2.24	.140	647	5.7	6.4	12	88	843	286	379	179
62	1.86	.048	354	4.0	6.1	54	46	1979	979	896	104
38	1.60	.020	158	8.7	5.6	82	18	850	0	500	350
38A	2.12	.012	100	5.3	6.0	100	0	1500	417	1000	83
72	1.74	.034	249	8.0	5.6	50	50	765	88	412	265
27	2.11	.076	372	8.2	4.9	46	54	947	132	395	421
47	1.96	.029	126	6.2	4.7	0	100	897	276	414	207
48	1.74	.299	730	6.0	5.3	26	74	690	140	345	205
51	1.29	.067	390	8.9	7.0	62	38	821	119	298	403
53	1.63	.065	188	9.9	8.0	89	11	292	15	92	185
52	1.56	.020	210	10.0	7.9	50	50	1250	100	250	900
82	2.82	.024	200	2.8	1.2	0	100	1667	1250	417	0
115	2.27	.037	240	6.7	10.0	26	74	1243	865	162	216
116	2.43	.055	220	5.4	5.4	5	95	1018	382	582	55
78	2.22	.065	298	5.9	4.4	97	3	1215	323	585	308
Average	1.99	.055	278	6.68	5.67	51	49	1051	342	461	248

^{1/} Non-territory size and thicket area are in acres.^{2/} Edge and branch height are in feet.^{3/} DBH is in inches.^{4/} Ponderosa pine.^{5/} Douglas-fir.

The average DBH (diameter breast high) of trees in the territory thickets was 4.9 inches which is significantly less ($p < .01$) than the 6.7 inch average occurring in the non-territory thickets, and the average number of trees per acre over 8 inches DBH was significantly less ($p < .01$) in the territory than in the non-territory thickets (105 trees per acre vs. 248 trees per acre). Thus, the males used thickets that were generally younger than those in non-territories.

Ages of the majority of trees contained in the territory thickets ranged from about 10 to 60 years with most of them in the 20 to 40 year range. Thickets with most trees younger than 10 or older than 60 years were seldom used except when they were of a growth form that provided protection without obscuring vision.

The species composition of thicket trees varied considerably with an increase in Douglas-fir as the elevation increased. There was no significant difference in species composition or overall densities of thicket trees between territories and non-territories.

The territories and non-territories were separated into three categories based on the species composition of thicket trees. The ponderosa pine type had thickets containing more than 75 percent pine, the Douglas-fir type had thickets containing more than 75 percent fir, and the mixed type had thickets in which neither species made up more than 75 percent of the total. A comparison of the results (Table 7) indicates that the Douglas-fir type territories contained less thicket

TABLE 7. THICKET CHARACTERISTICS OF TERRITORIES AND NON-TERRITORIES GROUPED ACCORDING TO TREE SPECIES COMPOSITION.

Type	Terr. Size ^{2/}	Thicket Area ^{2/}	Edge ^{3/}	Ave. DBH ^{4/}	Branch Ht. ^{3/}	Trees per Acre			
						All	1-3"	4-8"	>8"
Territories									
Ponderosa Pine (7) ^{1/}	1.94	.233	636	6.1	5.6	1018	309	525	184
Mixed (6)	2.03	.250	681	4.7	5.5	723	315	347	61
Douglas-fir (14)	1.99	.183	696	4.3	5.2	1507	666	761	84
Non-territories									
Ponderosa Pine (10)	1.94	.041	221	8.3	6.3	852	102	442	286
Mixed (9)	1.76	.084	361	6.7	6.2	1070	440	344	286
Douglas-fir (8)	2.11	.057	293	5.3	5.0	1460	607	654	199

^{1/} The number of territories or non-territories in each group.

^{2/} Territory size and thicket area are in acres.

^{3/} Edge and branch height are in feet.

^{4/} Average DBH is in inches.

area than the other types. The greater tree density in these thickets could make them more secure and account for the smaller area. These higher densities could be due to the relative shade tolerance of Douglas-fir and the younger age of the thickets. The ponderosa pine thickets were less dense and contained, on the average, larger trees. The relative intolerance of pine to shade and the lack of young pine thickets in the area could account for this.

The open areas of territories contained mostly herbaceous vegetation with occasional areas of shrubby cover. The density profile of

the shrubby vegetation on territories and non-territories is presented in Figure 9. Since the growth of herbaceous vegetation occurs largely after the peak of grouse breeding activity, only the profile of the shrubby vegetation was determined. There is an indicated increase in the shrubby vegetation density in the territories from the ground level upward while the opposite is apparent in the non-territories. This difference is due to both the amount of shrub cover and its growth form. Only ten of the territories had significant amounts of shrub cover while 13 of the non-territories had significant amounts. In the 10 territories and 13 non-territories, shrub cover averaged 1400 and 6300 square feet, respectively.

Small amounts of shrub cover may be used for escape and resting cover as indicated by Bendell and Elliott (1967); however, large amounts probably cause too much vision obstruction and are thus avoided.

Large, mature ponderosa pine and/or Douglas-fir trees were present in most of the territories, but their presence is probably not necessary for territory occupancy. They were occasionally used for escape cover since the birds often flew into them when flushed. Bendell and Elliott (1967) noted that no large trees were present on the breeding areas they studied on Vancouver Island.

Physical Characteristics

Various physical characteristics of the 27 territories are recorded in Table 8. Overall territory size was included in Table 5.

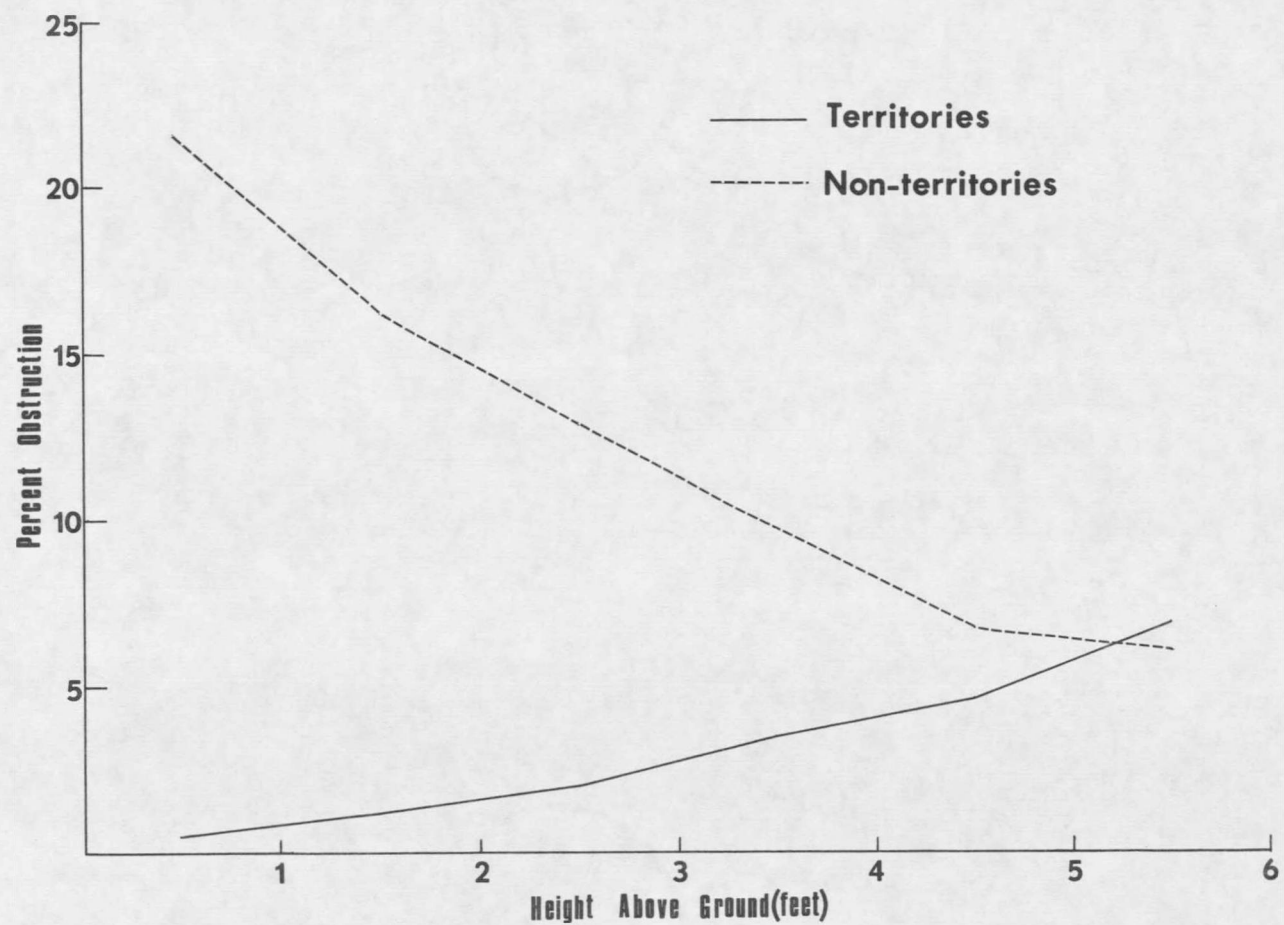


Figure 9. Shrubby vegetation density profile of territories and non-territories.

TABLE 8. PHYSICAL CHARACTERISTICS OF 27 MALE BLUE GROUSE TERRITORIES.

Terr. No.	Altitude	%Slope	%Crown Cover	No. of Thickets	Distance to Neighbor ^{1/}	Exposure
103A	5420	18-35	18	4	460	NE,SW
104	5430	72	25	4	395	E-SE
105	5380	35-65	23	1	525	NE,SW
42	5400	65	19	3	395	SE
32A	5380	58	21	4	395	SE
32B	5460	65	27	2	525	S-E
30	5470	23-47	43	5	395	SE-SW
30A	5510	23-54	33	3	395	E-SW
65	5430	62	39	2	395	E
73A	5610	13-25	31	6	660	N,S
54	5490	57	29	4	460	W
94	5510	45-66	34	4	460	SW-NW
94A	5470	34-44	32	4	660	W-N
62	5400	44	32	4	460	E
38	5380	48	34	2	330	W
38A	5400	58	29	3	330	SW-NW
72	5410	58	28	5	525	W-NW
27	5120	27	25	5	810	SW
47	5000	65	26	6	595	W
48	4950	39-56	26	2	395	SW-NW
51	4910	60	65	5	460	NW
53	4820	59	37	9	460	NW
52	4670	56	30	6	725	W
82	4620	57	31	4	660	SW
115	4680	0-60	24	5	330	W,E
116	4650	20-34	23	4	330	SE-NW
78	4960	70	33	4	395	W
Average		46	30	4.1	478	

^{1/} Feet

Territory size ranged from 1.14 to 3.60 acres, but only one territory was larger than 2.82 acres. The average size was 1.99 acres which is slightly larger than the size determined by Bendell and Elliott (1967) who worked with several different population densities. From their studies, they concluded that territory size varies inversely with population density. No such conclusion could be drawn from this study since male density remained stable.

There appeared to be some relationship between the age of a male and the size of its territory. Nine territories that had been occupied by the same males for a maximum of two years averaged 2.25 acres, while ten territories that had been occupied by the same males for more than two years averaged 1.76 acres, but this difference was not statistically significant.

The altitudes of the territories ranged from 4620 feet to 5510 feet; however, territories are known to occur at considerably higher elevations in other nearby areas. Slopes of the territories located on ridge lines were relatively level, but most of the territories had rather steep slopes because of the general aspect of the terrain.

Tree crown cover on the territories averaged 30 percent which is the same crown cover figure arrived at for the entire study area. Mussehl (1962) reported that the average crown cover was 41 percent on 12 blue grouse territories in the Judith Mountains of Central Montana,

Exposure of the territories included all compass directions; however, the majority faced south or west. Several of the territories were located on ridgelines extending in northwest to southeast or west to east directions so that they contained portions of the heavily wooded north or northeast side of the ridge and the open, treeless, south or southwest side (Figure 10). In such territories, the males often used the ridgeline for displaying.

The distance from the center of one territory to the center of the nearest neighbor territory was measured on the aerial photographs (Table 8). In order to evaluate the significance of this spacing, the distance-to-the-nearest-neighbor method of Clark and Evans (1954) was used. This involves the calculation of a R value which is indicative of the degree to which the pattern of distribution deviates from random expectation. R ranges in value from 0 for maximum clumping to 2.1491 for an evenly spaced distribution. An R value of 1 represents a random distribution.

The calculated R value, determined by dividing the average distance between territories by a figure derived from the territorial male density on the area, was 1.32. This is a significant departure from a random distribution and indicates that the males are rather evenly spaced over the area.

The eight-year history of territories on the study area was used to separate them into three categories: those occupied intermittantly, those occupied continuously by different birds, and those occupied



Figure 10. A sloping ridgeline that is open on the south side and heavily wooded on the north side which was often used by a territorial male blue grouse.

continuously by the same bird for five or more years. The only relationship noted between these groupings and the physical and vegetation data, other than that noted between territory size and male age, was that all the territories with continuous occupancy by the same male occurred at the higher altitudes.

The positioning of territories in relation to the density of conifers on the study area is presented in Figure 11. Small coniferous thickets were associated with all territories even though they may not be so shown in the figure.

A comparison between territories and non-territories with respect to the relative percentages of open areas, thickets, and shrub cover occurring in each is presented in Figure 12. The open areas were designated as consisting of herbaceous vegetation with or without scattered mature conifers. The composition of the non-territories with respect to the three categories should be indicative of the composition of the areas not used by males. If this is so, then there is apparently less shrub cover and open area, and more thicket types incorporated into the territories than in the unused portions of the area. Considering just the thicket and open types, the opposite would probably occur in areas with abundant thickets and infrequent openings.



Figure 11. The location of territories with respect to coniferous vegetation on the study area.

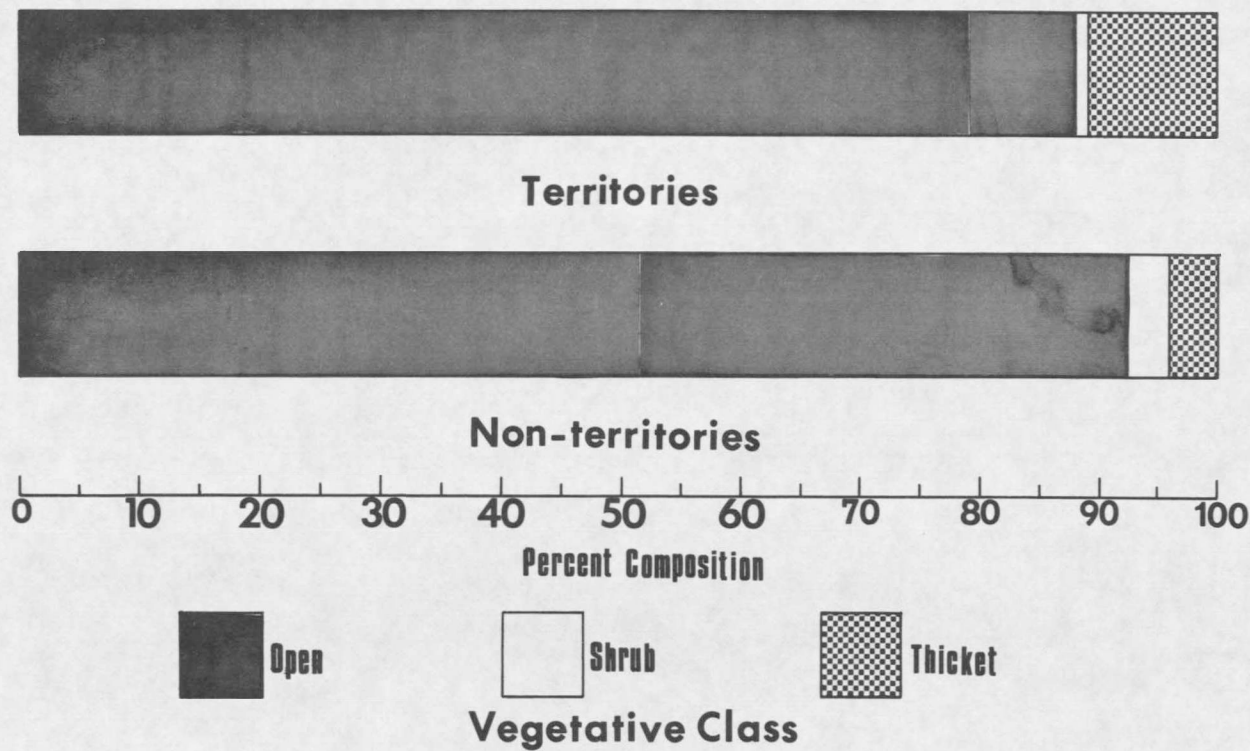


Figure 12. The composition of territories and non-territories with respect to the relative occurrence of three vegetative classes: open, shrub, and thicket.

Discriminant Function Analysis

Four combinations of variables were used in the discriminant function analyses to determine which were the most important. In the first analysis, all ten variables were used (Tables 5 and 6); in the second, thicket area, edge, and trees per acre in the three diameter categories were used; in the third, thicket area, edge, and average tree DBH were used; and in the fourth, only thicket area and edge were used. The choice of the different combinations of variables was based on the results of the analyses of variance mentioned previously. A condensed version of the results is presented in Table 9. The results of the individual analyses are included in Appendix Tables 10 through 13.

The discriminant function analyses suggest that the vegetational structure of male blue grouse territories can be distinguished from that occurring on areas not used by breeding male blue grouse. The analysis in which ten variables were used provided the best results. As the number of variables in the analysis was reduced, the quality of the results decreased. Thus, all the variables measured, except possibly species composition of the thickets, were of some importance.

There appeared to be considerable interaction between variables which made it rather difficult to choose the most important ones. However, a rather high degree of discrimination was shown when only thicket area, edge, and average tree DBH were used in the analysis, so these

TABLE 9. DISCRIMINANT FUNCTION ANALYSES OF TERRITORIES AND NON-TERRITORIES IN WHICH FOUR COMBINATIONS OF VARIABLES WERE USED.

	Number of Variables Used in the Analysis			
	10	5	3	2
<u>Territories</u>				
Classified as:				
Territory	27(3) ^{1/}	27(6)	27(7)	27(9)
Non-territory	0	0	0	0
<u>Non-territories</u>				
Classified as:				
Territory	2(1)	2(1)	2(1)	2(1)
Non-territory	25(3)	25(4)	25(6)	25(7)

^{1/} The number in parentheses is the number of territories or non-territories out of the total which had a less than 95 percent chance of being assigned to the indicated class by the discriminant function.

variables may be the most pertinent ones. The most important aspect of the vegetational structure was probably the amount of edge provided by the thickets since this was the least variable measurement.

LAND-USE AND SUCCESSIONAL RELATIONSHIPS

Logging

Selective logging has occurred on the study area since 1948, and there appears to have been no overall detrimental effects to the breeding habitat. This logging method may be beneficial because it opens up the canopy which allows the regeneration of trees in the form of scattered thickets. However, there are two side-effects that may be deleterious to the breeding habitat. First, this logging method often results in the destruction of thicket areas during log removal and spur road and skid trail construction. Secondly, large areas of slash, like large areas of shrubby cover, seem to be avoided by males, possibly because it obstructs their vision.

Although the clear-cut harvest method was not used on the study area because of the wide spacing of merchantable trees, it was commonly used on other nearby areas. If this method was used on blocks of ten to 60 acres as recommended by Lutz (1957), it may be beneficial to blue grouse because it would open up the canopy and provide the opportunity for the regeneration of new thickets. Large clear-cut areas, if reforested to even-aged stands, would not be suitable for blue grouse breeding habitat.

A relatively new practice on large clear-cut areas is a treatment method commonly referred to as terracing (Figure 13). Such areas are contour furrowed by bulldozers at about 20 foot intervals and planted

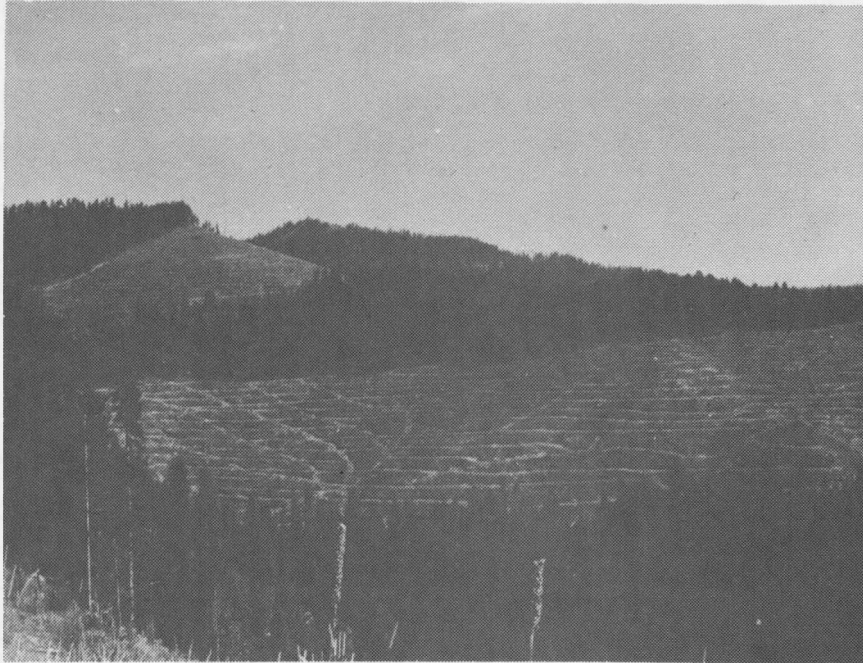


Figure 13. Terracing on a clear-cut area in the Douglas-fir vegetational zone near the study area.

to ponderosa pine. The purpose of this method is to produce conditions suitable for the growth of pine at elevations where it occurs naturally only as a fire successional stage. Aside from degrading the area aesthetically, this practice removes for the present virtually all suitable cover and may delay reestablishment of blue grouse breeding habitat.

Overall, logging must be considered as being beneficial to blue grouse because it results in subclimax vegetation formerly produced by fire which is necessary for breeding habitat. However, the concept of multiple-use of forested areas should be taken into consideration where logging is to take place, and when possible, logging and reforestation methods should take into account the ecology of a particular area as suggested by Lutz (1957).

Silvicultural Practices

Small portions of the study area were clear-cut by the U. S. Forest Service in an attempt to control heavy dwarfmistletoe infestations in thickets of Douglas-fir reproduction. This resulted in the destruction of several thickets (Figure 14) used by territorial male blue grouse and could be considered detrimental to blue grouse breeding habitat. According to Childs (1963), control of this parasite is not economically feasible in heavily infested and densely stocked young tree stands such as those that were cut on the study area. Because of this and because mistletoe spreads very slowly (Pierce 1960), there appears to be little justification for attempts at such control. Also, according to Pierce



Figure 14. A Douglas-fir thicket destroyed in a dwarfmistletoe control program. It was once used by a territorial male blue grouse.

(1960), it generally is more prevalent in situations where trees are ill-adapted to the particular site. So perhaps from the multiple-use viewpoint, attempts to control mistletoe should be limited to the more productive sites and to those that are not important blue grouse breeding areas.

Thinning, although not practiced on the study area, is another silvicultural method which could be detrimental to blue grouse breeding habitat. However, thinning is generally practiced only on large areas of young, even-aged stands of trees where it is said to be economically practical. Thus, the application of the practice is most likely restricted to areas unfavorable for breeding blue grouse.

Successional Relationships

Fire was undoubtedly once the principal creator of blue grouse breeding habitat. With the advent of zealous fire control, logging has become the major disturbances factor responsible for creating new opportunities for succession to take place. However, the seral communities following fire disturbance may differ from those following logging. These differences should be considered since early successional or immature climax stages are desirable for blue grouse breeding habitat.

Breeding habitat in the study area was generally associated with a ponderosa pine fire successional stage in the Douglas-fir vegetational zone, or with immature climax stages in both the ponderosa pine and

Douglas-fir vegetational zones (Daubenmire 1953). The entire area consisted of uneven-aged stands of pine and fir which, according to Weaver (1967), were probably the result of periodic burning. Most of the regeneration present is Douglas-fir which appears to be replacing the mature pine, especially in the cutover areas.

The oldest trees in territory thickets ranged from about 40 to 60 years. Thickets in which most trees were older than 60 years were seldom used and there was little or no use of thickets under 10 to 20 years of age. The longevity of thicket use by males in this area is apparently about 40 to 50 years. On Vancouver Island where precipitation is high, the longevity of breeding areas is closer to 20 years (Bendell and Elliott 1967).

A photo sequence of forest succession over a 40-year period following logging on a nearby area shows what might be expected on the study area (Figures 15-A, B, C, and D). The thickets shown in Figure 15C are probably of about the age when the first use would take place. In a sequence with ponderosa pine reproduction (Figures 16-A and B), the thickets in Figure 16B (about 40 years old) would probably be excellent for male blue grouse territories.

Presently, the regeneration of Douglas-fir thickets following logging on the upper portions of the study area seems adequate. Selective logging in this area may speed up succession because it favors Douglas-fir. On lower portions of the study area, there seems to be



A



B

Figure 15. A photo sequence of forest succession over a 40-year period following logging. The photos were taken in 1909(A), 1927 (B), 1938(C) and 1948(D) (Courtesy U.S. Forest Service).



C



D

Figure 15. (Continued).



A



B

Figure 16. A photo sequence showing the growth of a ponderosa pine thicket over a 20-year period. The photos were taken in 1938(A) and 1958(B) (Courtesy U.S. Forest Service).

little ponderosa pine reproduction even in areas that have been logged.

This may be due to the fact that pine is more dependent than fir on fire for regeneration (LeBarron, 1957).

DISCUSSION

Coniferous tree thickets appeared to be the primary component of male blue grouse breeding territories. This component occurred in all territories and males did not establish territories where it was not present. Thickets used by males varied in number and size but provided a relatively constant amount of edge. Although the density of thicket trees was variable, territorial thickets of greater tree density were usually of less total area. Thickets not used by territorial males were generally made up of younger or older trees than those used by males. The edges of extensive thickets received moderate use, but small isolated thickets were rarely used.

Extensive areas of shrubs were lacking in territories and are probably avoided by males. Shrub cover occurred in much greater quantities on areas not used for territories than it did on areas defended by males. Shrubs that were present on territories were usually of a different growth form.

Since measurable differences do occur between used and unused thickets, it seems reasonable to assume that males select for certain types of thickets. In a discussion of habitat selection in birds, Hilden (1965) mentioned that habitat components such as thickets could be considered both a proximate and an ultimate factor in habitat selection, since they apparently stimulate the selection of a particular

site, and they provide shelter from both enemies and adverse weather. Shrubby areas probably evoke a negative response which may be stronger than the positive response toward a particular group of thickets.

Once a territory has been established, a male will return to it each successive year until he dies, regardless of changes in the vegetational aspect (Bendell and Elliott 1966). For this reason, emphasis in a study such as this should probably be placed on the younger males whose territories have had little chance to change. However, in the present study there was relatively little difference between territories which had been occupied for more than two years and those which had been occupied for two years or less, even though the area had been subjected to periodic selective logging.

Open areas are also an important territorial component, but their importance was not stressed in this study because of their abundance. Since a negative correlation exists between thicket and open areas, the relative importance of one in a given habitat is directly dependent on the other. Barring disruptions in the succession of a unit of forest, a situation where thickets are at a premium and one where openings are at a premium denote the beginning and end, respectively, of suitability of that area for breeding male blue grouse. The importance of openings is shown by the seeming preference by males to hoot or display in areas where, at ground level, unrestricted vision permits ready surveillance of the territory. Prominances such as rocks or stumps are often used

as hooting stations, and in the present study, logging roads were frequently used.

Using the distance-to-the-nearest-neighbor method of Clark and Evans (1954), it was determined that the spacing of males tended toward an even distribution. This distribution may be due to territorial behavior of the males, an even distribution of the necessary vegetation, or a combination of these two factors. Spacing due to territorial behavior alone cannot be accepted in light of the vegetational data from territories and non-territories. Since territories do consist of components which are measurably different from non-territories, spacing of breeding male grouse is probably governed initially by habitat requirements and/or selection and secondarily by territorial behavior.

In sparse populations, Bendell and Elliott (1967) found a random distribution of males in dense and very dense cover which they attributed to the influence of cover pattern. However, in both dense and sparse populations in open cover, they found that males tended toward even spacing which they attributed to territorial behavior.

Although males spend less than one-third of each year on territories, this is the period when their display activities in open areas would probably make them more vulnerable to predation. Thus, the history of territorial occupancy may be indicative of the relative degree of security provided by the vegetation. Eng (1959) reported that the greatest loss of ruffed grouse (*Bonasa umbellus*) to goshawks.

(*Accipiter gentilis*) was during the spring drumming season.

Territories that were occupied continuously during the eight years were generally smaller than those that were occupied intermittantly (1.79 acres vs. 2.33 acres), while most other characteristics were similar. The size difference could be indicative of the aggressiveness of the male as Watson (1964) found in red grouse (*Lagopus scoticus*). Since thicket size and other variables were similar, the security level may in some way be related to the distributional pattern of thickets, which, unfortunately, was not investigated. The larger average size of intermittantly used territories in conjunction with the fact that total thicket areas were similar indicates that the thickets may have been more widely dispersed. Birds occupying such territories were probably more vulnerable to predation, particularly by avian predators. However, it should be noted that of the six predator-killed males found, all appeared to be victims of coyotes (*Canis latrans*).

The greater density and smaller total area of territory thickets composed mostly of Douglas-fir (Table 7) suggests that they provide better protection than thickets of ponderosa pine. Since different tree species have different growth forms, the species comprising most of the thicket trees may be relatively important, although it is basically the growth form rather than the tree species itself that is of major importance. Gullion and Marshall (1968) concluded that it was the growth form or physical characteristics of trees rather than

the species that affected ruffed grouse survival in Minnesota.

Longevity of males did not seem to be influenced by habitat type (ponderosa pine vs. Douglas-fir zones) as was reported for ruffed grouse by Gullion and Marshall (1968). However, differences in longevity as related to habitat types were probably more easily determined for ruffed grouse males since their annual turnover rate is about 50 to 70 percent (Eng 1959; Frank 1947; and Gullion and Marshall 1968) compared to about 30 percent for blue grouse males (Mussehl and Schladweiler 1969; Bendell and Elliott 1967).

Most of the measured characteristics of thickets were inter-related and dependent on age. As a thicket increased in age, natural processes would increase the average tree DBH and the average live branch height and decrease the tree density. Also, thicket area and edge might increase slowly because of regeneration and radial increment at thicket perimeters. Species composition might shift because of interspecific competition between pine and fir. Unfortunately, definite relationships such as this are difficult to quantify because of the variation in site quality encountered in mountainous terrain. In an area that is relatively homogenous with respect to site quality, it may be possible to measure a lesser number of selected variables and determine from them the suitability of thicket areas for blue grouse breeding habitat.

The discriminant function analysis proved to be quite valuable in evaluating male blue grouse territorial characteristics. Using ten variables, 96 percent of the 54 areas (27 territories and 27 non-territories) were classified correctly. This high degree of discriminating power was made possible through a known history of territories which in turn permitted separating areas used for territories from those which were not. In other studies using this statistical technique (Klebenow 1969), problems arose because there was no assurance that selected areas were not suitable for a particular organism, even though it was not found there.

Selective logging, and the resulting forest succession, is probably necessary to maintain this area as suitable blue grouse breeding habitat. This is particularly true in the absence of uncontrolled fires. Other types of logging and most silvicultural practices should be avoided in multiple-use management where blue grouse breeding habitat is paramount. The aim of management in such areas should be to produce uneven-aged stands of timber in which conifer thickets 20 to 60 years of age are numerous. Pynnönen (1954) suggested similar management practices for hazel grouse (*Tetrastes bonasia*) in Finland. Territories in the ponderosa pine zone may become increasingly scarce because of the apparent lack of pine reproduction, which may also be due to the curtailment of fire.

APPENDIX

TABLE 2. A COMPREHENSIVE LIST OF THE FLORA PRESENT ON THE STUDY AREA.

Taxon	Common Name
EQUISETACEAE	
<i>Equisetum arvense</i>	Horsetail
PINACEAE	
<i>Abies lasiocarpa</i>	Alpine fir
<i>Picea engelmanni</i>	Engelmann spruce
<i>Pinus contorta</i>	Lodgepole pine
<i>ponderosa</i>	Ponderosa pine
<i>Pseudotsuga menziesii</i>	Douglas-fir
CUPRESSACEAE	
<i>Juniperus communis</i>	Common juniper
<i>scopulorum</i>	Rocky Mountain juniper
GRAMINEAE	
Tribe Festuceae	
<i>Bromus brizaeformis</i>	Rattlesnake chess
<i>inermis</i>	Smooth brome
<i>marginatus</i>	Mountain brome
<i>tectorum</i>	Downy chess brome
<i>Catabrosa aquatica</i>	Brookgrass
<i>Dactylis glomerata</i>	Orchard grass
<i>Festuca elatior</i>	Meadow fescue
<i>idahoensis</i>	Idaho fescue
<i>octoflora</i>	Six-week fescue
<i>scabrella</i>	Rough fescue
<i>Poa compressa</i>	Canada bluegrass
<i>pratensis</i>	Kentucky bluegrass
<i>secunda</i>	Sandberg bluegrass
Tribe Hordeae	
<i>Agropyron cristatum</i>	Crested wheatgrass
<i>dasystachyum</i>	Thickspike wheatgrass
<i>repens</i>	Quackgrass
<i>spicatum</i>	Bluebunch wheatgrass
<i>Lolium perenne</i>	Perennial ryegrass
Tribe Aveneae	
<i>Arrhenatherum elatius</i>	Tall oatgrass
<i>Danthonia unispicata</i>	One-spike oatgrass
<i>Deschampsia elongata</i>	Slender hairgrass
<i>Koeleria cristata</i>	June grass
<i>Trisetum spicatum</i>	Spike trisetum

TABLE 2. . (CONTINUED)

Taxon	Common Name
Tribe Agrostideae.	
<i>Agrostis alba</i>	Redtop
<i>Calamagrostis purpurascens</i>	Purple reedgrass
<i>rubescens</i>	Pinegrass
<i>Phleum pratense</i>	Timothy
<i>Sporobolus microspERMUS</i>	Sixweeks dropseed
<i>Stipa columbiana</i>	Columbia needlegrass
<i>comata</i>	Needle-and-thread
Tribe Paniceae	
<i>Setaria viridis</i>	Green bristlegrass
CYPERACEAE	
<i>Carex geyeri</i>	Elk sedge
<i>Carex</i> spp.	
JUNCACEAE	
<i>Juncus</i> sp.	Rush
<i>Luzula glabrata</i>	
LILIACEAE	
<i>Allium cernuum</i>	Nodding onion
<i>Brodiaea grandiflora</i>	Brodiaea
<i>Disporum trachycarpum</i>	Rough-fruited fairy-bells
<i>Erythronium grandiflorum</i>	Dogtooth lily
<i>Fritillaria pudica</i>	Yellow bell
<i>Streptopus amplexifolius</i>	Large twisted-stalk
<i>Trillium ovatum</i>	Trillium
<i>Zigadenus elegans</i>	Mountain death camas
ORCHIDACEAE	
<i>Calypso bulbosa</i>	Fairy slipper
<i>Corallorrhiza striata</i>	Striped coral-root
SALICACEAE	
<i>Populus angustifolia</i>	Narrowleaf cottonwood
<i>tremuloides</i>	Quaking aspen
<i>Salix bebbiana</i>	Bebb willow
<i>geyeriana</i>	Geyer willow
<i>scouleriana</i>	Scouler willow
BETULACEAE	
<i>Betula occidentalis</i>	Water birch
URTICACEAE	
<i>Urtica dioica</i>	Stinging nettle
LORANTHACEAE	
<i>Arceuthobium douglasii</i>	Mistletoe

TABLE 2. (CONTINUED)

Taxon	Common Name
POLYGONACEAE	
<i>Eriogonum umbellatum</i>	Sulfur eriogonum
<i>Polygonum aviculare</i>	Prostrate knotweed
<i>douglasii</i>	Douglas knotweed
<i>Rumex acetosella</i>	Sheep sorrel
<i>crispus</i>	Curl dock
CHENOPODIACEAE	
<i>Chenopodium album</i>	Lamb's quarter
<i>Monolepis nuttalliana</i>	Nuttall monolepis
AMARANTHACEAE	
<i>Amaranthus retroflexus</i>	Redroot pigweed
PORTULACAEAE	
<i>Claytonia lanceolata</i>	Western spring beauty
<i>linearis</i>	Narrowleaved spring beauty
<i>perfoliata</i>	Miner's lettuce
<i>Lewisia rediviva</i>	Bitterroot
CARYOPHYLLACEAE	
<i>Arenaria congesta</i>	Ballhead sandwort
<i>Cerastium arvense</i>	Field chickweed
<i>vulgatum</i>	Big chickweed
<i>Lychnis alba</i>	White cockle
<i>Silene cucubalus</i>	Bladder silene
<i>menziesii</i>	Menzies silene
<i>noctiflora</i>	Nightflowering silene
<i>Vaccaria segetalis</i>	Pink cockle
RANUNCULACEAE	
<i>Anemone patens</i>	Pasque flower
<i>Clematis columbiana</i>	Rock clematis
<i>linquisticifolia</i>	Western white clematis
<i>Delphinium bicolor</i>	Low larkspur
<i>Ranunculus acris</i>	Tall buttercup
<i>cymbalaria</i>	Shore buttercup
<i>glaberrimus</i>	Sagebrush buttercup
<i>Thalictrum occidentale</i>	Western meadow rue
BERBERIDACEAE	
<i>Berberis repens</i>	Oregon grape
CRUCIFERAE	
<i>Alyssum alyssoides</i>	Pale alyssum
<i>Arabis holboellii</i>	Holboell rockcress
<i>Camelina microcarpa</i>	Littlepod false-flax
<i>Capsella bursa-pastoris</i>	Shepherd's purse
<i>Descurainia pinnata</i>	Pinnate tansy mustard

TABLE 2. (CONTINUED)

Taxon	Common Name
<i>Draba crassifolia</i>	Rocky Mountain draba
<i>nemorosa</i>	Woods draba
<i>Erysimum asperum</i>	Plains wallflower
<i>Physaria didymocarpa</i>	Common twinpod
CRASSULACEAE	
<i>Sedum stenopetalum</i>	Yellow stonecrop
SAXIFRAGACEAE	
<i>Heuchera cylindrica</i>	Roundleaved allumroot
<i>Lithophragma parviflora</i>	Smallflower woodlandstar
<i>Saxifraga rhomboidea</i>	Diamondleaf saxifrage
GROSSULARIACEAE	
<i>Ribes cereum</i>	Squaw currant
<i>sertosum</i>	Redshoot gooseberry
HYDRANGEACEAE	
<i>Philadelphus lewisii</i>	Mock-orange
ROSACEAE	
<i>Amelanchier alnifolia</i>	Western serviceberry
<i>Cercocarpus ledifolius</i>	Curl-leaf mountain mahogany
<i>Fragaria virginiana</i>	Virginia strawberry
<i>Geum triflorum</i>	Prairie smoke
<i>Physocarpus malvaceus</i>	Ninebark
<i>Potentilla arguta</i>	Tall cinquefoil
<i>glandulosa</i>	Gland cinquefoil
<i>gracilis</i>	Northwest cinquefoil
<i>Prunus americana</i>	Wild plum
<i>virginiana</i>	Chokecherry
<i>Purshia tridentata</i>	Antelope bitterbrush
<i>Rosa woodsii</i>	Wood's rose
<i>Rubus idaeus</i>	Red raspberry
<i>parviflorus</i>	Thimbleberry
<i>Spiraea betulifolia</i>	White spiraea
LEGUMINOSAE	
<i>Astragalus</i> sp.	Milkvetch
<i>Glycyrrhiza lepidota</i>	Wild licorice
<i>Lupinus sericeus</i>	Silky lupine
<i>Medicago lupulina</i>	Black medic
<i>Melilotus alba</i>	White sweetclover
<i>officinalis</i>	Yellow sweetclover
<i>Trifolium hybridum</i>	Alsike clover
<i>pratense</i>	Red clover

TABLE 2. (CONTINUED)

Taxon	Common Name
GERANIACEAE	
<i>Erodium cicutarium</i>	Alfilaria
<i>Geranium carolinianum</i>	Carolina geranium
<i>viscosissimum</i>	Sticky geranium
EUPHORBIACEAE	
<i>Euphorbia esula</i>	Leafy spurge
CELASTRACEAE	
<i>Pachistima myrsinites</i>	Myrtle pachistima
ACERACEAE	
<i>Acer glabrum</i>	Rocky Mountain maple
VIOLACEAE	
<i>Viola adunca</i>	Western violet
<i>orbiculata</i>	Western round-leaved violet
LOASACEAE	
<i>Mentzelia dispersa</i>	Scattered stick-leaf
CACTACEAE	
<i>Opuntia polyacantha</i>	Plains pricklypear
ONAGRACEAE	
<i>Epilobium angustifolium</i>	Fireweed
<i>glaberrimum</i>	Glaucous willow-herb
<i>minutum</i>	Small willow-herb
<i>Gayophytum nuttallii</i>	Nuttall's groundsmoke
<i>Oenothera biennis</i>	Rydberg's evening primrose
UMBELLIFERAE	
<i>Lomatium dissectum</i>	
<i>triternatum</i>	Nineleaf lomatium
<i>Osmorhiza occidentalis</i>	Western sweetroot
<i>Perideridia gairdneri</i>	Yampa
CORNACEAE	
<i>Cornus stolonifera</i>	Red dogwood
ERICACEAE	
<i>Arctostaphylos uva-ursi</i>	Kinikinnick
<i>Vaccinium occidentale</i>	Western huckleberry
PRIMULACEAE	
<i>Dodecatheon pauciflorum</i>	Southern shooting star
GENTIANACEAE	
<i>Gentianella amarella</i>	Annual gentianella
APOCYNACEAE	
<i>Apocynum androsaemifolium</i>	Spreading dogbane

TABLE 2. (CONTINUED)

Taxon	Common Name
POLEMONIACEAE	
<i>Collomia linearis</i>	Narrowleaved collomia
<i>Microsteris gracilis</i>	
HYDROPHYLLACEAE	
<i>Hydrophyllum capitatum</i>	Waterleaf
<i>Phacelia heterophylla</i>	Virgate phacelia
<i>linearis</i>	Linear-leaf phacelia
BORAGINACEAE	
<i>Cryptantha bradburiana</i>	Miner's candle
<i>Cynoglossum officinale</i>	Hound's tongue
<i>Lappula redowskii</i>	Western stick tight
<i>Lithospermum ruderale</i>	Western gronwell
<i>Mertensia oblongifolia</i>	Oblongleaf bluebell
LABIATAE	
<i>Agastache urticifolia</i>	Nettle-leaf giant hyssop
<i>Monarda fistulosa</i>	Horsemint
<i>Prunella vulgaris</i>	Common selfheal
SOLANACEAE	
<i>Solanum dulcamara</i>	Climbing nightshade
SCROPHULARIACEAE	
<i>Castilleja hispida</i>	
<i>miniata</i>	Scarlet Indian paintbrush
<i>Collinsia parviflora</i>	Blue-eyed Mary
<i>Mimulus guttatus</i>	Common monkey-flower
<i>Orthocarpus tenuifolius</i>	Thin-leaves orthocarpus
<i>Pedicularis contorta</i>	Coiled pedicularis
<i>Penstemon albertinus</i>	Alberta penstemon
<i>procerus</i>	Littleleaf penstemon
<i>wilcoxii</i>	Wilcox penstemon
<i>Verbascum thapsus</i>	Flannel mullein
<i>Veronica americana</i>	American speedwell
<i>peregrina</i>	Purslane speedwell
<i>serpyllifolia</i>	Thymeleaf speedwell
PLANTAGINACEAE	
<i>Plantago major</i>	Broadleaf plantain
<i>purshii</i>	Woolly plantain
RUBIACEAE	
<i>Galium aparine</i>	
<i>boreale</i>	Northern bedstraw
<i>trifidum</i>	

TABLE 2. (CONTINUED)

Taxon	Common Name
CAPRIFOLIACEAE	
<i>Linnaea borealis</i>	Twin-flower
<i>Sambucus melanocarpa</i>	Black elderberry
<i>Symphoricarpos albus</i>	Common snowberry
VALERIANACEAE	
<i>Valeriana dioica</i>	Marsh valeriana
<i>occidentalis</i>	Western valeriana
CAMPANULACEAE	
<i>Campanula rotundifolia</i>	Roundleaf harebell
COMPOSITAE	
<i>Achillea millefolium</i>	Yarrow
<i>Agoseris glauca</i>	Pale agoseris
<i>Anaphalis margaritacea</i>	Pearly everlasting
<i>Antennaria racemosa</i>	Raceme pussytoes
<i>rosea</i>	Rose pussytoes
<i>Arnica cordifolia</i>	
<i>sororia</i>	
<i>Artemisia frigida</i>	Fringed sagewort
<i>ludoviciana</i>	Cudweed sagewort
<i>Michauxiana</i>	Michaux sagebrush
<i>tridentata</i>	Big sagebrush
<i>Aster foliaceus</i>	Leafybract aster
<i>Balsamorhiza sagittata</i>	Arrowleaf balsamroot
<i>Centaurea maculosa</i>	Spotted knapweed
<i>Chrysopsis villosa</i>	Golden-aster
<i>Chrysothamnus viscidiflorus</i>	Green rabbitbrush
<i>Cirsium arvense</i>	Canada thistle
<i>vulgare</i>	Bull thistle
<i>Crepis atrabarba</i>	
<i>Erigeron acris</i>	Bitter fleabane
<i>canadensis</i>	Horseweed fleabane
<i>compositus</i>	Fernleaf fleabane
<i>divergens</i>	Spreading fleabane
<i>philadelphicus</i>	
<i>speciosus</i>	Oregon fleabane
<i>subtrinervis</i>	Three-veined fleabane
<i>Filago arvensis</i>	Field fluffweed
<i>Hieracium cynoglossoides</i>	Houndtongue hawkweed
<i>Lactuca serriola</i>	
<i>Matricaria matricarioides</i>	Pineapple weed
<i>Microseris nutans</i>	Nodding microseris

TABLE 2. (CONTINUED)

Taxon	Common Name
<i>Senecio camus</i> <i>lugens</i>	Woolly groundsel
<i>Solidago missouriensis</i>	Goldenrod
<i>Tanacetum vulgare</i>	Common tansy
<i>Taraxicum officinale</i>	Common dandelion
<i>Tragopogon dubius</i>	Common salsify

TABLE 10. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSIS IN WHICH ALL TEN VARIABLES WERE USED

Terr. No.	Classified as: ^{1/}	Probability of Correct Class. ^{2/}	Non-terr. No.	Classified as:	Probability of Correct Class.
103A	T	0.999	103A	N	0.989
104	T	0.999	104	N	0.991
105	T	0.999	105	N	0.997
42	T	1.000	42	N	0.955
32A	T	0.902	32A	N	0.991
32B	T	0.996	32B	N	0.998
30	T	0.933	30	N	0.999
30A	T	0.991	30A	N	0.994
65	T	0.998	65	N	0.997
73A	T	0.999	73A	N	1.000
54	T	0.955	54	N	0.999
94	T	0.992	94	N	0.994
94A	T	0.998	94A	T	0.877
62	T	0.999	62	N	0.887
38	T	0.966	38	N	0.999
38A	T	0.999	38A	N	0.997
72	T	0.999	72	N	0.999
27	T	0.959	27	N	0.995
47	T	0.997	47	N	0.999
48	T	0.965	48	T	0.997
51	T	0.999	51	N	0.995
53	T	0.999	53	N	0.999
52	T	0.971	52	N	0.999
82	T	0.728	82	N	0.999
115	T	0.999	115	N	0.999
116	T	0.999	116	N	0.999
78	T	0.957	78	N	0.985

^{1/} T stands for territory and N for non-territory.

^{2/} Probability that the area was classified correctly by the discriminant function.

TABLE 11. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSIS IN WHICH FIVE VARIABLES WERE USED (THICKET SIZE, EDGE, TREES PER ACRE IN THREE CATEGORIES).

Terr. No.	Classi- fied as: ^{1/}	Probability of Correct Class. ^{2/}	Non-terr. No.	Classi- fied as:	Probability of Correct Class..
103A	T	0.996	103A	N	0.953
104	T	0.999	104	N	0.992
105	T	0.999	105	N	0.997
42	T	1.000	42	N	0.937
32A	T	0.873	32A	N	0.957
32B	T	0.998	32B	N	0.997
30	T	0.915	30	N	0.999
30A	T	0.980	30A	N	0.985
65	T	0.995	65	N	0.996
73A	T	0.999	73A	N	0.999
54	T	0.953	54	N	0.999
94	T	0.987	94	N	0.995
94A	T	0.996	94A	T	0.833
62	T	0.998	62	N	0.931
38	T	0.975	38	N	0.999
38A	T	0.999	38A	N	0.996
72	T	0.999	72	N	0.999
27	T	0.948	27	N	0.990
47	T	0.995	47	N	0.999
48	T	0.972	48	T	0.995
51	T	0.999	51	N	0.994
53	T	0.999	53	N	0.999
52	T	0.837	52	N	0.999
82	T	0.600	82	N	0.999
115	T	0.999	115	N	0.999
116	T	0.996	116	N	0.992
78	T	0.934	78	N	0.989

^{1/} T stands for territory and N for non-territory.

^{2/} Probability that the area was classified correctly by the discriminant function.

TABLE 12. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSIS IN WHICH THREE VARIABLES WERE USED (THICKET SIZE, EDGE, AVERAGE DBH).

Terr. No.	Classified as: ^{1/}	Probability of Correct Class. ^{2/}	Non-terr. No.	Classified as:	Probability of Correct Class.
103A	T	0.986	103A	N	0.959
104	T	0.999	104	N	0.991
105	T	0.990	105	N	0.663
42	T	0.999	42	N	0.939
32A	T	0.942	32A	N	0.931
32B	T	0.997	32B	N	0.999
30	T	0.903	30	N	0.999
30A	T	0.943	30A	N	0.977
65	T	0.990	65	N	0.997
73A	T	0.999	73A	N	0.999
54	T	0.931	54	N	0.999
94	T	0.984	94	N	0.999
94A	T	0.990	94A	T	0.937
62	T	0.999	62	N	0.948
38	T	0.958	38	N	0.999
38A	T	0.999	38A	N	0.999
72	T	0.995	72	N	0.998
27	T	0.924	27	N	0.975
47	T	0.964	47	N	0.999
48	T	0.962	48	T	0.996
51	T	0.995	51	N	0.979
53	T	0.999	53	N	0.999
52	T	0.588	52	N	0.999
82	T	0.573	82	N	0.993
115	T	0.999	115	N	0.997
116	T	0.995	116	N	0.994
78	T	0.958	78	N	0.983

^{1/} T stands for territory and N stands for non-territory.

^{2/} Probability that the area was classified correctly by the discriminant function.

TABLE 13. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSIS IN WHICH TWO VARIABLES WERE USED (THICKET SIZE, EDGE).

Terr. No.	Classified as: ^{1/}	Probability of Correct Class. ^{2/}	Non-terr. No.	Classified as:	Probability of Correct Class.
103A	T	0.984	103A	N	0.660
104	T	0.999	104	N	0.991
105	T	0.989	105	N	0.897
42	T	0.999	42	N	0.976
32A	T	0.923	32A	N	0.879
32B	T	0.996	32B	N	0.999
30	T	0.853	30	N	0.999
30A	T	0.909	30A	N	0.967
65	T	0.980	65	N	0.995
73A	T	0.998	73A	N	0.999
54	T	0.863	54	N	0.997
94	T	0.960	94	N	0.999
94A	T	0.982	94A	T	0.931
62	T	0.998	62	N	0.969
38	T	0.894	38	N	0.999
38A	T	0.999	38A	N	0.999
72	T	0.988	72	N	0.995
27	T	0.875	27	N	0.934
47	T	0.945	47	N	0.999
48	T	0.952	48	T	0.996
51	T	0.991	51	N	0.928
53	T	0.999	53	N	0.996
52	T	0.643	52	N	0.998
82	T	0.842	82	N	0.998
115	T	0.999	115	N	0.995
116	T	0.988	116	N	0.995
78	T	0.953	78	N	0.981

^{1/} T stands for territory and N stands for non-territory.

^{2/} Probability that the area was classified correctly by the discriminant function.

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