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Winter habitat selection by female spruce grouse in a mixed coniferous forest

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WINTER HABITAT SELECTION BY
FEMALE SPRUCE GROUSE IN A MIXED CONIFEROUS FOREST

By

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Winter habitat selection by female spruce grouse (Canachites canadensis franklinii) in a mixed coniferous forest (96 pp.)

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Captured spruce grouse were fitted with solar powered radio transmitters and/or color coded leg bands. The movements, areas used, social groupings, and food habits of radioed and banded birds were monitored during the fall and winter seasons. Meterological conditions were monitored to evaluate the effects of extreme temperatures, winds, and snow conditions on habitat selection of grouse. Sites used by grouse were analyzed to determine the horizontal and vertical structure of vegetation. Areas utilized by observed grouse were compared to unused available areas on the basis of vegetation species composition, basal area, relative density, canopy cover, and the vertical distribution of foliage.

The topographic diversity of spruce grouse habitat in the intermountain west influences not only vegetation community structure and distribution, but also thermal and radiant energy regimes. Over the winter period spruce grouse activity is concentrated within areas subject to tolerable microclimatic conditions. Ridges, upper slope positions, and southerly aspects are selected over drainage bottoms and northerly aspects. In coincidence with the physiographic features selected, certain forest vegetation communities with distinct structures (horizontal and vertical), and furthermore, specific sites exhibiting distinct structures were selected for daytime activities and night roosting.

Needles of ponderosa pine (Pinus ponderosa) were major food consumed by spruce grouse during the winter period.

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INTRODUCTION

The native grouse which inhabit western forests have adapted over time to the prevailing conditions imposed by biotic and abiotic components of their environments. Through the slow process of evolution they have become equipped to occupy distinctive niches in the forest ecosystem. However, the rate of man's modification of forest systems species composition, physical structure, and internal spatial arrangement easily outstrips the forest grouse's ability to adjust. Given the increasing perturbation of existing habitats and control or modification of natural factors, such as wildfire, which create and maintain natural habitats, it is no longer safe to assume that the vegetation communities which result will continue to provide the proper mix of conditions necessary for the survival of current populations or individuals of a species. In order to assess the impacts of natural and man-caused disturbances on a species' environment we must understand the functional relationships which exist between the species and its environment. This is especially true with respect to the vegetal component of the species' environment, for it is this component which we most often modify.

This study deals with the habitat relations of Franklin's race of spruce grouse (*Canachites canadensis franklinii*). It is second only to the ruffed grouse (*Bonasa umbellus*) in terms of areal distribution (Johnsgaard, 1973). Despite this wide geographic distribution spruce grouse have received relatively little attention from the research community.

Throughout the species' geographic range spruce grouse habitat is found exclusively within the coniferous forest environment. As a function of their ecologic distribution spruce grouse are particularly susceptible to the impact of activities and forces which modify their forest habitat. With the ever increasing demand for wood products has come associated forest protection, fire suppression and logging activity which have seemingly replaced wildfire as the major sources of forest habitat modification. Given the current body of knowledge of spruce grouse ecology it is difficult to evaluate the impacts of resource management related activities on the species' habitat.

Over their broad geographic range spruce grouse occupy a variety of environments, differing in physiographic conformation; plant community composition and structure; and climatic regime. This environmental diversity exists within geographic regions as well as among them. For example, in western Montana Franklin's race of spruce grouse is found in association with a variety of forest types ranging from high elevation fir-spruce communities to pure lodgepole pine (*Pinus contorta*) and mixed coniferous forest communities at lower elevations. Forest management practices and other resource use can reasonably be expected to differ over the range of these areas. Spruce grouse responses to environmental perturbations may likewise differ locally, regionally, and seasonally. Greater understanding of the functional relationships between spruce grouse and those factors of their habitat which they perceive will facilitate the evaluation of habitat modification and management across the species' range.

PAST RESEARCH

General

Courtship behavior, territory establishment and territory size have been described by investigators from Alaska (Ellison, 1968 and 1971), Alberta (McDonald, 1968), Minnesota (Anderson, 1973), and Montana (Stoneberg, 1967). Quantitative descriptions of the structural configuration of vegetation at display sites has been presented by Anderson (1973) from Minnesota and Ellison (1971) from Alaska. Quantitative descriptions of habitats used by spruce grouse during the spring and summer season for nesting and brood rearing are provided by Ellison (1964, 1968) from Alaska, McCourt (1969), McCourt et al. (1973) from Alberta, and Haas (1974) from Minnesota. A quantitative description of habitats used by spruce grouse during the summer season in Michigan, without specification of sex or activity, can be found in Robinson (1969).

Home range sizes and movements of female spruce grouse during the nesting and brood rearing seasons have been investigated by Haas (1974) in Minnesota and McCourt (1969) in Alberta. Seasonal movements of male and female spruce grouse have been studied in Alaska (Ellison, 1973). The seasonal social organization of spruce grouse in Alaska has also been reported by Ellison (1973).

The food habits of spruce grouse have been reported from many different areas over the species' range. Quantitative information pertinent to the spring, summer, and fall diets of spruce grouse is available for Alaska (Ellison, 1966), Alberta (Pendergast and Boag, 1970), and Montana (Jonkel and Greer, 1963). Qualitative information about the spruce grouse diet during spring, summer, and fall has been reported by observers from points over much of the species' range (Bent, 1932; Johnsgaard, 1973). The nutritional quality of the spruce grouse diet has been described by Pendergast and Boag (1971), Ellison (1966, 1972) and Gurchinoff and Robinson (1972).

Winter

Information pertinent to the winter season is relatively limited compared to that available for the other seasons. The composition of the spruce grouse winter diet is described by Bent (1932) and Ellison (1972) for Alaska, Pendergast and Boag (1970) for Alberta, Crichton (1963) for Ontario, and Jonkel and Greer (1963) for western Montana. In all of these studies conifer needles were consumed to the practical exclusion of other foods during the winter season. The species of conifer needle selected varied with geographic region, and selectivity for certain species was exhibited by spruce grouse. Needles of jack pine (*Pinus banksiana*) were almost exclusively used on study areas in Ontario (Crichton, 1963) and Michigan (Gurchinoff and Robinson, 1972). The needles of white spruce (*Picea glauca*) were selected exclusively over the equally abundant needles of black spruce (*Picea mariana*) in Alaska (Ellison, 1972). Needles of lodgepole pine (*Pinus contorta*) were selected over other coniferous species in Alberta (Pendergast and Boag, 1970). Jonkel and Greer (1963) observed that needles of western larch (*Larix occidentalis*) were predominantly selected during the fall in north-western Montana. As larch needles became unavailable spruce grouse selected needles of lodgepole pine and Engelmann spruce (*Picea engelmannii*). In no case was food supply or nutritional content considered limiting (Pendergast, 1970 ; Ellison, 1972). Changes in the length and weight of the spruce grouse small intestine, large intestine, and ventriculus occur seasonally, apparently in response to increasing amounts of fiber in

nd Boag, 1973). These changes in internal anatomy facilitate the attainment of energy and nutritional needs from a high fiber, low quality food source by providing for a high rate of food passage through the digestive tract.

The physical structure of habitats selected by spruce grouse has not been investigated sufficiently to allow more than general characterization of winter habitat structure. The only quantitative description of sites used by spruce grouse during the winter is from the Kenai peninsula of Alaska where Ellison (1965) examined 200 roost sites. The roost sites were located during April and May 1965, and identified on the basis of droppings found on the snow surface. Quantitative data from 48 sites were collected. The forest communities from which this information was collected were dominated by white spruce, black spruce, and birch (Betula vesinifera). One hundred and ninety-nine of the 200 roost trees examined were spruce (species not indicated). Roost trees were located in both dense and sparesely stocked stands of timber dominated by spruce. The mean canopy cover for the 248 sites was 21 percent. No other parameters of stand structure, except the species composition of trees, were provided. In a later study, Ellison (1972) observed spruce grouse using dense micro-stands of spruce located within moderately open to open stands of mixed spruce and birch. However the nature of his study excluded consideration of habitat structure and no pertinent structural data were presented.

The social organization of spruce grouse during the winter period has been reported by Ellison (1973) from Alaska. During the winter, Ellison observed spruce grouse singly and in flocks of as many as 10 birds. Ellison noted that flocks (defined as 2 or more birds) rarely remained intact for more than 2 or 3 days, i.e., flock size and composition changed frequently. Adult females and immature spruce grouse of both sexes commonly associated in winter flocks. It appeared, however, that adult males avoided each other during the winter season as well as during the remainder of the year.

Ellison (1973) also monitored the movements of spruce grouse and estimated home range sizes. Based on observations of adult grouse banded before the winter study period, Ellison hypothesized that adult spruce grouse used the same general area yearlong. Two adult males radio-tracked through the winter subsequently established breeding territories within their winter ranges. Seven immature grouse were radio-tracked from mid-October through mid-November. None of these birds moved more than 1.3 km. from the point of capture. Ellison observed that during the winter, spruce grouse were "dispersed throughout the forest on overlapping home ranges, and given birds (traveled) about and (fed) in (their) range either singly or in temporary association with other grouse".

In determining winter home range size, Ellison (1973) suggested that on his area, 40 observations were the minimum number required. His home range size data for 10 Alaskan spruce grouse (5 immature males, 2 immature females, 1 adult female and 2 adult males) are presented in Table 1.

Table 1. Winter home range size (hectares) of ten Alaskan spruce grouse (from Ellison, 1973).

Male		Female	
Adult	Juvenile	Adult	Juvenile
99.8	37.6	39.0	3.2
101.6	112.7		21.7
			41.5
			75.3
			86.0

OBJECTIVES

There is evidence that the relationship of forest grouse to their habitat is substantially different in mountainous regions than in regions of relatively flat relief. Hungerford (1951) noted the effect of cold air drainage, temperature inversion, and vertical temperature gradient on ruffed grouse habitat selection and use. He stated:

> Throughout the year ruffed grouse used cover at those locations where the most moderate temperature prevailed. In winter the ridge habitat experienced the warmest temperatures. Throughout the spring the mating grouse and young broods are on those parts of the slope experiencing warmest night time temperatures and moderate day time temperatures.

Based on Hungerford's finding I hypothesized that forest grouse, including spruce grouse, in western Montana are subject to similar micro-environmental factors and select seasonal habitats which most effectively ameliorate environmental pressures.

The objectives of the current study are to determine:

1. The vegetation species composition and physical structure of sites selected by Franklin's Grouse during the winter season.
2. The influence of micro-climate, food supply, and conspecifics on site selection by Franklin's Grouse.
3. Winter home range size and associated pattern of movements of Franklin's Grouse.

The field work was conducted between September 1, 1975 and Februarv 29, 1976.

STUDY AREA

The study area was located on the lower North Fork of Elk Creek, in the eastern portion of the Lubrecht Experimental Forest, approximately 30 miles northeast of Missoula, Montana (Figure 1). The area included in this study (Figure 2) covered approximately 282 hectares (1.1 sq.mi.).

The North Fork of Elk Creek (North Fork) flows generally from east to west; however, within the study area the stream course runs from NNE to SSW. The resultant general slope exposures are NNW and SSE. Micro-topographic variation is extensive. Elevations on the study area range from approximately 1256 m. (4082 feet) above sea level at the mouth of the North Fork to 1538 m. (5000 feet) at the highest point.

Soils on the study area are Inceptisols formed from quartz monzonite. Soils on the north facing aspects are well developed (up to 100 cm. in depth) in comparison to the shallow, young soils on southerly exposures (Brenner, 1968).

Climatic data for the period 1956-1975 has been collected at the Greenough Post Office, approximately 5 miles from the study area and at a similar elevation (1297 m.) (Steele, 1975). Air temperature was also measured at a base station on the study area.

A winter temperature summary for the study period is given in Table 2. These data indicate that the study period was slightly colder than the previous 19 winter periods. Mean annual precipitation at Greenough for the period 1959-1975 was 46.6 cm. (18.34 in.), including rain and snow. The mean maximum snow accumulation for the period 1959-1976 at Greenough was 40.9 c.m (16.1 in.) and the maximum snow depth recorded was 68.6 cm. (27 in.) in 1972 (Steele, 1975).

Figure 1. Location of Study Area

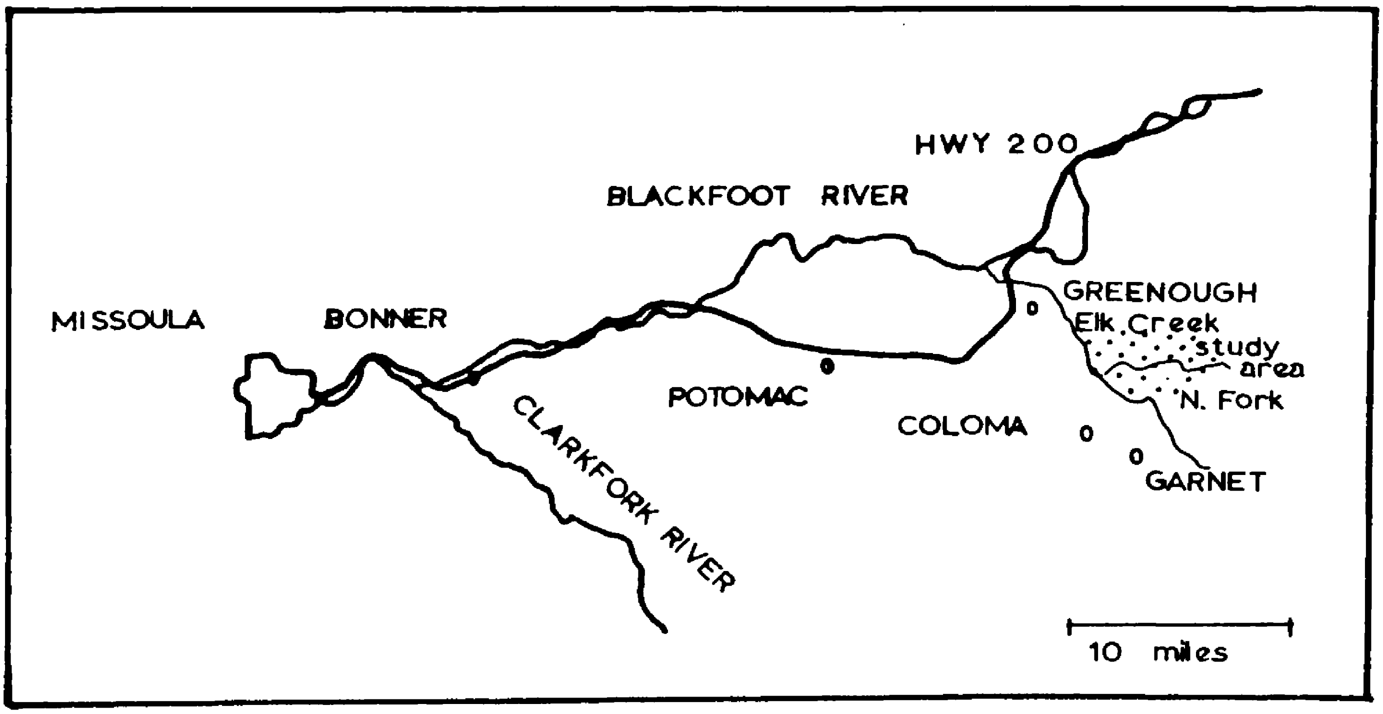

HWY 200
BLACKFOOT RIVER
MISSOULA
BONNER
GREENOUGH
Elk Creek
study area
N. Fork
POTOMAC
COLOMA
GARNET
CLARKFORK RIVER
10 miles

Figure 2. Aerial Photograph of the Study Area on the North Fork of Elk Creek

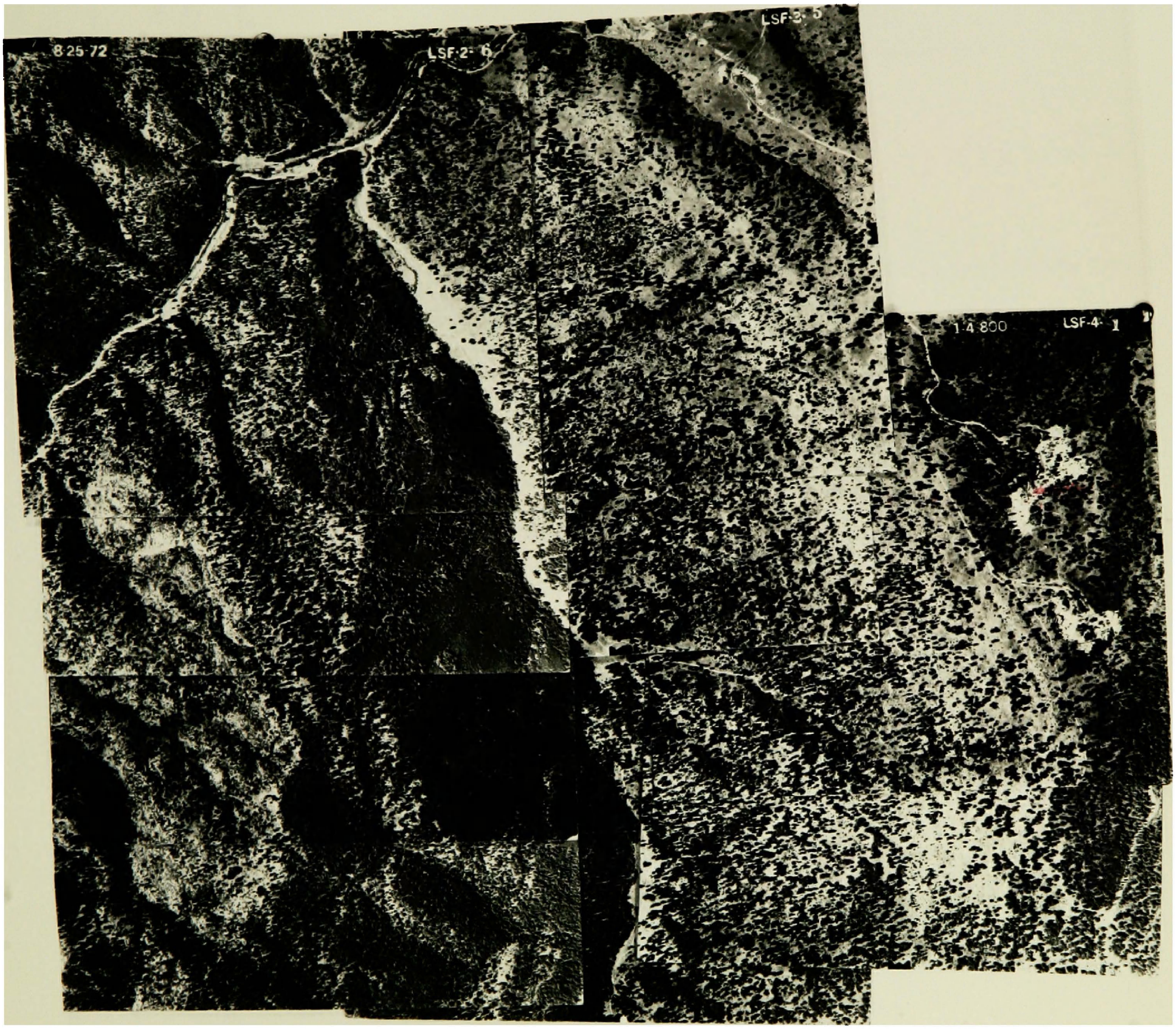

8-25-72
LSF-2- 6
LSF-3- 5
1:4,800
LSF-4- 1

Table 2. Winter temperature summary for Greenough, MT, and the North Fork of Elk Creek study area (°F).

	Mean Daily Maximum			Mean Daily Minimum			Daily Mean			No. of Days when Temperature <32°F.		
	18-year* Mean	1975** Greenough	1975*** N.Fork	18-year Mean	1975 Greenough	1975 N.Fork	18-year Mean	1975 Greenough	1975 N.Fork	18-year Mean	1975 Greenough	1975 N.Fork
November	37.3	35.7	38.5	18.2	15.9	19.6	27.7	25.8	29.2	28	29	29
December	28.1	32.1	30.4	11.0	14.9	11.9	19.6	23.5	21.2	30	29	29
January	26.3	25.0	31.2	7.4	8.8	11.2	17.4	16.9	21.2	29	31	31
February	34.1	29.4	36.2	13.8	7.8	11.1	25.0	18.6	23.7	28	28	29

* 18 year average through 1974, data collected at Greenough
** 1975 data collected at Greenough
*** 1975 data collected on the North Fork of Elk Creek Study area

The Anaconda Company built a railroad into the North Fork of Elk Creek drainage in 1927, and initiated logging activity in 1928 (Cauvin, 1961). The tree species removed included Douglas fir (Pseudotsuga menziesii var. glauca [Beisn.] Franco), western larch, ponderosa pine (Pinus ponderosa Doug.), and Engelmann spruce. All trees of these species greater than 35.6 cm. (14 in.) diameter at breast height (dbh) were removed, except for those which could not be skidded by horses.

Shortly after completion of the logging operation, a fire burned through portions of the study area, primarily south of the North Fork (Crabtree, unpub. Senior Thesis, School of Forestry, University of Montana).

The forest vegetation on the study area was classified on the basis of species composition and physical structure. The following nine types were recognized on the north facing aspect of the drainage:

1. Engelmann spruce
2. Western larch
3. Western larch/lodgepole pine
4. Lodgepole pine (1)
5. Lodgepole pine (2)
6. Ponderosa pine/Douglas fir (on the North Fork - Elk Creek divide)
7. Douglas fir/western larch
8. Douglas fir/lodgepole pine (on the North Fork - Elk Creek divide)
9. Douglas fir/ponderosa pine (on the North Fork - Elk Creek divide)

The forest tree associations on the southerly aspects of the drainage are less diverse in terms of species composition and structural arrangement.

The lower third of the slope is covered by a mixture of Douglas fir, lodgepole pine, ponderosa pine and larch. Moving upslope larch decreases in importance. In the middle third of the slope larch is not present; Douglas fir, ponderosa pine, and lodgepole pine constitute the forest cover. Despite the slight difference in species composition, the horizontal structure of the lower two-thirds of the slope appears relatively homogeneous. The upper third of the south facing slope is covered by a relatively open stand of Douglas fir/ponderosa pine. The vegetation structure of the study area is summarized in Table 3.

Table 3. Summary of study area horizontal structure.

Cover Type	% of Total Basal Area	Area (ha)	% of Study Area	Mean Basal Area Per Acre	Standard Deviation	Mean Tree Density Per Acre	Standard Deviation	Index of Aggregation
Engelmann spruce	ES (29.8)	21.1	4.3	140	45	1969	1675	.68
	LPP (30.4)							
	DF (23.8)							
	WL (7.7)							
Western Larch	WL (61.8)	2.6	.9	169	78	6969	6215	.59
	DF (23.1)							
	LPP (9.7)							
	PP (5.4)							
Western Larch/ Lodgepole pine	WL (43.3)	2.2	.8	123	22	3388	2561	.46
	LPP (35.5)							
	DF (21.2)							
Lodgepole pine (1)	LPP (63.9)	19.9	7.1	193	50	5296	3581	.44
	WL (29.9)							
	DF (3.9)							
	PP (2.5)							
Lodgepole pine (2)	LPP (59.8)	9.5	3.4	150	56	1647	1652	.93
	WL (21.3)							
	DF (12.1)							
	PP (6.9)							
Ponderosa pine/ Douglas fir (North Fork-Elk Creek Divide)	PP (48.7)	13.4	4.8	124	51	449	568	1.49
	DF (21.7)							
	WL (23.7)							
	LPP (6.4)							

Table 3. Continued.

Cover Type	% of Total Basal Area	Area (ha)	% of Study Area	Mean Basal Area Per Acre	Standard Deviation	Mean Stems Per Acre	Standard Deviation	Index of Aggregation
Douglas fir/ Western Larch	DF (38.0) WL (31.0) ES (11.7) PP (7.5) SAF (2.7)	7.7	2.7	146	45	646	596	.75
Douglas fir/ Lodgepole pine (North Fork-Elk Creek Divide)	DF (38.5) LPP (35.2) WL (15.9) PP (10.4)	17.8	6.4	120	56	1172	1477	1.51
Douglas fir/ Ponderosa pine (North aspect)	DF (79.4) PP (14.4) WL (6.2)	3.8	1.4	190	32	717	461	.31
Douglas fir/ Lodgepole pine (South aspect- lower third of slope)	DF (45.2) LPP (24.7) PP (19.4) WL (10.7)	65.0	23.2	69	42	559	971	2.92
Douglas fir/ Ponderosa pine (South aspect- mid slope)	DF (55.2) PP (37.3) LPP (7.5)	62.1	22.2	62	42	595	971	2.52
Douglas fir/ Ponderosa pine (South aspect- upper slope)	DF (68.9) PP (31.1)	55.9	19.9	41	24	162	393	5.60
Unavailable		8.1	2.9					

METHODS AND MATERIALS

Radio-tracking

Spruce grouse were located by searching the study area on foot. Once located, grouse were snared using a telescoping, extensible fishing pole fitted with a noose at the tip, similar to that described by Zwickel and Bendell (1967). Grouse which were wary of the noosing pole were herded into a mist net stretched between shrubs and/or small trees.

Once captured, all spruce grouse were fitted with four anodized, aluminum, color-coded leg bands for future identification. Initially, five female spruce grouse were fitted with radio transmitters. This number approached the maximum I was operationally capable of monitoring under the prevailing conditions. The same grouse were not followed all winter because of losses due to radio failure and natural mortality.

The radio telemetry equipment used was manufactured by Wildlife Materials, Inc., of Carbondale, Illinois. Both standard battery-powered and solar-powered transmitters were used. The transmitters were operated on discrete frequencies within the 150-159 megahertz range. The harness system used was similar to that described by Brander (1968). The radio packages, located on the birds' back, weighed approximately 23 gms. A hand held 3 element yagi antenna was used for signal reception.

Radio marked hens were relocated from 1 to 3 times during each day spent in the field. Visual sightings were made when possible: however, it was often necessary to triangulate on a grouse's position in order to determine its exact location. This procedure was required after nightfall and in cases in which the subjects were situated in a tall tree or extremely dense canopy and were not visible.

Re-locations of a radio-marked grouse were recorded on acetate overlays of aerial photographs of the study area. The aerial photographs used were 1:4800 in scale. The distance between subsequent radio locations was measured directly from the aerial photographs. Measurements were made only within the center portion (effective area) of the aerial photographs to minimize measurement error due to distortion near the photograph margins (F.L. Gerlach, Pers. Comm.).

The distance between daytime activity areas and night roosts for individual birds was measured only in cases in which subsequent radio locations were less than 6 hours apart. Distances moved by individual birds during the feeding-loafing period (daytime activity) were measured only when at least 2 successive radio locations were made during a given day (feeding-loafing period).

Home Range

Home range sizes were determined by measuring the area encompassed by a line on the aerial photograph connecting the outermost location points for each grouse (Odum and Kuenzler, 1955). Areal coverage was measured with a compensating polar planimeter, again utilizing only the effective area of the photographs. A modified minimum area method (Harvey and Barbour, 1965) was used to estimate the area utilized within each individual grouse's home range.

Disturbance of radio-marked grouse during observation was minimal. Observation of located grouse from concealed positions for periods of up to 2 hours indicated that normal behavior was not excessively disrupted after the initial disturbance caused by the location procedure. When approached by humans, spruce grouse normally froze in position. Birds on the ground often tolerated human presence to within approximately 3 meters before moving.

Flushing response to disturbance was seldom observed. Grouse in trees remained motionless until disturbing activity ceased. Activities such as feeding, preening, loafing, or a combination of these were interpreted as normal behavior. When disturbed excessively, grouse in trees either fled or sat motionless. Generally, normal activity resumed within several minutes of detection, depending on the subsequent activity of the observer and the position of the grouse with respect to the observer.

Habitat Measurements at Observation Sites

Each time a spruce grouse was located a record was made of the time of day (Mountain Standard Time), sexes and ages of all grouse present, cloud cover, precipitation occurrence and type, general wind intensity and direction, and air temperature at breast height (137 cm.). The birds' locations were noted with respect to slope inclination and aspect. Activities and food habits were observed and recorded. When a grouse was located on the ground, its position with respect to overhead cover, stumps, logs, boulders, etc., was recorded. Tree species, height, diameter at breast height (dbh), crown form (Miller and Keen, 1960), and crown length were recorded for all trees used by spruce grouse. In cases where concealment was afforded a grouse by the view obstruction of 2 or more contiguous tree canopies, the effective crown length represented by these trees, i.e., length of canopies considered as one, was recorded.

A Relaskop was used to measure the basal area of the trees per acre at the site of each grouse location. Trees which fell within the variable radius plot were recorded by species and dbh class. Six dbh classes were arbitrarily selected, 0-5.0 c.m (0.2 in.), 5.1-10.1 c.m (2-4 in.), 10.2-20.3 cm. (4-8 in.), 20.4-38.0 cm. (8-15 in.), 38.1-76.2 cm. (15-30 in.), and 76.2 cm. + (30 in. +).

The percent canopy coverage for the area of the sample plot was estimated. The vertical distribution of foliage in the area of the sample plot was recorded in terms of estimated canopy coverage contributed by layers of foliage and their corresponding depths and heights above ground. Percent canopy coverage was estimated on the basis of the percent of sky obscured by foliage, limbs, branches, and tree boles. Heights were determined with the Relaskop. Vertical foliage profile diagrams were constructed for groups of observations such as night roosts and feeding-loafing sites. Frequency of occurrence and the density of the trees, on a per acre basis, both by species and dbh class, were calculated from the sample plot data. A non-parametric statistical method, Mann-Whitney rank test, was used to test for significant differences in tree density and tree basal area between feeding-loafing sites and night roosts selected by observed spruce grouse (Sokal and Rohlf, 1969).

General Habitat Measurements

Forest cover types were delineated on acetate overlays of aerial photographs of the study area. Delineations were based on tree species composition and differences in physical structure of stands. A compensating polar planimeter was used to determine the areal coverage of individual types.

The vegetation in that portion of the study area south of the North Fork of Elk Creek was sampled during the fall of 1975 in a study conducted by Gregory Shaw. In each designated cover type, reference points for the placements of variable radius plots were subjectively located on representative sites. One plot was placed 30 meters from the reference point in each of the cardinal directions. A minimum of 4 plots was placed in each designated forest cover type. Since areas covered by the same cover type were scattered in patches of varying size, the date from several geographically separate areas were often combined.

The northern portion of the study area was sampled during the spring of 1976. Due to time constraints, I selected a sampling method which required less time than that used by Gregory Shaw. The only difference between the two methods was in the determination of plot location. Paced transects were established in a randomly selected direction and at randomly selected distances apart in each of the designated cover types. Plots were spaced at 45 meter intervals along the transects.

Basal area of trees was recorded by species and diameter class at each sample point. Frequency of occurrence of trees and density of trees on a per acre basis were calculated from the sample plot data and recorded according to species and dbh class. An index of aggregation was calculated for each cover type from the ratio of the variance (associated with the mean density of trees per acre) to the mean density of trees per acre (Pielou, 1969). The variability in vertical foliage structure within cover types was great. Without means of expressing this variability, foliage profile diagrams for general cover types were considered marginal in value.

Sampling efficiency was determined by plotting the variance associated with basal area estimates for the i^{th} cover type against the number of plots (n_i) associated with s_i^2 (Smith, 1966). When the curve associated with the graph of s_i^2 versus n_i leveled off, sampling was terminated. I reasoned that additional sampling effort would not decrease sample variance sufficiently to warrant further effort.

Habitat Selection

Habitat selection by female spruce grouse was evaluated on the basis of cover types available within the study area as a whole, rather than cover

ɿird's home range alone. Consideration of the cover types present within a bird's home range alone may reflect the bird's preference for associated vegetation structure and environmental conditions, but ignores the differential effect of the various cover types on initial habitat selection. This is the same procedure used in an evaluation of habitat selection by sharp-tailed grouse (Ramharter, 1976).

Based on the hypothesis that wintering spruce grouse were distributed randomly throughout the study area, expected frequencies of radio locations for each cover type were computed by multiplying the total number of radio locations by the fraction of the total study area comprised of the given cover type. The hypothesis was tested by comparing the observed number of radio locations to the expected number for each cover type via a single classification Chi-square goodness of fit test with one degree of freedom.

Weather Data

Air temperatures were measured at various points within the study area to determine the location and magnitude of air temperature gradients. A hygrothermograph was placed at each of the following locations: the stream bottom (H1) at approximately 1277 m. (4120 ft.) above sea level; on the North Fork - Elk Creek divide, which marks the southern boundary of the study area, (H2) at approximately 1495 m. (4860 ft.) above sea level; and on the south facing slope (H3) at approximately 1406 m. (4570 ft.) above sea level. An attempt was made to place the hygrothermographs on level sites. A transect of maximum-minimum thermometers was established, running from the creek bottom upslope on both the north and south exposures. Thermometers were set at 30.7 m. (100 ft.) elevational intervals such that the transects ran through areas used by radio-marked grouse. The hygrothermographs and maximum-minimum thermometers were placed at 1.37 m. (4.5 feet) above the ground.

RESULTS

Performance and Effects of Radio Telemetry Equipment

The solar powered radio transmitters functioned well under bright light conditions. However, when the duration of exposure to bright light or light intensity diminished below optimum conditions, the storage batteries failed to fully recharge and the period of transmitter operation was substantially curtailed. When a radio-marked grouse remained for relatively long periods in dense cover where light intensity was low and the solar plate was in shadows, the storage battery did not recharge. Similarly when the grouse preened feathers over the solar plate the efficiency of the transmitter was reduced, particularly under low light conditions. Overcast sky conditions and the occurrence of precipitation reduced the intensity and amount of light available to recharge solar cells regardless of grouse behavior.

Only 2 of the radio packages consistently transmitted signals during daylight hours. However, on days during which heavy precipitation occurred, even the most reliable radio package failed to transmit a signal for more than 4 hours during mid-day. None of the radio packages stored enough energy to allow signal transmission through the night into early morning hours. As a result, locations of night roosts and early morning locations were not often attained.

All of the radio packages were operating at the end of the study (Table 4). One adult female (No. 2739) carried a radio package for over 200 days without any apparent difficulty or adverse effects. Only 1 radio-marked grouse died during the study period (No. 335). The cause of death was unknown. This adult female had raised a brood during the previous summer. When examined in September of 1975, the bird appeared healty except for a retarded primary

ubsequently became emaciated and died in mid-November,

Table 4. Summary of radio telemetry observations.

Bird No.	Sex	Age*	Fate**	Period Observed	No. Days Observed	No. of Observations	Mean No.Daily Observations
226	F	I	2	1/22/76-1/27/76	5	5	1.0
235	M	A	2	10/1/75-10/10/75	3	3	1.0
236	F	I	1	12/10/75-2/29/76	25	27	1.1
237	F	A	1	2/13/76-2/28/76	5	6	1.2
243	F	I	1	11/3/75-2/29/76	38	43	1.1
245	F	A	1	10/8/75-2/29/76	59	75	1.3
335	F	A	3	9/1/75-11/16/75	19	21	1.1
2739	F	A	1	9/1/75-2/29/76	61	73	1.2
Total					213	253	1.1

* A = Adult, I = Immature

** 1 = Alive at end of study period.
2 = Radio failed, fate unknown.
3 = Died of unknown natural cause.

1975. I do not feel that the radio package caused the bird's death. However, it undoubtedly affected the grouse while under stress.

A summary of observations of banded spruce grouse without radios is presented in Table 5.

Temperature regimes

Recorded winter temperature gradients reflected the physiographic features of the drainage (Figures 3, 4, 5). Warmest temperature conditions consistently occurred on the south-facing slope. Air temperatures on ridges and the upper portions of the slopes were generally warmer than in drainage bottoms and lower portions of the slopes at night and during the coldest portions of the day.

The weekly mean maximum temperature recorded at H3 (south-facing slope) ranged between 1.7°C. (3°F.) and 5.5°C. (10°F.) above the weekly mean maximum temperature recorded at H1 (creek bottom) and between 1.1°C. (2°F.) and 5.5°C. (10°F.) above that recorded at H2 (ridge). Weekly mean maximum temperatures recorded at H2 ranged between .6°C. (1°F.) and 7.2°C. (13°F.) below those temperatures recorded at H1.

The weekly mean minimum temperatures recorded at H3 (south-facing slope) ranged between 0 and 3.9°C. (7°F.) above those recorded at H2 (ridge station) and between 2.2°C. (4°F.) and 9.4°C. (17°F.) above those recorded at H1 (creek bottom) 1267 m. (4120 ft.). The weekly mean minimum temperatures recorded at H2 ranged between 3.3°C. (6°F.) and 5.5°C. (10°F.) above those recorded at H1.

Temperature inversions occurred on 23 of 28 nights for which data are available between December 16, 1975 and February 29, 1976 (Figure 5). Cold air accumulation was detected in the North Fork drainage bottom resulting

Table 5. Summary of observations on banded and unmarked spruce grouse (10/1/75 - 2/29/76).

Bird No.	Sex*	Age**	No. of Observations
229	F	I	1
231	F	I	1
239	M	A	1
241	F	I	1
242	M	A	1
238	M	I	1
unmarked	M	A	24
unmarked	M	I	6
unmarked	M	U	18
unmarked	F	A	18
unmarked	F	I	16
unmarked	F	U	62
			150

* M = Male
F = Female

** A = Adult
I = Immature
U = Unknown

Figure 3. Mean maximum temperature for one week intervals measured at the three study area weather stations.

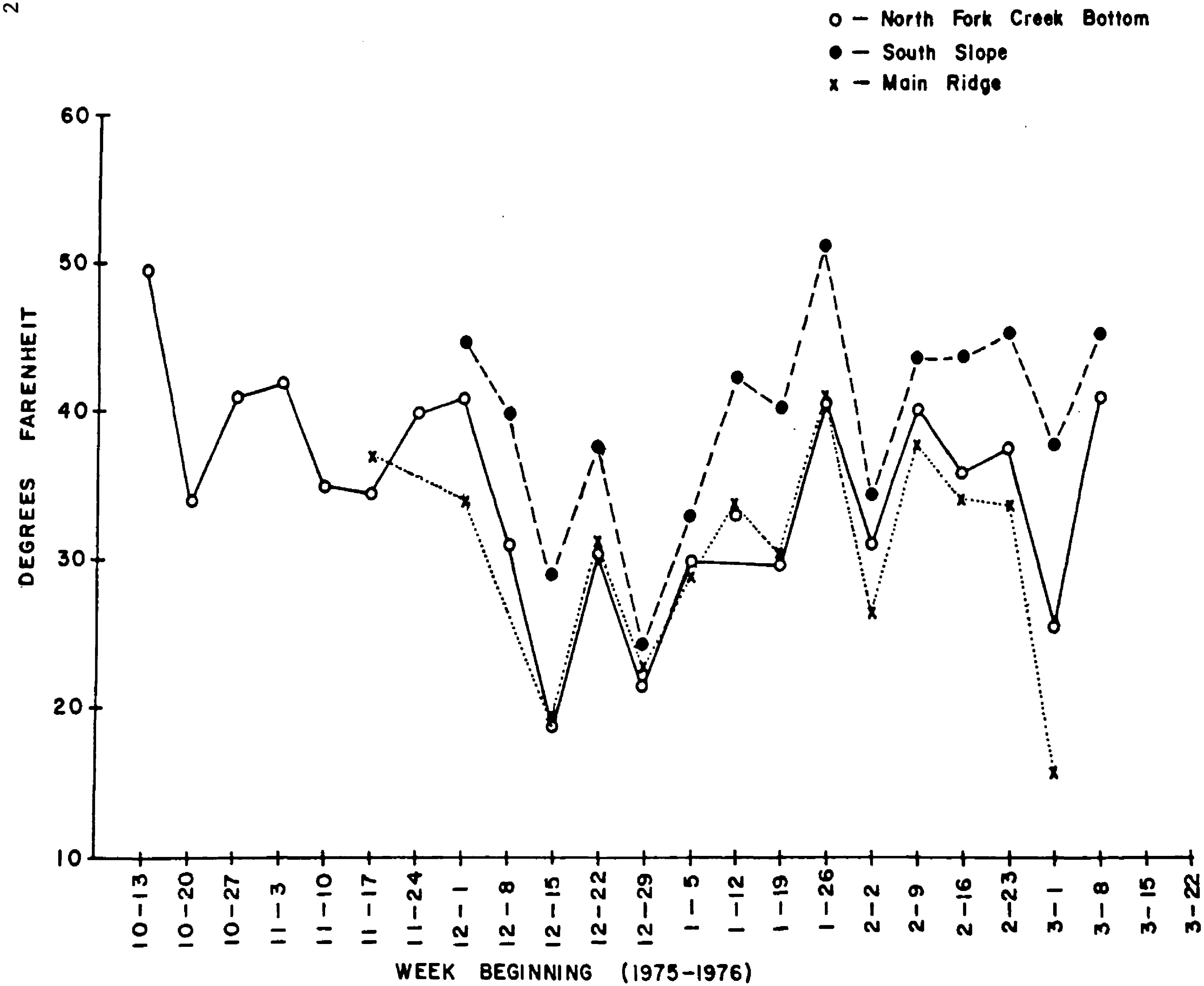

o — North Fork Creek Bottom
● — South Slope
x — Main Ridge
DEGREES FARENHEIT
60
50
40
30
20
10
10-13
10-20
10-27
11-3
11-10
11-17
11-24
12-1
12-8
12-15
12-22
12-29
1-5
1-12
1-19
1-26
2-2
2-9
2-16
2-23
3-1
3-8
3-15
3-22
WEEK BEGINNING (1975-1976)

Figure 4. Mean minimum temperatures for one week intervals measured at three study area weather stations.

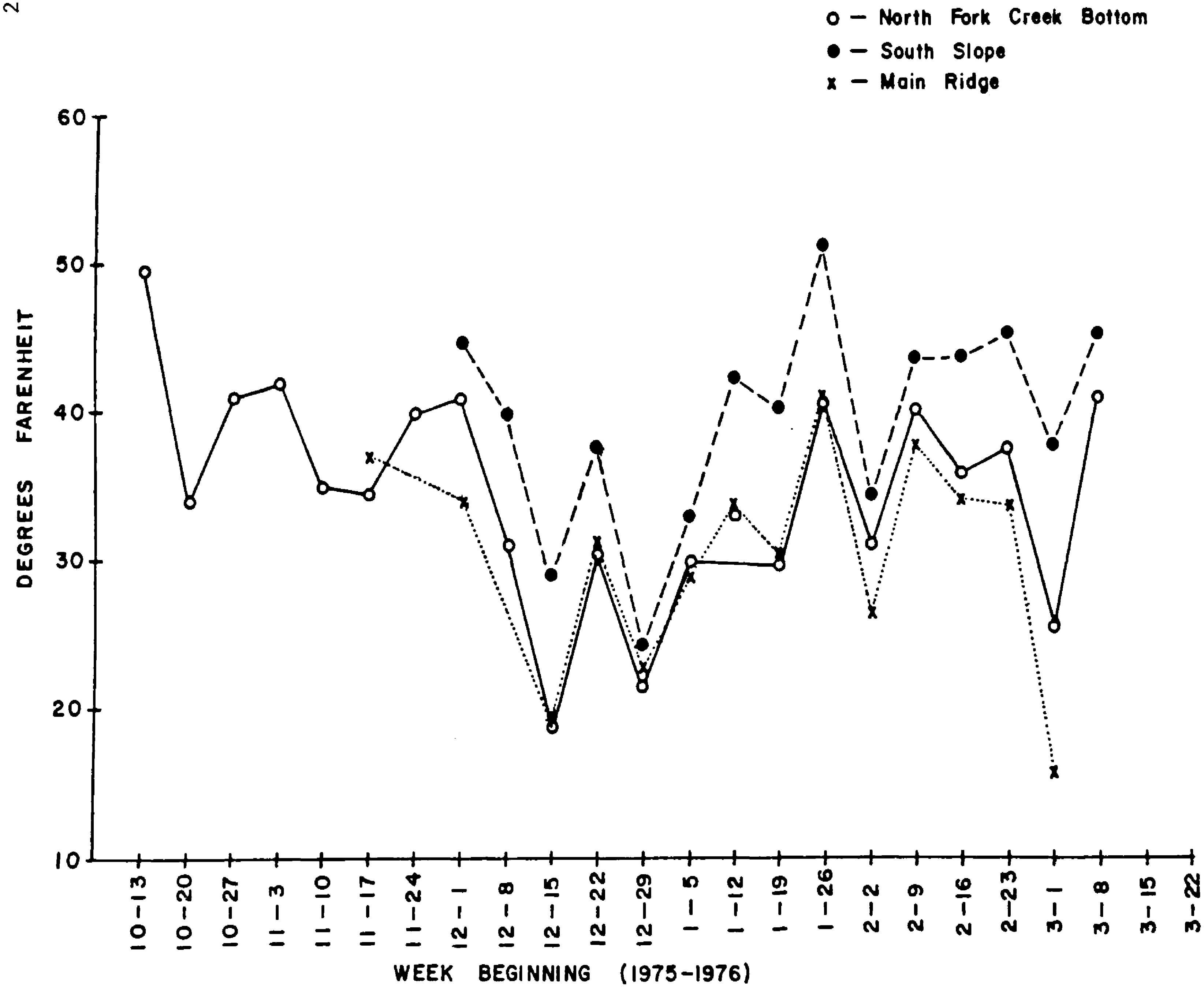
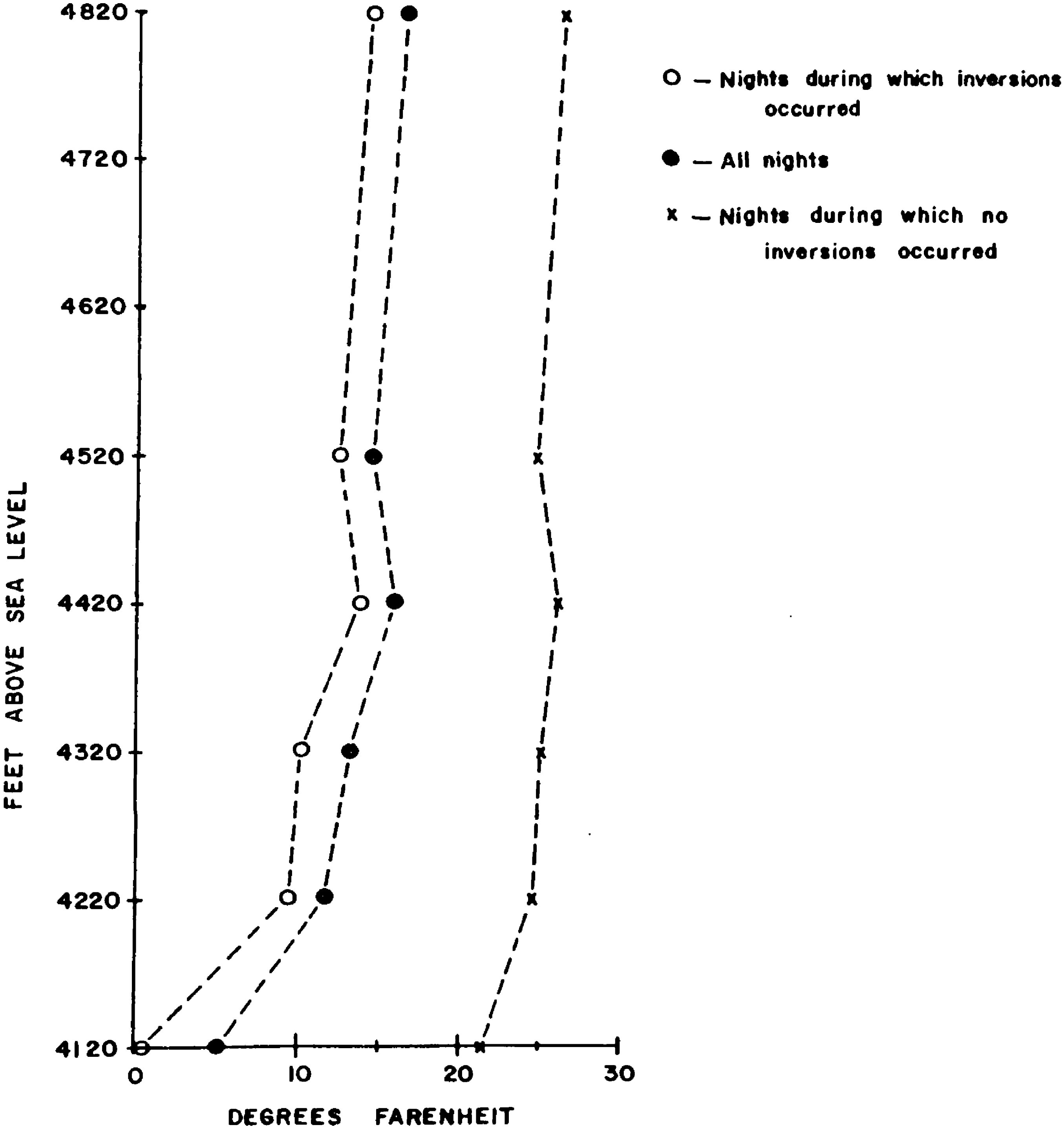

o — North Fork Creek Bottom
● — South Slope
x — Main Ridge
DEGREES FARENHEIT
60
50
40
30
20
10
10-13
10-20
10-27
11-3
11-10
11-17
11-24
12-1
12-8
12-15
12-22
12-29
1-5
1-12
1-19
1-26
2-2
2-9
2-16
2-23
3-1
3-8
3-15
3-22
WEEK BEGINNING (1975-1976)

Figure 5. Average minimum temperatures measured at 100 ft. elevation intervals in the North Fork drainage.


4820
4720
4620
4520
4420
4320
4220
4120
FEET ABOVE SEA LEVEL
0
10
20
30
DEGREES FARENHEIT
O — Nights during which inversions occurred
● — All nights
x — Nights during which no inversions occurred

in a 4.9°C. (8.8°F.) difference in mean minimum ambient air temperature between 1267 m. (4120 ft.) and 1298 m. (4220 ft.) above sea level. There was a 7.8°C. (14°F.) difference in mean minimum air temperature between the drainage bottom (1267 m. (4120 ft.) and ridge above the northerly aspect (1483 m. (4820 ft.). On cloudy and overcast nights, minimum temperatures were generally warmer and the gradient between the drainage bottom and ridges was smaller.

On the 5 nights during which no temperature inversion was recorded, there was 2.0°C. (5.3°F.) difference in mean minimum air temperature between the drainage bottom (1267 m. (4120 ft.) and the ridge above the north-facing slope (1483 m. (1820 ft.).

<u>Cover type selection</u>

Cover types used by radio-marked spruce grouse during the winter season differed radically from those used during the spring and summer seasons. During the spring and summer of 1975, both radio-marked and unmarked spruce grouse were observed using lower, mid, and upper slope positions on northerly aspects of the North Fork and Elk Creek drainages. Courtship and breeding activity took place in the lodgepole pine cover type and upper slope portions of the Engelmann spruce-subalpine fir cover type. During brood rearing, radio-marked hens with broods moved extensively about the northerly exposures and wet draws on south-facing exposures.

By the first of October, radio-marked spruce grouse had moved from brood rearing areas on northerly exposures across drainage bottoms to southerly exposures. Non-radio-marked grouse were observed on southerly exposures and on the upper portions of northerly aspects. By December, all spruce grouse activity observed occurred on southerly aspects, ridges, and portions of northerly aspects within 46.2 m. (150 ft.) (vertical distance) of ridges. Southerly aspects and upper slope positions of northerly aspects were covered by types dominated by Douglas fir and ponderosa pine. Ninety percent of the sites at which spruce grouse were observed between October 1, 1975 and February 29, 1976 were concentrated in the following cover types:

1. Douglas fir/lodgepole pine type located on the lower third of southerly aspects of the study area (65.0 ha, 160.6 ac.).
2. Douglas fir/ponderosa pine cover type located on the middle third of the southerly aspects of the study area (62.1 ha, 153.5 ac.).
3. Douglas fir/lodgepole pine cover type located on the ridge marking the southern boudnary of the study area (17.8 ha, 43.9 ac.).
4. Douglas fir/ponderosa pine cover type located on the extreme upper portions of northerly aspects of the study area (3.8 ha, 9.39 ac.).
5. Ponderosa pine/Douglas fir cover type located on the ridge marking the southern boundary of the study area (13.4 ha, 33.1 ac.).

A Chi-square goodness of fit test indicated strong selection for three of these cover types at the .05 significance level (Table 6). The Douglas fir/lodgepole pine cover type on the lower third of the south-facing aspects of the North Fork drainage was used to a much greater extent than would be expected, based on its areal coverage and the assumption of a random distribution of spruce grouse. The same was true of the ponderosa pine/Douglas fir cover type found on the North Fork - Elk Creek divide (southern boundary of the study area) and the Douglas fir/ponderosa pine cover type found on upper slope, northerly aspects of the divide. Due to their small size and correspondingly small number of associated observations, these 2 cover types were combined for the purpose of the Chi-square analysis.

Only 2 cover types (larch and larch/lodgepole pine) were used in propotion to their availability. These 2 cover types were not important, since their combined areal coverage amounted to only 1.7% of the study area.

The following 7 cover types were apparently avoided:

1. Engelmann spruce
2. Lodgepole pine (1)
3. Lodgepole pine (2)
4. Douglas fir/larch
5. Douglas fir/ponderosa pine (on the North Fork - Elk Creek divide)
6. Douglas fir/ponderosa pine (mid-slope of south-facing aspects)
7. Douglas fir/ponderosa pine (upper slope of south-facing aspects).

This apparent avoidance was statistically significant in the case of the Engelmann spruce, lodgepole pine (1), and Douglas fir/ponderosa pine (mid-slope of southerly aspects of the North fork drainage) cover types.

Activity patterns

The activity of wintering spruce grouse were classified into 2 categories: night roosting and feeding-loafing activity. After leaving the night roost, spruce grouse moved to a site at which they generally spent the entire day intermittently feeding, preening and loafing. Feeding periods ranged in

Table 6. Cover type selection by radio-marked, female spruce grouse as indicated by Chi-square goodness of fit test.

Cover Type	% of Study Area	Frequency of Occurrence**
Engelmann Spruce	4.3	2 (1%) -*
Western Larch Western Larch - Lodgepole	1.7	3 (1.5%) 0 n.s.
Lodgepole pine (1)	7.1	0 (0) -*
Lodgepole pine (2)	3.4	3 (1.5%) - n.s.
Ponderosa Pine - Douglas fir Douglas fir/Ponderosa Pine (North Aspects)	6.2	28 (15%) +*
Douglas fir/Western Larch	2.7	0 (0) - n.s.
Douglas fir/Lodgepole pine (Ridge Aspect)	6.4	3 (2%) - n.s.
Douglas fir/Lodgepole pine (South Aspect-Low)	23.2	130 (69%) +*
Douglas fir/Ponderosa pine (South Aspect-Mid)	22.2	19 (10%) -*
Douglas fir/Ponderosa pine (South Aspect-Upper)	19.9	0 (0%) -*

* Indicates significance at the .05 level

** Selection and avoidance of cover types indicated by + and -, respectively. "0" indicates use in proportion to availablility. The percent of total observation is indicated in ( ).

duration from several to 30 minutes. A vigorous feeding period occurred in the early morning. The duration of this feeding period was not established. Another major feeding period occurred in the evening just prior to the bird's move to a night roost. The duration of the evening feeding period was approximately 30 minutes, in most cases. Spruce grouse flew to their night roosts in all cases.

Movements

Distances moved between night roosts and feeding-loafing areas are summarized in Table 7. Some radio-marked spruce grouse roosted in the same group of trees in which they spent the day. However, in most cases, feeding-loafing areas were not used for night roosts.

Spruce grouse often used areas of .045 ha. (.01 ac.) to .31 ha. (.7 ac.) in size for both feeding-loafing and night roosting for periods as long as 9 days (maximum observed). In some cases a single tree or clump of trees was used solely as a day roost for up to 6 days. The large range of values for distance between night roosts and daytime activity areas is a result of occasional movements to entirely new areas of use (activity areas). Most night roosts were used repeatedly as evidenced by the accumulation of droppings below the roost tree or within a clump of trees. In many instances, radio-marked grouse used a day roost area for a single day only, moving on to a new area that very night and next day.

I could find no relationship between changing meteorological conditions and the relatively long movements by radio-marked grouse to new activity areas. However, short movements within activity areas were apparently influenced by changing weather. Wind conditions appeared to be the major factor stimulating movement. Radio-marked spruce grouse exposed to winds sufficiently intense to ruffle the bird's feathers often flew to sites protected from the wind. Given equivalent intensities, gusty winds did not stimulate movement to the same extent as constantly blowing winds. The longest move witnessed under gusty wind conditions (n=3) was approximately 250 m. (813 ft.). In most cases spruce grouse were able to find suitable protection from the wind by shifting their position within the roost tree or clump of trees being used.

Precipitation and fluctuating temperatures did not apparently influence spruce grouse movement during the feeding-loafing period beyond limited position adjustment within a given tree. During periods of precipitation spruce grouse often roosted beneath clumps of needles in the roost tree, and exhibited no difficulty in finding adequate cover at feeding-loafing sites.

On clear, cold days wintering spruce grouse appeared to take advantage of direct solar radiation by roosting at positions on or in the canopy of the roost tree which were directly exposed to the sun's rays. On warm, clear days, the grouse often perched in the shade of clumps of needles, the bole of the tree, or other tree canopies.

The availability of food at a given roost site did not appear to significantly affect grouse movement, since needles were abundant either in the crown of the roost tree or in the thicket in which the roost tree was located.

Food habits

Ninety-one observations of feeding grouse were obtained (Table 8). In 76.9% of the observations ponderosa pine needles were being consumed. In all cases in which ponderosa pine was available during observed feeding periods, it was selected. However, in the absence of ponderosa pine, lodgepole pine was an apparently acceptable substitute.

Table 7. Summary of distances moved between night roosts and feeding-loafing areas and within feeding-loafing areas.

	Mean	Standard Deviation	Range	Sample Size
Distance moved between night roots and feeding-loafing areas	47.3 meters	49.2 meters	0-226.9 meters	30
Rate of movement within feeding-loafing areas	1.9 meters/ hour	---	0-12.3 meter/ hour	9

Home Range

Home range data is summarized in Table 9. Data from grouse number 335 is not included in the analysis because of the limited number of times she was observed before her death in mid-November, 1975.

Radio-marked spruce grouse established their home range principally in the following cover types:

Nos. 236, 245, 335, 2739: Douglas fir/lodgepole pine on the lower third of south aspects.

No. 243: Ponderosa pine/Douglas fir on the North Fork Elk Creek Divide and Douglas fir/ponderosa pine on the upper portion of north aspect.

Home range sizes ranged between 17.0 ha. (37.4 ac.) and 34.6 ha. (76.1 ac.). The extent to which home range size is indicative of home range quality is difficult to assess. Food is not limiting to spruce grouse during the winter season. However, the structural arrangement of vegetation, including diameter distribution of stems, horizontal pattern of tree distribution and the vertical distribution of foliage may influence the availability of sites for spruce grouse use and activity. Variation among individuals due to differences in age and sex was not assessed due to the small sample size.

A modified minimum area method (Harvy & Barbour, 1965) was used to estimate the area utilized within the individual home ranges. One-fourth of the distance between the most widely separated points in a grouse's home range was used as the criterion for determining which points to connect on the home range map for estimating more accurately the utilized home range area. Since, in the case of spruce grouse, this distance was greater than the mean daily movement distance of individuals, it was adopted as a conservative criterion for determining utilized home range.

Table 8. Winter food habits of spruce grouse

Species	No. of Observed Uses	Percent of Total Observations
Ponderosa pine	70	76.9
Lodgepole pine	8	8.8
Western larch	3	3.3
Douglas fir	3	3.3
Other	7	7.7
Total	91	100.0

Table 9. Home range size and percent of home range utilized by radio-marked spruce grouse. (10/1/75 - 2/29/76).

Bird No.	Sex/Age	Home Range Area	Estimated % Utilized	No. of Observations	Period Observed
236	F/I	20.3 ha. (44.6 ac.)	18.9	27	12/10/75 - 2/29/76
243	F/I	34.6 ha. (76.1 ac.)	29.9	43	11/3/75 - 2/29/76
245	F/A	24.4 ha. (53.7 ac.)	25.3	75	10/8/75 - 2/29/76
2739	F/A	17.9 ha. (37.4 ac.)	31.0	73	10/1/75 - 2/29/76
335*	F/A	12.75 ha. (21.8 ac.)	--	21	10/1/75 - 11/16/75
Mean		24.1 ha. (53 ac.)	26.3		
Standard Deviation		7.5 ha. (16.5 ac.)	5.5		

* This grouse died on 11/16/75. Home range data for this bird is not included in the computation of the Mean Home Range size.

The estimated percent of home range actually utilized by spruce grouse varied from 18.9% to 30%. These low percentages may be a result of the patchy horizontal distribution of trees within the home range. However, it did appear that many suitable areas were not used by the grouse over the winter period. Grouse exhibited a high degree of fidelity to both day roost and night roost sites, using many sites repeatedly over the winter season.

With only 7 exceptions, all observations of radio-marked spruce grouse between October 1, 1975 and February 29, 1976 were made above 1299 m. (4220 ft.) elevation. Thus, all radio-marked grouse established their winter home ranges above the level of temperature inversion. All unmarked grouse were also observed above 1299 m. (4220 ft.). After February 29, 1976 radio-marked female spruce grouse began to wander from their winter home ranges.

Vegetation structure

If spruce grouse were not selective in terms of the vegetation structure of sites used, I would expect parameters of vegetation structure at sites selected by the grouse to approximate those parameters obtained from a random sample of the forest cover types. This was not the case. Sites selected by radio-marked spruce grouse were distinct in terms of certain components of horizontal and vertical vegetation structure. The vegetation of selected sites varied according to the activity of the grouse.

Horizontal pattern of tree distribution

The distribution of tree stems within cover types used by spruce grouse was classified visually as aggregated or clumped. This subjective classification was supported by calculated indices of aggregation for the types (Table 3).

Importance values

Douglas fir, ponderosa pine, lodgepole pine and western larch were the principal species of importance in the cover types within which radio-marked spruce grouse established their home ranges (Table 10).

The calculated Importance Value (Relative Density + Relative Frequency + Relative Basal Area) of ponderosa pine was consistently greater at feeding-loafing sites than at night roosts. The calculated Importance Value of Douglas fir was greater at night roosts than at feeding-loafing sites, except in the case of No. 243. No clear trend in the magnitude of Importance Value at feeding-loafing sites vs. night roosts was apparent in the case of lodgepole pine. Western larch was more important at feeding-loafing sites than at night roosts in all cases (Table 11).

Density of trees

The mean density of trees at feeding-loafing sites and night roosts selected by spruce grouse was generally greater than the mean density of trees for the cover type in which the grouse had established their home ranges (Table 3, 12).

The average density of trees at night roosts (2143 trees/acre, s = 1746) was significantly greater than at feeding-loafing sites (1508 trees/acre, s = 1844) at the .05 significance level (Table 12, Figure 6).

The relative density of individual tree species at sites selected by grouse differed in certain aspects from that computed from the random sample of plots taken from the cover types in which home ranges of the grouse were established (Table 13). With respect to spruce grouse observed on the south-facing slope of the drainage (nos. 236, 245, 335, 2739), the most apparent difference was in the consistently greater relative density of

Table 10. Importance Values of tree species in the cover types selected by radio-marked spruce grouse during the winter season.

	Ponderosa pine	Douglas fir	Lodgepole pine	Western larch	Subalpine fir	Engelmann spruce
Douglas fir/lodgepole pine lower third, south aspects	66.3	132.4	89.4	11.9	0	0
Ponderosa pine/Douglas fir North Fork-Elk Creek Divide	107.9	189.3	2.8	0	0	0
Douglas fir/ponderosa pine upper third, north aspect	83.4	216.6	0	0	0	0

Table 11. Importance values of coniferous tree species at feeding-loafing sites and night roosts.

	No. 236		No. 243		No. 245		No. 2739		No. 335	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
Ponderosa pine	105.7	100.7	71.1	58.4	104.3	41.5	108.5	82.4	90.6	N/A
Lodgepole pine	23.4	0	18.1	74.1	31.3	39.8	43.8	25.3	38.5	N/A
Douglas fir	158.5	199.3	155.7	137.9	161.2	218.8	113.9	188.3	159.8	N/A
Western larch	12.4	0	48.1	39.6	3.2	0	26.7	4.0	11.1	N/A
Subalpine fir	0	0	0	0	0	0	1.5	0	0	N/A
Engelmann spruce	0	0	0	0	0	0	5.6	0	0	N/A

* Feeding-loafing sites

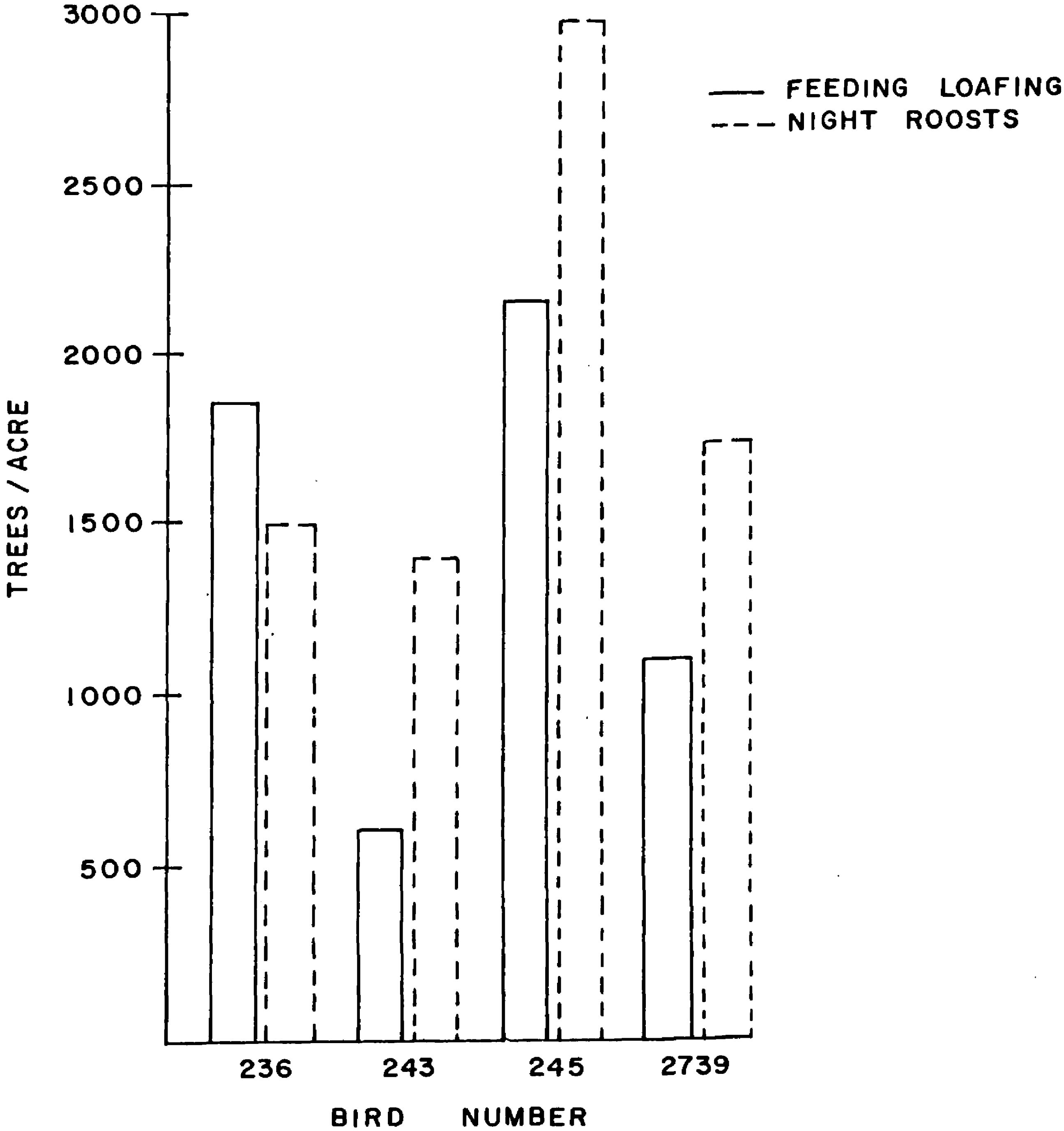
** night roosts

Table 12. Density of trees at feeding-loafing sites and night roosts of radio-marked and banded spruce grouse.

	Feeding-loafing Sites			Night Roosts		
Bird No.	Mean Density of Trees	Standard Deviation	n*	Mean Density of Trees	Standard Deviation	n
236	1857	1031	20	1504	754	2
243	604	681	36	1395	1094	6
245	2175	1981	50	3003	2380	7
335	1564	1478	14	--	--	-
2739	1121	1745	58	1748	1334	11
All Birds	1508	1844	229	2143	1746	28

* n = number of observations

Figure 6. Density of trees at feeding-loafing sites and night roosts of radio-marked spruce grouse.


3000
2500
2000
1500
1000
500
TREES / ACRE
FEEDING LOAFING
NIGHT ROOSTS
236
243
245
2739
BIRD NUMBER

ponderosa pine at feeding-loafing sites than expected, based on random samples of the cover types used by the radio-marked grouse. The relative densities of Douglas fir, lodgepole pine, and western larch at grouse feeding-loafing sites did not exhibit any definite trends.

At night roosting sites the relative density of ponderosa pine was consistently lower than expected, and the relative density of Douglas fir was generally, but not always, greater than expected. No clear trends were recognized in comparing the observed relative densities of lodgepole pine and western larch to the relative densities expected for the two species.

The areas used by the radio-marked spruce grouse (No. 243) and associated unmarked spruce grouse on the north-facing slopes of the study area are more heterogeneous in terms of vegetation structure and composition than the south-facing slopes of the drainage. The relationships between spruce grouse site selection and the relative density of tree species present on the north slope and ridge habitat do not exhibit any clear relationships (Table 13).

The relative density of the trees in the three diameter classes between 0-20.3 cm. (0-8 in.) was generally greater at night roosts than in the overall cover types in which the grouses' home ranges were established. The opposite was true in the case of the 2 diameter classes between 20.3-76.2 cm. (8-30 in.) (Table 14). No clear relationship between site selection by grouse and the relative density of trees in the six diameter classes was noted in the comparison of feeding-loafing sites vs. night roosts (Table 14, Figure 7).

For ponderosa pine the following relationships were noted (Tables 15, 18):

1. The relative density of ponderosa pine in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at feeding-loafing sites than in the general cover types used.

Table 13. Relative density of tree species (%) at feeding-loafing sites, night roosts, and cover types in which individual grouse established their home ranges.

	Feeding-Loafing Sites						Night Roosts						Cover types in which Home ranges established					
Bird No.	PP	DF	LPP	WL	SAF	ES	PP	DF	LPP	WL	SAF	ES	PP	DF	LPP	WL	SAF	ES
236	32.6	61.0	4.4	2.0	0	0	11.3	88.7	0	0	0	0	12.5	42.8	42.8	1.8	0	0*
243	15.4	72.7	3.1	8.8	0	0	14.1	58.4	23.1	4.4	0	0	34.9	61.2	.14	3.7	0	0**
													12.8	85.2	0	2.1	0	0***
245	28.4	61.8	9.8	0	0	0	2.8	94.3	2.9	0	0	0	12.5	42.8	42.8	1.8	0	0*
335	18.4	76.1	5.3	.2	0	0	--	--	--	--	--	--	12.5	42.8	42.8	1.8	0	0*
2739	31.2	47.7	12.5	7.3	.4	.9	11.8	86.4	1.9	0	0	0	12.5	42.8	42.8	1.8	0	0*

* Douglas fir/lodgepole pine cover type, lower third of south aspect.
** Ponderosa pine/Douglas fir cover type, North Fork-Elk Creek Divide.
*** Douglas fir/ponderosa pine cover type, upper third of north aspect.

Table 14. Relative density of trees (%) in the six diameter classes at feeding-loafing sites, night roots, and cover types in which individual radio-marked grouse established their home ranges.

Bird No.	Feeding-loafing Sites						Night Roosts						Cover types in which Home ranges established					
	0-2 in.	2-4 in.	4-8 in.	8-15 in.	15-30 in.	30+ in.	0-2 in.	2-4 in.	4-8 in.	8-15 in.	15-30 in.	30+ in.	0-2 in.	2-4 in.	4-8 in.	8-15 in.	15-30 in.	30+ in.
236	34.6	43.3	18.5	3.4	.2	0	30.5	37.2	27.9	2.9	1.4	0	58.2	19.4	13.8	8.1	1.3	0*
243	50.6	15.9	17.7	12.7	3.1	0	32.9	40.2	20.9	5.4	.6	0	40.5	16.9	20.0	2.7	0	0**
													31.0	0	48.8	17.5	1.7	0***
245	67.5	19.6	10.9	1.9	.2	0	65.4	23.7	9.6	1.2	.1	0	58.2	19.4	13.8	8.1	1.3	0*
335	58.6	24.2	2.7	.1	0	--	--	--	--	--	--	--	58.2	19.4	13.8	8.1	1.3	0*
2739	55.0	26.5	12.7	5.1	.7	0	57.2	24.4	15.9	2.3	.2	0	58.2	19.4	13.8	8.1	1.3	0*

* Douglas fir/lodgepole pine cover type, lower third of south aspect.
** Ponderosa pine/Douglas fir cover type, North Fork-Elk Creek Divide
*** Douglas fir/ponderosa pine cover type, upper third of north aspect.

Table 15. Relative density of ponderosa pine (%) in the six diameter classes of feeding-loafing sites and night roosts.

Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	9.87	0	15.90	0	5.40	8.46	1.30	1.48	.05	1.31	0	0
243	0	0	4.22	9.73	6.56	2.74	3.22	1.37	1.35	.23	0	0
245	18.55	0	4.25	1.45	3.84	1.21	.65	.15	.10	.02	0	0
335	4.19	-	6.51	-	6.63	-	1.02	-	.08	0	0	0
2739	15.52	0	7.99	5,83	4.9	5.03	2.27	.76	.55	.12	0	0

(Diameter Classes)

* feeding-loafing sites
** night roosts

Figure 7. Mean relative density of trees in the six diameter classes at feeding-loafing sites and night roosts for the radio-marked spruce grouse.

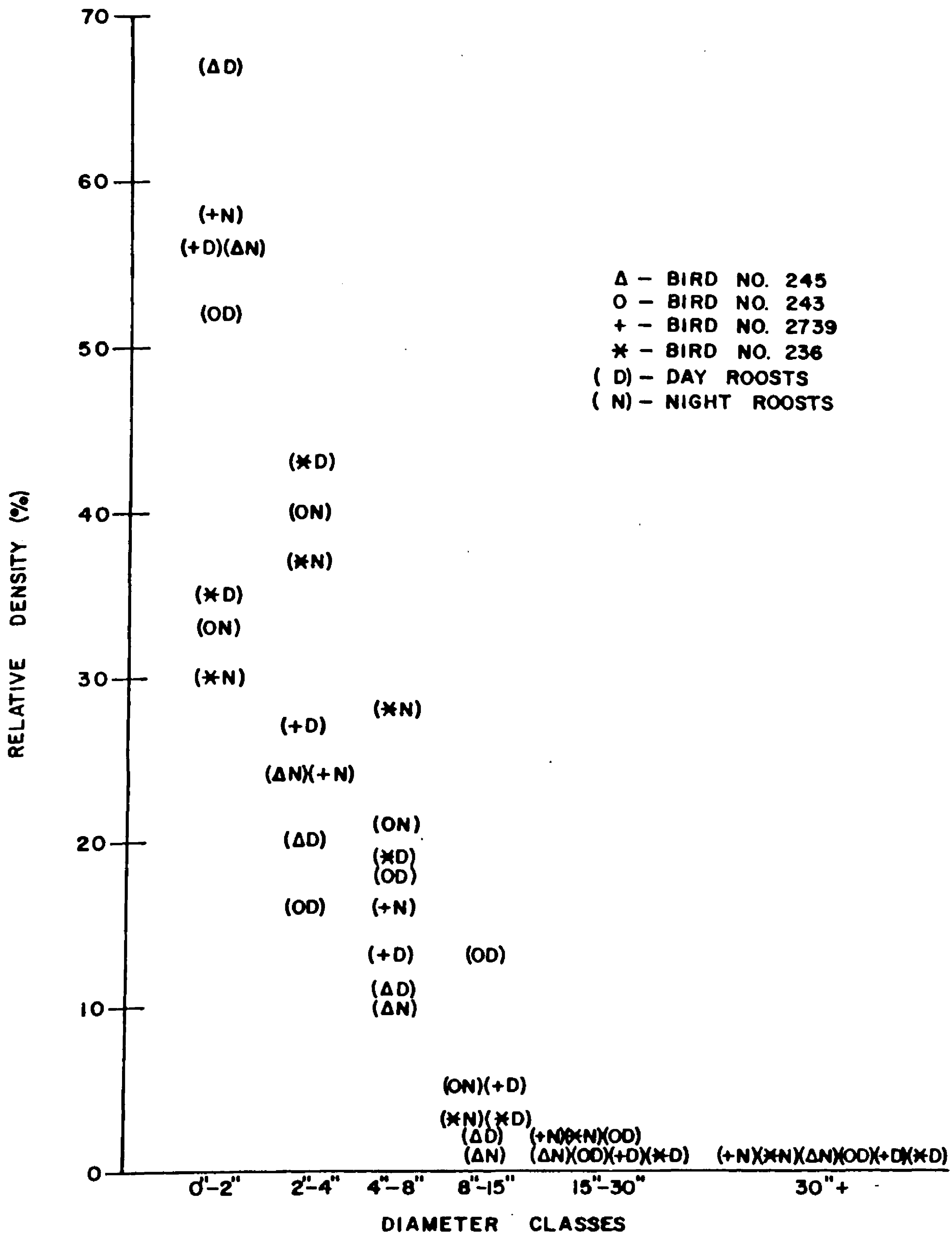

RELATIVE DENSITY (%)
DIAMETER CLASSES
0"-2"
2"-4"
4"-8"
8"-15"
15"-30"
30"+
Δ – BIRD NO. 245
O – BIRD NO. 243
+ – BIRD NO. 2739
✱ – BIRD NO. 236
(D) – DAY ROOSTS
(N) – NIGHT ROOSTS

Table 16. Relative density of Douglas fir (%) in the six diameter classes at feeding-loafing sites and night roosts.

	Diameter Classes											
Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	24.68	30.5	23.58	37.2	10.97	19.5	1.66	1.5	.14	.10	0	0
243	46.4	32.5	10.30	15.82	7.73	6.69	7.27	2.74	.97	.32	0	0
245	41.31	65.4	13.58	21.8	5.71	6.3	1.15	.7	.05	.04	0	0
335	54.41	--	15.35	--	4.88	--	1.37	--	.04	--	0	0
2739	31.03	57.22	10.66	18.54	4.23	9.01	1.62	1.49	.15	.09	0	0

* feeding-loafing sites
** night roosts

Table 17. Relative density of lodgepole pine (%) in the six diameter classes at feeding-loafing sites and night roosts.

Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	0	0	2.19	0	1.78	0	.39	0	.01	0	0	0
243	0	0	.47	13.38	2.11	9.43	.53	.30	.03	0	0	0
245	7.59	0	.75	.48	1.36	2.06	.06	.33	0	0	0	0
335	0	--	2.33	--	2.79	--	.17	--	0	0	0	0
2739	4.23	0	5.49	0	2.12	1.85	.63	0	.01	.02	0	0

Diameter Classes

* feeding-loafing sites
** night roosts

Table 18. Relative density (%) of ponderosa pine, Douglas fir, and Lodgepole pine in the six diameter classes in the cover types in which radio-marked spruce grouse established home ranges.

			Diameter Classes						
Cover Type	Radio-Marked Grouse*	Tree Species**	0-2 in.	2-4 in.	4-8 in.	8-15 in.	15-30 in.	30+ in.	Total
			Relative Density (%)						
Douglas fir/ lodgepine pine, Lower-third, south aspects	236	PP	5.29	2.35	2.79	1.65	.38	0	12.46
	245	DF	21.16	9.99	6.47	4.3	.84	0	42.76
	335	LPP	31.75	5.88	3.53	1.73	.06	0	42.94
Ponderosa pine/ Douglas fir, North Fork-Elk Creek Divide	243	PP	0	6.75	14.34	12.02	1.79	.03	34.93
		DF	40.50	10.13	5.06	4.92	.62	.01	61.24
		LPP	0	0	0	.14	0	0	.14
Douglas fir/ ponderosa pine, Upper third, north aspects	243	PP	0	0	10.66	2.0	.10	0	12.76
		DF	31.97	0	37.3	14.43	1.49	0	85.19
		LPP	0	0	0	0	0	0	0

* Radio-marked grouse which established home ranges in the corresponding cover type

** PP = ponderosa pine
DF = Douglas fir
LPP= Lodgepole pine

2. The opposite was true for diameter classes between 20.3-76.2 cm. (8-30 in.).
3. No relationships appeared in the comparison of the relative density of ponderosa pine in the six diameter classes at night roosts and the general cover types used.
4. In all diameter classes, the relative density of ponderosa pine was greater at feeding-loafing sites than at night roosts.

For Douglas fir, the following relationships were noted (Tables 16, 18):

1. Relative density of Douglas fir in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at feeding-loafing sites and at night roosts than in the general cover types used.
2. Relative density of Douglas fir in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was lower at feeding-loafing sites and night roosts than in the general cover types used.
3. The relative density of Douglas fir in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at night roosts than feeding-loafing sites.
4. The relative density of Douglas fir in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was greater at feeding-loafing sites than at night roosts.

The relative density of lodgepole pine in all diameter classes was generally greater within the cover types used by spruce grouse than at specific feeding-loafing sites or night roosts (Tables 17, 18). The relative density of lodgepole pine was greater at feeding-loafing sites than at night roosts in all diameter classes except the 10.2-20.3 cm. (4-8 in.) class, in which case the opposite was true.

Western larch, subalpine fir, and Engelmann spruce occurred only rarely on sites used by spruce grouse.

Basal area of trees

The basal area of trees was generally greater at feeding-loafing sites and night roosts than in the general cover types used by spruce grouse (Table 19).

The basal area of trees at feeding-loafing sites was, on the average, lower than at night roosts (Table 19).

With respect to the relative basal area (RBA) of ponderosa pine, the following relationships were noted (Tables 20, 21):

1. RBA of ponderosa pine was greater at feeding-loafing sites than in the cover types used.
2. RBA of ponderosa pine was greater at feeding-loafing sites than at night roosts.
3. No clear relationship between night roost selection by spruce grouse and RBA of ponderosa pine was noted in the comparison of night roosts and cover types used.

Analysis of the relative basal area (RBA) of Douglas fir yielded the following information (Tables 20, 21):

1. Generally the RBA of Douglas fir was lower at feeding-loafing sites than at night roosts.
2. RBA of Douglas fir was greater at night roosts than in the cover types used by spruce grouse.
3. No clear relationship between the RBA of Douglas fir and feeding-loafing site selection was apparent.

For lodgepole pine the data indicates (Tables 20, 21);

1. The relative basal area (RBA) of lodgepole pine is lower at feeding-loafing sites and night roosts than within the cover types used by spruce grouse.
2. No relationship between the RBA of lodgepole pine and the selection of feeding-loafing sites or night roosts.

Sites dominated by western larch, subalpine fir, and Engelmann spruce were avoided by spruce grouse during the winter season (Tables 20, 21).

Analysis of the relative basal area (RBA) of trees in the five diameter classes between 0-76.2 cm. (0-30 in.) showed the following relationships (Tables 22, 23):

1. RBA of trees in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at feeding-loafing sites than within the cover types used by spruce grouse.
2. RBA of trees in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was lower at feeding-loafing sites than in the general cover types used by spruce grouse.
3. At night roosts the RBA of trees in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater than within the general cover types used by spruce grouse.
4. At night roosts the RBA of trees in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was lower than within the general cover types used by spruce grouse.
5. RBA of trees in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at night roosts than at feeding-loafing sites.

Table 19. Mean basal area (sq. ft./acre) of trees at feeding-loafing sites, night roosts and in principal cover types in which radio-marked spruce grouse established their home ranges.

	Feeding-loafing Sites			Night Roosts			Cover Types	
Bird No.	Mean	Standard Deviation	n	Mean	Standard Deviation	n	Mean	Standard Deviation
236	168	43	10	178	39	2	69*	42
243	122	43	36	164	18	6	190**	32
							124***	51
245	115	57	50	134	38	7	69*	42
335	104	32	14	-	-	-	69*	42
2739	110	55	58	122	56	11	69*	42

* Douglas fir/lodgepole pine cover type, lower third, south aspects
** Douglas fir/ponderosa pine cover type, upper third, north aspects
*** Ponderosa pine/Douglas fir cover type, North Fork-Elk Creek Divide

Table 20. Relative basal area (%) of tree species at feeding-loafing sites and night roosts of radio-marked spruce grouse.

	Grouse Number									
	236		243		245		335		2739	
Tree Species	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
Ponderosa pine	33	39	32	21	32	10	39	--	46	31
Douglas fir	56	61	49	45	57	75	47	--	32	62
Lodgepole pine	9	0	4	23	8	15	13	--	13	6
Western larch	2	0	15	12	1	0	2	--	6	0
Subalpine fir	0	0	0	0	0	0	0	--	1	0
Engelmann spruce	0	0	0	0	0	0	0	--	3	0

* feeding-loafing sites
** night roosts

Table 21. Relative basal area (%) of tree species in the principal cover types in which radio-marked spruce grouse established home ranges.

Cover Type	Radio-Marked Grouse*	Tree Species: ponderosa pine	Douglas fir	lodgepole pine	western larch	subalpine fir	Engelmann spruce
Douglas fir/ lodgepole pine, lower-third, south aspects	236 245 335 2739	21.5	54.3	21.5	2.7	0	0
ponderosa pine/ Douglas fir, North Fork - Elk Creek Divide	243	61.9	26.2	0.8	11.1	0	0
Douglas fir/ ponderosa pine, upper-third, north aspects	243	14.7	80.6	0	4.7	0	0

* radio-marked grouse using this cover type

Table 22. Relative basal area (%) in the six diameter classes at feeding-loafing sites and night roosts of radio-marked spruce grouse.

Bird No.	Diameter Classes											
	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	2.4	1.7	23.7	15.6	40.2	46.4	29.6	19.6	4.1	16.7	0	0
243	1.6	1.8	4.1	16.9	17.2	34.9	49.2	35.5	27.9	10.9	0	0
245	7.0	8.2	18.0	25.9	40.9	41.5	18.0	21.5	6.1	2.9	0	0
335	4.8	--	18.3	--	42.3	--	31.7	--	2.9	--	0	0
2739	2.7	4.1	13.6	17.2	25.5	45.1	40.9	25.4	17.3	8.2	0	0

* feeding-loafing sites
** night roosts

Table 23. Relative basal area (%) in the six diameter classes in the principal cover types in which radio-marked spruce grouse established home ranges.

Cover Type	Diameter Classes					
	0 - 2 in.	2 - 4 in.	4 - 8 in.	8 - 15 in.	15 - 30 in.	30+ in.
Douglas fir/lodgepole pine lower-third, south aspect	2.9	7.4	20.6	51.5	17.6	0
ponderosa pine/Douglas fir North Fork-Elk Creek Divide	0.8	3.2	14.2	55.9	25.2	0.7
Douglas fir/ponderosa pine upper-third, north aspect	0.5	0	36.3	52.1	11.1	0

Table 24. Relative basal area (%) of ponderosa pine in the six diameter classes at feeding-loafing sites and night roost of radio-marked spruce grouse.

	Diameter Classes											
Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	.60	0	8.90	0	11.90	14.1	11.3	10.1	1.2	15.7	0	0
243	0	0	.8	4.3	6.6	4.9	12.3	9.2	12.3	3.1	0	0
245	1.7	0	5.2	1.5	13.9	5.2	9.6	3.0	3.5	8.0	0	0
335	0	--	4.8	--	19.2	--	12.5	--	1.9	--	0	--
2739	.9	0	3.6	4.1	10.0	13.9	18.2	8.2	13.6	4.1	0	0

* feeding-loafing sites
** night roosts

Table 25. Relative basal area (%) of Douglas fir in the six diameter classes at feeding-loafing sites and night roosts of radio-marked spruce grouse.

Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	1.8	1.7	8.9	0	11.9	14.1	11.3	10.1	1.2	5.7	0	0
243	0	0	0.8	4.3	6.6	4.9	12.3	9.2	12.3	3.1	0	0
245	1.7	0	5.2	1.5	13.9	5.2	9.6	3.0	3.5	0.8	0	0
335	0	--	4.8	--	19.2	--	12.5	--	1.9	--	0	-
2739	0.9	0	3.6	4.1	10.0	13.9	18.2	8.2	13.6	4.1	0	0

* feeding-loafing sites
** night roosts

Table 26. Relative basal area (%) of lodgepole pine in the six diameter classes at feeding-loafing sites and night roosts of radio-marked spruce grouse.

Bird No.	0 - 2 in.		2 - 4 in.		4 - 8 in.		8 - 15 in.		15 - 30 in.		30 + in.	
	F-L*	N-R**	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R	F-L	N-R
236	0	0	1.2	0	3.6	0	0	0	0	0	0	0
243	0	0	0	5.5	2.5	15.9	2.5	1.8	0	0	0	0
245	0.9	0	6.9	6.8	5.2	9.0	0.9	6.0	0	0	0	0
335	0	--	1.9	--	8.7	--	1.9	--	0	--	0	--
2739	0	0	2.7	0	4.5	4.9	5.5	0	0	0	0	0

* feeding-loafing sites
** night roosts

Table 27. Relative basal area (%) of ponderosa pine, Douglas fir, and lodgepole pine in the six diameter classes in the principal cover types in which radio-marked spruce grouse established home ranges.

Cover type	Radio-Marked Grouse*	Tree Species	Diameter classes 0-2	2-4	4-8	8-15	15-30	30+
Douglas fir/	236	Ponderosa pine	0.1	1.5	4.4	10.2	5.8	0
lodgepole pine,	245	Douglas fir	1.5	4.4	10.2	17.5	11.6	0
lower third,	335	Lodgepole pine	1.4	2.9	5.8	11.6	0	0
south aspect	2739	Western larch	0	0	0	0	2.9	0
ponderosa pine/	243	Ponderosa pine	0	1.6	10.3	34.1	16.7	0.8
Douglas fir		Douglas fir	0.8	1.6	4.0	14.3	5.6	0
North Fork-Elk		Lodgepole pine	0	0	0	0.8	0	0
Creek Divide		Western larch	0	0	0.8	7.9	3.2	0
Douglas fir/	243	Ponderosa pine	0	0	7.9	5.8	0.5	0
ponderosa pine ,		Douglas fir	0.5	0	27.9	42.6	10.0	0
upper third,		Lodgepole pine	0	0	0	0	0	0
north aspects		Western larch	0	0	0.5	3.2	0.5	0

* radio-marked grouse which established home ranges in these cover types

6. RBA of trees in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was greater at feeding-loafing sites than at night roosts.

Analysis of the relative basal area (RBA) of ponderosa pine, Douglas fir, and lodgepole pine in the 6 diameter classes at feeding-loafing sites, night roosts, and within the general cover types used by spruce grouse yielded the following relationships (Tables 24-27):

1. RBA of ponderosa pine was greater at feeding-loafing sites than in the general cover types used in the 4 diameter classes between 0-38.1 cm. (0-15 in.).
2. No relationships between selection of night roosts and RBA of ponderosa pine were apparent for any diameter class except the 0-5.1 cm. (0-2 in.) and 10.2-20.3 cm. (4-8 in.) diameter classes in which the RBA of ponderosa pine was greater at night roosts than within the cover types used.
3. RBA of ponderosa pine was greater at feeding-loafing sites than at night roosts only in the 0-5.1 cm. (0-2 in.) and 20.3-38.1 cm. (8-15 in.) diameter classes. No relationships were apparent in the comparison of RBA in the other diameter classes.
4. RBA of Douglas fir in the three diameter classes between 0-20.3 cm. (0-8 in.) was greater at feeding-loafing sites than within the cover types used.
5. RBA of Douglas fir in the two diameter classes between 20.3-76.2 cm. (8-30 in.) was lower at feeding-loafing sites than within the cover types used.
6. RBA of Douglas fir in all diameter classes was generally

lower at night roosts than within the cover types used.

7. RBA of Douglas fir in the 3 diameter classes between 0-20.3 cm. (0-8 in.) was greater at night roosts than at feeding-loafing sites.
8. RBA of Douglas fir in the 2 diameter classes between 20.3-76.2 cm. (8-30 in.) was greater at feeding-loafing sites than at night roosts.
9. RBA of lodgepole pine was generally lower at feeding-loafing sites than within the cover types used by spruce grouse in all diameter classes.
10. RBA of lodgepole pine at night roosts was lower than within the cover types used in the 0-5.1 cm. (0-2 in.) and 20.3-38.1 cm. (8-15 in.) diameter classes; no relationship between night roost selection and RBA of lodgepole pine was apparent in any other diameter class.
11. No consistent relationships were apparent in terms of RBA of lodgepole pine in the comparison of night roosts and feeding-loafing sites.

Vertical distribution of vegetation at feeding-loafing sites and night roosts

Even though substantial differences existed among individual radio-marked grouse in terms of the distribution of crown volume at observation sites, expressed as height distribution of canopy coverage, a consistent trend is apparent. The "mean" condition for all observed spruce grouse is depicted in Figures 8 and 9. It is difficult to exhibit the variability associated with the individual birds in such a diagram, but it should be noted that a great deal of variation existed in the height of night roost trees, effective crown lengths at roost sites, and the heights above ground at which grouse roosted at both feeding-loafing sites and night roosts (Table 28). In general, night roosting sites were characterized by a relatively dense crown volume of 50% to 90% canopy cover within a 10 m. radius, contributed by tree crown biomass between 3 to 36 feet (1-12 m.) above ground (Appendix Figures 10-14, Table 29). Canopy cover figures exhibited in the Appendix for each radio-marked grouse do not show this amount of canopy coverage, since they depict canopy coverage out to the limits of the variable radius plot taken at each bird observation site. Usually, plots extended beyond the limits of the "micro" stand in which the grouse roosted, thus the understatement of canopy coverage.

The density of the crown volume at typical feeding-loafing sites is generally less than at night roosts, and distributed over greater vertical distance (Appendix Figures 10-14, Figures 7, 8). That is, at feeding-loafing sites 30-70% canopy cover was distributed between 5 to 60 feet above ground at a "typical" site. As noted earlier, some sites used by radio-marked grouse served as both feeding-loafing sites and night roosting sites. These sites included a food source in the upper zone of the crown volume (i.e. at least one ponderosa pine or lodgepole pine tree) and cover in the middle and lower zones of the crown volume. These conditions existed at many sites where Douglas fir saplings were growing up under the less shade tolerant ponderosa pine.

It is apparent that the mean roost heights of spruce grouse coincide with the middle and upper zone of maximum crown volume at both feeding-loafing sites and night roosts (Appendix Figures 10-14). This trend is consistent among the radio-marked grouse, despite the difference in location, in terms of heights, of the zone of maximum volume.

Figure 8. Typical vertical distribution of tree crown foliage at feeding-loafing sites of radio-marked spruce grouse.

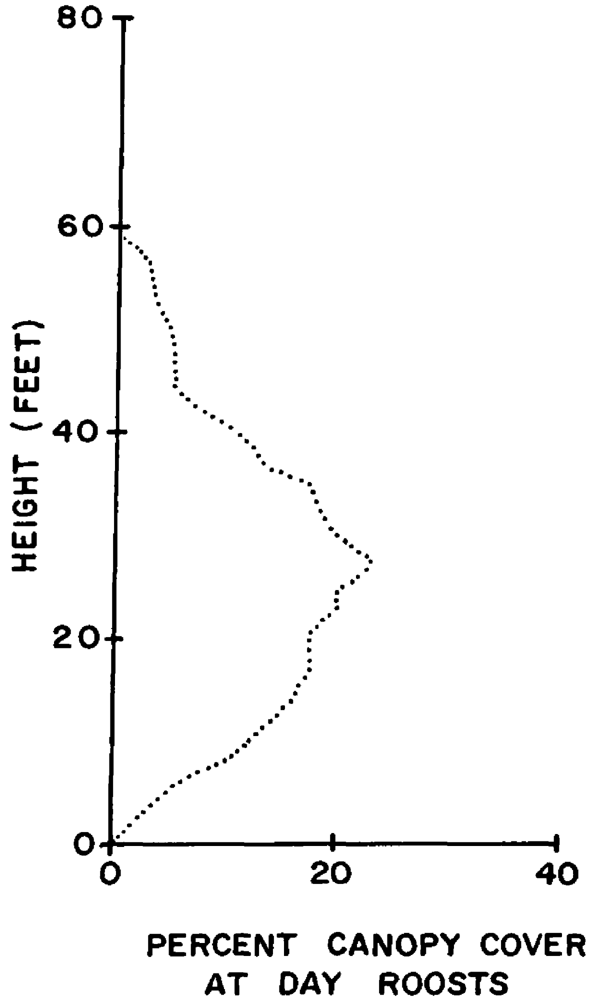

80
60
40
20
0
HEIGHT (FEET)
0
20
40
PERCENT CANOPY COVER
AT DAY ROOSTS

Figure 9. Typical vertical distribution of tree crown foliage at night roosts of radio-marked spruce grouse.

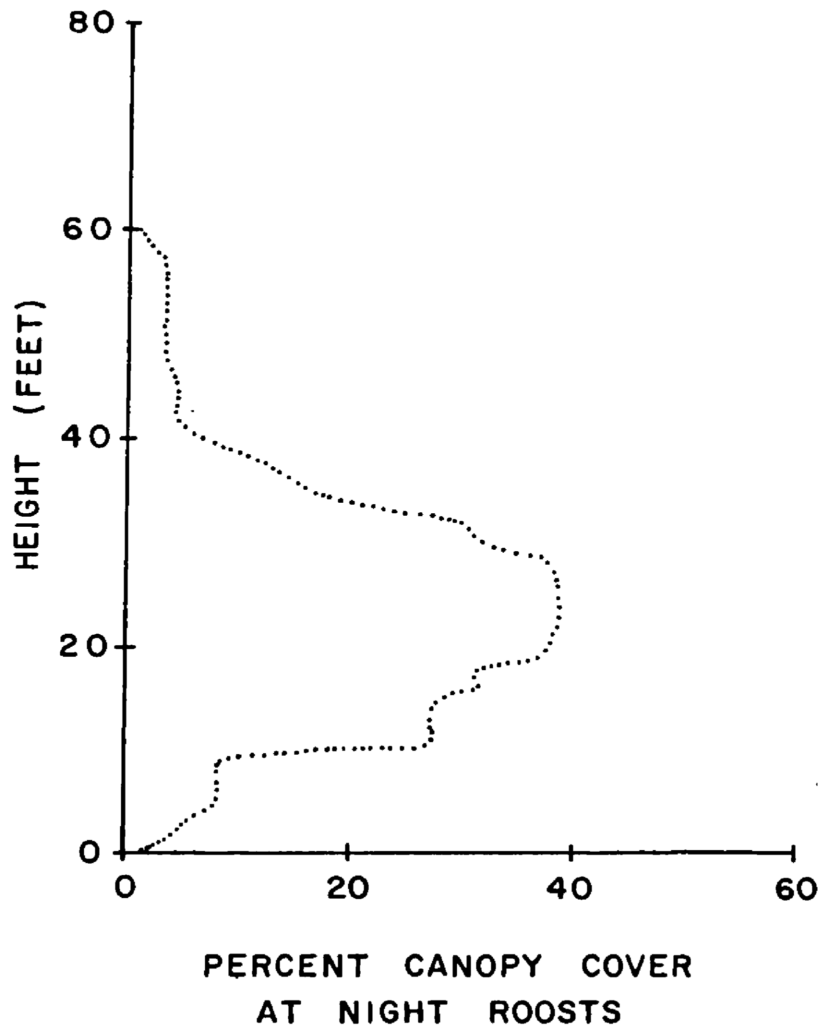

80
60
40
20
0
HEIGHT (FEET)
0
20
40
60
PERCENT CANOPY COVER
AT NIGHT ROOSTS

Table 28. Roost tree heights, effective crown lengths, and height of bird roost above ground at night roost and feeding-loafing sites.

		Roost Tree Height		Effective Crown Length		Grouse Roost Height			Roost Tree Height		Effective Crown Length		Grouse Roost Height	
Bird No.	n	$\bar{x}$*	s**	$\bar{x}$	s	$\bar{x}$	s	n	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
236	21	45.5	13.5	43.3	14.9	24.2	9.6	2	55.5	2.1	54.0	12.7	27.5	7.8
243	39	61.9	15.7	45.1	12.2	38.6	14.9	6	48.8	19.8	44.2	14.2	22.5	4.1
245	50	44.0	9.8	41.5	9.4	26.1	8.9	2	36.5	12.0	34.0	5.7	21.0	8.5
335	6	44.3	13.7	33.7	19.3	29.2	11.1				no data			
2739	50	55.3	22.7	48.9	17.6	36.3	20.3	3	30.3	6.8	31.0	13.9	16.0	5.3

* mean

** standard deviation

Table 29. Number of feeding-loafing and night roost sites occurring within the 10 canopy cover classes.

	Canopy Cover Classes (%)									
	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Feeding-loafing sites	0	0	8	42	54	56	48	14	7	0
Night roosts	0	0	1	3	1	6	10	5	2	0

SUMMARY AND DISCUSSION

Five radio-marked female spruce grouse established their winter home ranges in areas quite different from those used during the spring and summer. These differences involved physiography, forest species composition and structure, and microclimate of utilized area.

The winter home ranges of four radio-marked female grouse were established on the predominantly south-facing slope of the North Fork drainage. One radio-marked female established her home range on the physiographic divide between the North Fork and Elk Creek.

On clear, cold nights in which atmospheric mixing was minimal, cold air subsidence resulted in a steep temperature gradient between 1267.7 m. (4120 ft.) elevation and 1298.5 m. (4220 ft.) elevation. Mean minimum air temperature was 4.9°C. (8.8°F.) warmer at 1298.5 m. (4220 ft.) than at 1267.7 m. (4120 ft.). There was a 7.8°C. (14°F.) difference in mean minimum air temperature between 1267.7 m. (4120 ft.) elevation and 1483. m. (4820 ft.) elevation. All of the established home ranges were located above the approximate level of nocturnal cold air accumulation (1286 m.) in the North Fork drainage bottom.

The opportunity for maximum exposure to direct solar radiation existed on the areas in which radio-marked female spruce grouse established their winter home ranges. Many areas on north-facing slopes were exposed to solar radiation for quite abbreviated periods due to the low zenith of the sun during winter and the steep slope inclinations (Lee and Baumgartner, 1966). The physiographic difference between areas selected for winter use and areas not selected, appeared to be partially and function of prevailing micro-climatic conditions associated with these sites. During cold periods, the maintenance of homeothermy would be facilitated by the warmer nocturnal thermal conditions and seemingly by potential diurnal exposures to solar radiation on south-facing slopes, upper north-facing slopes (which may receive substantial amounts of direct solar radiation) and ridges.

However, the energy gains resulting from exposure to solar radiation may be insignificant. Evans and Moen (1975) found that sharp-tailed grouse (*Pedioecetes phasianellus*) feathers have a very low heat conductivity. This low heat conductivity makes feathers a good insulator which prevents heat gain as well as heat loss. However, the insulatory effect of a grouse's feathers may be adjusted by an individual grouse through piloerection or the lack thereof. Whether significant energy gains are available to a wintering grouse through exposure to solar radiation is still questionable.

Habitat utilization

The areas in which the radio-marked female spruce grouse established their home ranges were covered principally by Douglas fir, ponderosa pine, lodgepole pine, and western larch. Needles of western larch (when available), ponderosa pine, and lodgepole pine were the principal foods consumed in order of apparent preference. Douglas fir was the most abundant species in the areas used by wintering spruce grouse and functioned as an important cover component of winter habitat.

Suitable habitat was not uniformly distributed throughout the areas in which radio-marked spruce grouse established their winter home ranges. Female spruce grouse utilized only 18-30% of the areas over which they ranged during the winter season. I could not determine whether this pattern of habitat use reflected the repeated use of preferred sites or the use of a

ıtable habitat.

Feeding-loafing and night roosting activity centered about a .045 to .3 hectare (.1-.7 ac.) area for short periods of time, generally 1 to 9 days. Changes in location of activity centers occurred frequently. I could not relate these changes in location of activity centers to changes in meteorological or local climate conditions with the data available. It is possible that these changes of activity center location are an adaptation to avoid detection by avian predators. A concentration of activity by avian predators in an area used by spruce grouse may provide the necessary stimulus for initiating such moves.

Radio-marked female spruce grouse were commonly observed in association with other spruce grouse. Adult female spruce grouse were most often associated with other adult females and immature grouse of both sexes. Adult male spruce grouse were infrequently seen and never observed in the presence of another known adult male. Circumstances preventing age determination of unmarked spruce grouse hampered my analysis of the effect of social interaction on habitat utilization, but, my data and evidence in the literature (Ellison, 1973; McCourt, 1971) indicates that social interactions among female and immature spruce grouse do not restrict winter habitat utilization. The common observance of females and immature grouse in association with each other without any evidence of aggression and the overlapping home ranges of radio-marked females support this statement. In addition, wintering spruce grouse do not depend upon flocking for winter survival as in the case of various other tetraonids (Ellison, 1973). On approximately 80% of the days on which spruce grouse were observed during the winter season, they were found alone.

Vegetation structure of sites utilized during the winter

One important factor determining winter survival of spruce grouse appears to be the availability of sites covered by vegetation of appropriate physical structure in areas with suitable micro-climatic regimes.

Female spruce grouse whose home ranges were established on the south-facing slopes of the drainage selected sites with more densely stocked forest than the cover type in general. Distinct patterns of habitat use were exhibited during the two identified activity periods (feeding-loafing and night roosting). During both activity periods radio-marked spruce grouse keyed on the tree crown volume of the habitat. The species composition of trees (expressed in terms of relative density), total density of trees, and the vertical distribution of tree foliage (expressed in terms of canopy coverage) reflect the characteristics which radio-marked spruce grouse appeared to select.

During daylight hours (feeding-loafing period) radio-marked female spruce grouse roosted in a single tree or group of trees. Movements were generally restricted to a 0.045 to 0.3 hectare area. The sites selected include the resources necessary for the simultaneous satisfaction of nutritional, behavioral, and cover requirements associated with the evolved survial strategy of spruce grouse.

Cryptic coloration and behavioral responses to the presence of predators, i.e., remaining motionless until pursued, allowed spruce grouse to use relatively exposed sites during daylight hours. Sites selected by radio-marked spruce grouse for day use simultaneously facilitated day-long exposure to a food source, avoidance of predators, and potential amelioration of thermal stress by exposure to solar radiation and shade.

The principal food source on the study area was needles of ponderosa pine. The crown biomass of this species, which is shade intolerant, and, therefore, does not produce large crowns in the understory, is distributed as isolated components of the canopy and/or in the upper zone of the canopy.

During the feeding-loafing period, spruce grouse intermittently fed on conifer needles. Feeding periods were generally short, lasting from less than a minute to 15 minutes. The majority of remaining time was spent loafing. A vigorous feeding period, lasting approximately 30 minutes, occurred just prior to night roosting.

Spruce grouse required long periods of exposure to their food source, probably because of the low quality of their winter diet in terms of energy content and nutritional value (Pendergast and Boag, 1971; Gurchinoff and Robinson, 1972; Ellison, 1966). The birds compensate for the low nutritional value and relative indigestibility of their food source by passing large quantities of needles through their digestive systems (Pendergast and Boag, 1971, 1973).

Micro-sites providing adequate cover for protection from predators and weather were apparently distributed over a wide range of heights. The vertical distribution of foliage at feeding-loafing sites ranged over an 80 foot distance, however, weather conditions strongly influenced the birds' selection of a site with respect to height above ground, and density of canopy cover. Convective heat loss due to wind is probably the most important adverse meteorological factor affecting spruce grouse during the winter period (Moen, 1973; Porter and Gates, 1962; Stevens and Moen, 1970). Observations of spruce grouse exposed to constantly blowing winds, sufficiently strong to ruffle their feathers, indicate that spruce grouse were unwilling or unable to tolerate those conditions. In each case, the grouse moved to a site protected, or at least partially protected, from the wind.

On cold days in which skies were clear, spruce grouse adjusted their behavior to retard heat loss. Postures which effectively reduced the bird's exposed surface area, particularly about the head region, were assumed. Piloerection of feathers and orientation of the body to maximize incident solar radiation was observed. These behavioral reactions to cold stress compliment internal heat production from body metabolism, reducing energy requirements for the grouse (Moen, 1973). The importance of such behavior in light of the low nutritional quality of spruce grouse winter diet may be substantial.

On relatively warm days in which skies were clear, exposure to direct solar radiation may result in excessive heat load for spruce grouse. However, those using the crowns of ponderosa pine could easily find shade behind the tree bole or groups of branches and needles.

On overcast days, ambient air temperatures were relatively uniform. Thermal radiation input occurred from all directions as a function of reflection and re-radiation of energy from snow, vegetation, and the atmosphere (Gates, 1962). Under these conditions, spruce grouse appeared less selective in terms of where they roosted within the tree. They often loafed in the interior of the crown, i.e., closer to the bole, possibly to avoid detection by predators.

Periods of precipitation did not alter the pattern of spruce grouse habitat use beyond that associated with overcast conditions and strong winds. Spruce grouse easily escaped the wetting effects of precipitation by adjusting their positions within the tree crown.

The species composition and measured physical structure of vegetation at sites selected for day roosting document the above mentioned pattern of habitat utilization. Tree species which appeared to provide preferred food supplies (ponderosa pine primarily) achieved maximum importance at feeding-loafing sites in terms of calculated importance values, relative density, and relative basal area. Sites used as day roosts were generally less dense in terms of tree stocking (25% less on the average) than sites used for night roosting. Approximately one-third of the basal area of trees at feeding-loafing sites were in the 8-15 inch dbh class. Approximately one-half of the basal area of trees at these sites were in trees larger than 8 inches dbh. Estimated canopy coverage of trees at feeding-loafing sites was generally less than at night roosts, varying between 30 to 70% canopy cover.

Spruce grouse always flew to their roosts before complete darkness set in. At night roosts, tree species most efficient in the provision of thermal and security cover were of maximum importance, Douglas fir appeared to be most valuable, as reflected by its high Importance Value and relative density at night roost sites.

Sites selected as night roosts by radio-marked spruce grouse were generally more densely stocked with trees than feeding-loafing sites (1.4 times as dense on the average). Approximately two-thirds of the total basal area was in trees smaller than 8 inches dbh, with more than one-third in trees between 4 and 8 inches dbh. The greater amount of tree canopy coverage present at night roosts (generally between 50% and 95%) than at feeding-loafing sites is partially a function of the distribution of basal area in the various diameter classes as indicated above. The distribution of canopy cover (crown volume) at night roosts was over a smaller vertical range than at feeding-loafing sites.

The dense crown volume present at night roosts functions to ameliorate environmental stresses imposed by weather conditions in several ways. Convective heat loss is minimized by the reduction of wind velocity within the relatively dense crown volume of the night roost (Geiger, 1965; Gates, 1962; Berger, 1971; Moen, 1973). One would expect lower wind velocities at night roost sites than at feeding-loafing sites or most sites at snow surface level.

Temperature conditions at night roosts are modified by the reflection, absorption, and reradiation of heat energy by and from crown foliage. Radiative heat loss from bird to space is thereby reduced (Geiger, 1965; Beall, 1974). The atmosphere absorbs radiation from the ground, snow, and vegetation within certain bands of the electromagnetic spectrum. Much heat energy which is not absorbed by the atmosphere is lost to space. As a result, the ground surface cools, and in turn, absorbs heat energy from the air immediately above it. Layers of air are sequentially cooled resulting in a gradient of increasing temperatures between the ground and tree canopy (Geiger, 1965). Consequently, temperatures at night roost sites within the canopy are warmer than at ground level or above the canopy.

A substantial amount of variation was associated with the mean values of absolute tree density and absolute tree basal area at feeding-loafing sites and night roosts. This statistically unexplained variation is attributed to four major factors. Thermal stress on spruce grouse varied with the weather conditions. As weather conditions change, microclimates and thermal stress associated with a set of structural conditions change correspondingly. In most cases, spruce grouse reacted to changing weather conditions by adjusting their position within a tree or group of trees. However, some changes to a different location entirely were stimulated by changing weather conditions, particularly wind. These more extensive movements probably contributed to the wide variation in the structural characteristics of sites used.

Differences in the effect of local topographic features on microclimatic conditions may compensate for certain features of vegetation structure. Local topographic features may serve to deflect wind or expose the site to increased amounts of solar radiation, allowing birds to use this site even if the vegetation structure is not functioning in these respects.

The sampling methods used may have measured components of stand structure not important to spruce grouse. For example, at many sites Douglas fir sapling are growing up under shade intolerant ponderosa pine. The resulting stand structures are functions of past logging and fire history. As mentioned, during feeding-loafing activity, spruce grouse used the crown portions of ponderosa pine, and occassionally lodgepole pine. At feeding-loafing and night roost sites, where understories of Douglas fir saplings occur beneath a few large ponderosa or lodgepole pines, the presence of Douglas fir may not have been required. However, the sapling-sized Douglas fir trees were included in the description of the site for that activity period, consequently, increasing the variability of the average structural conditions.

Finally, unrecognized differences in behavioral responses to weather conditions exhibited by the individual radio-marked grouse undoubtedly added unexplained variation in terms of structural differences of sites selected.

CONCLUSIONS AND MANAGEMENT CONSIDERATIONS

The results presented here are based on a small sample of spruce grouse and should be extrapolated outside the study area only with considerable caution. However, there are certain basic functional relationships between the birds and their habitat which probably hold throughout the species' range.

In the intermountain west, the topographic diversity of spruce grouse habitat influences not only vegetation community structure and distribution, but also thermal and radiant energy regimes. Over the winter period, spruce grouse activity is concentrated within areas subject to tolerable microclimatic conditions. Ridges, upper slope positions, and southerly aspects are selected over drainage bottoms and northerly aspects. In coincidence with the physiographic features selected, certain forest vegetation communities with distinct structures (horizontal and vertical), and furthermore, specific sites exhibiting distinct structures were selected for daytime activities and night roosting. At the sites selected, radio-marked spruce grouse appeared able to maximize energy inputs from solar and thermal radiation and food sources. Additionally, they appeared able to minimize energy losses from convection (wind), conduction, and radiation.

Certain key factors under the control of land managers greatly influence the quality of spruce grouse winter habitat;

1. The species composition of the stands.

   The species composition of forest stands directly affects spruce grouse winter food supply. Needles of ponderosa pine and lodgepole pine appear to be the most important winter foods for spruce grouse in the United States and southern Canada (Jonkel and Greer, 1963; Crichton, 1963; Pendergast and Boag, 1970). However, forest stands need not consist totally of ponderosa or lodgepole pine to satisfy spruce grouse winter nutrition needs. Ponderosa pine and lodgepole pine trees in the 4-15" dbh class appear to be of the most value at feeding-loafing sites for wintering spruce grouse in the second growth forests on the North Fork study area. The mean density of winter food tree species (ponderosa and lodgepole pine combined) in the 4-15" dbh class at sites used by radio-marked female spruce grouse range between 75 stems/acre and 167 stems/acre. These densities represented 8.9% to 12.4% of the total number of trees at sites used for feeding-loafing activity (Table 15, 17). Management practices resulting in minimum tree densities and relative densities of ponderosa pine and lodgepole pine within these limits should provide an adequate winter food supply for spruce grouse in similar low elevation forests.

2. The distribution of affected stands with respect to topography.

   Ridges, extreme upper slope positions on northerly aspects, and southerly aspects provide potential exposure to solar radiation. Sites at elevations above nocturnal cold air accumulation (temperature inversion) further enhance energy conservation for spruce grouse.

3. The horizontal and vertical structure of affected stands.

   From the data collected, forest stands with the following characteristics provided suitable cover (escape and thermal) for wintering spruce grouse:

Mean Basal Area:	51 sq.ft./acre - 190 sq. ft./acre
Mean Density:	499 stems/acre - 717 stems/acre
Index of Aggregation:	1.49 - 2.92

Within such stands, "micro" sites (.045-.3 ha.) (.1 m. - .75 ac.) with the following characteristics are desirable for feeding-loafing activity:

Mean Basal Area:	122 - 178 sq. ft./acre
Mean Density:	1395 - 3003 stems/acre

Pure stands (with respect to species composition) do not appear to provide the diversity of conditions preferred by spruce grouse for winter habitat in low elevation forests. This may not be the case at higher elevations.

Relative densities of tree species within the following ranges provide suitable feeding-loafing sites on low elevation forests:

ponderosa pine:	2.8 - 14.1%
lodgepole pine:	0 - 23.1%
Douglas fir:	58.4 - 94.3%

At both feeding-loafing sites and night roosts the crown biomass associated with living trees should be distributed over 9.2 - 15.4 m. (30-55 ft.) vertical distance. At feeding-loafing sites canopy coverage ranging between 30% and 70% is desirable. At night roosts canopy coverage should range between 50% and 80%.

The forest stand parameters presented above represent unevenaged stands which provide relatively diverse microclimates under any set of meteorological conditions in addition to providing protection from predators.

4. The areal coverage of affected forest stands.

   The average winter home range of observed spruce grouse covered 24.1 ha. (53 ac.). The appropriate structural characteristics of forest stands should be maintained on habitat blocks of this size in areas managed to maintain spruce grouse populations. Habitat blocks should not be separated by more than 50 meters on the average to facilitate movement by spruce grouse between habitat blocks.

5. The effect of forest succession on forest stand structure and distribution.

   Forest management practices can be used to counteract the adverse effects that forest succession may impose on spruce grouse habitat. The length of time over which adequate spruce grouse winter habitat persists was not determined in this study.

The development of an ecological model for spruce grouse would greatly facilitate the evaluation of impacts associated with forest management on a species habitat. Some major components of spruce grouse winter habitat have been identified and can be related to an individual grouse's attempt to maintain its energy budget. However, quanitification of energy fluxes between spruce grouse and their environment is needed before a complete habitat model can be constructed.

The integration of energy flux over time must be calculated to properly evaluate a grouse's energy budget, since instantaneous and short-term energy deficits can be tolerated. It is the long run energy balance which is of importance (Moen, 1973).

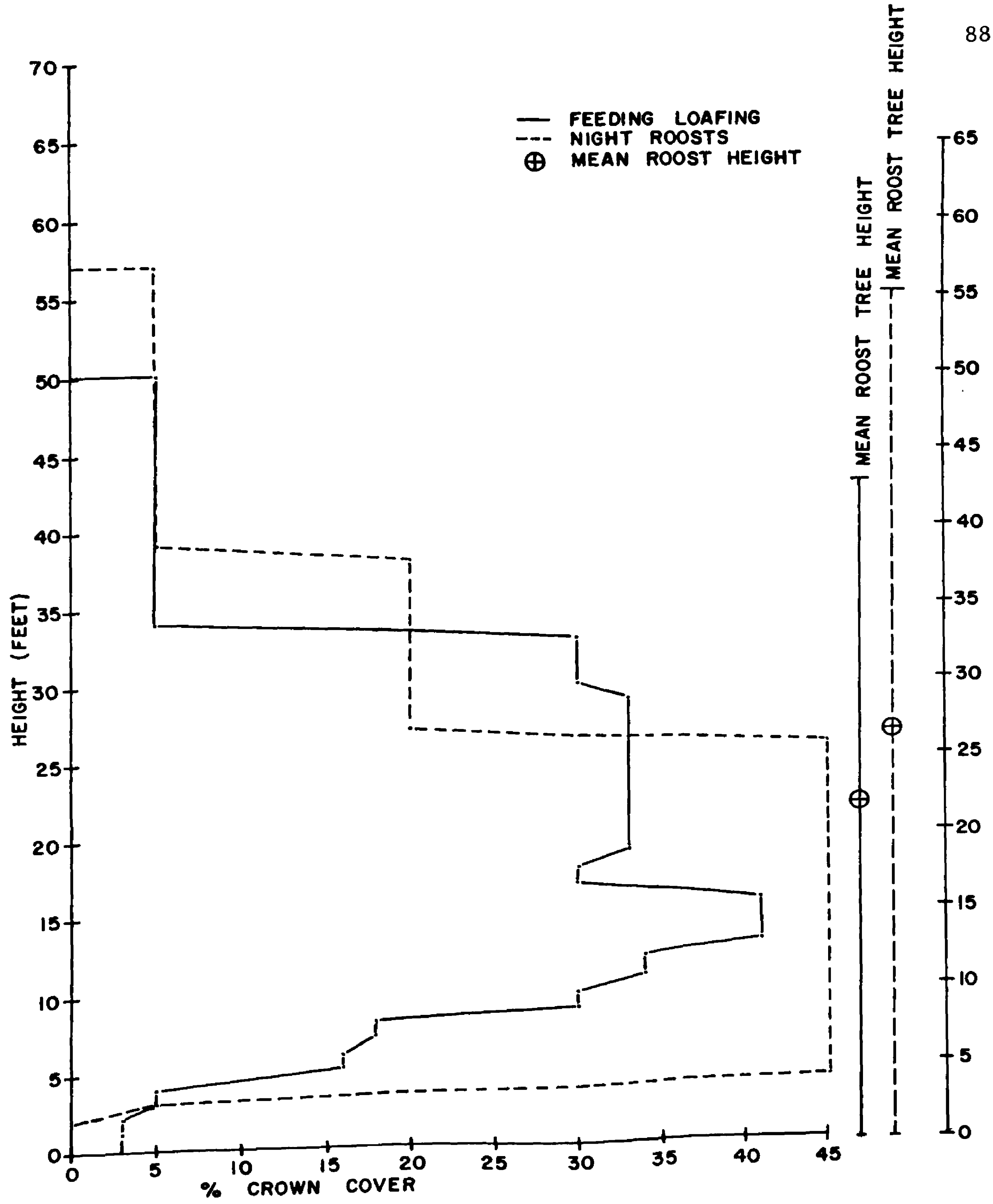
An understanding of the effect of forest stand structures on energy input and losses is essential to predict the effect of silvicultural practices and natural phenomenon on the survival value of a particular habitat for spruce grouse.

Furthermore, expansion of consideration to those components of the wildlife community with similar ranges of mobility and using the same areas would facilitate an integrated approach to habitat management.

APPENDIX

Vertical Distributions of Tree crown foliage, mean roost heights, and mean roost tree heights at feeding-loafing sites and night roosts for each radio-marked spruce grouse.

Figure 10. Typical vertical distribution of tree crown foliage, mean roost height, and mean roost tree height at feeding loafing sites and night roosts of bird No. 236.



FEEDING LOAFING
NIGHT ROOSTS
MEAN ROOST HEIGHT
MEAN ROOST TREE HEIGHT
MEAN ROOST TREE HEIGHT
HEIGHT (FEET)
% CROWN COVER
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70

Figure 11. Typical vertical distribution of tree crown foliage, mean roost height, and mean roost height at feeding-loafing sites and night roosts of bird No. 243.

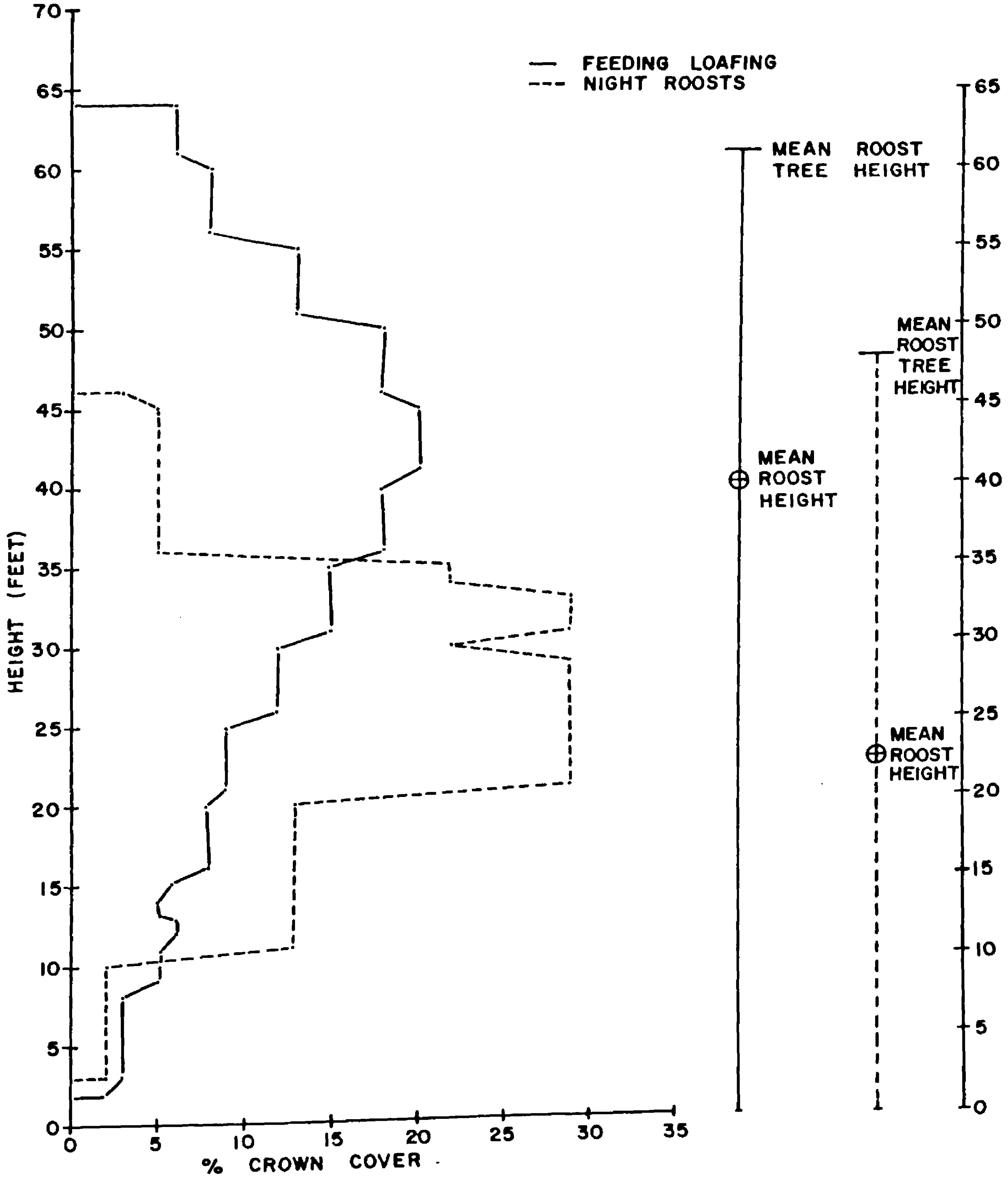
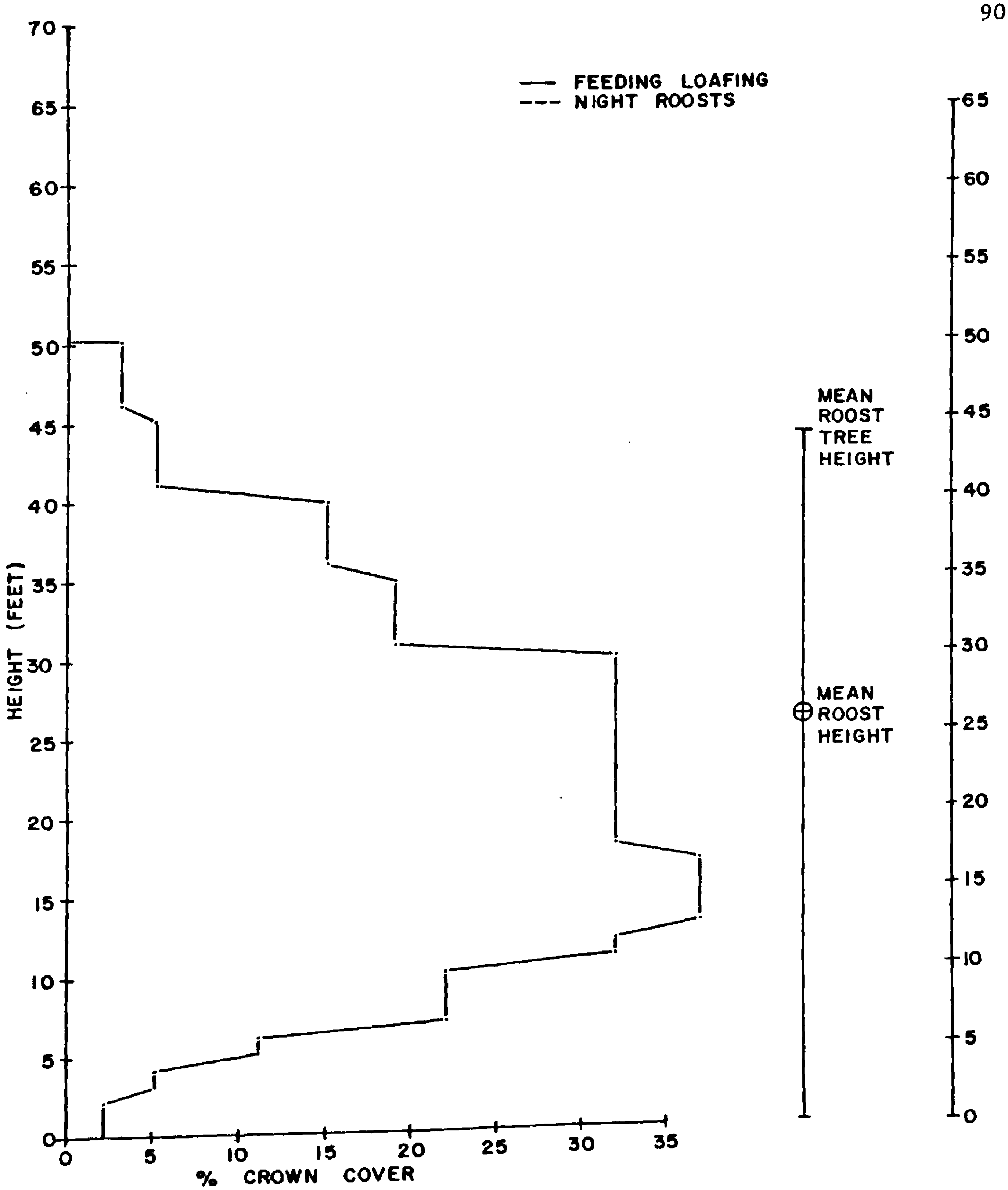
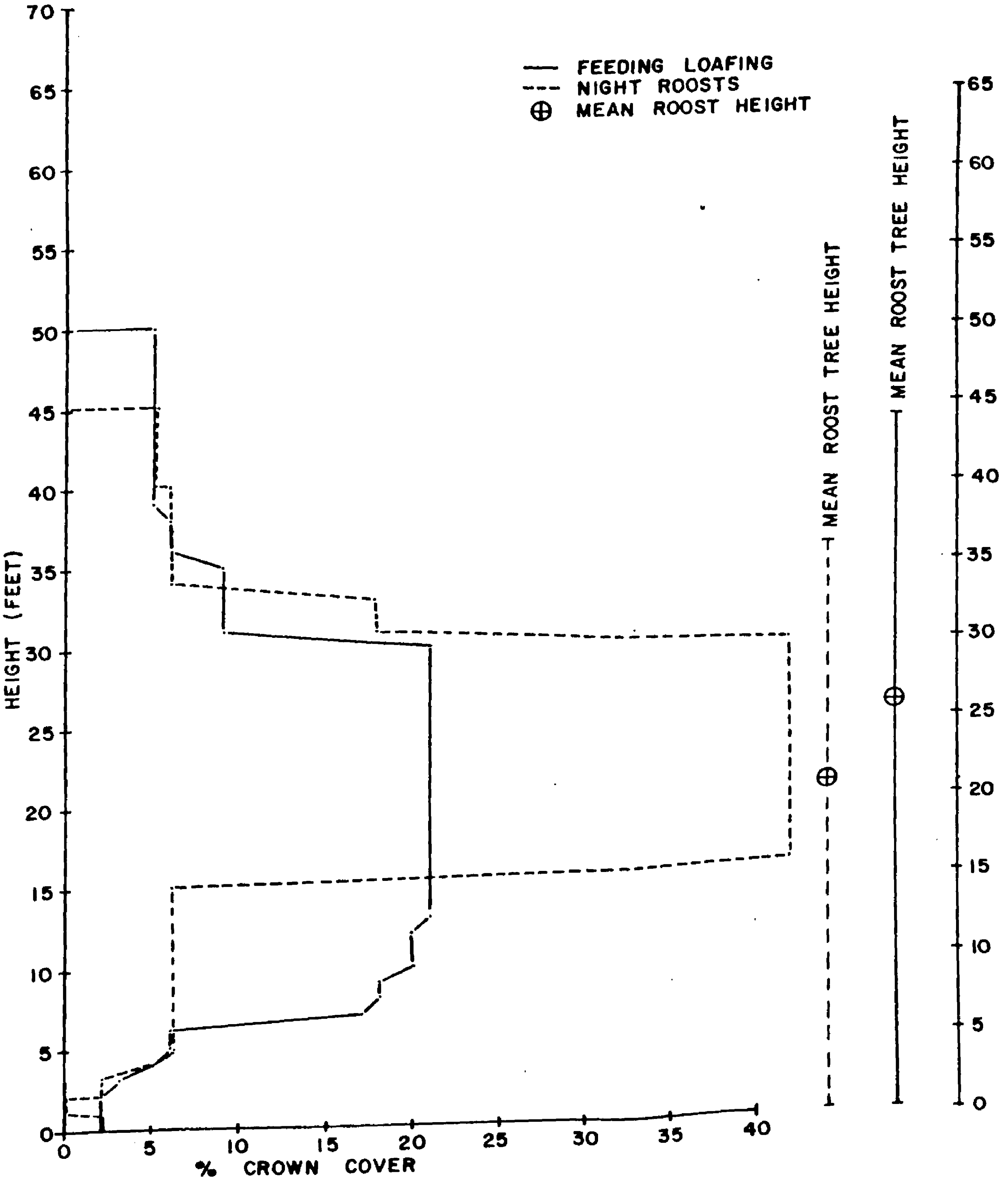

FEEDING LOAFING
NIGHT ROOSTS
MEAN ROOST TREE HEIGHT
MEAN ROOST HEIGHT
MEAN ROOST TREE HEIGHT
MEAN ROOST HEIGHT
HEIGHT (FEET)
% CROWN COVER
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70

Figure 12. Typical vertical distribution of tree crown foliage, mean roost height, and mean roost tree height at feeding-loafing sites of bird No. 335.



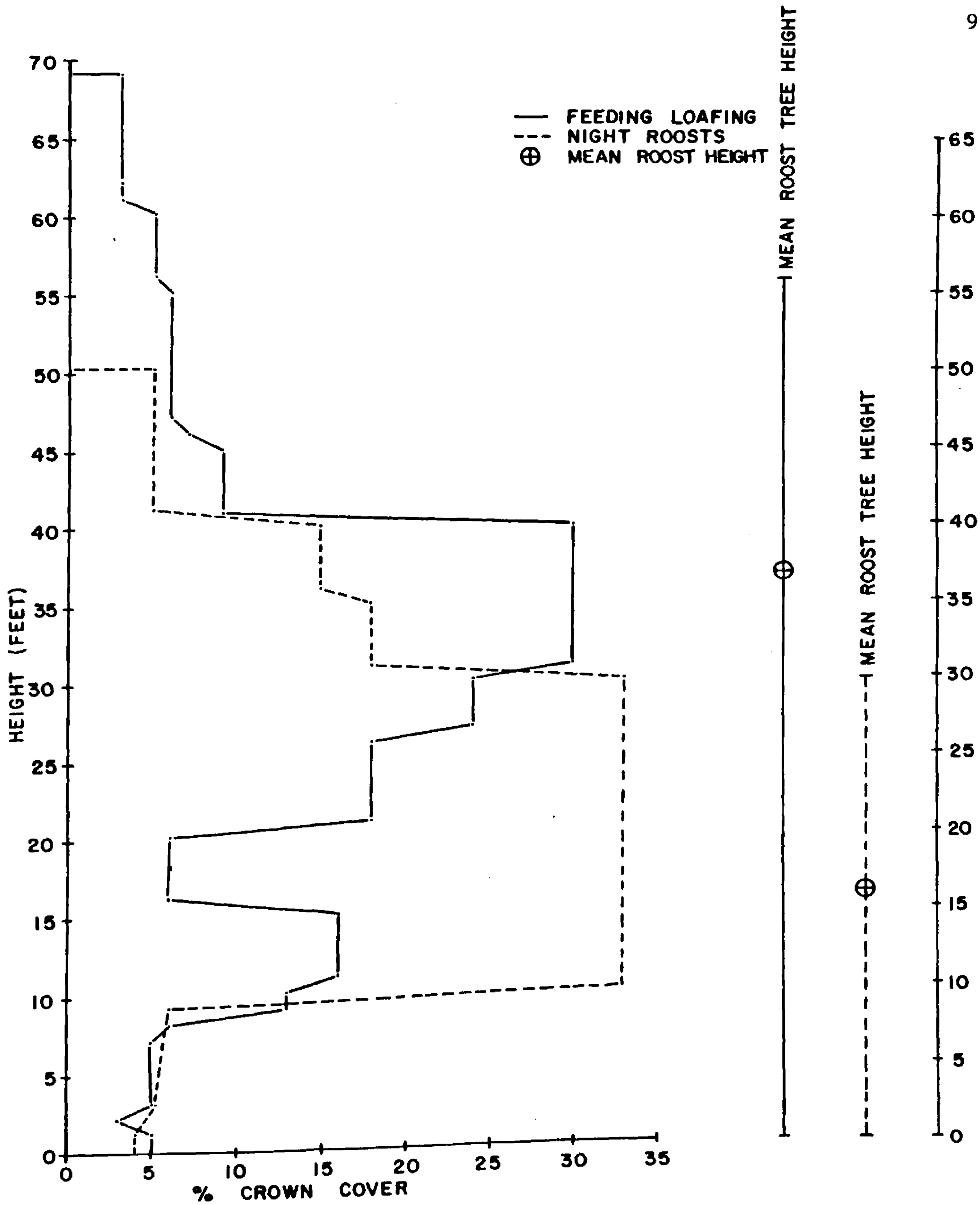
FEEDING LOAFING
NIGHT ROOSTS
HEIGHT (FEET)
% CROWN COVER
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
MEAN ROOST TREE HEIGHT
MEAN ROOST HEIGHT

Figure 13. Typical vertical distribution of tree crown foliage, mean roost height, and mean roost tree height at feeding-loafing sites and night roosts of bird No. 245.



FEEDING LOAFING
NIGHT ROOSTS
MEAN ROOST HEIGHT
HEIGHT (FEET)
% CROWN COVER
MEAN ROOST TREE HEIGHT
MEAN ROOST TREE HEIGHT
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70

Figure 14. Typical vertical distribution of tree crown foliage, mean roost height, and mean roost height at feeding-loafing sites and night roosts of bird No. 2739.


FEEDING LOAFING
NIGHT ROOSTS
MEAN ROOST HEIGHT
MEAN ROOST TREE HEIGHT
MEAN ROOST TREE HEIGHT
HEIGHT (FEET)
% CROWN COVER
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70

REFERENCES CITED

Anderson, Leon J., 1973. Habitat use, behavior, territoriality and movements of the male Canada Spruce Grouse of northern Minnesota. M.S. thesis, University of Minnesota, Minneapolis.

Beall, Robert C., 1974. Winter habitat selection and use by a western Montana elk herd. Ph.D. dissert., University of Montana.

Bent, Arthur Cleveland, 1932. Life Histories of North American Gallinaceous Birds. New Yrok: Dover Publications, Inc.

Berger, James D., 1971. Vertical profiles of windspeed in a pine stand. Forest Science 17(3): 314-321.

Brander, R.B., 1968. A radio package for game birds. Journ. Wildl. Mgt. 32:630-632.

Brenner, Robert L., 1968. The Geology of Lubrecht Experimental Forest. M.S. thesis, University of Montana, Missoula.

Cauvin, D.M., 1961. Management plan for Lubrecht Forest. M.S. thesis, Montana State University, Missoula.

Crichton, V., 1963. Autumn and winter foods of the spruce grouse in central Ontario. Journ. Wildl. Mgt. 27(4): 597-601.

Ellison, L.N. Alaska Department of Fish & Game Job Progress Report W-G-R-5, 6, Job No. 3, 1964.

__________. Alaska Department of Fish and Game Job Progress Report W-B-R-1, Job No. 4, 1965.

__________. 1966. Seasonal foods and chemical analysis of the winter diet of Alaskan Spruce Grouse. Journ. Wildl. Mgt. 30(4):729-735.

__________. 1968. Movements and behavior of Alaskan Spruce Grouse during the breeding season. Mimeo. Trans. Cal-Nev. section, Wildlife Society.

__________. 1971. Territoriality in Alaskan Spruce Grouse. Auk 88(3): 652-664.

__________. 1972. Role of winter food in regulating numbers of Alaskan Spruce Grouse. Ph.D. dissert. University of California, Berkeley.

__________. 1973. Seasonal social organization and movements of Alaskan Spruce Grouse. Condor 75(4): 375-385.

Evans, K., and Aaron N. Moen, 1975. Thermal exchange between Sharp-tailed Grouse (Pedioecetes phasianellus) and their winter environment. Condor 77: 160-168.

Gates, D.M., 1962. Energy exchange in the biosphere. New York: Harper and Row.

Geiger, Rudolph, 1965. The climate near the ground. Cambridge: Harvard University Press.

Gurchinoff, S., and W.L. Robinson, 1972. Chemical characteristics of Jack pine needles selected by feeding Spruce Grouse. Journ. Wildl. Mgt. 36(1):80-87.

Haas, George H., 1974. Habitat selection, reproduction, and movements in female Spruce Grouse. Ph.D. dissert., Univeristy of Minnesota, Minneapolis.

Harvey, M.J., and R.W. Barbour, 1965. Home Range of Microtus ochrogaster as determined by a modified minimum area method. Journ. Mamm. 46(3): 398-402.

Hungerford, K.E., 1951. Ruffed Grouse populations and cover use in northern Idaho. Trans. of North American Wildlife Conference 16:216-224.

Johnsgaard, Paul A., 1973. Grouse and Quails of North America. Lincoln: Univeristy of Nebraska Press.

Jonkel, C.J., and K.R. Greer, 1963. Fall food habits of Spruce Grouse in northwestern Montana. Journ. Wildl. Mgt. 27(4):593-596.

Lee, Richard, and A. Baumgartner, 1966. The topography and insolation climate of a mountainous forest area. Forest Science 12:258-267.

MacDonald, S.D., 1968. The courtship and territorial behavior of Franklin's race of the Spruce Grouse. The Living Bird 7:5-25.

McCourt, K.H., 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in Southwestern Alberta. Unpub. M.S. thesis, Univ. of Alberta, Edmonton.

______________. 1971. Dispersion and dispersal of female and juvenile Franklin's grouse in southwestern Alberta. M.S. thesis, University of Alberta, Edmonton.

McCourt, K.H., D.A. Boag, and D.M. Keppie, 1973. Female Spruce Grouse activities during laying and incubation. Auk 90(3): 619-623.

Miller, J.M., and F.P. Keen, 1960: Biology and control of the western pine beetle. USDA Misc. Pub. 800.

Moen, Aaron N., 1973. Wildlife Ecology. San Francisco: W.H. Freeman and Company.

Odum, E.P., and E.J. Kuenzler, 1955. Measurement of territory and home range size in birds. Auk 72(2):128-137.

Pendergast, B.A., and D.A. Boag, 1970. Seasonal changes in the diet of Spruce Grouse in central Alberta. Journ. Wildl. Mgt. 34(3):605-611.

______________________________. 1971. Nutritional aspects of the diet of Spruce Grouse in central Alberta. Condor 73(4):437-443.

______________________________. 1973. Seasonal changes in the internal anatomy of Spruce Grouse in Alberta. Auk 90(2):307-317.

Pielou, E.C., 1969. An introduction to mathematical ecology. New York: Wiley-Interscience.

Porter, W.P., and D.M. Gates, 1969. Thermodynamic equilibria of animals with environment. Ecol. Mono. 39:227-244.

Ramharter, Brentt G., 19761 Habitat selection and movements by Sharp-tailed Grouse (Pedioecetes phasianellus) hens during the nesting and brood rearing periods in a fire maintained brush prairie. Ph.D. dissert., University of Minnesota, Minneapolis.

Robinson, W.L., 1969. Habitat selection by Spruce Grouse in Northern Michigan. Journ. Wildl. Mgt. 33(1):113-120.

Smith, Robert L., 1966. Ecology and Field Biology. New York: Harper and Row.

Sokal, Robert R., and F. J. Rohlt, 1969. Biometry, San Francisco: W.H. Freeman and Company.

Steele, Robert W., 1975. Weather Data Summary, 1956-1975, Lubrecht Experimental Forest, Greenough, Montana. Forest and Conservation Experiment Station, Misc. Pap. No. 8. University of Montana.

Stevens, D.S., and Aaron N. Moen, 1970. Functional aspects of wind as an ecological and thermal force. Trans. of N. Am. Wildl. Nat. Res. Conf. 35:106-114.

Stoneberg, R.P., 1967. A preliminary study of the breeding biology of the Spruce Grouse in northwestern Montana. M.S. thesis, University of Montana, Missoula.

Zwickel, F.C., and J.F. Bendell, 1967. A snare for capturing Blue Grouse. Journ. Wildl. Mgt. 31:202-204.