

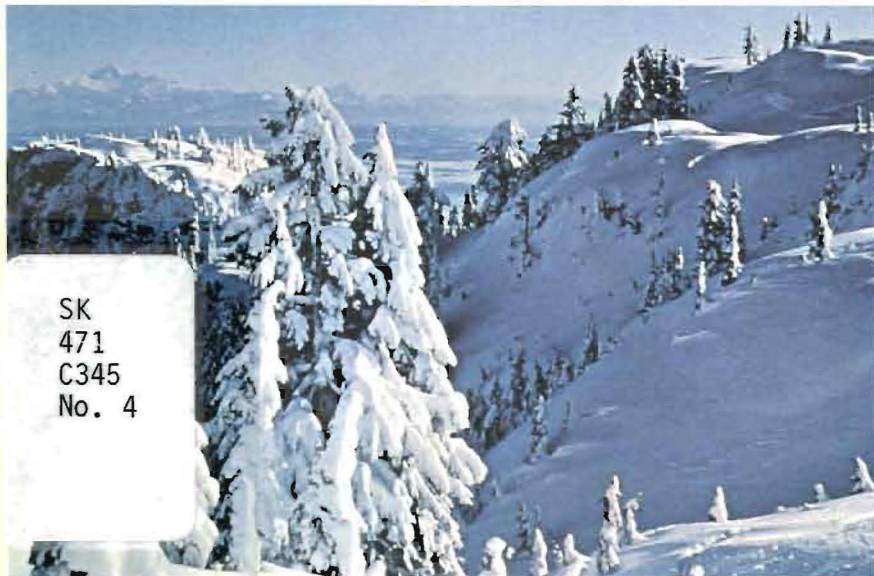


J. F. BENDELL AND P. W. ELLIOTT

Behaviour and the regulation of numbers in blue grouse



CANADIAN WILDLIFE SERVICE REPORT SERIES—NUMBER 4



SK
471
C345
No. 4

7003479F
Jean-Luc Desgranges

**Behaviour and the
regulation of numbers in blue grouse**

by J. F. Bendell and P. W. Elliott



**Canadian Wildlife Service
Report Series—Number 4
Ottawa, 1967**

**Department of
Indian Affairs and Northern Development**

Cover

Top left—Summer range (J. F. Bendell).

Top right—Adult male (F. C. Zwickel).

Bottom left—Winter range (D. A. King).

Bottom right—Summer range (J. F. Bendell).

Issued under the authority of the
Honourable Arthur Laing, P.C., M.P., B.S.A.,
Minister of
Indian Affairs and Northern Development

Acknowledgements

We are grateful to the people who worked with us in the field and gave useful advice and criticism. Student assistants who helped gather data were Messrs. R. Pasin, A. Bohn, D. Belcher, D. Hancock, W. Munro, R. Jakimchuk, K. Wade, and F. Gornall, Jr. Messrs. S. Teeple and J. Loyns worked in several years and were able to get onto the burns before the arrival of grouse.

Dr. F. Zwickel participated in the field work, gave much constructive criticism, and provided several photographs. Dr. D. Boag read the manuscript and made helpful suggestions for its improvement. Dr. D. Chitty helped us in the interpretation of our data. The illustrations were prepared by Mr. R. Henzler.

Financial support that made the study possible came from the National Research Council of Canada, British Columbia Fish and Wildlife Branch, the Canadian National Sportsmen's Show, and Canadian Industries Limited. Part of the work was done while the senior author was with the Canadian Wildlife Service. We thank the Service for the editing and publication of the manuscript.

Abstract

The importance of behaviour to the regulation of numbers was studied in blue grouse (*Dendragapus obscurus fuliginosus*) on two summer ranges on Vancouver Island. Data were gathered over 10 years from dense and sparse populations that occupied cover which varied from very open to very dense. Grouse were shot to determine the effect of residents on recruitment.

Grouse on the summer range apparently do not regulate their density. Territorial behaviour appears to provide the undisputed use of area for successful mating. The rate of loss of young from autumn to spring is high in comparison to that of older grouse and may relate to a process of population regulation.

Males precede the females onto the summer range and establish a display and mating type of territory. Males are promiscuous. Some of the auditory and visual display of males and females is described. Territorial males tend to space themselves evenly but this may be altered by the pattern of cover. Most adult males are territorial, while most yearlings move widely and are attracted by territorial males. Some yearlings will occupy territory if the resident is removed. Most yearling males are apparently immature and dominated by territorial males.

Hens appear to occupy home ranges, are attracted by hooting males, and travel over a number of territories. Hens with brood move independently over the summer range and travel farther than hens in spring. The migration in autumn is begun by most males in July, and by hens with brood after August and before mid-September. The migration is a dispersal, so birds from a breeding population apparently winter apart.

The mean annual death rate of grouse beyond a year of age appears low and constant at approximately 28 per cent. Virtually all hens on the summer range appear to breed, and mean size of clutch is 6.22 ± 0.29 eggs. The proportion of yearlings in each population was the same each year although there were apparently fewer yearlings in the dense than in the sparse population.

Hunting is apparently a negligible cause of mortality. The relevance of some of our findings to management is discussed.

Roger Duhamel, F.R.S.C.
Queen's Printer and Controller of Stationery
Ottawa, 1967. Cat. No. R65-8/4
Price: \$1.00

Contents

Acknowledgements, 2
Introduction, 5
Study areas and methods of study, 6
The vegetation and topography of the study areas, 8
Results and conclusions, 11
The behaviour of grouse on the breeding range, 13
Migration, 13
Behaviour of the breeding male, 15
Territories of breeding males, 19
Return to territory in successive years, 20
Relation of territories to vegetation, 24
Spacing of territories, 24
Size of territories, 27
Group activities of males, 31
Behaviour of yearling males, 32
Numbers of yearling males, 35
Death rate of adult and yearling males, 37
The results of shooting grouse from the removal area, 39
Effect of resident males on yearling males, 39
Effect of resident males on the addition of new adults to the breeding population, 39
Numbers of grouse shot each month, 41
Replacement of males by place and time, 41
Distribution of yearling males on the removal area, 45
The behaviour of the breeding female, 45
Movements of females and females with brood, 48
Numbers of yearling hens, 51
Numbers of breeding hens and size of clutch, 53
Return and death rate of females, 54
Interaction among hens, 54
The return and death rate of young, 54
The autumn migration, 55
Discussion, 58
Research and management, 64
The outlook, 64
Habitat requirements, 65
Utilization, 65
Information and management, 68
Summary, 68
Résumé, 71
Literature cited, 74

List of tables

- 1a Major elements of cover and the average percentage of ground covered by them in the four types of habitat at Middle Quinsam Lake, 1962, as measured by line-intercept, 11
- 1b Major elements of cover and the average percentage of ground covered by them in the four types of habitat at Middle Quinsam Lake, 1962, as measured by quadrat, 11
- 2 Build-up and departure of grouse from the breeding range at Middle Quinsam Lake, March through August 1960, 14
- 3 Spacing of territorial males in relation to density and cover, and spacing after males were removed, 26
- 4 Movements of silent yearling males, Middle Quinsam Lake, 33
- 5 Numbers of adult and yearling males sampled as hooting or silent from March through August, Middle Quinsam Lake, 1958 through 1962, 35
- 6 Return of adult males each year after banding, 1959 through 1962, Middle Quinsam Lake, 38
- 7 Return of yearling males each year after banding, 1959 through 1962, Middle Quinsam Lake, 38
- 8 Estimate, from mapping of territories and shooting, of number of new adult hooting males on the reference and removal plots, 40
- 9 Number of new adult hooting males on the reference plots, by calculation, 41
- 10 Time and place of recording grouse on the removal area, Middle Quinsam Lake, 44
- 11 Distance between sightings of territorial males, hens, and hens with brood in dense population at Lower Quinsam Lake and sparse population at Middle Quinsam Lake, 48
- 12 Percentage of yearlings in the hen population, April through June, June through August, and pooled data, Middle Quinsam Lake, 1958 through 1962, 51
- 13 Number of banded grouse available to, and shot by, hunters at Middle Quinsam Lake, 1959 through 1966, 67

List of figures

- 1 General area of study at Middle Quinsam Lake, reference and removal plots, and the distribution of open, very open, dense, and very dense types of vegetation, 7
- 2 Middle Quinsam Lake, March 1961, showing in the foreground open vegetation and in the background very dense and very open types. A main reference plot was located in the foreground, and removal plots were on the hill, 8
- 3 (a-d) The four types of habitat recognized at Middle Quinsam Lake, 1962: (a) very open, (b) open, (c) dense, and (d) very dense, 9
- 4 Profiles of the types of habitat at Middle Quinsam Lake, 1962: very open, open, dense, and very dense, 11
- 5 (a-e) Territorial behaviour of the male: (a) male in alert posture (by H. Laing); (b) adult hooting (by H. Laing); (c) a hooting station in open vegetation (the male hooted from the crevice in the log at the marker stick); (d) full courting display before a female (by F. Zwickel); and (e) threat posture, 16
- 6 Territories of males on a study plot, April through August, Lower Quinsam Lake, 1952, 19
- 7 Territories and locations of nests, 1950 through 1952, Lower Quinsam Lake, 20
- 8 Distribution of cover on a study plot, 1952 and 1957, Lower Quinsam Lake, 21
- 9 (a-d) Territories, yearling males, females, nests, and broods on the main reference plots, Middle Quinsam Lake: (a) 1959, (b) 1960, (c) 1961, and (d) 1962, 22
- 10 Territories, males, and females on the main reference plots, 1959 through 1962, Middle Quinsam Lake, 25
- 11 The relationship between number of observations of hooting males and size of territory in sparse and dense population, 29
- 12 Points where grouse were shot or observed on the removal area, Middle Quinsam Lake, 1959 through 1962, 42
- 13 Sequence of removal of hooting and silent adult and yearling males from territories on the removal plots, Middle Quinsam Lake, 1959 through 1962, 43
- 14 (a-e) (a) Hen in neutral posture, (b) defence display of female, (c) hen on nest (by F. Zwickel), (d) nest, (e) nest site, 46
- 15 Direction and minimum distance of movement of grouse (mostly hens with brood) beyond the study area at Lower Quinsam Lake, 1950 through 1952, and Middle Quinsam Lake, 1959 through 1966, 56

Introduction

An important question in population ecology is to what extent animals determine their own local abundance and distribution. Wynne-Edwards (1962) summarized much of the literature on the subject and concluded that, as a general rule, animals regulate their own density and dispersion by their social behaviour. He gave as evidence territorial behaviour, the existence of non-breeding surplus populations of adults, and habitat selection by which a population is spread through habitats of different quality.

A number of students of populations of birds have concluded that territorial behaviour limits numbers by regulating the density of the breeding population (Carrick, 1963; Hensley and Cope, 1951; Jenkins, 1961; Stewart and Aldrich, 1951; and others). Kluyver and Tinbergen (1953) concluded that territorial behaviour in titmice (*Parus* spp.) resulted in the regulation of population in good habitat and caused excess birds to occupy poor habitat. Jenkins *et al.* (1963) found that red grouse (*Lagopus lagopus scoticus*) regulated their density by territorial behaviour in the autumn. As a result of this interaction birds were chased into inferior habitat. These birds did not breed, had a higher death rate than the established and breeding members of the population, and were the expendable surplus.

On the other hand, Lack (1954, 1966) disputes the importance of territorial behaviour in the regulation of numbers. He argues its main functions are those of spacing animals, and preventing disturbance of reproducing pairs. As will be seen, we reach the same conclusions with respect to the territorial behaviour of blue grouse in spring.

The main objective of the present study was to determine whether established male blue grouse (*Dendragapus obscurus fuliginosus*) regulated their own density by preventing some males from joining the breeding population. The excluded birds would form a surplus of non-breeders. While emphasis was placed on the behaviour and population statistics of males, hens and young were also studied to find how their behaviour and population statistics related to the regulation of numbers.

We worked on the problem in two ways. Grouse were studied in sparse and dense populations and in different habitats. This enabled us to relate behaviour to density of population and to habitat. A second approach was to remove resident males from an area to determine whether new males joined the population. This allowed us to single out some of the effects of territorial males.

Our experimental method was essentially that of Stewart and Aldrich (1951) and Hensley and Cope (1951). They postulated that if resident males prevent new males from joining the breeding population, new males should replace males that are removed. Also, an area from which males are removed should yield more birds than a similar area where resident birds are not disturbed. Both predictions were satisfied by experiments in which birds of various species were counted, shot, and counted again in the same area (Stewart and Aldrich, 1951; Hensley and Cope, 1951). These workers concluded that territorial behaviour limited the density of breeding birds and created a surplus of non-breeders.

The blue grouse (*Dendragapus obscurus*) is a common member of the avifauna of the mountain regions of the West. A striking feature of its life history is an altitudinal migration of some populations between a winter range in the mountains and a summer or breeding range on the lowlands. The migration occurs between mid-March and early April and takes the birds from subalpine coniferous forests to relatively open areas that are used as breeding range. On the breeding range, the adult males (23 months of age and older) establish a display and mating type of territory. Yearling males (11 to 16 months of age) rarely occupy territory and travel relatively widely. Females do not show territorial behaviour and move over the territories of a number of males. Mating is believed to be promiscuous. Both yearling and adult females may breed. Before and after mating the sexes appear to live separate lives. The young hatch in mid-June. By the end of July most of the cocks have abandoned their territories and returned to the winter range. They are followed by the hens and broods in August and September. The migration in autumn appears to be a dispersal over a relatively large winter range. This sketch of the life history of blue grouse comes from reports by Bendell (1954, 1955a), Boag (1958, 1964), Buss (1960), Hoffmann (1956), Fowle (1960), Mussehl (1960), and others.

Study areas and methods of study

The data presented in this report are from breeding ranges near Middle and Lower Quinsam Lakes, approximately 12 miles southwest of Campbell River, Vancouver Island. The land about the Quinsam Lakes is part of an extensive and rolling plain which lies between the Island mountains to the west and the Strait of Georgia to the east. Middle Quinsam Lake is at an elevation of about 1,000 feet and is approximately 4 miles east of the first range of mountains. The study area at Lower Quinsam Lake was approximately 6 miles east of Middle Quinsam Lake and at an elevation of about 500 feet.

The original forest of the area is described by Rowe (1959) as the Southern Pacific Coast Section of the Coastal Forest Region. By the classification of Krajina (1959) the area is between the Douglas-Fir and Western Hemlock Bioclimatic Zones. According to records of the B.C. Forest Service (Forest Cover Series, Map 49°-125°, No. 11) the trees of the original forest were western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*). The forest was logged from about 1930 on and burned in a severe fire that swept some 75,000 acres in 1938. In 1952 another severe fire (the Elk Fire) burned approximately 25,000 acres including part of the 1938 burn near Middle Quinsam Lake. A fire road stopped the fire from spreading farther into the old burn. Thus the summer range at Middle Quinsam Lake consisted of two sharply separated areas with plant growth dating from 1938 and 1952, respectively. The breeding range at Lower Quinsam Lake was deep within the vegetation dating from the burn of 1938.

Grouse were studied on each breeding range by systematic search of a general study area and study plots. A general area was approximately 4 square miles; a study plot consisted of 25 or 36 acres. The general study area at Middle Quinsam Lake is illustrated in Figure 1. Approximately two thirds of it was open vegetation and one third was dense and very dense forest. The layout of the general study area at Lower Quinsam Lake, containing two reference plots and a single removal plot, is given in Bendell (1954).

Intensive studies of grouse were made on the study plots. At Middle Quinsam Lake there were 14 plots, 8 in open and the rest in dense and very dense vegetation (Fig. 1). The four plots enclosed in double lines in the figure were the removal areas where we attempted to shoot all grouse except hens with brood. The plots marked by a single line

were reference areas where grouse were observed and, if possible, banded. Two main reference plots were located south of the Argonaut Mine road, with one on each side of the fire road.

The removal and reference plots were searched until it was certain that all hooting or breeding males were found. In May and June one or two men spent full time on them and they were crossed almost every day in July and August. The frequent traversing of all parts of the main reference plots gave data for the plotting of territories and ranges of grouse. Much searching was done in the early morning and evening hours when grouse are most active and vocal (Bendell, 1955a). We believe that virtually all hooting males on the reference plots were detected, and in some years almost all on the removal plots at Middle Quinsam Lake were shot within a day or two of commencing to hoot.

We detected grouse on all areas by sound, sight, and sign. Pointing dogs were of invaluable assistance and were used throughout the study at Middle Quinsam Lake. They were particularly useful in finding birds that were silent, in dense vegetation, or on nests. Grouse were observed and, if possible, captured, banded, and released or collected. Data obtained included location, sex, age, weight, behaviour before disturbance, and the type of vegetation in which the grouse was found. Most grouse were captured in a sliding noose attached to the end of a 10- to 12-foot bamboo pole (Zwickel and Bendell, 1967). A bird captured for the first time was individually marked with coloured plastic and numbered metal bands.*

When hooting males were captured or shot at Middle Quinsam Lake, a red stake with relevant data marked on it was placed nearby. This enabled easy check of the territory in the same and subsequent years.

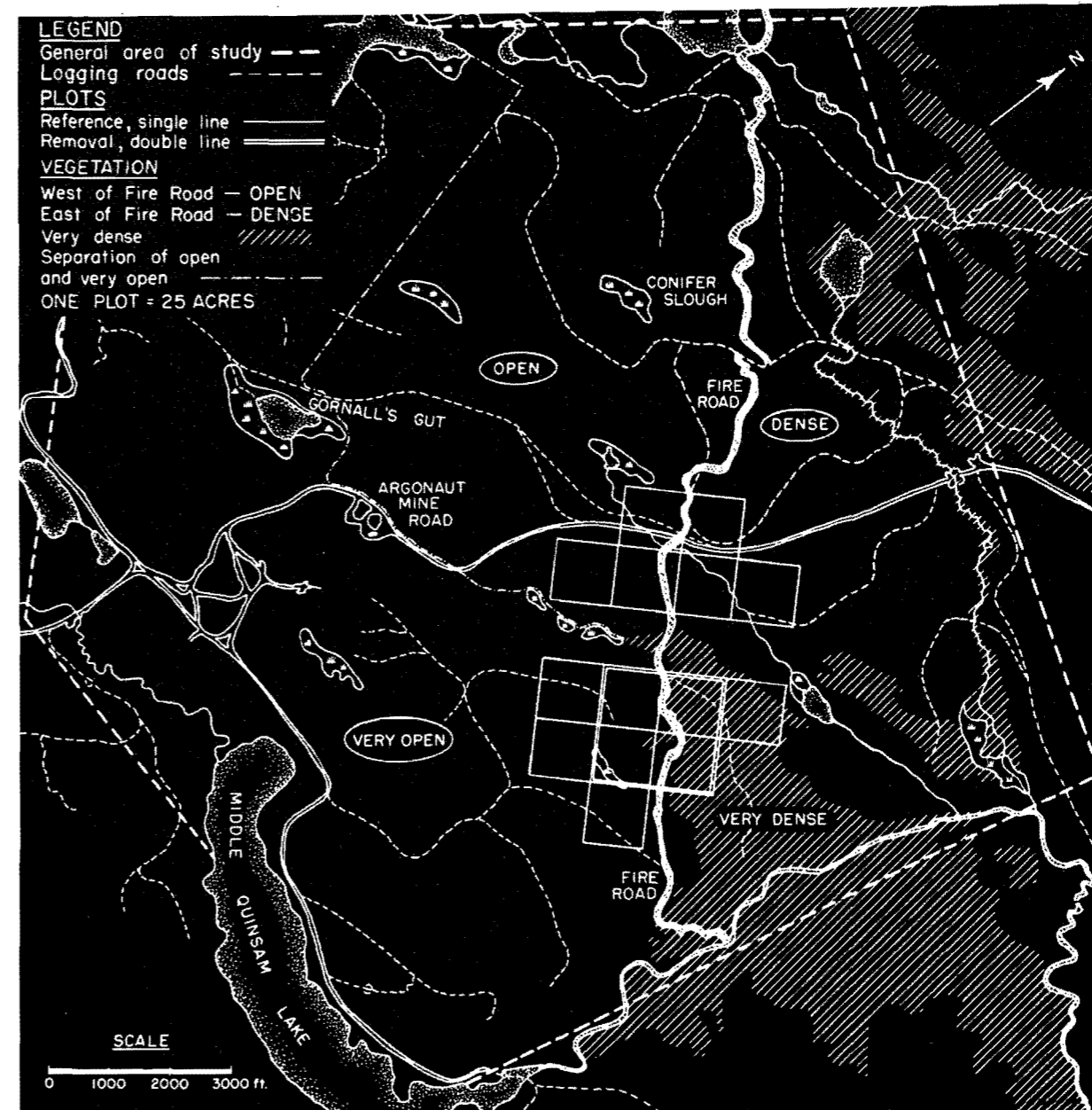
The positions of grouse were determined by reference to the network of used and disused logging roads that laced the areas. These roads are marked with broken lines in Figure 1. The boundaries of the removal and main reference plots at Middle Quinsam Lake were marked at intervals of 100 feet. This also facilitated the accurate locating and later plotting of positions of grouse.

Most of the work was done between May and early September from 1950 to 1953 at Lower Quinsam Lake and from 1959 through 1962 at Middle Quinsam Lake. In 1952, work began in April; in 1960, in March; and in 1962, a week was

*Two series of numbers were used—Nos. 1-500± at Lower Quinsam Lake and 1-1000± at Middle Quinsam Lake.

spent on the area in March and again in April before the continuous work of the summer began. The number of people in the field varied from one to seven.

1 General area of study at Middle Quinsam Lake, reference and removal plots, and the distribution of open, very open, dense, and very dense types of vegetation. (Other than the plots, from aerial photograph, B.C. 2312:53, 1957; and B.C. Reforestation Division, Part of North Portion, Map No. 11 including Block 26, map of plantations to 1963).



The vegetation and topography of the study areas

Features of the burns that might affect the local distribution of grouse were density of vegetation and elevation. The vegetation at Middle Quinsam Lake separated easily into large areas of open and dense which related to their development after fire. Figure 2 is a photograph of the study plots taken from the Argonaut Mine road in March 1961. The snow shows the amount of open ground. The fire road, separating open and dense types of vegetation, ran from the middle of the left edge of the picture onto and over the hill.

While open and dense types of cover were clearly distinct, each type varied within itself. This was most noticeable in dense vegetation where there had been more time for the development of differences in growth. Most of the open area and approximately one half of the dense area had been planted at different times to Douglas-fir. These trees were important in the structure of dense vegetation and made an increasing contribution to the density of the open vegetation. Other variations in vegetation occurred in areas of shallow standing water, streams, and places where patches of trees had not been killed by fire.

To relate grouse and habitat four main kinds of cover were recognized at Middle Quinsam Lake. The open and dense types were each divided on the basis of density to give the following habitats: open, very open, dense, and very dense (Fig. 3 a-d). Their distribution is illustrated in Figure 1. The open type was planted to fir in 1954, the very open in 1958. The difference in time of planting and therefore in size of trees was the main reason for the two cover types in the young and open burn. The dense vegetation represented planting and natural succession from the 1938 fire. Approximately one half of this area was stocked in 1944 and 1949 to Douglas-fir. The very dense cover was mostly natural growth.

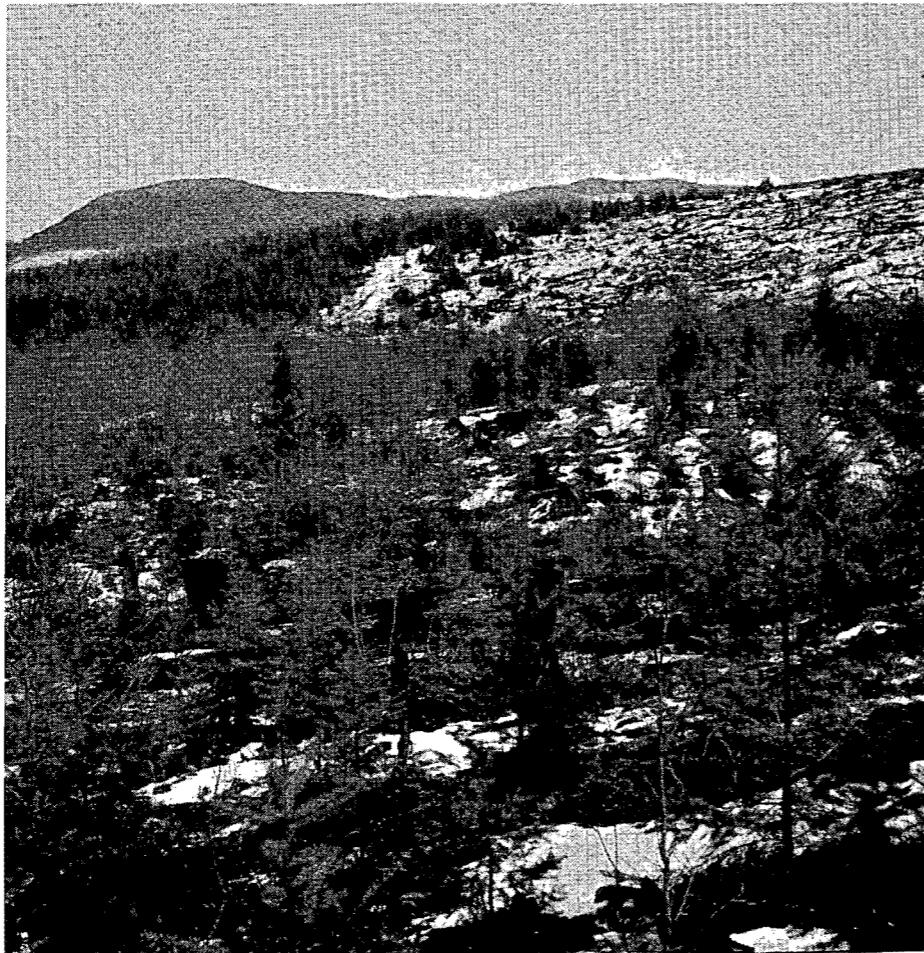
Three reference plots were in open vegetation, three in very open, three in dense, and one in very dense. Two removal plots were placed in very open and two in very dense types. Thus the behaviour of grouse and the replacement of shot birds could be compared in very open to very dense types of habitat.

The two main reference plots at Middle Quinsam Lake were sampled to describe open and dense vegetation. The two northernmost removal plots were taken as examples of very open and very dense types. Line intercepts and yard quadrats were used to sample the cover types in July and August of 1962. A 100-foot steel tape was laid over the ground,

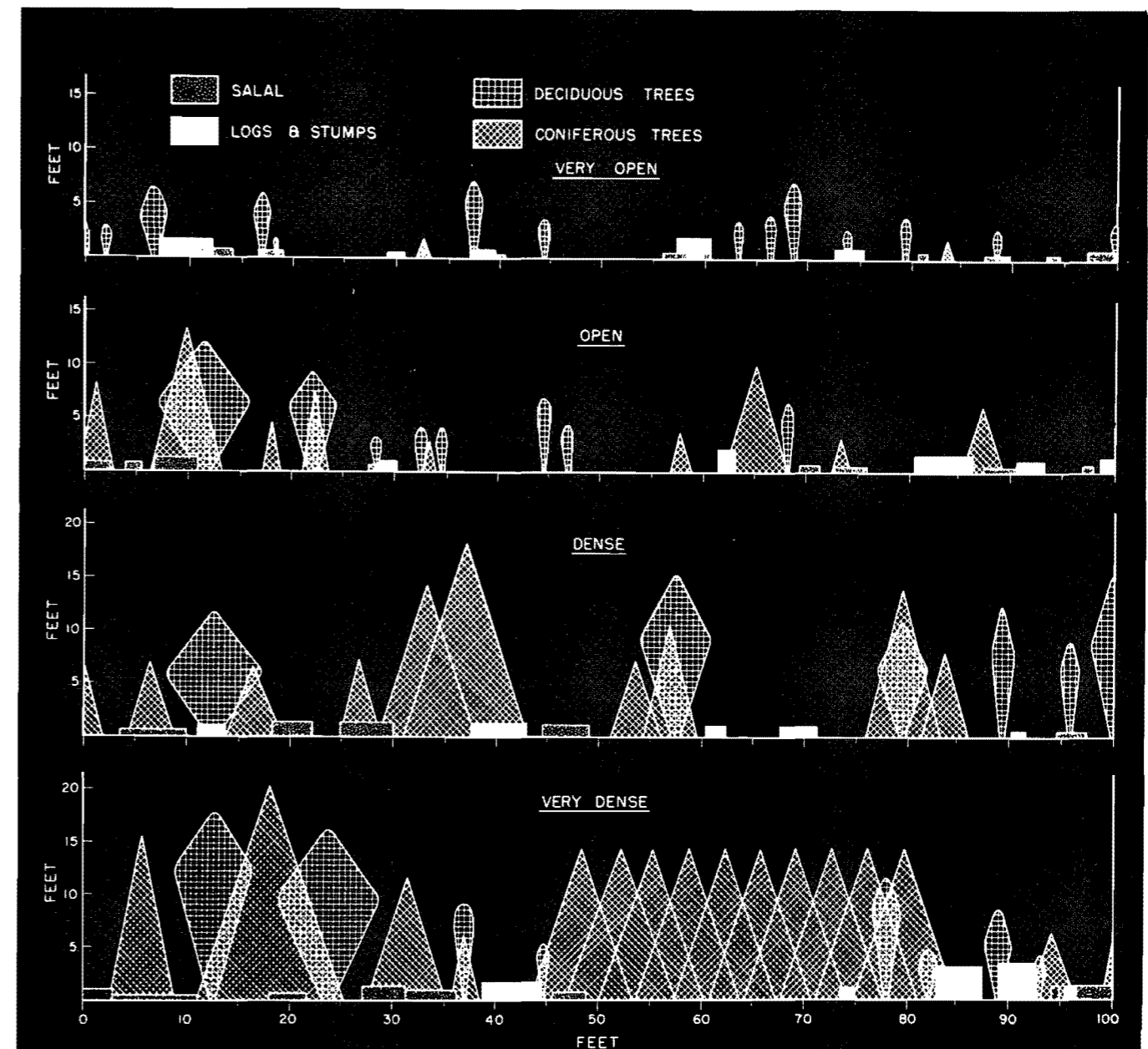
and the position, height, and extent of major elements of habitat were noted from the tape in feet and inches. A yard quadrat was placed on the ground at every 20 feet on the tape, and the amount of ground covered by each element of cover within the quadrat was estimated in per cent. The line intercepts were placed at regular intervals along three lines across a plot. One line was in the centre of a plot, the other two were 400 feet to either side of it. Generally, every other 100 feet of line was sampled. Sample lines that fell in wetland were discarded.

The results from the lines and quadrats were averaged to give a quantitative description of the types of cover on each plot. To further illustrate the habitats, a line intercept was selected that was most like the average for a plot, and measurements from the line were used to make a profile of cover.

2 Middle Quinsam Lake, March 1961, showing in the foreground open vegetation and in the background very dense and very open types. A main reference plot was located in the foreground, and removal plots were on the hill.



3 (a-d) The four types of habitat recognized at Middle Quinsam Lake, 1962: (a) very open, (b) open, (c) dense, and (d) very dense. Each large section of the stick is 1 foot.



4 Profiles of the types of habitat at Middle Quinsam Lake, 1962: very open, open, dense, and very dense.

TABLE 1a Major elements of cover and the average percentage of ground covered by them in the four types of habitat at Middle Quinsam Lake, 1962, as measured by line-intercept

Density of cover	Very open	Open	Dense	Very dense
Number of line-intercepts	13	13	13	11
Coniferous trees	2.0	28.0	45.0	75.0
Deciduous trees	13.0	16.0	26.0	24.0
Logs and stumps	14.0	11.0	25.0	15.0
Salal (<i>Gaultheria shallon</i>)	11.0	15.0	22.0	31.0
Bracken fern	16.0	29.0	15.0	5.0

Note: The lines under the values join those taken arbitrarily as similar and separate those regarded as different. The amount of cover in a habitat may be greater or less than 100 per cent because elements of cover were measured separately.

TABLE 1b Major elements of cover and the average percentage of ground covered by them in the four types of habitat at Middle Quinsam Lake, 1962, as measured by quadrat

Density of cover	Very open	Open	Dense	Very dense
Number of quadrats	71	63	68	60
Herbs	21.0	20.0	36.0	44.0
Duff	68.0	73.0	81.0	83.0
Bare soil and rock	24.0	17.0	3.0	5.0

Table 1 gives the results from the line intercepts and quadrats. Figure 4 presents a typical profile for each type of vegetation. Since bracken fern (*Pteridium aquilinum*) was not available to the grouse until June, several months after their arrival, it was

not included in the profiles. Figure 4 therefore represents cover in spring.

The amount of ground cover provided by trees, salal, logs, and stumps ranged from approximately 40 per cent in very open habitat to 60 per cent in open, 80 per cent in dense, and approximately 100 per cent in very dense habitat. Logs and stumps were important elements of cover throughout the study areas. The range in density of vegetation was such that whereas a person could walk without touching branches and with virtually unobstructed vision in the very open type, in the very dense type visibility was restricted and branches frequently blocked progress. The amount of bare ground in the open types contributed to the ease of travel through them.

At Middle Quinsam Lake, the density of coniferous trees was the main aspect of cover that determined each of our habitat types. In descending order of importance, the trees were Douglas-fir, western hemlock, and western red cedar. In dense vegetation, Douglas-fir was least important. The most conspicuous deciduous trees in all types of cover were willow (mostly *Salix sitchensis*) and alder (*Alnus rubra*). Salal was everywhere on the burns and thickest in the dense types of cover.

Bracken fern was also widely distributed, growing most thickly in the open types and sparsely in the dense vegetation. It grew from a foot to 4 feet in height and added cover wherever it occurred.

The term herb was given to a number of small and common plants on the burns. These included, in order of descending importance, trailing blackberry (*Rubus ursinus*), mosses (mainly *Polystichum munitum*), lichens (mainly *Peltigera aphthosa*), hare's ear (*Hypochoeris radicata*), pearly everlasting (*Anaphalis margaritacea*), white hawkweed (*Hieracium albiflorum*), and Oregon grape (*Mahonia nervosa*). As might be expected, the amount of duff or litter on the ground increased with increased density of vegetation. As the amount of litter increased, the amount of rock and bare soil decreased through the types of cover.

The very open habitat was in near natural plant succession after a burn. It is noteworthy that 11 years after fire, approximately 25 per cent of the ground was still in bare soil and rock.

The vegetation of the study areas changed over the time of field work. A measure of this is given by a comparison of very open and open habitat in Table 1. The amount of cover from all sources in the two types is about the same with the exception of Douglas-fir. The very open habitat was planted

in 1958, the open in 1954. Thus, in 4 years, the growth of fir increased the amount of cover from coniferous trees from negligible to nearly 30 per cent. When the study began in 1959 at Middle Quinsam Lake, all open areas were of the very open type. By 1961, the two types of open were identified. The amount of coverage by vegetation in areas of dense type also increased over the period of study but not as quickly as in the open area.

The topography of the study area at Middle Quinsam Lake is flat to gently rolling. The main reference plots (Fig. 1) were on more or less level land. The removal and adjacent reference plots were on the shoulder and top of a hill. Figure 2 shows the hill with the relatively flat land of a main reference plot in the foreground. The hill began approximately on the north boundary of the removal plots, rose about 150 feet, and then sloped gently to the east, west, and south. The old logging road that enters the northwest corner of a removal plot in Figure 1 follows the shoulder of the hill.

The types of cover at Lower Quinsam Lake and their use by blue grouse are described by Bendell (1954). As might be expected from the proximity of Middle and Lower Quinsam Lakes and their comparable history of land use, the types of habitat described for one area were found on the other. Types of cover described at Lower Quinsam Lake and their equivalents at Middle Quinsam are as follows: log open = very open, fir open = open, and fir dense = very dense. There were no important features of topography on the study plots at Lower Quinsam Lake.

The behaviour of grouse on the breeding range

Migration

The migratory behaviour of blue grouse causes a seasonal ebb and flow in their numbers on the breeding range. Time of arrival, peak build-up of numbers, and departure delimit the period of breeding activity and provide a natural time scale for working with grouse. Changes in numbers throughout the year may be related to processes of population regulation.

Anthony (1903) suggests that the females arrive on the summer range after the males. Until recently, we were not in the field early enough to record the arrival of grouse. In 1960, S. Teeple and J. Loyns began work on March 13. Between March 13 and 19, they cruised the area at Middle Quinsam Lake for 31 hours without finding signs of grouse. In the period March 20 to 26, during 39 hours searching, they observed 16 silent males. The first females were discovered between March 27 and April 2. In this time, 43 hours searching produced 2 hooting and 12 silent males, and 2 females. These data suggest that the first grouse on the breeding range were males and that in 1960 they arrived between March 20 and 26. The first females arrived approximately a week later. Some males were on the breeding range for approximately a week before beginning to hoot.

Incomplete data obtained in March and April 1951, 1952, and 1962 correspond with the pattern of arrival of grouse noted in 1960. At Lower Quinsam Lake, 8 hours in the field on March 6, 1951, yielded a silent male. On April 13 of 1952, this area was populated by breeding grouse of both sexes. At Middle Quinsam Lake in 1962, the general study area was searched in March and April. Between March 24 and 28, for 38 hours of search, the tally was one silent male. In the period April 15 to 18, for 25 hours abroad, we saw 1 hooting and 15 silent males, and 6 females. Again, most early males arrived before the females and were silent. The arrival of grouse in 1962 seemed later than in 1960. The observations from Lower Quinsam Lake also suggest that time of arrival may vary from year to year.

We have few data on the behaviour of males on arrival on the breeding range because relatively little time was spent in the field in March and April. In 1960, however, the main reference plots at Middle Quinsam Lake were searched thoroughly before and while males arrived on them.

Most males when first observed were on their

territories of the previous year. They were noted as follows: March 21, two silent banded males; April 11, one hooting male; April 14, one silent banded male; and April 20, 24, and 25, a hooting banded male on each date. The last male to arrive on the plots was first observed as a hooter on territory on April 26. These males were observed on their territories from time of arrival to departure. Thus, breeding males appear to migrate directly to their territories in spring. The time of arrival and early silent behaviour of the males on the main reference plots fit data already noted and the data to be presented shortly from observations over the whole breeding range.

Males stay on their territories through the spring and appear to move directly to winter range at the end of the summer. We banded 121 hooting males, most in May and June. Ninety, or 74 per cent, were observed in a subsequent year and all were virtually at the same point where banded. Most males banded as hooting or territorial males, if seen again, were within areas that could be considered their territories. Of nine silent adults banded in April, May, and June, six (67 per cent) were observed on territory at the point of banding in a subsequent year. Compared to this, of eight silent adults banded in July and August, and presumably migrants, only one (13 per cent) was observed again. These data suggest that territorial males remain on their territories until the end of their breeding activity and then move directly to the winter range.

Several records tend to contradict our conclusion that males come and go directly from their territories. On April 20, a banded male was observed for the first time on a study plot. He was hooting 675 feet from his territory of the previous year and on the territory of another banded male. On April 22, a fight was observed between the banded male and the owner of the territory. The banded male was chased away and over the rest of the spring and summer hooted from the area he had occupied the previous year. The second record was a banded male observed on April 26. This male was silent and 1,700 feet from his territory of the year before. Later in the year, the male was relocated frequently on his original area.

A few males were observed off their territories in late summer prior to departure from the breeding range. One banded male was observed 250 feet and later 1,200 feet from its territory after it had stopped hooting. A second silent banded male was noted in August, 500 feet from its territory. This male showed no reaction to two females that were sitting

TABLE 2 Build-up and departure of grouse from the breeding range at Middle Quinsam Lake, March through August 1960

Period	Hours of search*	Hooting males per hour	Silent males per hour	Lone females per hour	Females with brood per hour
March 12-April 2	58	.017	.35	.00	.00
April 3-16	54	.15	.24	.15	.00
April 17-30	48	.56	.15	.15	.00
May 1-14	78	.81	.17	.17	.00
May 15-28	35	.66	.086	.23	.00
May 29-June 11	50	.60	.24	.24	.020
June 12-25	87	.32	.25	.069	.10
June 26-July 9	116	.16	.086	.095	.14
July 10-23	112	.12	.11	.063	.17
July 24-Aug. 6	51	.059	.059	.059	.18
Aug. 7-20	80	.00	.025	.038	.28
Aug. 21-Sept. 3	83	.00	.00	.00	.29

*Men searching singly and without dogs in open cover.

nearby. However, another male observed off territory in July began to hoot and court when it met a hen. However, compared to these three, about 75 other banded cocks simply disappeared when they ceased hooting. This supports the contention that most males migrate directly to and from their territories.

The silence of males upon arrival deserves further comment. In late March and early April males on the burns are residents or perhaps migrants. It seems likely that migrants move quickly through the area. It appears that most resident males remain silent for about a week after arrival on territory. Hooting apparently begins with the appearance of the females, which suggests that their arrival is related to the beginning of song.

The rise and decline of numbers of grouse over the spring and summer are shown by the number of birds observed per hour for successive periods of search. Data to illustrate the build-up and departure of grouse from the area at Middle Quinsam Lake are presented in Table 2.

Table 2 shows that for the period March 12 to April 2 males outnumbered females on the breeding range. Most males observed were silent. From March 12 to May 14 the numbers of "hooters" and females increased, and, as would be expected, the number of males observed as silent decreased. By May 1-14, hooting males had reached peak abundance and this appeared to coincide with the levelling off in the number of hens. Thus, the build-up of the population of breeding males and females appeared completed in the period May 1-14.

In May, there was a decline in the number of hooting males observed per hour and this continued

through June. During the same period, the number of silent males observed remained approximately the same. Doubtless, some males abandoned territory in May and June, as noted at Lower Quinsam Lake (Bendell, 1955a). However, the fact that numbers of silent males did not diminish suggests that the main cause of the decline in hooting males was a reduction in the frequency of hooting rather than a disappearance of males from the summer range. Thus, while breeding males may be reduced slightly in abundance through April, May, and June, during this time the frequency of hooting is reduced.

Table 2 also shows the departure of males from the breeding range. In July, the numbers of both hooting and silent males observed per hour decreased. While hooting activity was again reduced in this time, the drop in silent males indicates that males had abandoned territory and left the summer range. A comparison between hooters observed per hour in the period June 12-25 and July 10-23 suggests that during July only about 37 per cent (.12/.32) of the hooting males remained on the breeding range. By August, hooting or silent males were seldom encountered as most had migrated.

The departure of the females from the breeding range is related to their success or failure in hatching and rearing a brood. The data in Table 2 indicate an apparent decreased abundance of hens in late May and June. This is because some hens were attending to nests and later to broods and therefore were not sampled as lone females on the study area. The further drop in the relative abundance of lone hens after the period July 24 - August 6 likely represents their departure from the breeding range.

Hence broodless hens appear to leave the summer range before hens with brood.

Hens with brood were observed in the period May 29 - June 11. Numbers observed per hour built up steadily to August 7-20. This trend is explained by the completion of the hatch and the increasing ease with which growing chicks are located. There was no indication in 1960 that hens with brood left their summer range before the end of August. Earlier migration was reported in 1 year in 3 (Bendell, 1955a).

Note that the numbers of males and females build up and decline in a fairly regular way over the spring and summer. There is no suggestion of a sudden dispersal and drop in numbers such as shown by Jenkins *et al.* (1963) for red grouse. We will return to this kind of consideration later.

In summary, in 1960, the first males arrived on the breeding range at Middle Quinsam Lake in the second half of March. The first females arrived about a week later than the males. Some cocks were on the summer range approximately 1 week before hooting was heard. The build-up in numbers of both sexes was completed by the first half of May. Numbers of males were maintained until July, and of lone females through July. By August most males and lone females had left the summer range. Hens with broods did not migrate until after August. The greater part of breeding activity apparently occurred between the middle of April and the end of June, with peak activity in the period May 1-14. There was no suggestion of a sudden dispersal of grouse from the study area. These results are comparable to those of other years at Middle Quinsam Lake and to published data from Lower Quinsam Lake (Bendell, 1955a).

Behaviour of the breeding male

The few large trees on our study areas in recent burns provided little opportunity for grouse to leave the ground. Virtually all the activities of grouse were on the ground or as part of low flights. This means that the space used was that of area rather than volume.

On the summer range, adult and a few yearling males establish territories. Territorial behaviour is taken as an indication of a breeding male and consists of an auditory display (hooting and wing fluttering), separation from adjacent breeding males, and restriction of movement to a relatively small area. On their territories, males court females and fight with or chase away intruding males. Routine activities of the territorial male, such as feeding, dusting, and sleeping, are carried out on their

territories.

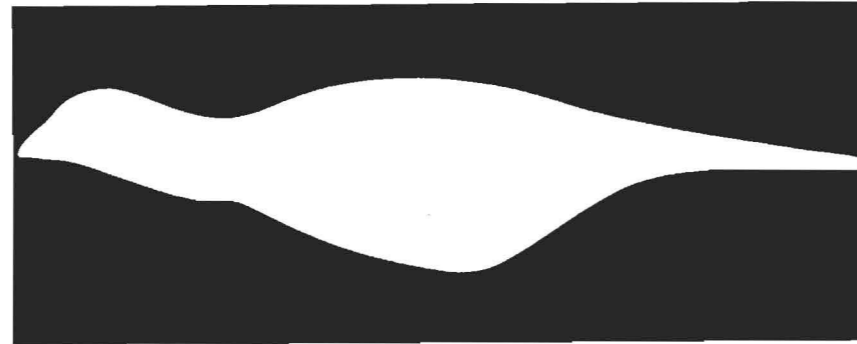
Territorial males were located most frequently by their hooting. We have noted already how the frequency of hooting changes over the spring and summer. The call or hoot of the Vancouver Island grouse is a series of hollow, low-pitched hoots usually given in six phrases, with an emphasis on the first and an inflexion on the fifth. Each complete song takes from 3 to 4 seconds. Stirling (1965) shows a sound spectograph of the call. The number of songs per minute varies from two to four in steady hooting to as many as six at times of sexual excitement when the song also gains in volume. When beginning to hoot, males do not give the full song. Several of the initial phrases occur, then a pause, and a repetition of the initial phrases of the call. After four or five of these attempts the full song is given and continued thereafter.

The distance that hooting can be heard is difficult to measure. The carrying power of the sound is affected by topography, vegetation, wind, and the loudness of the song. At times, males were accurately located by their hooting at 500 feet. Some were heard at 1,500 feet, and others, producing a subdued song, were inaudible beyond 100 feet.

When hooting, males assume a typical stance (Fig. 5b). The oesophagus appears inflated and the head is tilted down near or upon the swollen neck. Each phrase of the song begins with a constriction of the body which probably forces air through the syrinx to cause the sound. There is no display of body parts or plumage in routine hooting. However, males were frequently observed to hoot while in full courting display.

While males frequent particular hooting stations they also call from many other positions on their territories. Hooting stations were usually located on an elevation in the ground and males called from within or beside the cover supplied by a log, shrub, or coniferous tree. A hooting station on a log in open cover is illustrated in Figure 5c.

It is unusual for males to call alone. Generally, groups of two to eight or more adjacent males hooted at the same time. One group of males might be vocal while a remote group was silent. Frequently, adjacent males were observed hooting. When one was disturbed and silenced, the others stopped calling as well. When one resumed song, the others began to hoot again. At times, males appeared to move to hooting stations that placed them close to an adjacent hooting male. Thus, a male hooted from one part of its territory with one neighbour and moved to another part closer to an



5 (a-e) Territorial behaviour of the male: (a) male in alert posture (by H. Laing); (b) adult hooting (by H. Laing); (c) a hooting station in open vegetation (the male hooted from the crevice in the log at the marker stick); (d) full courting display before a female (by F. Zwickel); and (e) threat posture.

active neighbour when the first was silent. These observations show that the hooting of males influences the hooting and movements of others.

Besides hooting, territorial males display by a loud flutter of their wings. This sounds like a ripping noise and is apparently given by a short and rapid beat of the wings. It cannot be explained as purely the sound of flight, for at times grouse fly and land silently. The flutter flight or wing rip is not peculiar to sex because hens may make a similar sound on take-off, in flight, and when landing. This sound, like hooting, was most frequently heard in spring. Males on territory were observed to make flutter flights when in pursuit of and landing close to hens, when landing after a chase of another male, and when flushed by an observer. Once a silent male made the sound while on the ground and under a small tree. The sounds of wing flutter excited territorial males and they moved toward them, at times in full display. The flutter flight of the *fuliginosus* or sooty form of blue grouse seems similar to but not as elaborate as the fluttering and tumbling flight described for *D.o. pallidus* or dusky blue grouse by Blackford (1958, 1963), Wing (1946), and others.

Both hooting and wing fluttering probably warn other males and attract females. The reverse may be the case in the calling and flutter flight of the female. The calls of females will be discussed later. It is noteworthy that both activities appear to be most frequent close to the time of year of peak sexual development of the male (Simard, 1964, and Table 2). Frequently, males stopped hooting when females appeared on their territories. In a few cases, males reacted antagonistically to hooting from one of us. These data, and the demonstration of the function of song in other species (Armstrong, 1963), indicate that vocal display may attract one bird to another and at times keep birds of the same sex apart. We show in Bendell and Elliott (1966) and will present other evidence later that hooting males attract males and females to their territories.

Females are courted vigorously by the males when they appear on their territories. All females observed with territorial males were courted by them. This included incubating females and hens with young. Individually banded females were observed on the territories of two or more males in spring. Males were observed to court up to six females in succession as they appeared on their territories. We conclude that males are promiscuous and females are likely the same.

The courting display of the male involves skin

and plumage, sound, and movement. A grouse landing with a wing flutter on the territory of a male usually causes the resident to hoot and move toward the sound in partial courting display. Males may fly and land with a wing flutter beside an intruder or move toward it on the ground.

Males in full courting display are a sight to see. The display occurs on the ground and turns the inconspicuous dark colours of a male into patterns of black, white, and orange. In full courting display (Fig. 5d) the oesophagus is inflated and feathers on each side of the neck are opened to expose the bare skin. This skin in spring is thickened, deeply wrinkled, and coloured an egg-yolk yellow. The surrounding feathers are white at the base with black tips. The total effect is that of two fried eggs—one on each side of the neck behind and under the bill. The bare skin over the eye enlarges, rises, and becomes lemon yellow in colour or sometimes a livid red. The tail is spread and held slightly over the back while the wings are dropped at the sides. As the male approaches the female his vent puckers and dilates. When 2 to 20 feet from the hen, he drops his wings and swoops toward her with stiff legs, rapid short steps, and outer primaries dragging and rustling on the ground. This movement is made in a slight arc so that the cock approaches from one side. In the approach, the head and neck are held broadside to the hen and the tail slightly askew. The head and neck are held so that they are framed against the background of the black tail. At the termination of the rush and almost touching the female the male dips his head and gives a loud "whoot"—a shorter and higher pitched call than the phrases of the song. At times, the call is almost instantly followed by a squeal which seems to be the sucking of air after the expiration of the courting note. If the female remains still, the cock postures beside her, raising and lowering its body and jerking its head so that a neck pouch and an eye crest are presented fully and in motion to the female. The posturing may last from 2 to 3 minutes and then gradually the male moves behind the female and begins to climb upon her back. In the field, all observed encounters ended at this point as the female walked or flew away. When this happened, the male made another sweeping advance, or, when the hen disappeared began to hoot. In the aviary, receptive hens squat. The male climbs upon the back of the hen, grasps the back of her head with his beak and holds her body between his wings. The female shifts her tail to one side and everts her vagina through the vent. The copulatory papillae

of the male protrude from the vent and are applied to the vagina of the female (Stirling, 1965).

The function of the whole or various parts of the display to the hen are unknown. Presumably it elicits an appropriate response from the receptive female. As discussed later, males react strongly to a recorded precopulatory call of a hen by hooting or hooting more loudly and assuming the courting display. This is explained by the view that hooting attracts hens from afar while the courting display provides recognition over a shorter distance. If display is a necessary prelude to copulation then a male would require time and undisputed use of an area to attract a female and copulate successfully with her. As will be discussed later, the main function of territorial behaviour in the blue grouse seems to be to provide this undisputed space for mating.

The "whoop" or courting call is heard only when a male is with a female. The sound carries well and often serves to reveal the position of a male and female at some distance in the bush. The call causes nearby males to hoot or to hoot more vigorously and to draw as close to the courting male as the extent of their territories permits.

When males are observed together in spring, antagonism is usually shown between them. The encounters between males may be described as of three kinds: rush and flight, threat and flight, and fighting. Rush and flight was the most frequently observed kind of encounter and occurred when yearling or adult males appeared within the territories of other males. The resident male might move toward the intruder in partial courting display. This is quickly replaced by a threat posture wherein the head and tail are depressed in a line with the back (Fig. 5e). In threat posture, all feathers of the bird are pressed tightly to the body. The threatening male then rushes at the intruder who quickly takes flight. Yearling males while moving over their home ranges at times trespassed on the territories of breeding males. Some adult males became trespassers when they flew after hens beyond the boundaries of their own areas, and before establishing or after leaving their territories.

At times, an intruding male holds its ground in a motionless standing position. Then the resident male approaches steadily in threat posture, and when within a few feet from the intruder emits a series of sounds which we identify as the threat call or rattle. The call sounds like the growl of a dog, but is given in short, staccato phrases. This is illustrated by a sound spectrograph in Stirling

(1965). While calling, the resident male paces in a 4- or 5-foot oval in front of or beside the intruder. After 1 to 3 minutes, the pacing male rushes at the other, who then takes flight.

The actual fighting of blue grouse is mentioned in the literature but is poorly described as compared to other elements of display. In fighting, both males pace in threat posture in tight ovals and give threat calls. They stop periodically and face each other with upstretched necks. They then return to threat posture and pacing. Suddenly they engage with vigorous pecking, buffeting of wings, and downward slashing of feet. The birds may break and resume pacing and threatening. It seems that one bird tries to get above the other on the surrounding ground and from this position another engagement results. Only two complete fights were observed. In one lasting 5 minutes, one bird suddenly broke away, was pursued about 15 feet, and disappeared; the victor then withdrew approximately 100 feet and began to hoot. In the second fight, the contact lasted about 25 minutes with about 1 minute of actual fighting. The encounter ended when the two pacing birds became separated by a mound of earth and vegetation. Each then withdrew toward the centre of its territory.

Fighting doubtless influences the dispersion or spacing of males. Ten fights were observed on study plots where it was possible to relate the position of the flight to the boundaries of the territories of the participants. In all cases, the fights occurred on the boundary between neighbours. Trespassing males are chased from within the territory of an established male. An example of this involving banded birds has already been given.

While blue grouse may threaten and fight when in contact, such behaviour seems relatively infrequent on the breeding range. Moreover, breeding males, as will be seen, spend relatively little time near the boundaries of their areas and are found most frequently at hooting posts within the territory. This suggests that hooting and other auditory display alone may separate males. Moreover, blue grouse probably come to know and accept a particular neighbour, as do ovenbirds (*Seiurus aurocapillus*) (Stenger Weeden and Falls, 1959). Blue grouse are long lived, and a few fights, if any, may serve to space the birds for a number of breeding seasons.

Males were frequently found on their territories when they were silent, or active in an inconspicuous way. Such males were resting, feeding, or dusting. These activities were carried out in places close to

where they displayed. As noted, territorial males appear to remain on their territories between time of arrival in spring and departure in midsummer.

The activities of grouse on the breeding range follow well-marked diurnal and seasonal rhythms. There is a peak of activity just before sunrise and another just after sunset each day (Bendell, 1955a). In the seasonal rhythm, grouse appear on the range, rapidly build up to a peak in abundance, then gradually disappear as they leave the summer range. The sounds of grouse are heard most frequently in April and May, become less frequent during June, and then cease in July and August. The wing flutter, fighting and threat calls, the calls of hens, and the single "whoop" of a male with a hen are heard most often in April and May. While hooting is heard from April to August, it is most frequent in April and May. This sequence suggests that hooting, wing flutter, threat, fighting, and courting are associated with the early phases of establishment of territory while hooting is the main method of display during occupancy.

The activities of males that make them conspicuous are clearly related to the breeding season and their stay on the breeding range. The peak of display of males and their migrations correlate with the development and regression of secondary sexual characteristics, and of the testes, as measured by their change in size and function over the spring and summer (Bendell, 1955a; Simard, 1964). All territorial males observed with females showed attempts to copulate, and all sampled showed good production of sperm (Simard, 1964). From these data it seems most likely that all territorial males were potentially breeding members of the population on the summer range.

Territories of breeding males

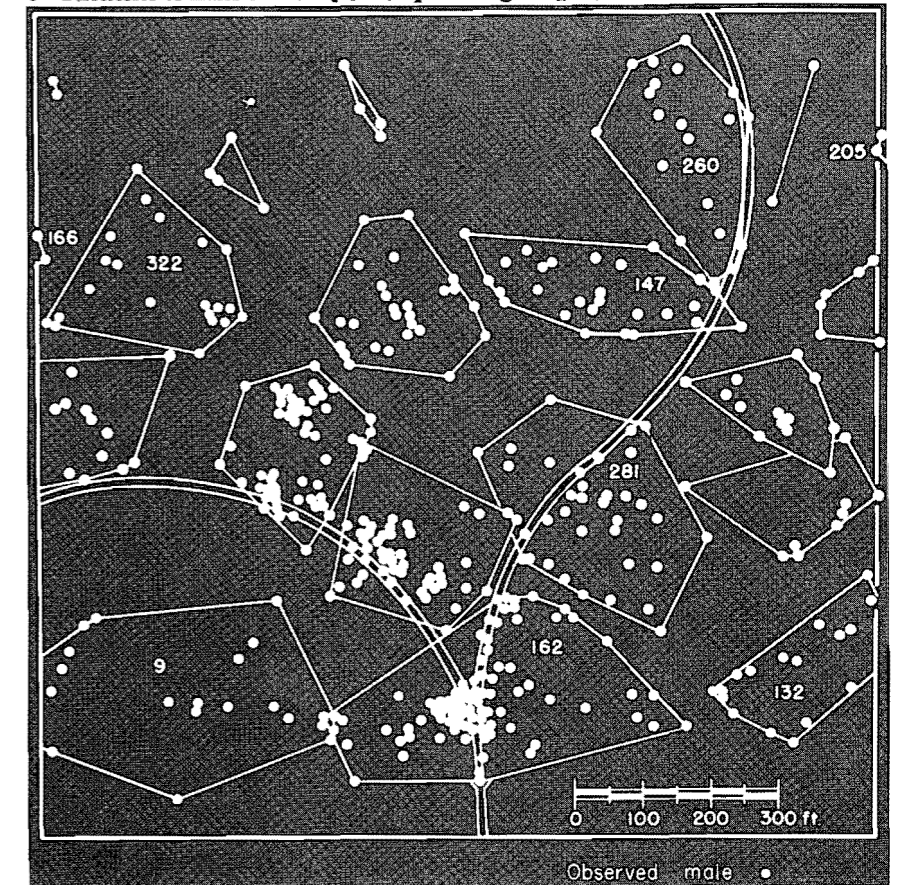
The purpose of this and following sections is to describe the territories of males and examine them in relation to density of population and cover. To describe territories, points of observation of hooting males on the study plots were mapped. Figure 6 illustrates the April to August distribution of 20 hooting males on a study plot of 36 acres at Lower Quinsam Lake in 1952. The density of these grouse, 0.55 per acre, is astonishing. Virtually all observations were of marked or banded males. The vegetation of the study plot was mostly open. Part of a bridge and two old logging grades occurred within the plot and are shown in the figure.

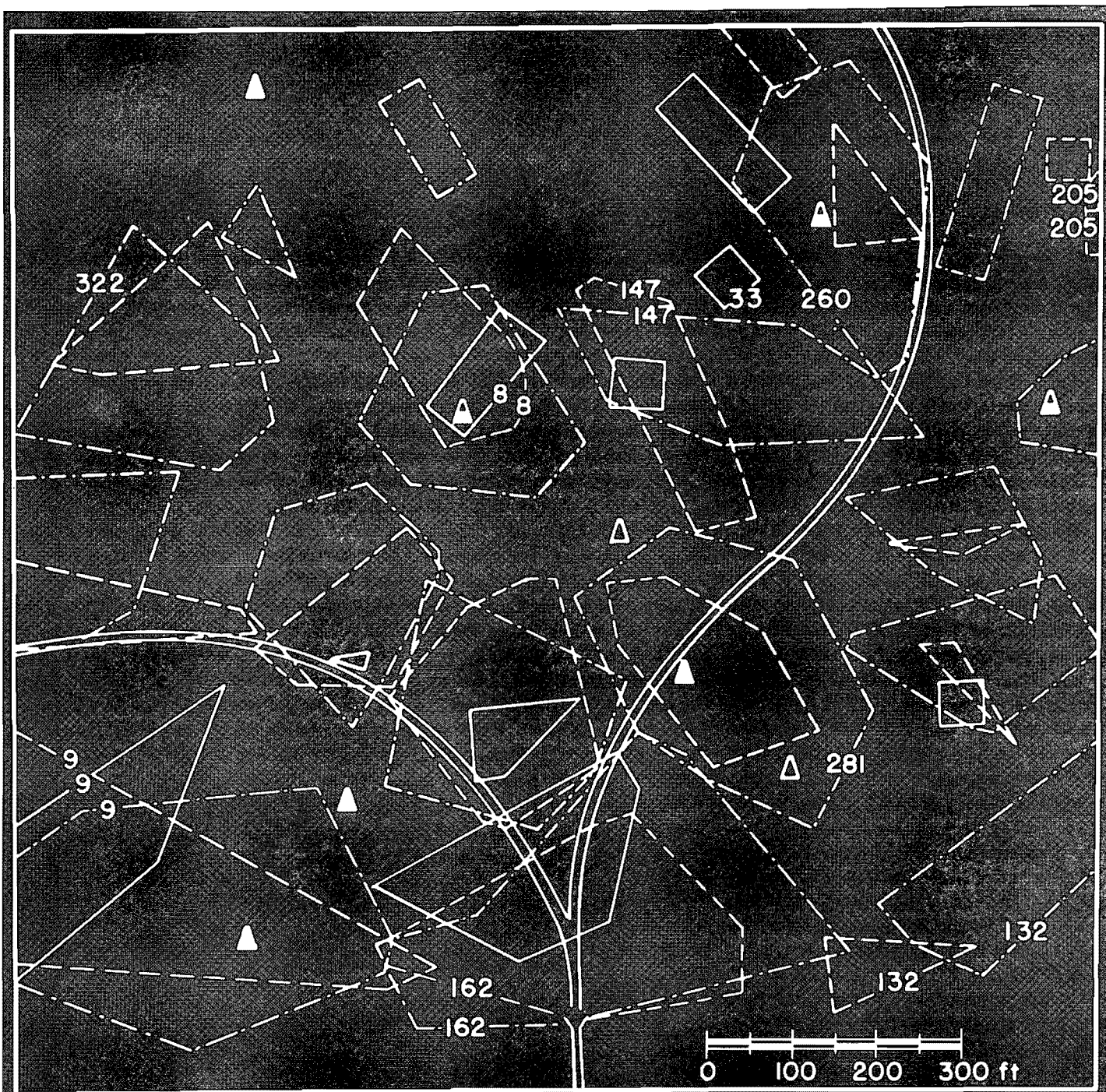
Note in Figure 6 that observations of each male are referable to an area where it displayed alone, or its territory. These were delimited by joining the

outermost points of observation of each male with a straight line. The method likely oversimplifies and enlarges the actual space within a territory recognized by a male. Despite this and the high density of males, there was little overlap of territories. Where there were many data on a bird, as on male No. 162, points of observation tended to cluster about a hooting post. When few data were obtained on a male it was not possible to more than note its position; extent of territory could not be determined. This was the case with four males at the top of Figure 6.

The most obvious manifestations of territorial behaviour were that males displayed and lived on separate areas throughout the breeding season. They also fought over positions and presumably warned others away by vocal display. As will be shown, the movements of hens were not confined to the territories of particular males. Clearly, male blue grouse show territorial behaviour in the accepted sense of persistent display from, and defence of, a restricted

6 Territories of males on a study plot, April through August, Lower Quinsam Lake, 1952.





YEAR	NEST	TERRITORY
1950	▲	—
1951	▲	- - -
1952	△	- · - ·

area. The territorial behaviour of the male sooty grouse is readily classified as the mating and display type described by Nice (1941).

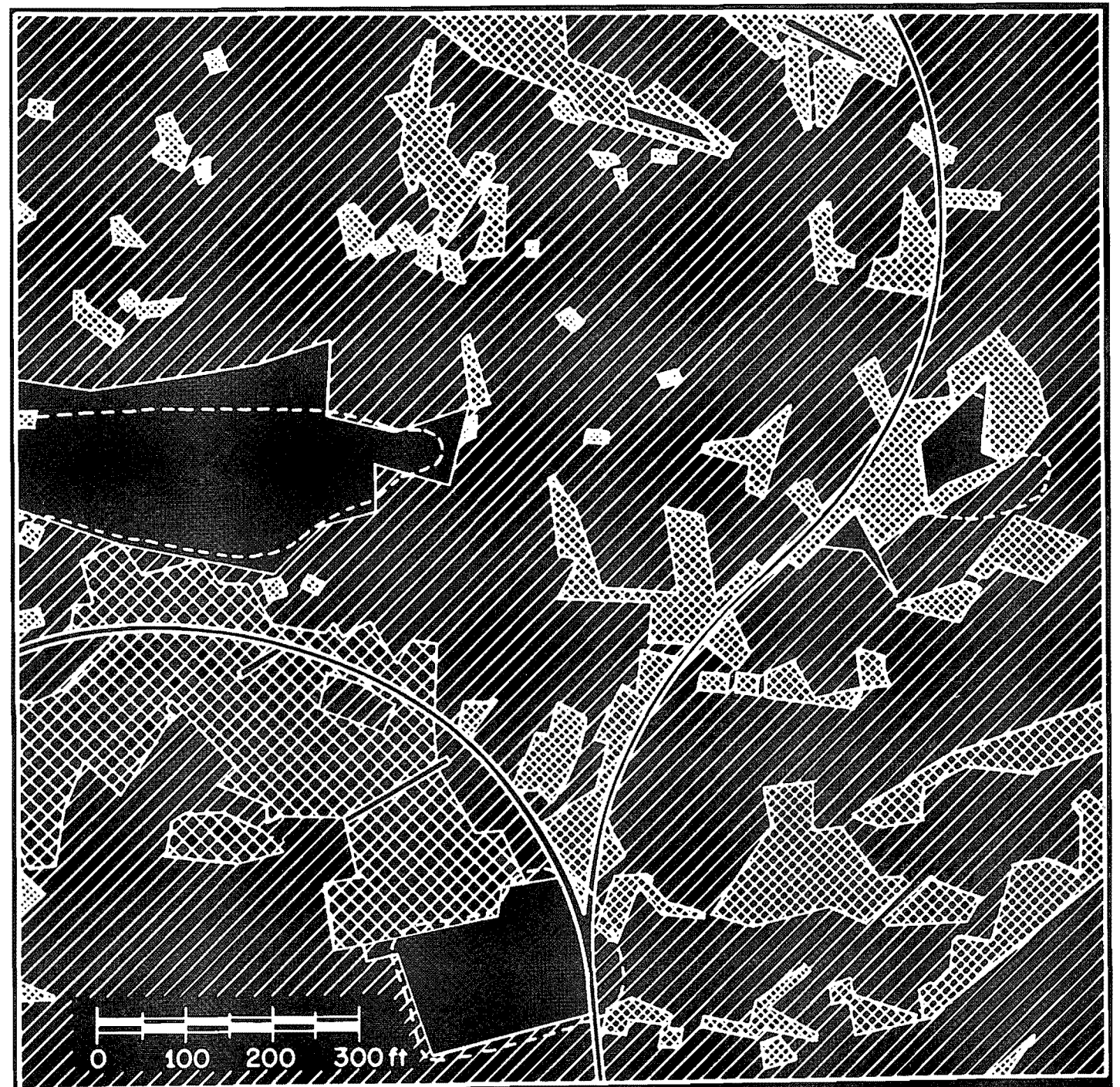
Return to territory in successive years

Once a male establishes a territory it returns to the same area in subsequent years. Thus, male No. 9 (Figs. 6 and 7) was banded on territory in 1950 and was observed on the same territory in 1951, 1952, and 1953. This was true of over 133 hooting males marked in one year, which, if recorded in subse-

quent years, were in their original areas, and in most cases under the same tree, log, or stump where first captured.

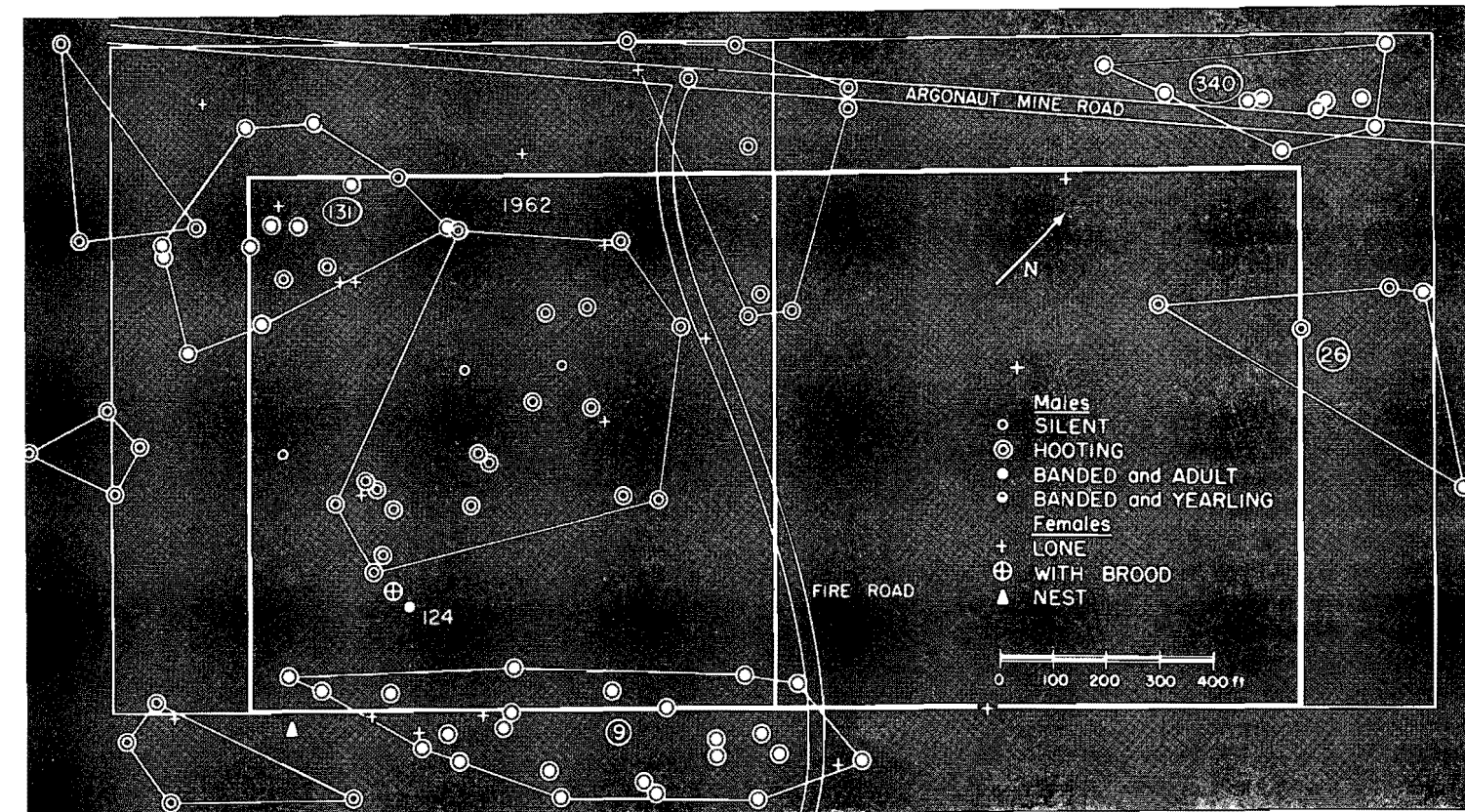
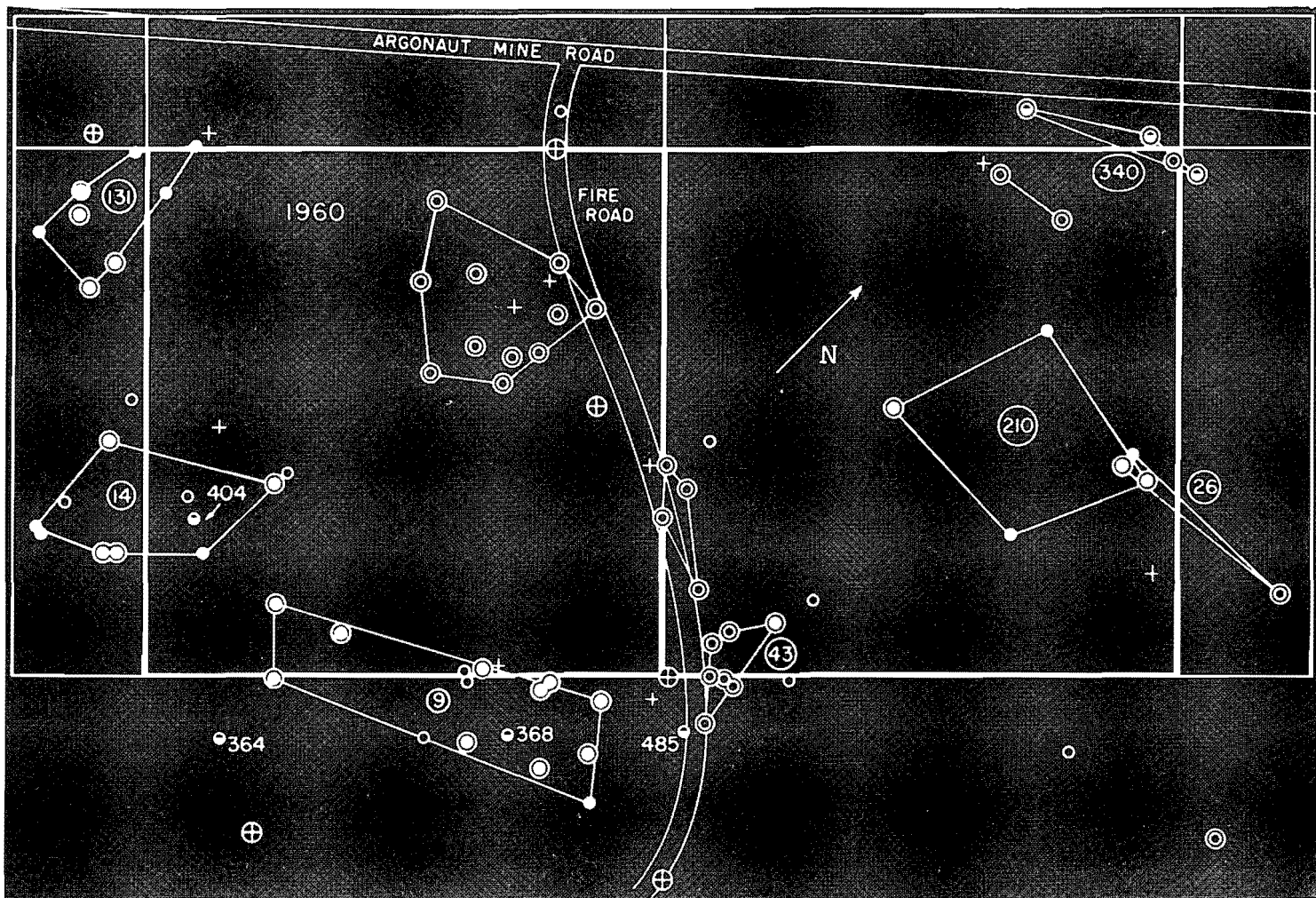
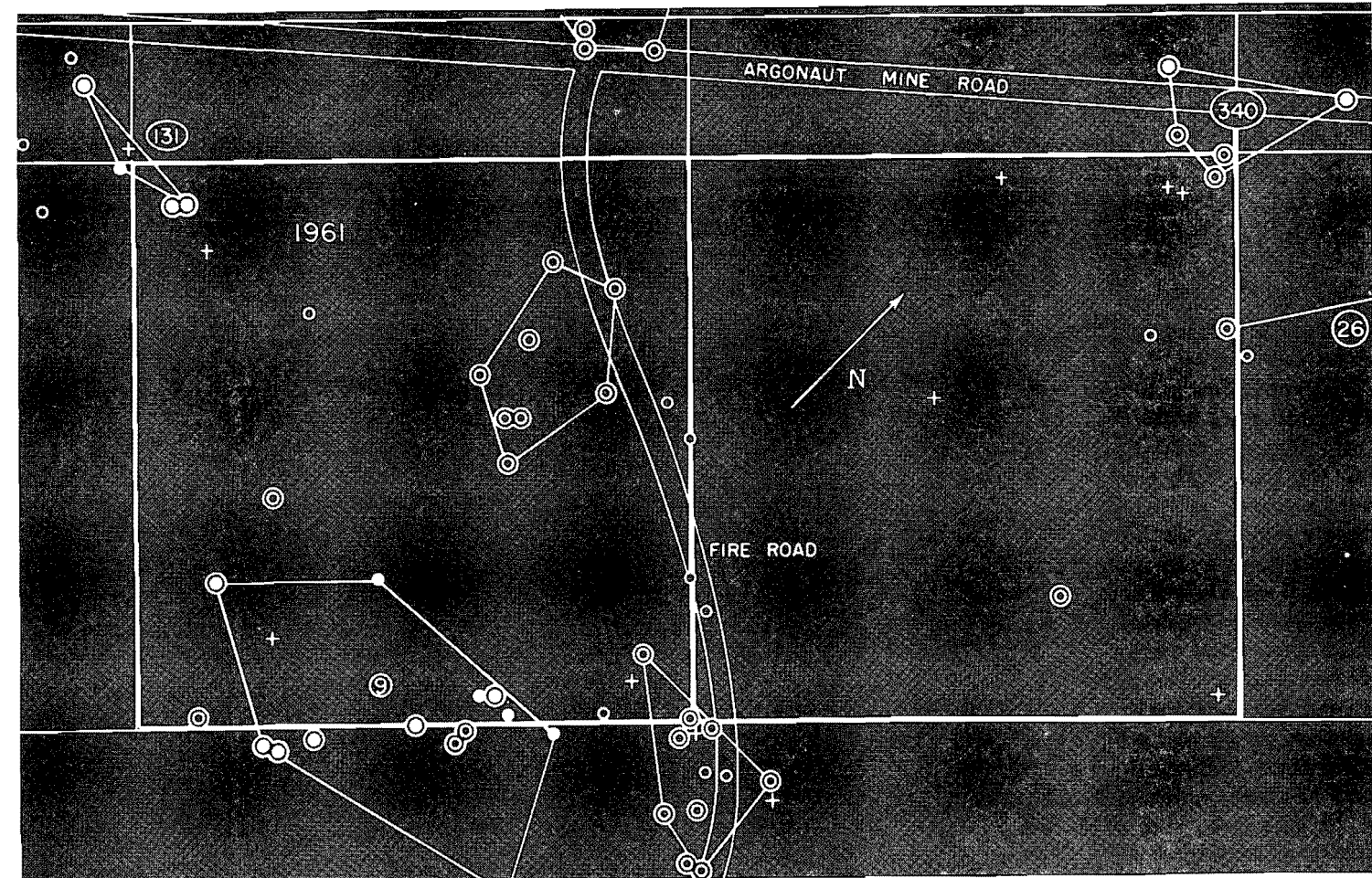
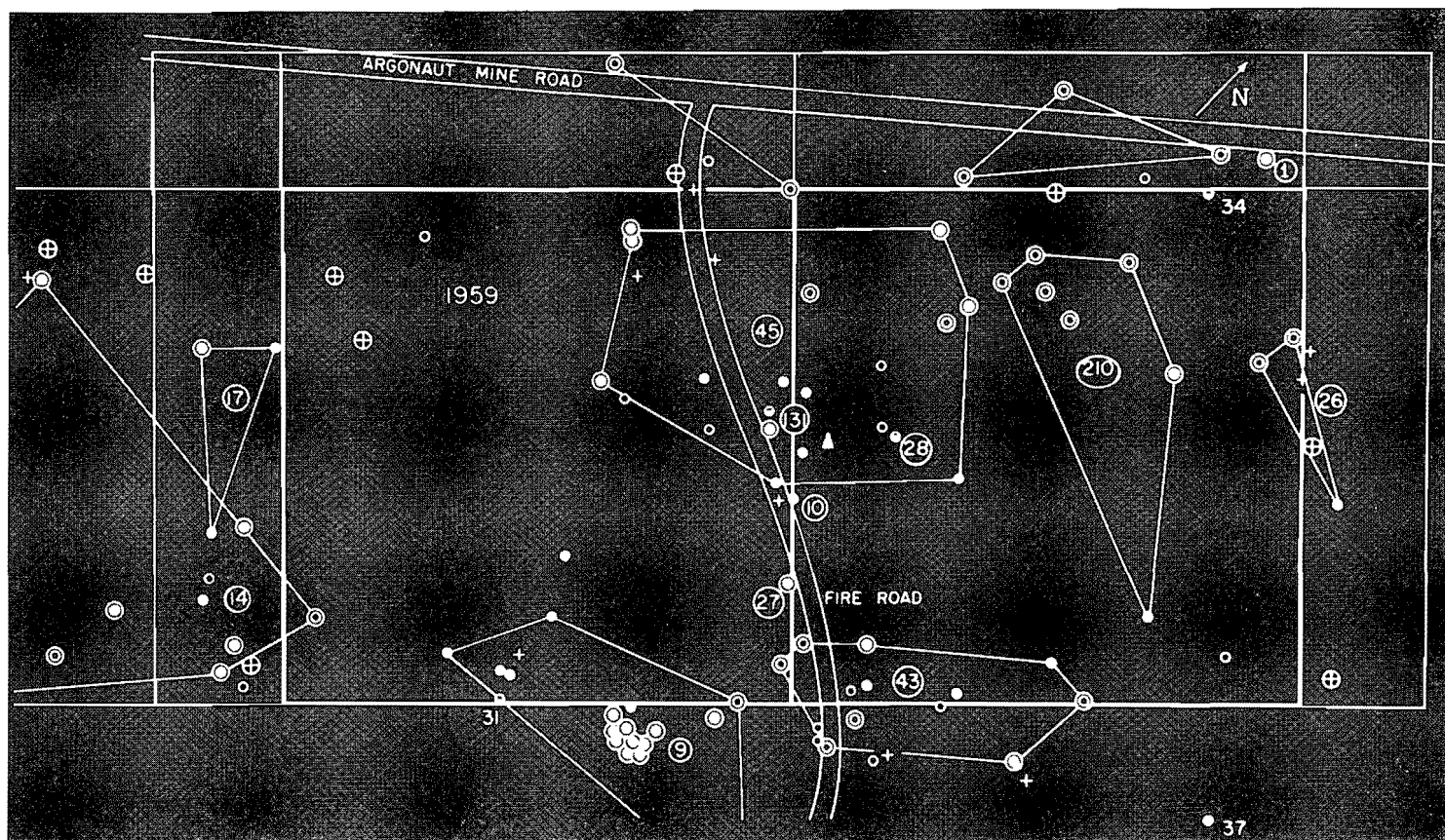
In April and May of 1957, the plot shown in Figures 6 and 7 was searched for males. By this time the vegetation had changed from predominately open to very dense with a few large openings (Fig. 8). Two males that were banded on the plot in 1951 and 1952 were still there and occupied areas included in their territories at time of banding.

7 Territories and locations of nests, 1950 through 1952, Lower Quinsam Lake.



1952		
VERY OPEN	—	▨
OPEN	—	▧
VERY DENSE	—	▩
1957		
OPEN	—	○

8 Distribution of cover on a study plot, 1952 and 1957, Lower Quinsam Lake.



9 (a-d) Territories, yearling males, females, nests, and broods on the main reference plots, Middle Quinsam Lake: (a) 1959, (b) 1960, (c) 1961, and (d) 1962.

These males returned to their territories despite the fact that the forest had grown up around them. A third male, banded outside this plot in the early years, was also found on its original territory.

The same return to territory was observed in males banded at Middle Quinsam Lake from 1959 through 1962. Figure 9 a-d shows the areas occupied by males on the two main reference plots over the

4 years. Banded males utilized the same areas each year until they disappeared. Places of display and rest were also reused.

The return of males to their territories year after year is important in the calculation of the rate of disappearance of males from the breeding population. Males are rarely seen off their territories and then presumably are migrating. In the absence of contrary evidence, we take the failure of a male to appear on territory to mean that it is dead. Thus, the annual death rate of breeding males is measured by the number of banded territorial males which return in successive years.

Relation of territories to vegetation

The distribution of very open, open, and very dense vegetation on the plot at Lower Quinsam Lake in 1952 is shown in Figure 8. Compare the location of males and their territories (Fig. 6) with the cover on the same area. Note that territories frequently included different types of cover, as well as parts of logging roads, and that males hooted from virtually all types of cover on the plot.

Similar observations were made at Middle Quinsam Lake from 1959 through 1962. The locations and territories of males on the two main reference plots are presented in Figure 9 a-d. The plot on the right was in dense vegetation, and the one on the left was in open. Some males ranged across roads and the two types of cover, while others were completely within one kind of habitat. We conclude that the position and extent of territories were not related to the pattern of open and dense vegetation and roads either at Lower Quinsam Lake in 1952 or at Middle Quinsam Lake from 1959 through 1962.

By 1957 at Lower Quinsam Lake, the vegetation and the number of breeding males had changed. Most of the plot was now in very dense cover with three open areas (Fig. 8). In May of 1957, there were three hooting males on the plot. Each territory included one of the open areas, and was separated from the others by approximately 500 feet of very dense cover. Where the cover was very dense with small openings, territories were clearly related to the openings. Hence, the position of territories in dense cover may depend upon the location of openings.

While the position and extent of territories may not relate to the pattern of cover, each territory includes places of importance to grouse as judged by their use and frequency of occurrence. Many hooting sites are on elevations in the ground and elevations may explain the location and extent of

territory in open cover (Bendell and Elliott, 1966). In addition to hooting sites, males use small thickets of vegetation, tangles of logs, and spaces under logs and stumps. These sites appear to be used for resting and concealment. The accumulation of droppings at some of them indicates they were used frequently.

Open areas for courting are another important feature of territories. On our study areas, openings occurred throughout the open types of vegetation and haphazardly within the dense types of cover. Openings were also created by old logging roads and side beds. Males are frequently found in or at the edge of openings and on small elevations. Such sites are more favoured if they offer shelter in the form of a clump of firs or a recessed log or stump. The arrangement seems to provide concealment and a vantage point for surveillance of the open area.

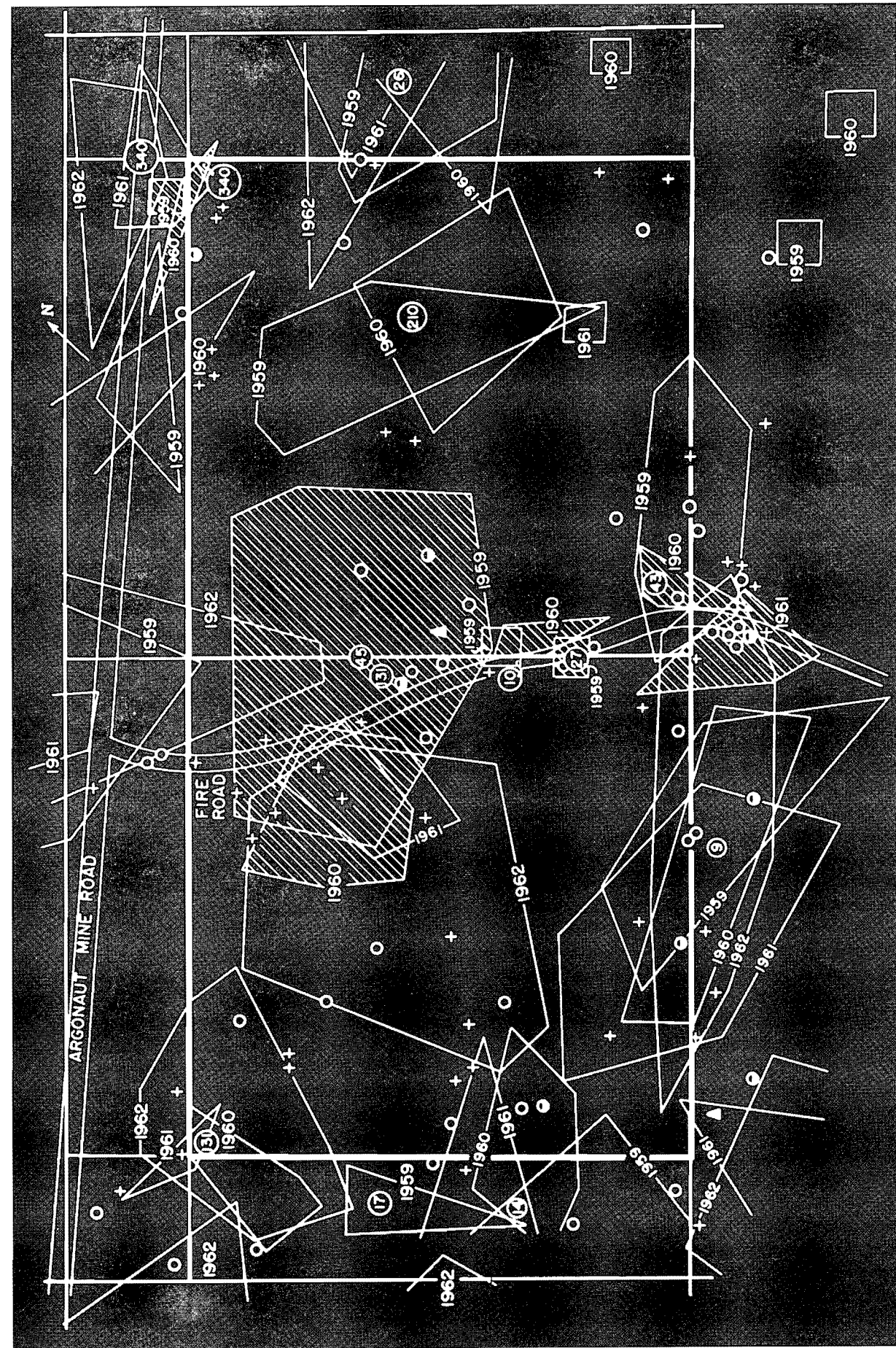
Note that when banded territorial males were located as silent birds, their positions were within, or close to the limits of, their territories as determined by their hooting positions (Fig. 9 a-d). Hence males found all their requirements on their territories.

The continuous use of an area by different males shows that areas have features of importance. Figure 10 shows the territories on the main reference plots from 1959 through 1962 at Middle Quinsam Lake. The eight shaded territories represent areas occupied by a succession of different cocks. In four out of five cases new males settled on areas or parts of them occupied by former residents. Similarly, new males at Lower Quinsam Lake seemed to prefer vacated territories to unused areas (Fig. 7). This suggests that the territories had features that made them attractive to grouse. The selection of habitat and a place for territory is considered in another report (Bendell and Elliott, 1966).

Spacing of territories

We studied the spacing of males in terms of the distance between them and the area of their territories. Distance and area were examined in relation to density of males and cover to determine how territorial behaviour spaced males and if it excluded others from the breeding population.

To examine the spacing between territorial males we used the distance to nearest neighbour method of Clark and Evans (1954). This involves the calculation of the value R which provides a measure of the degree to which the pattern of distribution of the observed population deviates from random expectation. R ranges in value from zero for maximum clumping to 2.1491 for a distribution where animals



10 Territories, males, and females on the main reference plots, 1959 through 1962, Middle Quinsam Lake.

TABLE 3 Spacing of territorial males in relation to density and cover, and spacing after males were removed

Population	Density (Males/acre)	Cover	No. measurements	Av. distance nearest neighbour (feet)	R*
Dense (L.Q.L.)	0.44	Open	20	232	1.63
		Very open	12	294	1.58
Sparse (M.Q.L.) Reference plots	0.13	Open	20	568	1.98
		Dense	17	348	1.12†
Removal plots	0.13	Very open	25	378	1.32
		Very dense	10	409	1.28†
		0.10	Very open	52	198
All males shot	0.26	Very open	52	198	0.99†

*R = The measure of spacing.

†Not significantly different from random spacing.

are as evenly and widely spaced as possible for a given density. An R value of one represents a random distribution; significant departures from one indicate a tendency for animals to gather together or spread apart.

Measurements were made of the distance between nearest territories on the two plots at Lower Quinsam Lake in 1952, and on the main reference plots and removal plots at Middle Quinsam Lake from 1959 through 1962. A centre of activity for each territory was determined subjectively from a best fit of where the male was observed most frequently, and often fell upon a hooting station. Hence, the distance to the nearest neighbour was a measure from the centre of activity of one male to that of its nearest neighbour. The use of a centre of activity avoids the problem of real size of territory. However, few observations on a male are not as likely to give as good a determination of the centre of its activity as a larger number. On the removal plots, the measurement was made between points where males were shot.

The density of hooting males on the two 36-acre plots at Lower Quinsam Lake in 1952 was 0.44 per acre. They are referred to as the dense population. The density of hooting males on the two 36-acre main reference plots at Middle Quinsam Lake from 1959 through 1962 was approximately 0.13 per acre. These males are referred to as the sparse population. The density of hooting males on the 100-acre removal area was comparable. In the dense population, there were approximately the same number of males on each plot. One plot was mostly open type with some very dense cover (Fig. 8); the other was predominantly very open, in the spring at least. In the sparse population, the density was approximately the same on each plot but one

reference plot was in dense vegetation, the other in open, while the removal plot was one half in very open and the rest in very dense cover (Fig. 1).

The spacing between males and its relationship to density and cover are presented in Table 3.

At both densities in open vegetation, males showed a tendency toward uniform distribution. The R values 1.63, 1.58, 1.98, and 1.32 are all statistically significant departures from a random distribution. In these tests and others throughout this report, the 5 per cent level of probability was used to decide on the validity of a difference between results. Hence, in dense and sparse populations in open cover, males tended toward even spacing. This result is in accord with the finding that territories were not related to the pattern of cover or roads on the study plots. The territorial behaviour of males apparently resulted in their even distribution on the breeding range.

The average distance to nearest neighbour gives the proximity of males. As might be expected, in dense population the centres of activities of males were closer together than in sparse population (Table 3).

In the sparse population in dense and very dense cover, the distribution of territorial males was not significantly different from random (Table 3). This may be a result of too few data, but, if accepted, suggests that in sparse population at least, the pattern of cover may influence the spacing of males. As already noted, territories were located at openings, which occurred in dense cover in a haphazard manner. Hence the location of territories may be influenced by interaction between males and openings in the vegetation.

The results from the removal plots are of special interest (Table 3). In very open cover, after the first

territorial males were removed, others were taken from the same territories. We will deal with this in greater detail later. However, for the present analysis, the R value for first males shot is 1.32. If all males shot are considered, the R value is 0.99. This is a change in a tendency toward a uniform distribution in the first males removed to a more clumped distribution in all males taken. The average distance to the nearest neighbour in first males and in all males was 378 and 198 feet respectively. The difference between them is statistically significant by t-test. We conclude that after established males were shot other males tended to replace them on their territories. As will be shown, most replacement males were yearlings.

Several observations may be cited to show how well the spacing between territorial males was maintained. Male No. 162 (Fig. 6) courted a banded female on the logging road that ran to the right through the plot. In full display, the male followed the hen to the edge of its territory, stopped, turned back, and began to hoot. The banded female continued on up the road toward male No. 281 who was hooting vigorously at the near edge of its territory. Male No. 281 broke into full courting display, picked up the hen approximately 60 feet from No. 162, and followed her through his territory. Similar observations were obtained several times with different males and females.

At times, male No. 162 was observed courting from one to six females in a clearing on his territory. Neighbouring males would usually come to the edge of the clearing and hoot and display. In all these observations, adjacent territorial males effectively spaced themselves during breeding activity. Males that displayed within areas occupied by others were chased and expelled by the resident male.

The cause of the even spacing between territorial cocks is of interest. We noted that they held position with respect to each other, and it is likely that hooting and other auditory display maintain the spacing. Note in Figures 6 and 9 that males were observed most frequently well within their areas and not at the edges. As noted, fighting is probably not the only method of establishing extent of territory since if it were males might be expected to patrol the edges and to fight more frequently than was observed. Males appeared to be spaced from time of arrival and extended their movements from their song posts during the breeding season. The positions where males are found suggest that hooting and other auditory display alone may space

breeding males.

Stenger and Falls (1959) show that ovenbirds learn the song of their neighbours. It seems likely that grouse learn boundaries to their territories. This point can be made from the data presented in Figures 9a and 10 which show territories on the main reference plots at Middle Quinsam Lake in 1959, and from 1959 through 1962, respectively. In 1959, there were three males on territory along the fire road (Nos. 45, 10, and 27) and three along the Argonaut Mine road (Fig. 9a). Males Nos. 10, 27, and 1 were killed early in May during banding. In no case was the territory of a killed male encroached upon or used in the year that it was destroyed despite the close proximity of neighbouring males (Fig. 9a). In 1960 all three areas were used by new males (Fig. 10). This suggests that males had learned a boundary between themselves and adjacent males for one breeding season at least.

Size of territories

Our other way of examining the spacing of males is through the size of their territories. If space for territory limited population then we would expect to find evidence for a minimum size of territory and wandering males that could not obtain a space. We were also interested in the influence of cover on the size of territory. The analysis was based on data from the two study plots at Lower Quinsam Lake in 1952 and the two main reference plots at Middle Quinsam Lake from 1959 through 1962. As noted, the populations on the plots ranged from dense to sparse and occurred in open and dense vegetation.

The estimate of size of territory varies with the number of observations. Size of territory tends to increase with number of observations until a maximum is reached whereupon more data do not add greatly to its extent (Odum and Kuenzler, 1955; Stenger and Falls, 1959). To overcome this effect we plotted the number of observations made on a male against the size of its territory (Fig. 11). If males tend to have territories of approximately the same area, then as observations are made the curve of area on number of observations should rise and then level off at the average real area of territory.

At Middle Quinsam Lake, the positions of silent males were used in the estimate of size of territory when they were banded territorial birds. That is, observations of silent males were used if they occurred before the end of June or if the male was observed hooting at a later date. Area was calculated by counting the number of squares of graph paper within a territory and converting the

total to acres.

Compare the size of territory in dense and sparse populations (Fig. 11). Note that for the same number of observations, the size of territory was consistently larger in sparse population. The cover on the plots which yielded the data for most of the comparison was virtually the same. Clearly, the territories of males were largest in the sparse population.

Males on small territories in high density expand their areas when density decreases. Between 1952 and 1953 the number of breeding males on one plot at Lower Quinsam Lake fell from 20 to 11. The territories of new and remaining males expanded to include most of the area vacated by birds that disappeared. By May 1957, as noted, only three males lived on the plot. One, banded in 1951, and observed 13 times in 1957, ranged over a territory approximately seven times as large as that occupied in 1951 and 1952 (male No. 132, Fig. 6). We conclude that size of territory of blue grouse varies inversely with density of population.

The calculation of area of territory is complicated by the number of observations—size of territory relationship already mentioned. Where there are few data, size of territory is likely to be underestimated. Moreover, where males are sparse they range over a larger area and may tend to increase the size of their territories over the summer. Hence many continuous data are needed to describe the extent of their movements. The small size of territories noted for 1950 at Lower Quinsam Lake shows the effect of few data on size of territory (Fig. 7).

In dense population of approximately 0.44 breeding males to the acre, where more than 20 observations were obtained on each male, the size of territory tended to reach a maximum of approximately 1.5 acres with a range of 1 to 2 acres (Fig. 11). In sparse population of approximately 0.13 breeding males to the acre there was little tendency for the observation—area curve to reach a maximum. The available data suggest that in sparse density territories were at least 5 acres and up to 11 acres in size. The territory of 11 acres is considered atypical and not included from now on.

An important question is the minimum and maximum size of territory. If a linear relationship is accepted between density and size of territory then the data from sparse and dense populations may be projected to estimate limits of size. Such a projection suggests that the maximum size of territory is approximately 8 acres. This estimate is supported

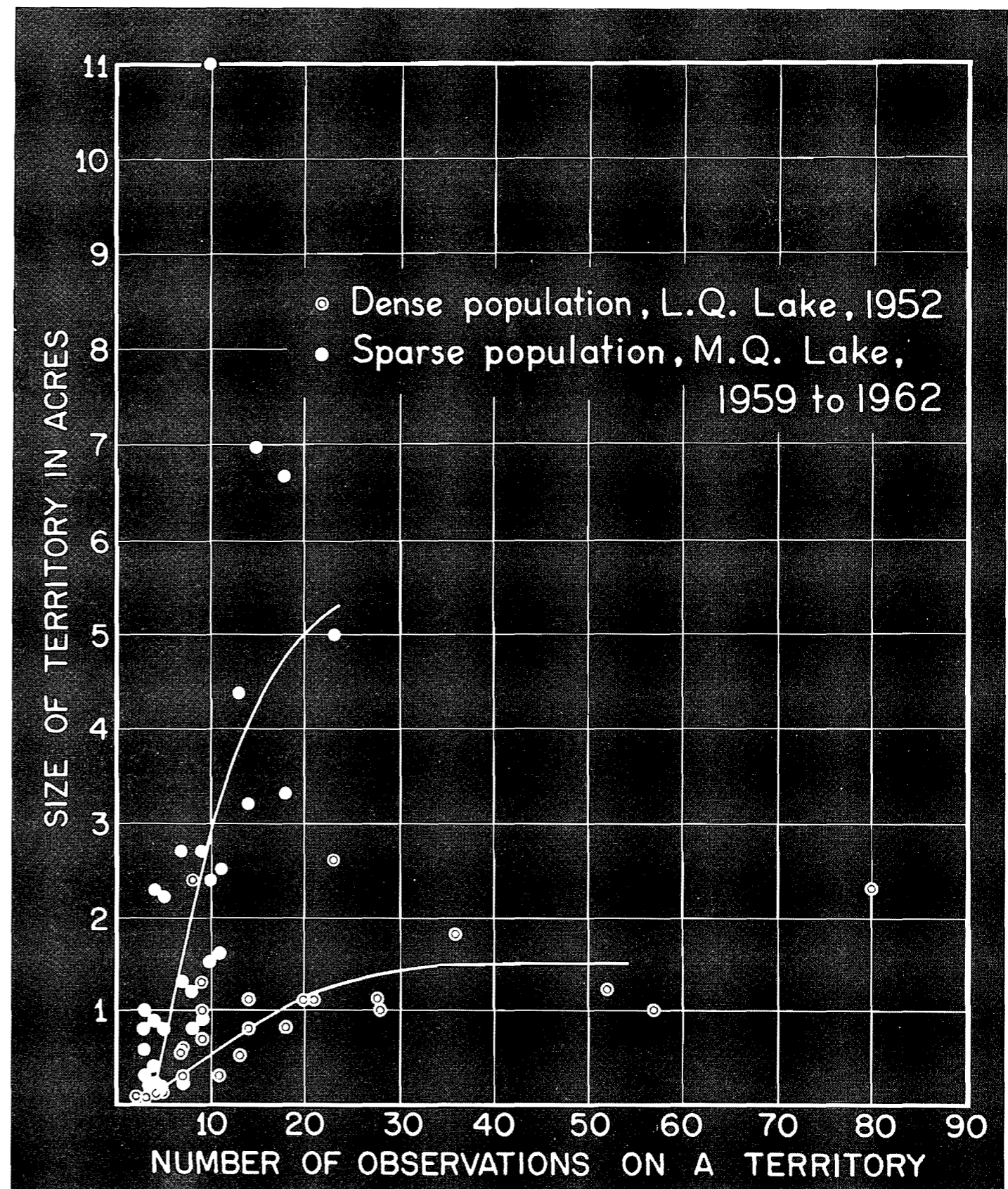
by direct observation. In studies of some 120 territories, a territory size larger than approximately 7 acres was recorded only once. In addition, several breeding males were studied that were apparently unrestricted in movement but did not range over an area greater than 7 acres. Male No. 9 restricted its movements to an area of 4 acres in 1961, and 5 in 1962 when virtually alone on the study plot (Fig. 9 c and d). Similarly, male No. 132 was one of three on a 36-acre study plot at Lower Quinsam Lake. It occupied a territory of approximately 6 acres.

How small territories might become is a more difficult question to answer. The regression of density on size of territory suggests that size becomes minimal at a density of about 0.6 males to the acre. Hence in an area of 36 acres there might be 22 males each with a territory of 1.6 acres. This estimate is rejected, for in nine territories in dense population with more than 20 observations on each, seven averaged approximately 1 acre in size. With the available data, minimum size of territory is estimated at approximately 1 acre or less. If this is true then saturation density is approximately one male to the acre and the limits to size of territory are approximately 1 and 8 acres. It follows that even in our dense population, at approximately 0.44 males to the acre, more males could have joined the breeding population, or, space for territory was not limiting at this high density.

Another approach to the minimum size of territory is the distance between hooting males. In 36 cases in the sparse population at Middle Quinsam Lake the distance between hooting neighbours averaged 290 feet. If the distance is assumed to represent the minimum spacing between males, and half of the distance is taken as the radius of territory, then minimum size of territory is approximately 1.5 acres.

Again, using this estimate more males might have been added to all areas studied, especially to the sparse population at Middle Quinsam Lake.

The size of territory was examined in relation to the kind of cover in which it occurred. This analysis was made with the data from sparse population at Middle Quinsam Lake where there were approximately equal densities of breeding males on the two main reference plots. One plot was in open, the other in dense vegetation. The data on area for number of observations were grouped for dense and open vegetation and tested by covariance analysis. The available data did not show a statistically significant difference in size of territory



11 The relationship between number of observations of hooting males and size of territory in sparse and dense population.

related to density of vegetation.

Consider now factors affecting the shape and extent of territory. Males may influence the extent of movement of adjacent males. In 1961, an unbanded male occupied a territory adjacent to male No. 9 on the reference plots at Middle Quinsam Lake (Fig. 10). In 1962, the territory of the unbanded male was empty and No. 9 extended its territory into the empty area. Clearly, the movement of No. 9 over part of its territory in 1961 was affected by its neighbour. Similar observations were obtained several times.

Another movement contributing to the extent of territory was pursuit by cocks. When males or females appeared, males frequently chased them on the ground or through the air. This resulted in relatively long movements by cocks and frequently in an increase in the areas measured as territories. Note that size of territory was more variable in sparse population (Fig. 11). This means that the limits of territories were better defined in dense than in sparse population. In sparse population, where males were less constrained, chance pursuits added extent and variability to the size of territories.

Finally, as noted, males appeared to change hooting stations to place themselves closer to a neighbour. For example, male No. 9 (Fig. 6) hooted in April 1952 close to the left boundary of the plot with a banded neighbour just off the plot. In June and July, when the banded male had disappeared No. 9 moved to the right of the plot line and hooted with male No. 162 and other males that were still hooting along the road.

Size of territory and age of male may be examined in Figures 7 and 10. The general conclusion is that where density remained the same, the territories of new adults and the same adults in successive years did not vary with age. For example, adult males No. 9 (Figs. 7 and 10) were observed for 4 years and occupied approximately the same area each year.* Male No. 131 (Fig. 10) was observed on territory as a 2-, 3-, and 4-year-old. Its size of territory did not show an appreciable change with age. Adult male No. 8 (Fig. 7) was observed on a territory of about the same size in 1950 and 1951. In 1952 it was replaced by a new adult, presumably 2 years of age. The new adult occupied the same size of territory as the banded male who in its last year was at least a year older than its replacement.

Twice yearling males were observed holding

territory. Male No. 340 (Fig. 10), banded as a hooting yearling, behaved as an adult on territory. A yearling male that replaced an adult male shot on the removal plot occupied a territory comparable in size to that of an adult. Size of territory was clearly not related to age.

In review, observations of breeding males and their use of space on the reference plots indicate that they did not prevent other adult males from holding territory or joining the breeding population. The size of territories varied inversely with density and few approached the estimated minimum size. In the dense population at Lower Quinsam Lake in 1952, there was apparently space for more males on both study plots. Moreover, in the years 1951 and 1953 there was a lesser density of males on both plots which indicates that space was not limited, at least in these years. At Middle Quinsam Lake the density of males on the main reference plots was approximately one third the peak density of males at Lower Quinsam Lake. Moreover, one main reference plot that contained males in 1959 and 1960 was virtually empty in 1961 and 1962. The density of vegetation was comparable at Middle and Lower Quinsam Lakes. Since males reached the high density recorded at Lower Quinsam Lake it is difficult to imagine a shortage of space for territories in the sparse population.

If adult males were excluded from holding territory on the breeding range they should be found as transients. As already noted the few transient males observed occurred early or late in the year and were probably migrants. In only one case was an adult male observed that might be regarded as an unsuccessful competitor for territory. In the dense population at Lower Quinsam Lake, a male was noted to court and display within the territory of another male. The transient was captured and observed several times in May on and off territories of other cocks. It did not establish territory in the year of capture but in the next year occupied the area of an adult male that disappeared. Hence, while interaction occurred between males to space them evenly, it seems unlikely that this prevented others from establishing themselves on the breeding range at the observed densities of population.

Direct observation thus provided little support for the hypothesis that resident males excluded others and regulated their own density. It may be argued that surplus males were missed or that males in sparse population held larger territories and so reduced density. The results of the removal experiments, to be presented shortly, refute these argu-

ments and support the conclusion reached by descriptive work that territorial males did not regulate their own numbers on the summer range.

Group activities of males

While territorial males live separately on the burns, they interact with their neighbours to produce group behaviour. A diurnal rhythm of activity was noted. This may be explained partly by the behaviour of individual birds at certain levels of light and partly by interaction among grouse of both sexes. Males also appear to influence the hooting activity of their neighbours.

The frequency of hooting seems related to the density of population. Males in dense population at Lower Quinsam Lake appeared to hoot more frequently throughout the day and later in the season than males in sparse population at Middle Quinsam Lake. In dense population, the number of hooting males observed per hour per week by mid-August was approximately 10 per cent of that recorded for mid-May (Bendell, 1955c). In sparse population, by mid-August, virtually no males were recorded either hooting or silent (Table 2). Hence, when males were abundant they stayed longer on the breeding range than when they were few. These observations suggest that intensity and length of hooting activity, and length of time on the breeding range are related directly to the density of males. Presumably, males stimulate each other more with increasing density.

While territorial males tended to space themselves uniformly on the plots, this was not always the case over the general study area. The distribution of hooting males occasionally appeared clumped. To illustrate this, approximately 7 miles of roadway through the general study area at Middle Quinsam Lake was divided completely by circular areas, each with a radius of 500 feet and centre on the roadway. It is believed that all hooting males in these areas were recorded. Thus the number of males within each circular area indicates their distribution along the grades. The data are from the years 1959 through 1962.

A total of 420 territorial males were tallied over the 4 years. From Table 3, the average distance between the centres of territory of nearest neighbours in open cover was approximately 600 feet. If the males along the grades were spaced similarly we would expect four or fewer males in each 1,000-foot circular area. In fact, 85 per cent (113) of the circular areas contained from one to four males, 10 per cent (13) contained five to six, and 5 per cent (7) contained seven to eight. Thus, most territorial

males were spaced along the grades as on the study plots. This result suggests that the sample plots reflected the density and spacing of males over the breeding range.

In 5 per cent (7) of the circular sample areas, seven or eight hooting males were found. In most of these, the males were 200 to 500 feet apart and formed a hooting group. When one member of the group was hooting the rest tended to chorus. Although the birds were close to each other their territories remained discrete.

Hooting groups produced on a small area the highest density of population recorded at Middle Quinsam Lake. A group of eight males within a circle 1,000 feet in diameter represents a density of approximately 0.44 males per acre—as dense as the population at Lower Quinsam Lake. This shows the compressibility of territory in that some males in the sparse population crowded as closely as those in the dense. Again the relationship of size of territory to density is shown between populations and within the same population. Note that census plots must be placed to represent general density, as a single plot in an area of local concentration of males may not represent the density and behaviour of males over a larger area.

Hooting groups appeared to be concentrated on a particular part of the breeding range. Favoured places were flat open areas surrounded by elevations with some cover. Thus one group of hooters was arranged around the shoulders of a large shallow gravel pit at the side of a grade. The flat and open floor presumably served as an area where hens were courted. The shoulders of the pit provided sheltered elevations that were used as hooting posts and appeared to offer excellent viewpoints to the floor and surrounding areas. In this hooting group, males were arranged around the gravel pit like spectators at an arena. Blackford (1958, 1963) and Hoffmann (1956) note that male blue grouse may hoot and display in groups to give an appearance of lek or communal behaviour as in the prairie grouse. Since male blue grouse defend areas and remain on them throughout the breeding season they are clearly of solitary behaviour, as are other forest grouse.

Hooting groups may be explained by the presence of highly attractive places for territory on the breeding range. Males concentrate on these areas to form a hooting group. We have already noted that openings in dense vegetation may influence the spacing between males. Hooting groups are regarded as another example of the influence of habitat on spacing. Here presumably the attractiveness of

*Owing to the two series of numbers (1-500± at Lower Quinsam Lake and 1-1000± at Middle Quinsam Lake), there were two No. 9 males.

the habitat offsets the tendency for males to space themselves farther apart.

Behaviour of yearling males

On the breeding range in spring, adult males are territorial while most yearling males are silent and move about widely. The yearlings might be regarded as surplus to the breeders and excluded from territory, or simply as immature birds that will establish territory when 2 years of age. Direct observation of yearlings and their response to the experimental removal of territory holders suggests that most are both immature and dominated by breeding cocks. Yearling grouse are birds in the plumage of their first autumn. In June, they are approximately 1 year of age. Yearlings can be separated from adults by plumage and weight until their second autumn when they become adult (Bendell, 1955b; Boag, 1965). Completely accurate determination of adults and yearlings can be made only with the bird in hand.

On the summer range, the yearling male is found either as a hooting or silent bird. Most of those found hooting, from our present data, have behaved as adult males on territory. Four hooting yearlings were captured and banded on the general study area at Middle Quinsam Lake from 1959 through 1962. Three of them returned to and hooted near the point of banding in subsequent years. This shows that these yearlings were located on territories comparable to those of adults.

We have a series of observations on one yearling hooting male. Male No. 340 established territory near the north corner of the main reference plot east of the fire road (Figs. 9 b, c, and d). When banded in April of 1960, it occupied part of the area used by two males in 1959. The yearling established territory with at least two adults as neighbours (Nos. 210 and 26).

Male No. 340 held territory as a yearling and as a 2- and 3-year-old. The bird was located at approximately the same positions each year. The size of its territory was approximately the same from yearling to adult, or from 1960 through 1962 (Figs. 9 b, c, and d, and 10). This agrees with a conclusion reached earlier that size of territory was not related to the age of the resident.

One change that may have been related to age in male No. 340 is time of leaving territory. When 1 and 2 years of age, the last dates on which the bird was recorded hooting were May 18 and May 4. At age 3 it was recorded hooting for the last time on June 15. Since the plots were covered repeatedly and the male was close to our access road, it is

believed that these dates represent the behaviour of the bird rather than the search effort of the observers.

An attempt was made to correlate date of departure from territory with age in 22 males of known age on the two main reference plots at Middle Quinsam Lake. The last dates of hooting for each male were recorded from 1959 through 1962. Most of the males ranged from 2 to at least 5 years of age. There was no clear relationship between age above 2 and the date when a male was last recorded hooting. All but two hooted in June, and six were last heard in July. However, male No. 340, as a yearling, was last heard in May. The behaviour of No. 340, and the decrease of hooting yearlings among hooting males over the general study area, as will be noted, suggest that 1-year-old males may abandon their territories earlier than males 2 years of age and older.

Forty-two yearling males were found as silent birds on the general study areas at Middle and Lower Quinsam Lakes. Virtually all were come upon as solitary individuals and usually moved from under logs and trees throughout the breeding range. As will be shown, yearling males move widely over the burns. One yearling was observed beside a female, and, although this was in May, the male showed no sexual excitement. Another silent yearling was observed to display and hoot when a hen landed nearby (Bendell, 1955a). In general, most yearlings appear as non-breeding males.

Silent yearling males were found on and off the territories of other males. Note the observations on banded silent yearlings (Figs. 9 a to d). As examples, in 1959, males Nos. 131 and 28 were banded on the territory of No. 45. In 1960, No. 364 was caught southwest of the territory of No. 9.

Silent yearling males apparently occur most frequently on the territories of other males. If silent yearling males were distributed at random over the two main reference plots then they should have been found on and off territories in the same proportion as the area of territories to remaining area. In 1959 and 1960 the territories of males took up approximately 40 per cent of the area of the plots. Thus in a random distribution of yearlings, 40 per cent should occur on and 60 per cent off territories. Actually seven yearlings were observed on territories and only one was observed away from a territory. The deviation from the expected distribution is statistically significant by Chi-square test. We conclude that silent yearling males occur most frequently on the territories of other males.

TABLE 4 Movements of silent yearling males, Middle Quinsam Lake

No.	Banded	1960	Dir.	Dist. (ft.)	1961	Dir.	Dist. (ft.)	1962	Dir.	Dist. (ft.)
34	June 1959 (S)							to June (H)	N	560
131	July 1959 (S)	to May (H) on (T)	SW	1,100	(H) on (T)			(H) on (T)		
364	May 1960 (S)				to May (S) shot	SE	1,200			
386	May 1960 (H) on (T)	to July (H) on (T)			to May (S) shot	E	1,300			
466	July 1960 (S)				to May (S)	S	300	to May (H)	W	600
620	May 16, 1961 (S)				to May 17 (S)	NW	3,460			
					to June 13 (S)	E	440	to May (H) shot	E	2,300
638	May 1961 (S)							to May (H) on (T)	SW	1,900
678	May 16, 1961 (S)				to May 22 (S)	NW	220			
					to May 23 (S)	S	1,730	to May (H) shot	E	2,600
721	July 1961 (S)							to June (H) on (T)	NW	6,900

Note: (S) = Silent; (H) = Hooting; (T) = Territory.

The data from Lower Quinsam Lake suggest the same conclusion. Of nine yearlings recorded, eight were on the territories of other males. However, with much of the area of the dense population in territories, the relationship between territories and silent yearlings was not clear.

The occurrence of silent yearlings on territories means that hooting males attract yearlings and (or) hooting males and silent yearlings select the same kind of habitat. Area for territory appeared to be unlimited in the relatively sparse population at Middle Quinsam Lake. It seems most likely that yearlings could find suitable areas without adults. We conclude that territorial males attract yearling males to them, presumably by their hooting. Additional evidence for this from the removal area is presented in Bendell and Elliott (1966).

Nineteen yearling males were banded as silent birds on the general study areas at Middle and Lower Quinsam Lakes. At Lower Quinsam Lake, two silent yearlings were captured and banded. One was observed in the same year at points approximately 1,000 feet apart and not seen again. The second was captured on the territory of an adult male in May of 1951. It was next observed a year

later hooting at a point 600 feet from the place of capture.

Repeat observations obtained on nine silent yearlings from 1959 through 1962 at Middle Quinsam Lake are presented in Table 4. In the table, distance and direction are calculated from a straight line between successive observations.

Compared to males on territory, most silent yearlings moved widely over the breeding range. Territorial males at Middle Quinsam Lake were rarely observed more than 400 feet from the centres of activity of their territories. Contrast this with yearling No. 678, for example, which moved at least 220 feet in 6 days, then at least 1,730 feet on the seventh day. The following year, it was located as a hooting male 2,600 feet from the last point of observation in the previous year. The longest movement was recorded for silent yearling No. 721. A year after banding it was observed as a hooting adult and had moved at least 6,900 feet between locations on the breeding range.

Generally, silent yearlings move relatively long distances and, as concluded earlier, they are apparently attracted by hooting males. Hence, in the course of their travels, silent yearlings probably

pass through the territories of a number of males.

Some of the silent yearlings made relatively short movements between observations. Males Nos. 34 and 131, for example, were observed at distances of approximately 560 feet and 1,100 feet from points of banding to where they located as adults. These males may have restricted their movements as yearlings and, therefore, made a start toward territorial behaviour.

The direction of movement of the yearlings does not follow a particular pattern. They seemed to move in all directions on the burn. During the study period, six silent yearlings were banded approximately 1,000 feet beyond the borders of the removal area at Middle Quinsam Lake. Three of the six yearlings were later taken on the removal plots as territorial males. The other three were observed on territory elsewhere than the removal plots and among neighbouring males. As reasoned for the distribution of yearlings on the main reference plots, we would expect three times as many yearlings to locate off as on the removal area. The even distribution, although not statistically significant, suggests that there was a tendency for yearlings, when adult, to establish territory on the removal area. This might be explained by the attractiveness of the area and (or) the absence of interference from neighbouring males.

Most silent yearlings, if located in subsequent years, were found as hooting adult males of 2 years of age and older. In 18 that were banded at Middle and Lower Quinsam Lakes, 10 (56 per cent) were observed in subsequent years on territory. This is a remarkable recovery considering that there must be mortality, and that silent males may move a mile or more in any direction over the breeding range. The wide movements of yearlings reduce the chance of finding them even after they begin to hoot. If the four yearlings observed on territory are added to the ten that became territorial as adults, then at least 64 per cent (14/22) of the yearlings banded joined the breeding population. We conclude that most of the yearling males on the breeding range augment the population of hooting adults when they are 1 and 2 years of age.

The histories of two yearling males illustrate the points we have made on their behaviour. Male No. 131 was captured in May of 1959 as a silent yearling on the territory of adult male No. 45 (Fig. 9a). It was next seen in April 1960 on territory on the main reference plot west of the fire road (Fig. 9b). This was a move of at least 1,100 feet to the southwest (Table 4). It is noteworthy that the

male established territory on unoccupied ground. It then held a territory in the same area in each breeding season from 1960 through 1962 (Figs. 9 c and d).

Male No. 638 was captured as a silent yearling, in May of 1961, on the territory of another male. It was next located in May of 1962, and observed repeatedly as a territorial male. The distance and direction between point of banding and point of recovery in the next year was 1,900 feet to the southwest (Table 4). This male replaced adult hooting male No. 713 which was banded in 1961 but not observed in 1962. Thus, these yearlings were found on the territories of adults, moved widely, and established territory in their second year. One settled on an unoccupied area, the other replaced an adult male.

The histories of yearling males Nos. 466 and 386 (Table 4) warrant comment. Yearling No. 466 was banded and observed in approximately the same locality a year later. In the third year it was observed hooting, again near the point of banding. The restricted movements of the male suggest that it was on territory as a yearling and older. Its hooting may have gone undetected until the last year of search.

Yearling No. 386 was captured as a hooting male on a removal plot in May of 1960 after hooting adult males were shot. It provides an example of a yearling that presumably would not have occupied territory in the presence of other territorial males. Since the male began to hoot only after adults were removed, it is included in the table of silent yearlings. The hooting of this bird seemed quieter and less frequent than that of fully territorial males.

No. 386 was observed six times, hooting and silent, between May 31 and July 9, 1960. The territory that it occupied was comparable in size to that of an adult for the same year and number of observations. In May of 1961, No. 386, now 2 years of age, was shot as a silent male, presumably on territory on another part of the removal area, 1,200 feet from its territory of the previous year. Thus, this male did not return to the same territory in a subsequent year as do adults. Like most silent yearlings, the bird settled as an adult far from where it was observed as a yearling bird.

The movements of yearling No. 386 are of interest for, as far as we know, they occurred without the interference of other males. After a number of hooting adults and yearlings were removed from the area in 1960, the bird was alone. In 1961, only one other adult male was shot on the removal area.

TABLE 5 Numbers of adult and yearling males sampled as hooting or silent from March through August, Middle Quinsam Lake, 1958 through 1962

	Hooting males										Silent males										
	1958		1959		1960		1961		1962		1958		1959		1960		1961		1962		
	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	Ad	Yr	
March-April	-	-	-	-	12	3	-	-	-	-	-	-	-	-	-	5	3	-	-	-	-
May	5	1	3	0	17	2	32	5	8	0	0	1	1	0	1	6	5	3	6	7	
June	13	1	18	2	25	2	6	0	5	0	1	0	6	3	4	2	0	1	4	7	
July	1	0	3	0	10	0	4	0	8	0	0	0	0	2	6	3	2	1	5	0	
August	0	0	0	0	1	0	0	0	0	0	-	-	0	0	1	0	0	0	5	0	

This suggests that the movement of No. 386 was voluntary and not affected by other males.

In review, all adult males on the summer range appear to be fully territorial and are taken as breeding birds. A few yearlings behave as adults and occupy territory. Territorial yearling males appear to abandon territory and leave the breeding range earlier than adults. Most yearlings are silent, move widely, and apparently are attracted by hooting cocks. Yearlings in spring were observed courting and unresponsive to hens. A yearling which replaced an adult on territory on the removal area did not seem as effective on territory as an adult, and did not return to the same territory in the next year as do adults. Most yearlings join the breeding population at 2 years of age and appear on new and old territories.

Bendell (1955a) and Simard (1964) have shown that the testes of yearlings are smaller than those of adults. Both hooting and silent yearlings show similar but less testicular development than adults (Simard, 1964). In spermatogenesis, for example, both age classes pass through the same stages but yearlings show slower recrudescence, shorter period of production of sperm, and an earlier and faster rate of testicular regression. When adult males were removed, yearlings began to hoot but they did not reach the weight or testicular development of adults until 2 years of age (Simard, 1964). Clearly, yearling males are immature and this partly explains their behaviour on the breeding range. Since some replace males that are shot then some are also apparently dominated by territorial cocks. Hence, yearling males on the breeding range may be described in the following ways: (a) all are immature; (b) a few establish territories but are probably not as strongly territorial as adult males; (c) some will replace territorial males that are removed and are presumably dominated by them; and (d) some move over the breeding range as apparently non-breeding males. Another possibility

is that some yearling males do not descend to the breeding range at all until after their second winter.

Numbers of yearling males

Males were sampled to find the numbers of yearlings in the breeding populations in each month and year. Data were obtained from the relatively dense population at Lower Quinsam Lake and the sparse population at Middle Quinsam Lake. For the present, data from the removal plots are not included. Thus the analysis represents the ratios of adults to yearlings in natural populations.

In dense population, 60 hooting males were captured or shot on their territories, mostly in May and June from 1950 through 1952. Only one (2 per cent) was a yearling male; the rest were adult. In the same time, 32 silent males were examined: nine (28 per cent) were yearlings. Clearly, most territorial males were adults and there were more adults than yearlings in the population.

The results of sampling males in sparse population at Middle Quinsam Lake are presented in Table 5.

The numbers of hooting adults to hooting yearlings may be compared by month. March and April are combined and represent a collection in a single year, so cannot be used in this comparison. The data in each month are few but are strengthened by the addition of those of successive years when similar. For example, in May of 1958 through 1960, the ratio of adults to yearlings was 25:3. This compares favourably with the ratio 32:5 for 1961. There were no apparent differences among any of the years in number of yearling males in the hooter population for each month considered. This suggests that the proportion of yearlings in the population of hooting males at Middle Quinsam Lake was virtually the same over the years 1958 through 1962.

Consider next the number of hooting males in each month of all 5 years. Since the ratios of adult to yearling males were the same, the samples from

each year were pooled by month to give total males examined by month. The ratios of hooting adults to hooting yearlings were: March and April, 12:3; May, 65:8; June, 67:5; July, 26:0; and August, 1:0.

The ratios were compared by Chi-square in a fourfold table. The data of May and June did not show a statistically significant difference and were therefore pooled. The data for March and April went to the 5 per cent level but not beyond. The ratio of adult to yearling hooters in July and August was significantly different from that in earlier months. From these comparisons we conclude that in the sparse population at Middle Quinsam Lake, most hooting males were adult, and the proportion of yearling males in the population of hooting males varied over the breeding season. If the data are accepted as they stand, yearling males made up the following percentages of the population of hooters over the spring and summer: March and April, 20; May and June, 9; and July and August, 0. March and April (considered together) are represented by a small sample and may not be different from May and June.

The result of the comparison of adult to yearling hooters may be extended. Since adult males are not added to the numbers of hooters over the summer, it appears that yearlings hoot most frequently in March and April, are less vocal in May and June, and by July cease to hoot. As noted, adults are most vocal in April and May, become less so in June, and by July many have stopped hooting and left their territories. Thus the hooting activity of the yearling seems to follow that of the adult but terminates earlier.

The behaviour of hooting yearlings should be considered when they are counted. Since their numbers change over the breeding season, statements of ratios of hooting adults to yearlings should be month-specific. Our estimate of number of yearlings in the population of hooting males is 132:13 (adults:yearlings) or 9 per cent for May and June. This was in the sparse population at Middle Quinsam Lake from 1958 through 1962.

In the dense population at Lower Quinsam Lake from 1950 through 1952, approximately 2 per cent of the hooting males sampled in May and June were yearlings. The difference between this and the 9 per cent hooting yearlings in the sparse population at Middle Quinsam Lake nearly reached statistical significance (Chi-square = 3.64 and $P = 0.05$).

Consider now the ratios of silent adult to silent yearling males in Table 5. The data of March and April are again omitted from the comparison. The

few data each month appear similar for all 5 years. This was to be expected if the conclusions on hooting yearlings in the hooter population apply to silent birds. The results suggest that the proportion of yearling to adult males was virtually the same over the years 1958 through 1962 at Middle Quinsam Lake.

Since the data on silent males appeared to be similar among years, they were pooled to yield the following ratios of silent adults to silent yearlings: March and April, 5:3; May, 13:17; June, 15:13; July, 13:6; and August, 6:0. The ratios March through June were not at variance statistically and were, therefore, pooled to give a March to June ratio of 33:33. Similarly, the data for July and August were pooled to give a ratio of 19:6 silent adults to silent yearlings. The two ratios tested significantly different by Chi-square in a fourfold table. Thus the proportions of yearlings and adults in the population of silent males varied between the periods of March through June and July through August. This supports the conclusion reached by examination of the changing ratios of hooting adults and yearlings.

The change in proportion of yearlings in the population of silent males can be explained by adult males becoming silent as the breeding season progresses and by the earlier departure of yearlings from the breeding range. As noted, yearlings appear to cease hooting earlier than adult males and adults leave the breeding range shortly after they silence. Hence it is likely that the change in ratio results from the relatively early departure of the yearling males.

Note that there were fewer hooting yearlings than adults. Among silent males, adults and yearlings were found in equal numbers although all adults spent time in hooting. This means that among the males there were more adults than yearlings in both dense and sparse populations.

The proportion of yearlings in dense and sparse populations may be compared by silent males. In the sparse population at Middle Quinsam Lake, among silent males sampled in May and June, there were 28 adults and 30 yearlings. In the dense population at Lower Quinsam Lake, mostly in May and June, there were 23 adults and 9 yearlings. The difference between populations is not statistically significant, however, as when hooting males were used in this kind of comparison, the Chi-square value went to the 5 per cent level. The data on hooting and silent males were pooled to give an age ratio of adults to yearlings in each population.

There was a highly significant difference between populations in numbers of yearling males. From this, the foregoing, and the age ratios of hens to be presented, we conclude that there were fewer yearling males in sparse population than in dense.

Note that in dense population the ratio of hooting to silent yearlings was 1:9. In sparse population the ratio was 13:30. These were not significantly different by statistical test but this may be the result of size of sample. If density affected the proportion of hooting yearlings in the population we would expect to find in dense population fewer hooting to silent yearlings. This was apparently the case, which suggests that density of population on the summer range was related to the number of hooting yearlings among the yearling males. This is in keeping with the view that adult males dominate yearlings.

The actual number of yearlings in the population of males on the breeding range is an important point. The ratio values do not provide a clear method of assessment because hooting males are found more frequently than silent cocks. Another complication is that yearlings and adults differ in the frequency and loudness of their hooting. These and other biases make deductions from ratios to actual numbers of hooting to silent males of doubtful value. With these qualifications consider the following argument.

At Middle Quinsam Lake, from March through June, the ratios of hooting to silent males were in adults, 144:33, and in yearlings, 16:33. If it is assumed that all adults hoot or remain silent for the same amount of time, then the data on hooting males may be converted into silent males. Thus, the 33 silent males represent 144 hooting males, or, males that are hooting are located 4.4 times more frequently than those that are silent. If yearling males that hoot behave as adults then the 16 hooting yearlings are equivalent to approximately four silent cocks. Hence a calculated ratio of adult to yearling males is 66:37. This suggests that in the population of males on the breeding range, approximately 36 per cent (37/103) were yearlings. Moreover, the number of yearlings that occupied territory or were hooters is estimated at approximately 11 per cent (4/37). The same calculation for the proportion of yearlings in the population of males at Lower Quinsam Lake in May and June gives 17 per cent and among these approximately 2 per cent were hooting males.

Death rate of adult and yearling males

Death rates are important statistics for a number of

reasons. We are concerned with them here because they provide another way to follow the fate of grouse on the breeding range. They are also important in calculating the number of new males that arrive on the reference plots in each year.

The average annual death rate of adult males can be calculated simply and accurately because of the faithfulness with which they return to their territories in successive years. Virtually all banded adult males were checked each year until not found (or found dead) and despite repeated searches in the same and ensuing years they were never observed again. Thus, a failure to record a banded adult male on territory means that it is dead.

The time of census and of banding males for the calculation of death rate needs explanation. Most of our males were banded in May and June, and checked in the same months. Hence, our year is from May and June of one year to May and June of the next. After May and June, hooting subsides and a significant number of males abandon territory so that they cannot be checked.

There is little problem in deciding when a male is territorial. Approximately 100 banded adult males were observed repeatedly. When observed hooting or silent in May and June, or observed hooting at any time, they were within or near the area of previous observation. Hence, adult males observed in May and June, and hooting males observed any time on the breeding range, are considered on territory. As another demonstration of this point, in May and June of 1959 through 1962 at Middle Quinsam Lake, 62 adult males were found and banded as hooters. In the year after banding 55 per cent (34) were observed again. In the same time, nine adult males were found and banded as silent birds. A year later, 67 per cent (6) were observed near the point of banding. Similarly, at Lower Quinsam Lake, of five adult males banded as silent birds in May and June, four were recorded on the same territory in a subsequent year. Another argument that silent adults are breeding is that all show the same degree of testes development as hooting birds (Simard, 1964). Therefore, adult males captured in May and June as silent birds are considered as hooting males from their faithfulness of return to territory and apparent potential to breed.

A similar comparison can be made between hooting males captured in May and June and those captured in July. In 3 years, 15 adult males were banded as birds hooting in July. In the year after banding, 53 per cent (8) were checked at their original points. This is comparable to the return of

TABLE 6 Return of adult males each year after banding, 1959 through 1962, Middle Quinsam Lake

Year	Number banded	Number returned		
		1960	1961	1962
1959	25	20 (19)*	16	12
1960	32		25 (22)	14
1961	26			16

*Numbers in brackets indicate reduction after collecting.

adult hooting males obtained in May and June and supports the conclusion reached above that July hooters are territorial.

The same cannot be said for silent males captured in July and August. As noted, some males have abandoned territory by this time and are presumably migrating toward the winter range. Eight adult males were banded as silent birds in July and August over 3 years. None was seen again. The data are too few to show statistical significance but we take them to mean that males banded as silent adults in July and August are likely not on territory. Therefore, they cannot be checked with accuracy in later years for a calculation of death rate.

We calculated the mean annual death rate of adult males from the records of males banded at Middle Quinsam Lake from 1959 through 1962. The data were taken from hooting males captured in May and June over the general study area and reference plots. The total number of adult males captured was 83 - 74 hooting and 9 silent cocks. The number of birds banded in each year and their return in subsequent years are given in Table 6.

The return of males each year appeared virtually the same. This is the more remarkable when one considers that adults may be up to 10 years of age when banded. We conclude that the death rate of males is constant with age.

The mean annual death rate was calculated by pooling the data from each year. Thus, 103 of 140 males present in one year returned the next. Therefore the mean annual death rate of adult males is 26 per cent.

The death rate of adult males in the sparse population can be compared with that in the dense population (Bendell, 1955c). In the relatively dense population at Lower Quinsam Lake from 1950 through 1953, the mean annual death rate of adult males was 31 per cent. This was calculated on 42 males where 77 were alive in one year and 53 returned in the next. In this sample also, death rate was constant and independent of age. Since the

TABLE 7 Return of yearling males each year after banding, 1959 through 1962, Middle Quinsam Lake

Year	Number banded	Number returned		
		1960	1961	1962
1959	6	4	3	3
1960	9		5 (2)*	2
1961	5			4

*Reduction of sample after collecting.

variation between the two rates was not statistically significant they were pooled. This gives a mean annual death rate for territorial adult males of 28 per cent calculated on a sample of 125 birds (42, Lower Quinsam Lake, plus 83, Middle Quinsam Lake). The similarity of death rates in sparse and dense populations suggests that they were independent of the observed densities. The mean annual death rate of adult males is low in comparison to that of other galliforms (Choate, 1963; Farner, 1955; and Hickey, 1955).

The mean annual death rate of yearling males was estimated in the same way as for adults. Except for the few yearlings that were on territory, however, the calculation overestimates their death rate. Yearlings banded in one year may be missed in the next because of their wide movements before locating on territory. The death rate of yearlings was determined from hooting and silent birds captured from May through July, 1959 through 1962, at Middle Quinsam Lake. The data are presented in Table 7.

From the table, a minimum estimate of the average annual mortality rate of yearling males is 27 per cent. This was calculated on 20 banded yearlings where 29 were present in one year and 21 returned the next. At Lower Quinsam Lake, two yearlings were banded and one was observed in the next year. If the data from the two areas are combined then a minimum estimate for the average annual mortality of yearling male blue grouse is 27 per cent calculated on 22 birds. The value is remarkably close to that calculated for the adult breeding cocks.

The minimum estimate of the mean annual death rate of yearling males provides the basis for two comparisons between yearlings and adults. Likely, the loss each year of yearling cocks was less than that of adult males. The simplest explanation for this is that the breeding behaviour of adult males increases their rate of death, presumably by predation. This is in keeping with the relative conspicuous-

ness of adult and yearling males on the breeding range.

As a second comparison, it may be argued that young, unestablished males are surplus to the breeding population. They are driven from adequate habitat by the adults and consequently die or are killed by predators (Boag, 1964; Jenkins *et al.*, 1963, 1964a). In the yearling male blue grouse sampled on the breeding range at Middle Quinsam Lake, the death rate was the same or less than that of adult cocks. Hence, in terms of death rate, yearlings were not at a disadvantage as compared to adults. This conclusion applies to yearlings on the breeding range and in their first winter as adults. The death rate of yearlings from their first autumn to spring (and on the winter range) will be discussed later.

The results of shooting grouse from the removal area

Effect of resident males on yearling males

The main purpose of the removal experiments was to find the effect of resident males on the addition of new males to the breeding population. This may be done in two ways: by comparing the number and age of males harvested or observed on the removal and reference plots, and by examining the replacement of males shot within the removal area.

From March through June of 1959 through 1962, on the reference plots and general study area, the age ratio among hooting males shot and captured was 144 adults to 16 yearlings. Over the same time on the removal area, where nearly all grouse were shot, the age ratio among hooting males was 19 adults to 18 yearlings. Since adults on the removal area had an annual rate of death of virtually 100 per cent their numbers must be adjusted to compare with the reference males. This was done by estimating that approximately five new adults arrived on the removal area each year and all died at the 28 per cent mean annual rate of death of adults. The adjusted ratio of hooting males on the removal area is approximately 40 adults to 18 yearlings. This compares with 144 adults to 16 yearlings on the reference and general study areas.

Compare next, the ratio of hooting to silent males among the yearlings. On the reference and general study areas over the 4 years, yearlings were sampled as 16 hooting to 33 silent. On the removal area, they were taken as 18 hooting to 10 silent. Clearly, there were more yearlings hooting on the area without adult males. The differences in the age structure of males on the removal and the reference areas are highly significant statistically. We conclude

that the removal of hooting adults and yearlings resulted in the increase of hooting yearlings. Hence, territorial males prevented some yearling males from hooting and holding territory. The result indicates that some of the silent yearling males on the breeding range are silent because of the presence of hooting males. Others may be silent because they are sexually immature.

The males removed from the removal plots can be used to estimate the percentage of yearling males in the population and the numbers that hoot. Assume that all males on the removal area were collected. This seems likely from the way the take of males dropped off at the end of May, as noted later. In 4 years the area yielded 27 adult males and 28 yearlings. The adults were all breeding males for, as noted, silent adults banded in spring are later found hooting. Take the 27 adults as seven new arrivals in each year. If they were not shot they would die at the rate of 28 per cent, the mean annual rate of death of adults. This means that in 4 years there would have been a ratio of adults to yearlings of 54:28. This suggests that for the 4 years, yearlings composed 34 per cent (28/82) of the population of males on the breeding range at Middle Quinsam Lake. The value is close to the 36 per cent estimate of the number of yearling males in the male population of the general study area. Moreover, if correct, the removal plots gave a valid sample of the proportion of yearling males in the population of males on the breeding range.

We can calculate the number of yearling males that will occupy territory if a resident is removed. If the 28 yearlings represent all that were present on the removal area when territorial males were shot, then since all territorial males were removed, 64 per cent (10/28) of yearling males will replace resident males on territory. Presumably the remaining or silent males were mature enough to migrate but lacked sufficient sexual development to become territorial. Finally, if 64 per cent of yearling males will occupy territory and in the natural population only 11 per cent did so, then established males apparently prevented approximately 53 per cent of the yearling males from adding to the breeding population.

Effect of resident males on the addition of new adults to the breeding population

The removal experiment shows that some yearlings were prevented from holding territory by established males. If, as direct observation suggests, all yearling males establish territory when adult, then the surplus of yearlings is not a complete explanation for the regulation of density by resident males. We

TABLE 8 Estimate, from mapping of territories and shooting, of number of new adult hooting males on the reference and removal plots

Cover	Reference plots								Removal plots					
	Very open			Open			Dense		Very dense		Very open		Very dense	
1960	2	1	3	2	3	2	4	1	2	3	4	3	3	2
1961	0	0	2	1	3	1	2	0	3	0	1	0	0	0
1962	2	5	3	1	2	1	2	0	0	0	4	1	1	0

need to know if there is a surplus or floating population of adult males on the breeding range.

In the dense population at Lower Quinsam Lake, a removal experiment was carried out on a study plot from May 1952 through June 1953 (Bendell, 1955c). In this experiment, yearling males did not replace adults and the area remained empty in 1952. The number of new adult males that appeared on the area in 1953 was what might be expected in a stable population. The experiment was done over only 1 year and with relatively few birds removed; however, the result suggests that no adults were made surplus by failure to obtain a territory in the dense population. Although the failure to find yearling replacements may be explained by the relatively few yearling males in the dense population, as noted earlier, the results of the removal experiment at Lower Quinsam Lake are in accord with those reached by direct observation. They also support the conclusions from the similar and larger study at Middle Quinsam Lake.

To find if there was a surplus of adult males at Middle Quinsam Lake we compared the number of new adult males that appeared each year on the removal and reference plots. If resident males excluded new males then there should be more new adult males shot from the removal plots than counted on the reference plots. It was relatively easy to count new adults on the removal area because the birds there were removed each year. This was not the case on the reference plots where an unbanded male might be the bird of a previous year or a new male.

Two methods were used to count new males on the reference plots each spring. The first used the mean annual death rate of adults and the fact that adult males return to the same territory each year until presumed dead. The hooting males were counted each year. We then calculated the number that would return the following year with a mean annual survival rate of 72 per cent. This gave the number of old birds in the second year. The difference between this expected number of old birds and the actual number of territorial males in the

second year was the number of new birds. For example, in 1959 there were 27 hooting males on the nine reference plots. With a 72 per cent survival the expected return was 20. From the census of 1960, there were 37. Thus the number of new males in 1960 was 37 minus 20 or 17. In counting hooting males, adults cannot be distinguished from yearlings. Since only 9 per cent of the hooters on the reference areas were yearlings this is considered a negligible error. Virtually all territorial males on the reference plots and general study area were adult birds.

The second method for estimating the number of new adult males was to map the distribution of new territories in previously vacant areas or note the broken occupancy of an old territory. The method underestimates the number of new males since some new males replace old from one year to the next and will be recorded as the old males. This error is reduced where banded males can be identified as continuous occupants of a territory.

Consider first the number of new adult males on the reference and removal plots by the method of mapping territories. The recruitment of new males to an area might be influenced by vegetation as well as the presence of established males. Hence the plots are classified by the kind of cover on them. The location and vegetation of the plots are illustrated in Figure 1. The estimate of the number of new adult breeding males in each year on the reference and removal plots as classified by cover is presented in Table 8. The data start in 1960, the first year that new birds were recorded.

Examine Table 8 for differences among the reference plots in the recruitment of new males. The data from all cover types when tested against each other by t-test did not differ significantly. However, we believe there were fewer males in the very dense cover. This conclusion is supported by data on the number of hooting males counted on all plots from 1959 through 1962. Here the numbers of hooting males on the reference and removal plots in very dense cover were significantly less than in all other types of vegetation. Hence, data

TABLE 9 Number of new adult hooting males on the reference plots, by calculation

Year	No. adult hooting males	Expected return	New males
1959	26		
1960	34	19	15
1961	34	24	10
1962	35	24	11

from the very dense vegetation are used separately and the rest are combined.

Note that in the table, a number of adult males were shot when silent. These are counted as hooting adults for reasons given earlier.

The reference and removal plots can now be compared for number of new males. From 1960 through 1962, on nine reference plots in open through dense cover, the average number of new adult hooting cocks per plot per year was 1.8. On two removal plots in very open type, over the same time, the average was 2.2. The two values do not show a statistically significant difference by t-test. Compare next the results from the reference and removal plots in very dense cover. On the one reference plot there was an average of one new male added each year. The same calculation for the two removal plots also gave an average value of one. We conclude from the method of mapping that virtually the same number of new adult males settled on the breeding range each year whether other territorial males were present or not.

Our other method of estimating numbers of new adult males was by calculation from the census of the plots and the mean annual mortality. On all reference plots except the one in very dense vegetation the numbers of adult hooters did not vary significantly, so they were pooled by year. The annual death rate was taken as 28 per cent, as determined earlier. The calculation of new birds for all reference plots except the one in very dense cover is set out in Table 9.

From Table 9, the nine reference plots contained 36 new adult hooting males, an average of 1.9 per plot per year. The two removal plots in comparable vegetation yielded 13, an average of 2.5 per plot per year (Table 8). The estimates of new males are close to those determined by mapping, and, similarly, the difference between the removal and reference areas is not statistically significant. The one reference plot in very dense cover received two new hooting males in 1960, and none in 1961 and 1962. The two removal plots in the same type of vege-

tation yielded six males over the 3 years. The results are in accord with those obtained on the other plots. Again, virtually the same number of new males were added to the breeding population whether territorial males were present or absent. Thus, at the densities of grouse observed at Lower and Middle Quinsam Lakes, territorial males apparently did not limit their density on the breeding range.

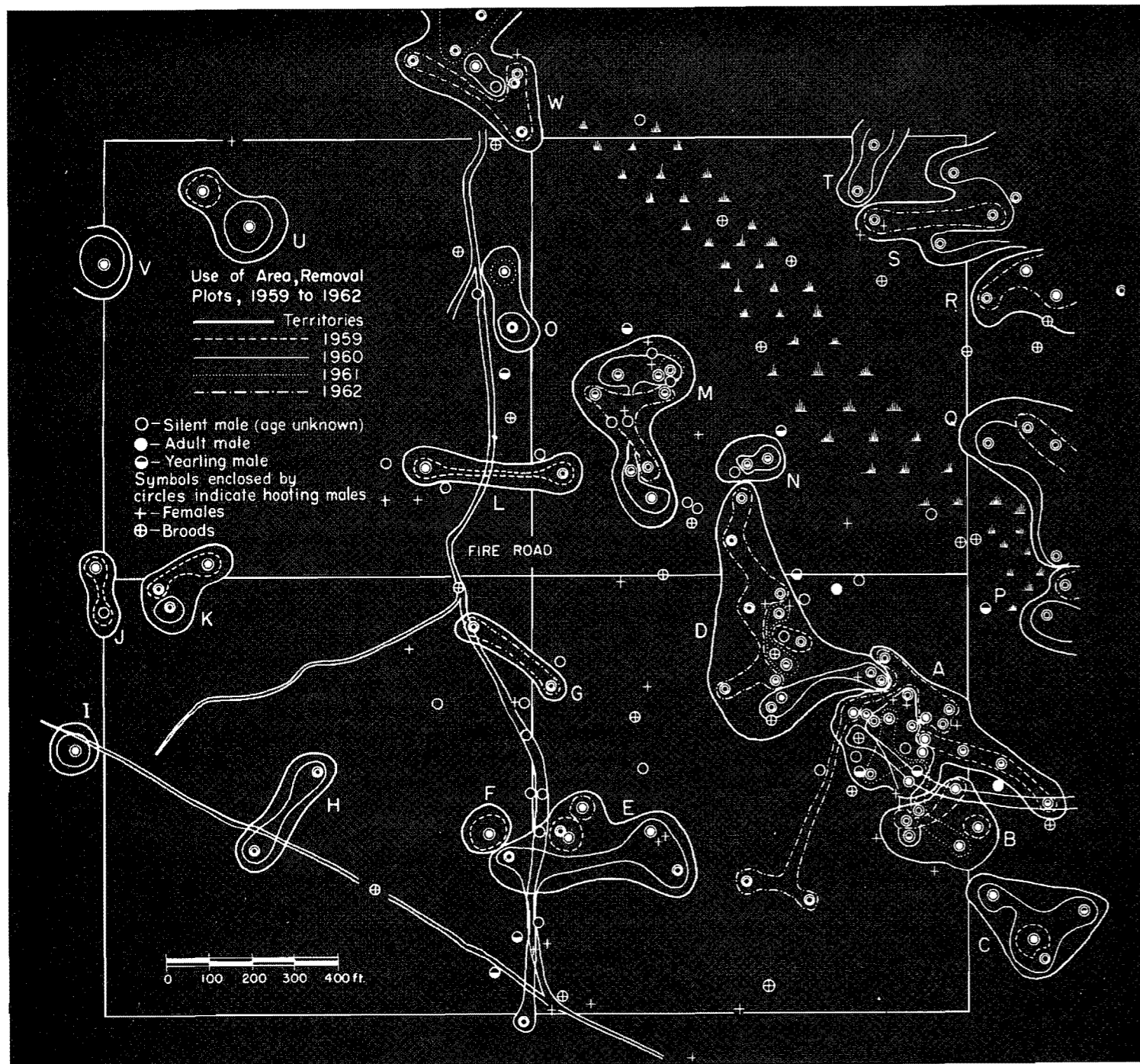
Numbers of grouse shot each month

Examine the kill of males on the breeding range in each month. This suggests that we were able to clear the removal area of male grouse. Each year, search and shooting began in early May at the latest and continued through August. The numbers of adults and yearlings taken by month from 1959 through 1962 were: March, 1; April, 12; May, 35; June, 4; July, 5; and August, 0. Clearly, most males were shot in May and the kill dropped markedly in June. Most of those shot in July can be regarded as migrants. Adult and yearling males, as noted, were found on the reference areas in the same numbers throughout May and June. Hence, most males were apparently collected from the removal plots each year. Moreover, once the area was cleared in May it remained virtually empty the rest of the summer. This is additional evidence that there was not a "floating" population of displaced males.

Replacement of males by place and time

The foregoing analysis was a treatment of the numerical data from the removal and reference plots. It is well established that breeding males occupy territory. Thus another way to determine how resident cocks affect others is through the analysis of the replacement of males on territories. We are concerned here with the place and sequence of shooting males from the removal area. If males on territory prevent new males from joining the breeding population, then when they are shot, surplus males should take their place. This contention is examined in adult and yearling males for each year.

Consider first the case of birds shot or observed on the removal area from 1959 through 1962 (Fig. 12). Most males were shot and their ages were determined. Others were simply observed and therefore could not be assigned to an age class. Note in Figure 12 that hooting males were shot in positions that tended to clump when data were plotted. These clusters are designated areas A to W. Silent adults and yearlings observed were generally close to, and easily placed with, a cluster of hooting

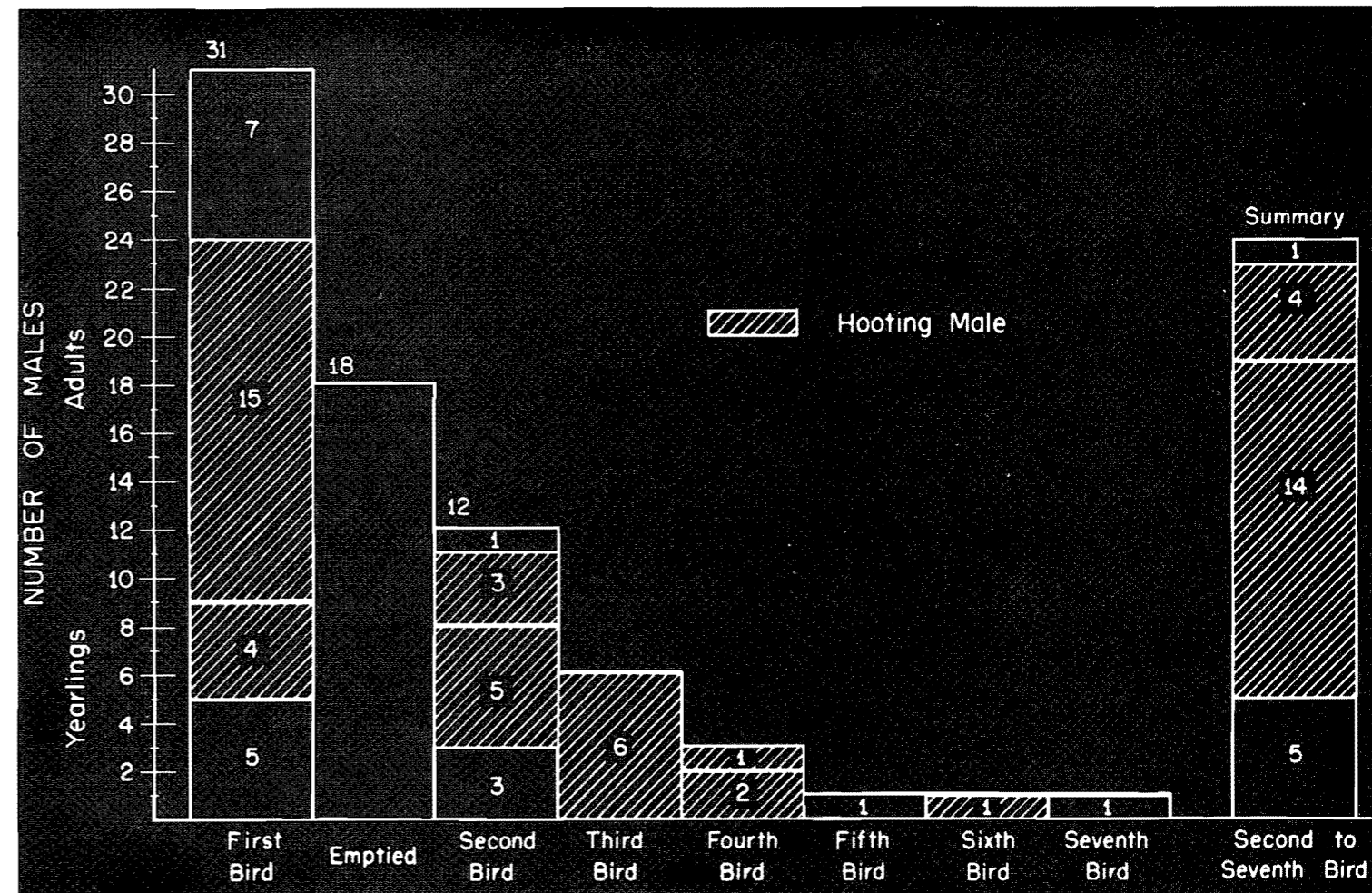


12 Points where grouse were observed or shot on the removal area, Middle Quinsam Lake, 1959 through 1962.

males. The areas are not territories in the usual sense for each is the space occupied by a succession of males. Nevertheless, the areas contained only one hooting male at a time and resemble in size and distribution the territories described on the reference plots. We regard the areas as territories. Some are of few points because only one or two males were shot or observed on them.

Much of the ensuing analysis of replacement and local distribution of grouse depends upon the argument that each area was the territory of one male. Therefore, this contention should be examined more closely. The number and position of areas were accurately determined from the location of hooting males. But when two or more birds were shot, was the second and later male a neighbour on another territory or a replacement on the same

territory? This question was resolved in a number of ways. The usual behaviour of neighbouring males is to hoot together. Thus when one bird was shot the observer noted the number and position of others remaining. The average distance between 36 hooting males measured in open vegetation was 290 feet. Hence, a male shot 300 feet or more from the position of another male could be taken as a neighbour. Most males considered replacements were shot or observed well under this distance and could be considered on the territory of an original male. If males replaced shot males, we would expect areas to be smaller than the territories of males on the reference plots for the same number of points. This is, in fact, the case. Then, the measurements to nearest neighbour provide evidence that males shot near the point of removal of a



13 Sequence of removal of hooting and silent adult and yearling males from territories on the removal plots, Middle Quinsam Lake, 1959 through 1962.

first male were replacement males. As noted, the average distance between first males shot on the removal area is larger than that between all males shot (Table 3). We believe that in most cases we distinguish correctly between two territories, and two males on one territory, that is, between a neighbour and a replacement bird. Doubtful cases are discussed as they occurred.

Consider first the sequence of replacement of males on the territories on the removal plots. The date and area of observing and shooting males over the 4 years are presented in Table 10. In the table, the territories that bordered on each other are grouped together. It was in these areas that replacement males and neighbouring males were most difficult to distinguish.

The data of Table 10 can be summarized graphically to show how males were replaced. The data from the 4 years were combined to give the total number of males shot first on the territories, the total number shot second, and so on for all males throughout a year. The males were also classified as to age and breeding behaviour. The analysis includes all males from March 22 through June. In July, only hooting males were counted; silent males were considered to be in migration. Two silent adult males shot on the removal area in July were excluded from the analysis. The results are presented in Figure 13.

From Figure 13, there were 31 times when a

male was shot in spring as the first bird on a territory. Eighteen (58 per cent) of these territories remained empty for the rest of the year after the first male was shot. This suggests that there was not a large number of males seeking territory or a shortage of space on the removal area.

In 12 cases where a male was shot from a territory a second male was taken from that area in the same year. Among these second or replacement males, four may be considered as breeding adults and five as hooting yearlings. Thus, where 26 breeding males were removed only 15 per cent were replaced by breeding adults that might be considered as surplus. If the "replacement" adults are examined, however, two may have been neighbours on areas A to D, and one was preceded by a silent yearling, and another by a silent adult very early in spring (Table 10). The silent male had relatively small testes and was likely migrating when shot. We conclude that when males were shot from their territories there was virtually no replacement by new adult males in that year. Again there was no apparent surplus of adult males to indicate their density was limited by territorial behaviour.

Note that among the second males taken from an area, five were hooting yearlings (Fig. 13). Where a third to seventh hooting male was shot virtually all were yearlings. One adult hooting male was shot as a fourth bird. It was on area A in

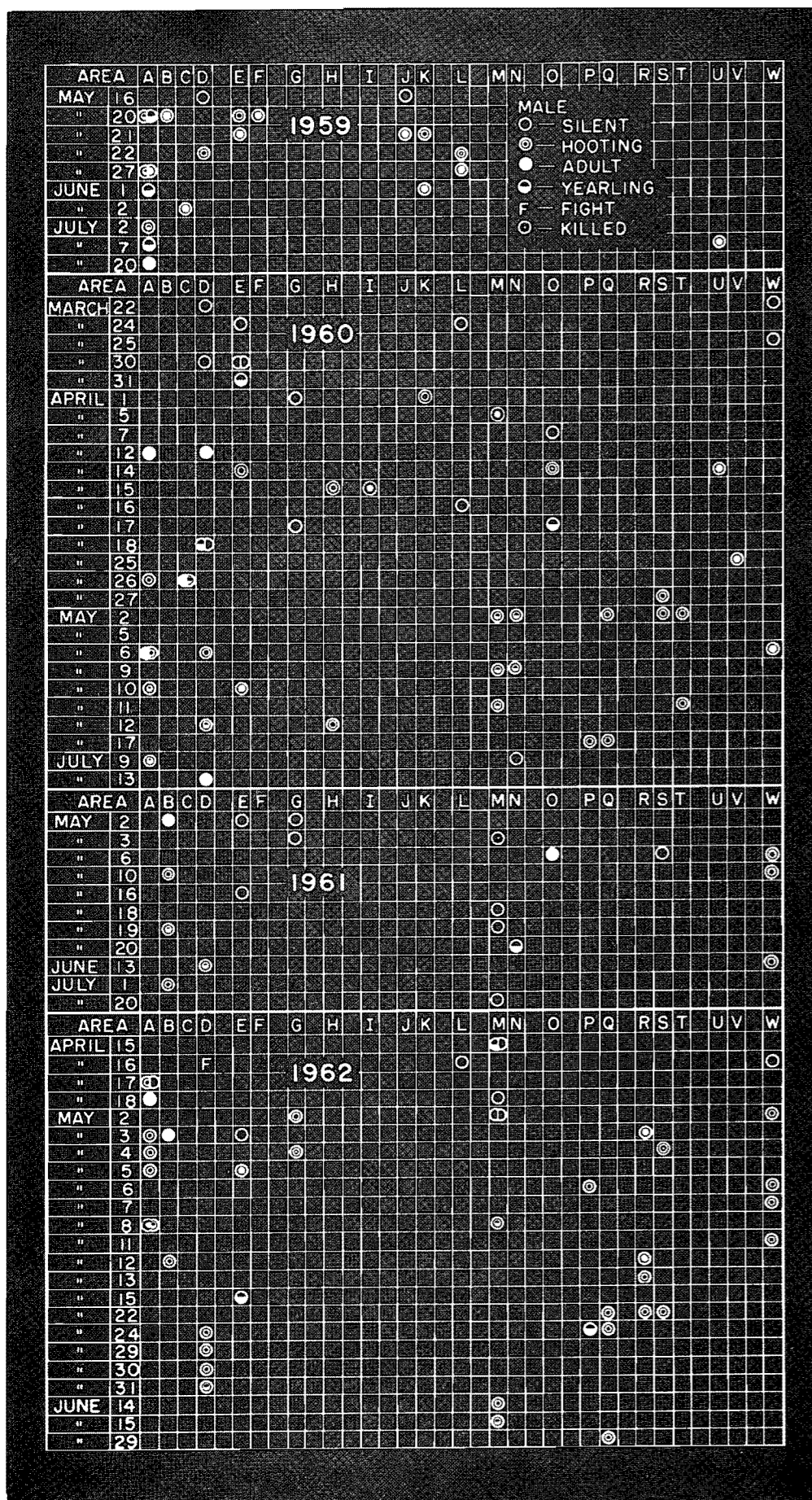


TABLE 10 Time and place of recording grouse on the removal area, Middle Quinsam Lake

1959, and might have been a neighbour to area C or D. Thus, after the first hooting birds of spring were shot, yearling males replaced some of them

and began to hoot. As the replacement yearlings were shot, some were replaced by other hooting yearlings. This result explains the difference in age

structure between hooting males of the removal plot and those from the reference areas. It also shows that territorial males prevented some yearling males from establishing territory.

The replacement of banded males that disappeared each year from the general study area provided a natural removal experiment to compare with the shooting of grouse. From 1960 through 1962, 39 males did not return to their territories in the year subsequent to banding. On these territories, 46 per cent (18) had new hooting males and 54 per cent (21) remained empty or were encroached upon by neighbouring males present the year before. This result supports the conclusion from the removal area that there were more suitable and available areas for territories than there were breeding males to fill them.

Distribution of yearling males on the removal area

As noted, yearling males were apparently attracted to the breeding cocks and therefore were found on their territories. Data from the removal area illustrate this point (Table 10). Yearling males were found on or near the territories of hooting males even though suitable areas for territory were available elsewhere on the removal plot. For example, in 1959 a hooting yearling was shot on May 27 in area A. It followed two yearlings, one hooting and one silent, shot on the same area on May 20. The male of May 27 might have located on areas such as G, M, N, or others used as territories in other years but empty in 1959 (Table 10). As was usual, the male turned up on an area that was previously occupied. Hence, some yearling males were apparently attracted to the territories of hooting males. Moreover, they did not hoot until the resident male was removed. Thus, yearling males were apparently attracted to territorial males and prevented from holding territory by them.

The length of time between the removal of a male from an area and its replacement by another shows the relationship between successive males on a territory. Over 4 years, 19 yearling males were shot as replacements. Approximately 80 per cent (15) were taken within a week after the first male was removed, and the rest within 2 to 6 weeks (Table 10). This suggests that most replacement yearlings were in the area of the male that they replaced, as would be expected if territorial males attracted yearlings.

The four yearlings that were taken on territories from 2 to 6 weeks after a hooting male was removed deserve comment. Since the established male was long gone before the later male occurred

on the area it is difficult to believe that the first male attracted and dominated its replacement. However, the replacement yearlings may have ranged widely for 2 to 6 weeks before returning to the territory of a particular male. As another possibility, the attractiveness of a site alone may elicit territorial behaviour (Bendell and Elliott, 1966). The males may have taken the time to come upon the territories.

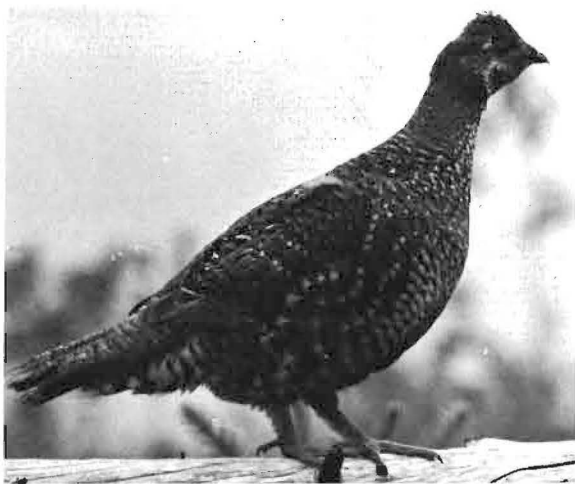
Behaviour of the breeding female

Our account of the female on the breeding range attempts, as does that of the male, to describe how their behaviour and population statistics relate to the regulation of numbers of grouse. Adult and yearling hens may be identified in the same way as described for males. The two age classes of hens are very much alike in behaviour, form, and colour and must be in the hand for accurate identification. We have found little difference between them in features important to population and therefore both ages are treated together unless noted.

On the breeding range, females are found most frequently alone. Occasionally, two hens are seen, apparently together. At times, particularly during the period of incubation, two to nine hens were observed at feeding areas, foraging within a few feet of each other. They come and go alone. Similarly, hens with brood seldom associate, although in late summer several broods may mingle in an area of lush vegetation. Rarely, two hens are observed with one brood, and one hen with a brood of chicks of two ages.

In the spring, most hens are located concealed under logs, stumps, and small conifers, in locations similar to those used for nest sites. When with broods, they are found relatively exposed on logs or stumps in open areas, particularly along the edges of old roads and in and around moist depressions with lush plant growth.

Like the cock, the hen has a number of elements of display consisting of sound, plumage, and movement, but we touch on only the most obvious here. The hens are not as vocal as the males but they have a much larger vocabulary. Like the males, they follow a diurnal rhythm of activity on the breeding range. Hens fly more than males and in the morning and evening they are most conspicuous by their sounds in flight. Before the hatch (approximately the last half of June), females fly and land without much sound or with a loud flutter of wings. The loud whirring of wings causes nearby males to hoot and move toward the sound, usually



14 (a-e) (a) Hen in neutral posture, (b) defence display of female, (c) hen on nest (by F. Zwickel), (d) nest, (e) nest site.

in full display. Females also make calls that excite the males.

One striking call of the hen is what we have named the whinny, and depicted in a sound spectrograph (Stirling, 1965; Stirling and Bendell, 1966). It is apparently the sound given by a hen to announce her presence and readiness to copulate. In preliminary tests of the call played from a record player on the breeding range, males began to hoot or hoot more loudly and broke into courting display. Males tended to move toward the speaker and this resulted at times in fights and the displacement of one male. Males seemed more aware of each other when the call was played and acted so as to space themselves and become conspicuous rather than move quickly and directly to the speaker. This is explained by our view that territorial behaviour functions to provide undisputed use of area for courtship.

When hens are flushed they usually cluck. Males never do this and so clucking may be used to distinguish the sex of a bird.

When with chicks, females display a different vocabulary. They make harsh calls or cackles which alarm the chicks, and soft clucking calls which draw and keep them together. Alarmed chicks crouch to the ground and remain motionless, or run a short distance and hide. Beyond about 2 weeks of age they flush and scatter widely when alarmed. They land in small trees or on the ground where they crouch motionless.

Chicks have a number of vocal signals. One, a soft whistle, elicits a soft cackle from the hen, and the same soft whistle from other chicks. The soft cackle with its variations and the soft whistle of the chicks cause the brood to gather on the hen or the chicks on each other. The whistle, when given loudly and quickly, usually elicits an intense defence display in the female (Fig. 14b). She rushes toward the chick and the cause of alarm. As chicks grow older they develop new calls of unknown function.

The defence display of the hen is most pronounced from the time of hatch of her young until they are 2 to 3 weeks of age. When a hen and brood are disturbed the female usually reacts with intense hissing and cackling, and rapid movements and plumage display. The head, neck, and wings are extended and the tail is spread. The feathers of the neck are elevated. The hen may rush at the observer with beating wings, and, at times, actually collide with him. After one or two attacks, the hen retreats 15 to 200 feet and walks in a circle in low

intensity defence display or on the alert and clucking. If a chick calls in alarm, the attack is renewed. If not, the hen moves away some 50 to 100 feet, crouches, and keeps silent until the first chick calls or she begins to gather her brood with a soft clucking. It is noteworthy that the defence display of the hen is similar to the courting display of the cock in a number of elements: elevation of the feathers of the neck and tail, tail spread, dragging wings, and perhaps the rush toward an intruder as a counterpart of the courting rush of the male.

Other plumage and movement displays of the hen resemble those of the cock although the comb above the eye is poorly developed and inconspicuous as compared to that of the male. Both sexes elevate the head and feathers of the crest and tail when alerted. The males when threatening, and both sexes when "freezing", compress their feathers and withdraw or flex their extremities.

The threat display of the male was not observed in females in the field. Antagonism between hens was rarely recorded and we have not found any particular display of hens that might function to fight or drive away another female. The defence display might fit into this category but it is found only in hens with young chicks. Hens make a variety of calls and perhaps some function to keep individuals apart, as suggested for the hooting of males.

Most lone females when alerted and pressed simply flush or walk away quickly. Once a hen without chicks was observed to give a display similar to the defence display. A male in full courting display and two females were together when disturbed. One female elevated the feathers of the neck and tail and dropped each wing. The tail was also slightly spread as she slowly walked away.

Hens on nest spend most of their time incubating (Fig. 14c). They leave the nest regularly for a short period in the morning and evening, deposit "clocker" droppings, feed, and perhaps dust. A clocker dropping is a large coiled dropping formed by a hen while incubating or brooding very young chicks. Movements from the nest may be as much as 1,000 feet and in a variety of directions. Hens move to and from their nests by flight or walking.

In addition to morning and evening movements, hens leave their nest infrequently and at irregular hours through the day. These movements are confined to a short distance from the nest. Again, they feed, dust, and evacuate.

When hens are disturbed from their nests they

flush, or jump erect and walk away. We have not observed a particular display of the hen that may be related to the defence of her nest or the distraction of an intruder from it.

Movements of females and females with brood

The movements of females in spring on the breeding range are of interest because they relate to the mating habits of blue grouse and possible interaction among females. Most of the data presented here on movements of lone hens and later hens with brood were obtained in the dense population at Lower Quinsam Lake from 1950 through 1952. Most of the data from both ranges were on grouse in open types of cover.

The movements of the female prior to the hatch are more extensive than those of the territorial male. Seven banded hens on a study plot at Lower Quinsam Lake were observed from 2 to 10 times each in April and May, 1952. Three of the hens were seen often enough to gain some impression of their range. This was achieved by drawing a line to join the outermost points of observation on each bird. A hen observed 10 times ranged an area of 12 acres on, and likely ranged as great an area off, the plot. Two hens seen five and six times had ranges of 4 acres. It is likely these observed ranges would have increased with more observations. On this plot, the average size of territory was 1.3 acres. Hence, the ranges of females were larger than the territories of males in the dense population at Lower Quinsam Lake.

Another way to describe and compare the movements of grouse is to measure the distance between successive sightings of a banded bird. If search is uniform over the range of movements then the

distance between sightings may be plotted as a frequency diagram to show extent of movement. This was done for the following kinds of birds in dense population at Lower Quinsam Lake and in sparse population at Middle Quinsam Lake: territorial males from April through August, hens from April through June, and hens with brood from June through August. The data from Lower Quinsam Lake were taken from 1952 for the males, 1951 and 1952 for the females, and from 1950 for females with brood. Data from Middle Quinsam Lake were from 1959 through 1962. The results of the analysis are presented in Table 11.

Approximately 80 per cent (215) of the sightings of males in dense population were less than 200 feet apart (Table 11). In sparse population, less than 40 per cent (61) of the sightings were this close. As noted, territories were larger and territorial males moved longer distances in sparse as compared to dense population.

In the analysis of the data from Lower Quinsam Lake, the distances between sightings of males were compared between April through May and June through August. The distances moved by males between observations were in the same frequency of occurrence for early and late in the season. This supports the point made earlier that males appear to establish the extent of territory early in spring and use it throughout the season.

Consider now the movements of lone females (Table 11). The data from Middle Quinsam Lake are too few to treat separately and are pooled with those from Lower Quinsam Lake. Note, in the females, only about 30 per cent (25) of the distances between sightings were less than 250 feet. Females

frequently moved at least 750 feet between sightings. Clearly, hens range over longer distances than do territorial males. Most movements by lone females are under 750 feet; moreover, their movements were in all directions. This suggests that they were on home ranges as shown by repeated observations of individual hens. The movements of females with brood are discussed later.

The movements of hens did not indicate interaction among them. The ranges of the seven banded females at Lower Quinsam Lake completely overlapped. The nests of two of the banded females were within the range of one and three other hens. Coupled with this, virtually no interaction was observed between hens. On mornings and evenings in May at Lower Quinsam Lake, two, three and at times as many as six hens foraged within 50 feet of each other in small clearings. Twice, one hen was observed to chase another. On two successive mornings an adult banded hen appeared in a clearing with another female. Each time, the adult chased the unbanded hen with a rush and cackle. The hen that was chased moved away a few feet and continued to forage. This kind of association in spring between an adult female and another hen may mean that a hen and some of her brood of the year before may remain together. The relationship may be broken by the aggressiveness of the adult hen.

What determines the distribution of lone hens on the breeding range in spring is largely unknown. Usually they appear evenly spaced although they show relatively little display of any kind. As shown later, hens appear to return to the same part of the breeding range in each year, and yearlings in their first spring disperse to areas beyond the range of their brood. We will also show that lone hens, like yearling males, are attracted to the territories of breeding males. Thus, at least, the distribution of hens, like that of yearling males, occurs in their first spring on the breeding range and is apparently related to the distribution of hooting males.

The ranges of hens relate to the breeding habits of blue grouse. The seven banded hens on a study plot at Lower Quinsam Lake were observed on the territories of a number of males in April and May. Each was noted on the territories of at least two males. One female was observed at different times on six territories, another on four, and a third was found on three. These data and the behaviour of breeding males suggest that both sexes are promiscuous in mating. There is good evidence that the male is promiscuous. We do not have complete enough observations on hens to rule out polyandry

or monandry as their mating behaviour.

Lone hens were observed most frequently on the territories of males. In 1951 and 1952 on two reference plots at Lower Quinsam Lake, the territories of males covered approximately 50 per cent and 30 per cent of each plot. Thus, if the sightings of hens were distributed at random, approximately 50 per cent and 30 per cent of hens seen on the two plots should have been on the territory of a male. On the plot with 50 per cent coverage by territories, 226 sightings were made of lone hens from April through June. Of these, 61 per cent (138) were on territories. Similarly, on the plot with 30 per cent coverage by territories, in 50 sightings of hens, 58 per cent (29) were on territories. Both deviations from the expected occurrence of sightings for a random distribution are statistically significant. The results suggest that lone hens occur most frequently on the territories of breeding males.

The same analysis was made with the data from the relatively sparse population at Middle Quinsam Lake. From April through June of 1959 through 1962, the observed territories of males covered approximately 33 per cent of the area of the two main reference plots. During the same period, of 47 sightings of hens, 72 per cent (34) were on or near a territory. Again, this departure from the expected distribution is statistically significant. Thus, in the sparse, as in the dense population, hens appeared to occur most frequently on the territories of breeding cocks.

There is support for the above method of analysis of distribution of hens from the results with clocker droppings, and hens with brood. Both data are from hens that are not likely associated with males. As noted later, there is no apparent association between territories and incubating hens (clocker droppings) and hens with brood. This suggests that the method does give a measure of association.

The occurrence of lone hens on the territories of cocks deserves further comment. As with yearling males, this can be explained by hens selecting the same habitat as cocks and (or) the cocks attracting the hens to their territories, presumably by hooting. Since the habitat used by the hens occurred throughout the study plots it seems most likely they were attracted by hooting males. While lone females were observed 47 times on the reference plots at Middle Quinsam Lake to the end of June from 1959 through 1962, only 19 sightings of hens were made on the removal plots during the same period. Since the two areas were similar except for the presence of males, we conclude that males attracted females

TABLE 11 Distance between sightings of territorial males, hens, and hens with brood in dense population at Lower Quinsam Lake and sparse population at Middle Quinsam Lake

		(Distance between sightings in feet)																		
Grouse		No. of grouse sightings	Total	0	50	100	150	200	250	300	350	400	450	500	550	600	650	700	750	+
				50	100	150	200	250	300	350	400	450	500	550	600	650	700	750	+	
Territorial males	L.Q.	7	266	34	63	71	47	26	12	5	4	2	1	1						
	M.Q.	8	159	10	8	20	23	22	10	12	9	11	7	15	3	3	4	0	2	
		(Distance between sightings in feet)																		
Lone females		No. of lone females sightings	Total	0	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000	3250	3500	3750	+
				250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000	3250	3500	3750	+	
Lone females	L.Q.	18	76	23	32	15	3	3	0	0	0	0								
	M.Q.	6	11	2	2	4	2	0	0	1	0	0								
		(Distance between sightings in feet)																		
Females with brood		No. of females with brood sightings	Total	0	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000	3250	3500	3750	+
				250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000	3250	3500	3750	+	
Females with brood	L.Q.	25	42	0	6	6	3	3	3	3	2	2	3	2	1	2	1	2	3	
	M.Q.	30	40	3	9	3	4	7	2	5	0	0	4	0	1	0	2	0	0	

to their territories. Thus, both yearling males and females are apparently attracted by territorial males. The occurrence of lone hens on the territories of males would be expected if one function of territorial behaviour was to attract a mate.

The distribution of nests was examined for their relationship to territories. A typical nest and the site of a nest in open vegetation are illustrated in Figures 14 d and e. The location of nests and territories on one plot at Lower Quinsam Lake from 1950 through 1952 is shown in Figure 7. The same data for Middle Quinsam Lake from 1959 through 1962 are shown in Figure 10. As noted, during 1951 and 1952 at Lower Quinsam Lake, territories of males covered approximately 30 and 50 per cent of each plot. The expected distribution of nests would have been one on to three off and one on to one off. The actual distribution was one on to four off and five on to four off. Of two nests found on the two main reference plots at Middle Quinsam Lake one was on and the other off the territory of a male. The few data suggest that the distribution of nests was not related to the territories of males.

Another approach to the distribution of incubating hens is by noting the occurrence of clocker droppings. At Lower Quinsam Lake in 1951 and 1952, where 30 per cent of one plot was in territory, 95 clockers were found. Of these, 29 per cent (28) were on and the remainder off a territory. On the other plot, with 50 per cent of the area in territory, 47 clockers were found. Of these, 55 per cent (26) were on a territory. These data suggest that there is no association between incubating hens and the territories of males.

Observations of hens with brood are important here as they pertain to the relationships between males and females, interaction between and within broods, and the range of broods. The last point bears on the locality and habitat selected by grouse at first breeding. Data on broods are taken from dense and sparse populations at Lower and Middle Quinsam Lakes. The distances between sightings of individually marked broods are presented in Table 11.

Compare the movements of females with brood in dense and sparse populations. The number of sightings at various distances was virtually the same. Hence, density of broods did not affect their movements. There is no suggestion from this comparison that broods interfered with the movements of other hens with brood.

The distances between sightings of hens with brood at Lower and Middle Quinsam Lakes were

pooled to compare with movements of other grouse. Approximately 60 per cent of the distances between sightings of marked hens with brood were greater than 1,000 feet (Table 11). Clearly, once the hens hatch their young they move relatively widely over the breeding range.

Hens with brood appear to move in all directions over the summer range. When direction of lines between sightings was noted all quadrants of the compass appeared equally represented. In 1950 at Lower Quinsam Lake, and from 1959 through 1962 at Middle Quinsam Lake, there was no indication of a substantial movement toward the winter range from June through August.

Some hens with brood move relatively long distances over the breeding range; others remain within a smaller area. Some idea of the range of broods is gained from the measurement of distance between first sighting and the farthest resighting. This measurement was made on 48 hens with brood on the two breeding ranges from June through August. Each hen with brood was observed from two to four times. The data were gathered in 1950 at Lower Quinsam Lake and 1959 through 1962 at Middle Quinsam Lake. Of the 48 hens with brood, 81 per cent (39) moved less than 3,000 feet, and 50 per cent (25) less than 1,500 feet. Nineteen per cent (9) of the sample ranged from 3,000 to 5,000 feet, which was the greatest distance from first to farthest resighting.

The ranges of females with brood are larger than those of hens prior to hatch, and most certainly larger than the territories of the males. This and the fact that most males leave the summer range during July show that there is apparently no relationship between territorial males and broods. This contention is supported by data on the distribution of hens with brood on the plots at Lower and Middle Quinsam Lakes. The analysis is the same as that used for relating the distribution of lone hens and clocker droppings to the territories of males. In 1951 and 1952 at Lower Quinsam Lake, 30 per cent of the area of one plot and 50 per cent of the other were in territory. In 40 sightings of broods on the first plot, 45 per cent (18) were on a territory. On the second plot, 67 sightings were made and 48 per cent (32) were on a territory. Hence, hens with brood occurred on territories by chance alone, as might be expected.

A comparison of the number of broods observed on the main reference and removal plots at Middle Quinsam Lake from 1959 through 1962 gives the same result. Compare the plots for number of

TABLE 12 Percentage of yearlings in the hen population, April through June, June through August, and pooled data, Middle Quinsam Lake, 1958 through 1962

Year	April through June (lone hens)			June through August (with brood)			Pooled % yearling
	Adult	Yearling	% yearling	Adult	Yearling	% yearling	
1958	—	—	—	6	0	0	0
1959	3	4	57	28	10	26	31
1960	7	19	73	46	23	33	44
1961	16	18	53	26	8	24	38
1962	14	10	42	38	13	25	31
Totals	40	51	56	144	54	27	36

broods as done for lone hens. From 1959 through 1962, 23 sightings of broods were made on or near the reference plots. On or near the removal plot in very open type, 25 sightings of broods were obtained. Thus, virtually the same number of broods was sighted on the area with territorial males as on the area without them. As noted, lone hens occurred more frequently on the areas with territorial males. From this and the foregoing analyses we conclude that the distribution of hens with brood is not related to the territories of males.

Like lone hens, hens with brood are observed most frequently alone. They seem to move independently over the burns. Different broods crossed and recrossed portions of the study areas, all appearing to share the summer range. Approximately 1,000 sightings were made of broods from hatch through August. Antagonism was never observed within or between broods. Chicks were held in an aviary in the field from hatch to the end of August. Although the density of young was much higher than in nature, little fighting occurred. With the lack of interaction between broods it is difficult to understand how they remain separate, for a number of factors tend to bring broods together. Perhaps, as speculated later for lone hens, broods simply avoid each other on the breeding range.

While most broods were observed singly, some occurred within several hundred feet of each other, and, at times, mingled. A few hens were observed with chicks of different age, indicating the exchange of young between broods. Opportunity for contact between broods is brought about by their behaviour and habitat selection. The chicks forage apart and up to distances of approximately 100 feet from the hen. Hens and chicks respond to the calls of other families. Moreover, broods are found most frequently in pockets and depressions with lush vegetation. These factors tend to bring broods together, particularly in the latter part of the summer when the vegetation over the burn is dry. In the dense

population at Lower Quinsam Lake, in and after July of a dry summer, groups of two and three hens with 10 to 20 young and single hens with 7 to 15 young were observed (Bendell, 1955a). This amount of association between broods is unusual.

Wing *et al.* (1944) report that the organization of broods begins to break down in late July. Other than as noted above, broods at Lower and Middle Quinsam Lakes appeared intact until early September, the latest time of observation. Our data indicate that most hens and their young migrate to the winter range as family units and without particular association with other broods.

In summary, lone hens live singly on home ranges and are apparently attracted by territorial males. There is no evidence from the behaviour and movements of hens that they interfered with one another. Antagonism was observed only once between lone hens and never between hens with brood or within broods. The ranges of hens overlap and include the territories of a number of males. Hens likely mate promiscuously. From time of incubation on, the movements of hens and of hens with brood are not related to the territories of males. Hens with brood move singly and widely over the summer range.

Numbers of yearling hens

The numbers of yearling hens provide a measure of the proportion of yearlings in the population on the breeding range. Unlike the males, all females appear to behave alike in spring so that each age class may be sampled without bias. The age structure and reproductive performance of females in sparse and dense populations may be compared as another measure of a possible interaction among hens that might be related to the regulation of numbers.

The data on hens sampled for age structure at Middle Quinsam Lake are in three parts: lone females observed April through June, females with brood observed June through August, and pooled values for each year. They are given in Table 12.

From the table, there was consistently a greater

percentage of yearlings in spring than yearlings with brood in summer. This cannot be shown statistically for each year. However, when the years are pooled, the greater number of yearling hens in spring as compared to summer is highly significant. In spring the proportion of yearlings was 56 per cent (51/91) and in summer, 27 per cent (54/198). As with the males, age ratios of females should be specific to time and stage of reproduction for they change from spring to summer. Our estimate of the percentage of yearling hens in the population of hens at Middle Quinsam Lake, from April through June, 1959 through 1962, is 56 per cent. In Table 12, 1960 appears a year of a strong yearling age class. The calculation ignores the possibility that the number of yearlings fluctuated from year to year.

As with males, there is the likelihood that the age structure changes within the periods designated as spring and summer. This can be examined as for males but there are fewer data for hens and these are broken by the changes in their breeding behaviour, as noted. The data on lone females were separated into the months of April, May, and June, from 1958 through 1962. The percentage of yearlings in each month was: April, 78 (7); May, 54 (31); and June, 54 (14). The relatively high percentage of yearlings in April was from 1960 and this carried through the summer (Table 12). We conclude that the percentage of yearlings among the hens on the breeding range remained virtually unchanged from April through June. This is an important point because it shows that some yearlings did not disappear as might be expected if interaction affected the dispersal of hens. Additional evidence for the contention that all hens on the summer range are part of the breeding population will be presented shortly.

The age structure of the hens at Middle Quinsam Lake represents the numbers of yearlings in spring in sparse population. A similar calculation of numbers of yearling females in spring was made for the dense population at Lower Quinsam Lake from 1950 through 1952. In 66 lone females sampled from April through June, 26 per cent (17) were yearlings. In 86 hens with brood, 20 per cent (17) were yearlings. The difference in age structure of hens between dense and sparse populations was statistically significant, that of hens with brood being at the 5 per cent level. When lone hens and hens with brood were pooled the difference in age structure between dense and sparse populations was highly significant. Hence, there were more yearlings among the hens in sparse population than in dense. This is the same result as obtained with males. With

the hen data, it seems most likely that there were fewer yearling birds in dense as compared to sparse population. If the age structure of the hens applies to the cocks, then the percentage of yearling birds of both sexes in spring was 26 percent at Lower Quinsam Lake and 56 percent at Middle Quinsam Lake.

The number of yearling males in the male population at Middle Quinsam Lake was calculated indirectly at approximately 34–36 per cent. The same calculation for Lower Quinsam Lake gave 17 per cent. If it is assumed that there is an equal sex ratio in all age classes, a likely assumption, then yearling hens apparently outnumber yearling cocks on the breeding range by a margin of approximately 2:1.

There is support from direct observation for the contention that more yearling hens than cocks occur on the breeding range. In spring, yearling cocks are apparently found as easily as yearling hens. Hence, the numbers of each sex banded or collected should show their relative abundance. At Lower Quinsam Lake, from 1951 through 1952, 17 hens were recorded to 7 males. At Middle Quinsam Lake, from 1959 through 1962, there were 37 females and 20 males. In both cases, hens outnumbered cocks by about 2 to 1, as predicted. Apparently then, in the yearlings on the breeding range, hens are almost twice as numerous as the cocks. Boag (1964) reports a sex ratio of 233 females to 100 males among yearlings at Gorge Creek, Alberta.

The absence of some yearling males from the lowlands is suggested by Beer (1943), Bendell (1955a), and Buss and Schottelius (1954). Since sex ratios of grouse older than a year of age appear equal (still to be proved) then the simplest explanation for the lower numbers of yearling males is that approximately half do not migrate from the winter range until they are adult, that is, in their second spring after hatch. As will be shown, virtually all yearling hens on the summer range breed. Hence, the absence of some yearling males links migration with reproduction and suggests the non-migrating males are sexually immature compared to hens of the same age and older grouse.

Note that apparently the same proportion of yearling males migrated onto the lowlands in both sparse and dense populations. This suggests that the numbers of yearling males on the breeding range were not related to density of grouse.

The change in age ratio of hens from spring to summer can be explained in a number of ways. First, yearling hens, as suspected of some yearling males, may leave the summer range shortly after arrival. Second, yearling hens are not as successful as adult

hens in raising young and therefore occur less frequently in the population of hens with brood. As a third possibility, there may be biases in the way adult and yearling hens are found each year that would affect their observed relative abundance. These might be amount of movement, time of nesting, and amount of re-nesting. Differences in these and other traits between age classes, particularly if they changed from year to year, would make an observed age structure depart as yet unknown amount from the true composition. The available data suggest that age structure does not change, at least from time of arrival until the end of June. Hence, the difference in age structure between lone hens and hens with brood is related to success in rearing young. Virtually all hens examined at Middle Quinsam Lake were breeding. This will be discussed later. We conclude that most yearling hens nested but were not as successful in rearing chicks as the adults. Note that in dense population yearling hens made up 26 per cent of lone hens and 20 per cent of hens with brood. In sparse population the proportions were 56 and 28 per cent. This suggests that yearling hens were less successful in rearing young in sparse as compared to dense population. The mortality of young is treated more fully in Zwickel (1965) and will be presented in a later report (Zwickel and Bendell, 1967).

The data on age ratios in hens, as in males, can be used to compare the proportion of yearlings each year in the breeding population. The numbers of adults and yearlings sampled in the spring and summer of each year were pooled. This gave the percentage of yearlings in the hen population from March through August in each year from 1958 through 1962 at Middle Quinsam Lake (Table 12). The values do not show a statistically significant difference. Hence, the age structure of the hens at Middle Quinsam Lake did not show a statistically significant variation over the years 1959 through 1962. This result is the same as that obtained from the analysis of age structure of the males (Table 5).

Note that the percentages of yearlings among females and females with brood in each year are lower than those calculated on hens in spring (Table 12). The latter calculation underestimates the percentage of yearlings because they drop from the population of hens with brood over the summer.

Numbers of breeding hens and size of clutch

Yearling hens appear to make up a greater proportion of the breeding population than yearling males. The numbers of hens breeding and clutch size are important points for they relate to the abundance

of grouse. Non-breeding hens and reduced size of clutch might be symptoms of some process of population regulation. At Lower Quinsam Lake, 70 per cent of yearlings and 96 per cent of adults were breeding (Bendell, 1955c). At Middle Quinsam Lake, in April through June of 1959 through 1962, 21 adult and 25 yearling females were examined for breeding condition. They were classified as breeding or non-breeding on the basis of size of reproductive organs, number of shed and maturing follicles, and presence or absence of a brood patch. In addition, hens were collected on nests.

Among the females not on nests when examined, 95 per cent (20) of the adults and 80 per cent (20) of the yearlings were breeding. Hence virtually all adult and most yearling hens in sparse population at Middle Quinsam Lake were breeding birds. The result is similar to that obtained from the dense population at Lower Quinsam Lake. When the data from both breeding ranges are pooled, 96 per cent (66/69) of adult hens and 76 per cent (29/38) of yearling hens were breeding.

The age structure of nesting hens reflects the proportion of yearlings in the population in spring. In 27 nests at Middle Quinsam Lake, 41 per cent (11) were those of yearling hens. If the proportion of yearling hens in the population in spring was approximately 56 per cent (as derived from Table 12) and 95 per cent of the adults and 80 per cent of the yearlings were breeding, then we would expect to find that of 27 nests, 48 per cent (13) belonged to yearling females. Actually 11 nests of yearlings were found. This is good evidence that most yearling hens in spring were breeding birds and remained on the breeding range at least through incubation. The latter point supports the same conclusion derived from the comparison of the age structure of hens in each month of spring.

Size of clutch was determined from the number of eggs under incubating hens. Clutch size in the dense population at Lower Quinsam Lake was estimated from six nests of adult hens as an average of 6.00 ± 0.66 eggs. The 0.66 gives the 95 per cent confidence interval. The size of clutch of yearlings appears to be the same as that of adults (Bendell, 1955c). In sparse population at Middle Quinsam Lake, from 1960 through 1963, we found 30 nests: 16 of adults, 9 of yearlings, and the rest unidentified as to age of hen. There was no statistically demonstrable difference in clutch size with year or age of hen. Average clutch size of the 30 nests was 6.27 ± 0.35 eggs. Note that in sparse and dense populations virtually the same numbers of hens

were breeding and produced approximately the same size of clutch. The result does not support the concept of a density-dependent interaction among grouse that would affect the numbers of hens breeding and their size of clutch. Birth rate appears high and constant from year to year.

Return and death rate of females

Breeding males return to the same territory each year until presumed dead. Females apparently return to the same breeding range but this cannot be documented as well as in the males. As noted, females range over a relatively large area and have neither territories nor song posts. Hence, finding hens in and between years was never certain, and therefore their death rate and homing tendency cannot be determined accurately.

As noted, seven hens banded in April and May, 1952, on a study plot were seen over the breeding season. Four hens were banded on the study plots at Lower Quinsam Lake in the spring of 1950. These areas were searched thoroughly and any grouse on them likely were seen at least once in a year. In the spring of 1951, three of the hens were observed and another eight were banded. In 1952, two of the first four and five of the eight were checked on the plots. These data suggest that hens return to the same home range each year, stay through the breeding season, and have a low annual mortality. A hen banded in 1952 was collected approximately 250 feet from the point of banding in 1958. The pooled data on hens banded in one year and resighted the next give an estimate of the mean annual death rate of hens of 33 per cent (5/15). This is remarkably close to the death rate of adult and yearling males and suggests that both sexes have the same death rate from yearling age in spring, and are committed from this age on to a particular portion of the breeding range. Zwickel (1965) banded and recensused 70 male and 68 female blue grouse on another breeding range approximately 25 miles away. He found the mean annual rate of death to be 27 per cent in males and 38 per cent in females. Death rates did not vary significantly between adults and yearlings or between sexes. These results are similar to our own and augment the few data we present on hens.

Interaction among hens

Data on hens were presented to determine how their behaviour and population statistics on the breeding range might relate to the regulation of numbers. Hens, and hens with brood, are usually found apart. In sparse and dense populations, virtually no antagonism was observed between hens,

between hens with brood, or within broods. The movements of hens when alone and with brood appeared similar in sparse and dense populations. There was no evidence from the numbers of grouse during spring or from age ratios that hens left the summer range before attempting to breed. In both populations, virtually all adult and most yearling hens bred, and size of clutch was the same. The few data suggest that the mean annual death rate of hens was low and comparable to that of males.

There were apparent differences between sparse and dense populations in age structure of hens and in loss of young by yearling hens. In the sparse population there were more yearlings of both sexes, and more yearling hens apparently failed to rear young.

The greater proportion of yearlings in the sparse population may relate to density, but there is no evidence that this was a result of interaction among grouse, at least on the summer range. Similarly, if interaction explained the loss of young by yearling hens then it is difficult to see why this apparently occurred more frequently in the sparse population. As shown, some yearling males were suppressed by adult males and apparently prevented from breeding. A comparable form of interaction could not have occurred among the hens, for virtually all bred. Thus, from the data we have on hens in the sparse and the dense populations, and with the lack of contrary evidence, there was apparently no interaction among hens important to the regulation of numbers on the breeding range.

The return and death rate of the young

Since adults and yearlings have a low and constant death rate, a high and constant birth rate, and do not disperse, then population regulation must be related to the fate of the young. By fate we mean their survival to 1 year of age and where they settle as breeding birds. Boag (1964), Bauer (1962), and Mussehl (1960) show the poor return of banded chicks to their natal range. A few chicks are resighted as breeding birds near the point of banding, but most are never seen again. Of 88 chicks marked in 7 years by Boag, only 5, or approximately 6 per cent, were resighted. From Bauer's data, Boag calculated that, of 600 chicks banded, only 5, or less than 1 per cent, were seen again. Our banding of chicks has yielded similar results. At Lower Quinsam Lake, from 1950 through 1951, we banded 37 chicks. None was resighted in a year subsequent to banding up to and including 1953. At Middle Quinsam Lake, from 1959 through 1962, we banded 250

chicks. Five, or 2 per cent, were resighted in subsequent years.

A measure of the direction and minimum distance of movement between banding and resighting of a chick is obtained by joining these points with a straight line. Two males banded as chicks in 1960 were recovered in 1962. One had moved 2,260 feet to the southeast, the other 6,860 feet to the west. One was collected as a hooting bird, the other as a silent male in May on the removal area.

Two hens banded as chicks in 1960 were recorded in later years. One of the hens was in the same brood as the male that moved 2,260 feet. The hen moved 5,800 feet to the southwest and was recaptured on May 23, 1961, as a lone hen. On two occasions later that year she was observed with a brood. These siblings settled as breeding birds more than a mile apart, consequently a mating between brother and sister was most unlikely.

The other hen banded in 1960 was located in 1961 as a lone breeding bird, 3,270 feet west of point of capture. She was observed later in the year with a brood approximately 500 feet to the south. The same hen was recorded with a brood in 1962, approximately 1,200 feet to the northeast. Note that the distance between capture as a chick and as a breeding hen was greater than that between observations of the same hen when with a brood.

The fifth and last recovery of a banded chick was a hen banded in 1961 and recovered as a breeding bird in May of 1962. She had moved 7,900 feet south from point of banding.

Two points may be made from the data on recovery of banded chicks. Most movements of broods, and of males between the age of yearling and adult, were less than 2,000 feet (Tables 4 and 11). The five banded chicks all moved more than 2,000 feet from point of capture to point of discovery as a breeding bird. The average movement was 5,200 feet with a range of 2,260 to 7,900 feet. The travels of the chicks were greater than the movements of hens with brood. Compared to the movements of chicks on the breeding range between years, silent yearling males appear settled. This suggests that the five chicks that were recovered had dispersed over the breeding range.

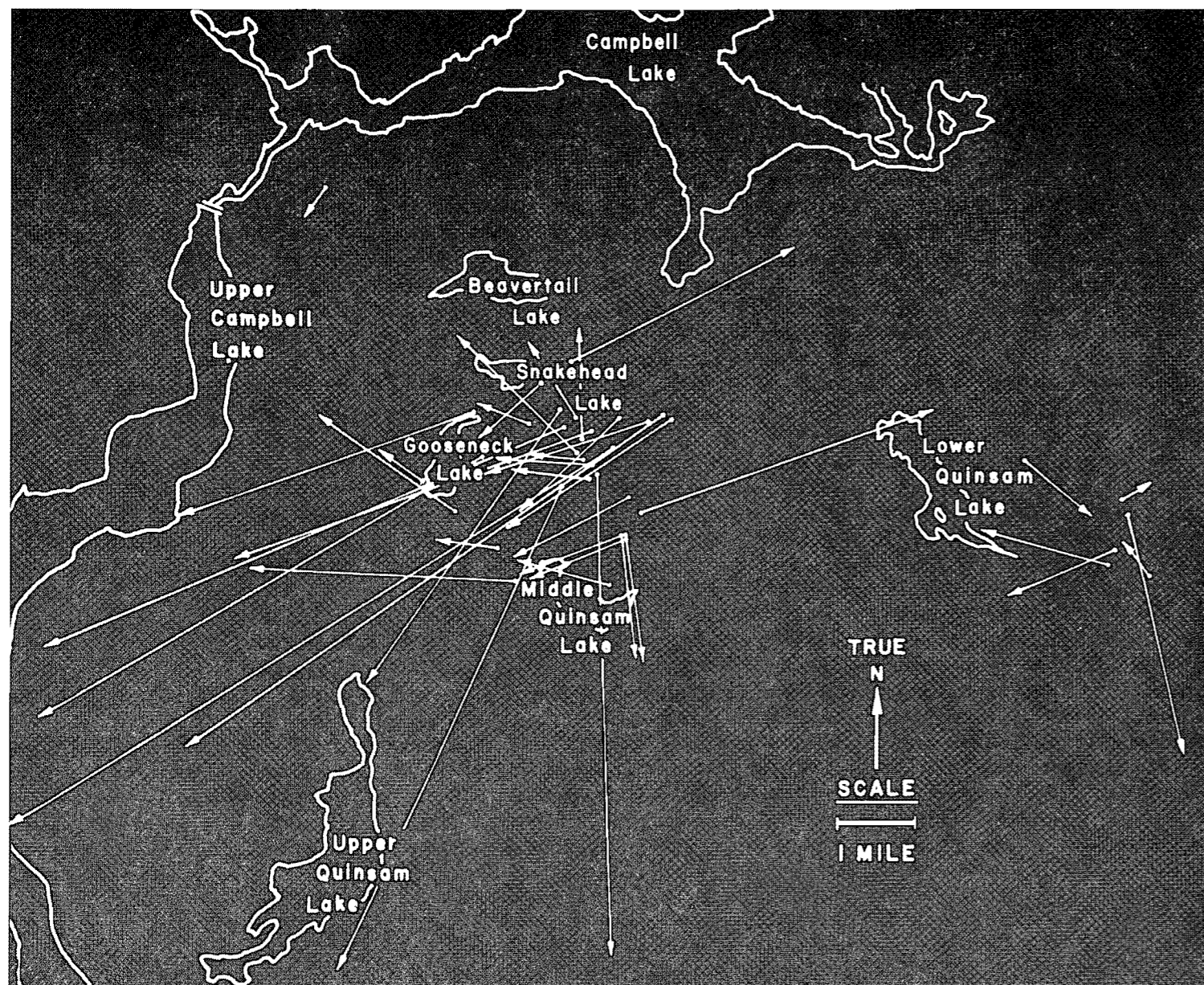
As a second point, the rate of dispersal and death of chicks between late summer and spring must be relatively high. There is heavy mortality of chicks in the first month of life but enough escape to increase population if later mortality and dispersal do not occur (Bendell, 1955c; Zwickel, 1965; Zwickel and Bendell, 1967). The sample of 250

chicks used here was selected from all those banded to provide birds robust enough to survive beyond the period of early mortality. There is very little further loss of young on the summer range (Bendell, 1955c; Zwickel, 1965; Zwickel and Bendell, 1967; and unpublished data). Moreover, as noted, most chicks remain on the lowlands in broods within a brood range at least through August. Hence, the disappearance of young occurs between September and April while they are beyond the breeding range. If banded chicks returned to the study areas we would expect to resight them nearly as frequently as silent yearlings are recovered as hooting adults. As noted, most of the yearling males banded in one year are observed the next. Of the sample of 250 banded chicks, 125 were males (Bendell, 1955b). Only two, or approximately 2 per cent, were seen again. Hence, the rate of death and dispersal of grouse from chick in autumn to yearling in spring appears to be high in comparison to older grouse. This loss of young might be part of the process of population regulation.

The autumn migration

The movement of blue grouse from the lowland summer range to a winter range in the mountains completes the cycle of their migratory behaviour. The autumn migration is interesting in itself and as a clue to where birds from a particular breeding population go for the winter. Some of the migration is coincident with the hunting season so that its time and speed within and between years will affect the harvest. As noted, observations of banded hens with brood and trends in grouse observed per hour indicate there is little movement of hens with brood from the summer range until after August. However, adult and yearling males and possibly lone hens leave before this time.

The return of bands from birds shot by hunters provided data on movements of grouse after August. When a band was returned we asked when and where it was taken and if the grouse was alone or with a brood when shot. We could check whether a bird was alone or with a brood when shot against what we had observed when the bird was last seen on the study area. A chick was usually shot as a member of a brood. Even if not so reported it was considered as an observation of a hen and brood because work on the winter range suggests that hens and their young remain together into the first range of mountains at least (David King, pers. comm.). Possibly the greatest weakness in the use of hunter returns to plot grouse move-



ments is that we do not know, as yet, the areas searched by hunters. This means that although the reports of bands show where birds were shot they may not provide a representative sample of the movements of grouse.

We obtained records from 49 grouse banded at Middle Quinsam Lake from 1959 through 1963 and in 1966. These data were augmented with six records from Lower Quinsam Lake obtained in the years 1950 through 1952. Three of the 55 grouse were adult males and the rest lone hens and hens with brood. Most were last seen in July and (or) August and approximately 80 per cent were

shot up to and including September 15.

The distance and direction moved by grouse were obtained by drawing a straight line between the point where they were last seen by us and the point where they were shot. This is illustrated in Figure 15 for grouse that had moved beyond the general area of study. Most movements of grouse were in a westerly direction and ranged from a mile to 10 miles. The movement of grouse to the west contrasts with the movement in all directions of broods observed until the end of August on the study areas. This is our main argument that grouse were migrating and not simply expanding their

15 Direction and minimum distance of movement of grouse (mostly hens with brood) beyond the study area at Lower Quinsam Lake, 1950 through 1952, and Middle Quinsam Lake, 1959 through 1966.

brood range. The westerly movement took the birds into the mountains and onto the winter range.

Figure 15 suggests that grouse from the dense population at Lower Quinsam Lake and sparse population at Middle Quinsam Lake were heading toward the mountains at all angles up to 180 degrees. Birds from the dense population apparently went to the same winter range as those from the sparse population. Moreover, from the spreading lines of travel it seems that grouse from a particular summer range winter many miles apart. As far as we know, the winter range of grouse has not changed; the same winter range has supported the dense and sparse populations. If grouse from a particular breeding population winter separately, it is difficult to see how social behaviour on the winter range can regulate their numbers on the summer range. Since the same winter range has apparently supported high and low numbers of grouse, differences in abundance must be related in part to some aspect of the summer range, some change in the quality of stock, or both. It seems certain that males and lone hens from a particular summer range winter apart. However, a brood stays together into the winter range and this association between hen and young and the quality of young produced from a particular summer range may be important to population regulation.

The directions moved by grouse beyond the general study areas were classified according to eight points of the compass. In 40 instances, 40 per cent headed southwest. This was the most direct way into the mountains and upland forests.

A measurement of the minimum distance of migration is given by the distance between point of last sighting and point where a bird was shot. In this analysis, all 55 grouse were included. Thirty-five per cent were shot under a mile from where last sighted on the study area, 40 per cent had travelled from 1 to 2 miles, and 25 per cent from 2 to 10 miles. Contrast this distribution of movements with that of hens with brood where first and last sightings were obtained in July and August. Here, 81 per cent of the movements were under approximately one-half mile and the maximum distance moved was 1 mile. Clearly, the movements of grouse during early September are longer, and directionally oriented, showing that migration was in progress. If grouse that had travelled less than 1 mile are considered as still moving over a brood range, then 35 per cent of the sample of grouse shot by hunters were still resident. Hence, by September 15, 65 per cent of the grouse at

Middle and Lower Quinsam Lakes had begun to migrate. As noted, we think there is little migration of broods until the end of August. If more than half the grouse begin to migrate between September 1 and September 15, this suggests a rapid onset of migratory behaviour. Most of the data were from hens with brood. Their departure, then, occurs at a faster rate than that of the cocks, which occurs over 2 or more months.

The average distance moved by 28 grouse considered as migrants was 3.6 miles with a range of 1-10 miles. If this movement occurred to September 15, then grouse (mostly hens with brood) were migrating at an average rate of approximately 2 miles per week. This suggests that by the end of September at least 65 per cent of the population at Middle Quinsam Lake would be an average of 8 miles from the summer range and into the mountains and subalpine forest. There they are in a habitat greatly different from the brood range and beyond the easy reach of hunters. As discussed later, few blue grouse are shot by hunters, and those taken are within a few days after the hunting season begins. This pattern of harvest is partly explained by the migratory behaviour of grouse.

The data on grouse shot by hunters were examined to determine whether broods pass through the study area in July and August, whether lone hens leave the summer range before hens with brood, and whether adult males migrate by hunting season. Hens and hens with brood were classified as to whether they were last seen in July or in August. Of 178 last seen in July, 18 were shot as residents and 11 as migrants. In 107 last observed in August, 12 were shot as residents and 9 as migrants. If birds last seen in July were migrating ahead of birds last seen in August, we would expect a larger percentage of August birds to be shot and also recorded as residents. Neither occurred, which suggests lone hens and hens with brood observed in July and August migrated at the same time.

The census of lone hens over the summer suggests that, like the males, they leave the lowlands before hens with brood. This was examined by classifying the data on hens and hens with brood into migrant and resident. Seven lone hens were shot as migrants and two as residents. Among the hens with brood, 23 were migrants and 18 residents. The difference between the ratios is not statistically significant, but the tend-

Discussion

ency is for more lone hens to be migrants. This supports the notion that broodless hens leave the summer range before hens with brood.

Very few adult males were taken by hunters. Three were shot that had migrated 4, 8, and 10 miles from their territories on the study area at Middle Quinsam Lake. The low return of banded males and their relatively long travels are in keeping with their early departure from the lowlands.

A number of authors have speculated on the cause of migration in blue grouse (Bendell, 1955a; in Buss, 1960; Mussehl, 1960; Wing, 1947). Arrival and departure are reputed to vary between years and to be related to extremes of weather, desiccation of the summer range, and failure of the food supply. One explanation given for the ascent in autumn is the later ripening of berries in the mountains. As we have seen, adult males leave before hens with brood, and there appears to be a relatively rapid movement into the uplands in the first half of September. There is apparently little difference in time of migration between years, although our data are too few to be sure of this. Buss (1960) notes that the migration of blue grouse is probably a fundamental characteristic of the species. Our observations also suggest that the migration of blue grouse is comparable to that of other migratory birds. In migratory species, migration is a twice-a-year movement, regularly timed, oriented, and determined largely by internal events. Since blue grouse appear to migrate in this manner, immediate circumstances, such as a ripening of berries, are unlikely to alter greatly their schedule for migration.

The main objective of this work was to determine whether blue grouse limited their own density on the breeding range. The concept of a species limiting its own numbers is not new and is usually considered possible when other limiting factors, such as shortage of food and predation, are not operative. Hence the principle of saturation density, or the idea that a species has a minimum compressibility, as expressed by Leopold (1933), Errington (1956), and others. If this concept is valid, territorial behaviour may limit the density of population at one time but not at another. And the importance of territorial behaviour as a factor regulating population may change with density and conclusions obtained at one density may not be applicable at another.

On the other hand, Wynne-Edwards (1962) maintains that animals constantly adjust their rates of mortality and natality through their behaviour and keep their numbers at an optimum level with respect to their resources. Hence, we might expect territorial behaviour to limit density and create a surplus of birds each year. In this connection, the work of Jenkins *et al.* (1964b) is probably most relevant because they worked with a tetraonid, the red grouse. They concluded, "In short, red grouse numbers are regulated by the number of cocks successful in obtaining territories, with the surplus mostly removed by predators and starvation." Territorial red grouse of both sexes, at all densities, excluded grouse of both sexes to make them surplus. Moreover, most surplus birds were at a disadvantage as compared to established pairs; they were driven into inadequate habitats and died of starvation or were killed by predators. Most surplus red grouse never contribute to the population. The presence of this surplus in all densities seems good evidence for autoregulation of population by established grouse.

Chitty (1960, 1964) and Krebs (1964) also see the behaviour of birds and mammals as an important part of the process of population regulation. However, they postulate that with increasing density of population there is a change in the genetic quality of its members and this in turn determines the amount of fighting between them. The amount of interaction affects rates of birth, death, and dispersal, and so regulates population. A change in body weight of an individual is taken as another indication of the change in genetic quality of members of a population. Animals of increasing and decreasing populations might be expected to show differences in aggressive behaviour, birth and death rates, and weight. Watson (1964) shows that the

size of territory in red grouse is related to the aggressiveness of males. The more aggressive cocks have larger territories.

We have studied blue grouse in densities of approximately 0.44 and 0.13 breeding males per acre. The dense population was stable or declining. The sparse population was stable or expanding. Adult males are strongly territorial on the breeding range. Direct observation of grouse gave no evidence that their behaviour determined their breeding density. A removal experiment conducted over 1 year in the dense population failed to reveal a surplus of males. A more detailed removal experiment carried on over 4 years in the sparse population indicated that virtually the same number of new adult males was added to the population in areas with and without resident territorial males. We did not find a surplus of adult males. Moreover, in observing grouse on the breeding range we have never encountered individuals that appeared as social outcasts and doomed to die.

Some yearling males might be considered surplus breeders for when adult males were shot, yearling males frequently replaced them and began to hoot. However, yearling males banded on the breeding range appear to have the same survival rate as adults, and establish territory among older males when they become 2 years of age. Hence, the surplus yearling males represent a delayed addition to the breeding population rather than a by-product of population regulation.

Our general conclusion is that the territorial behaviour of males in spring did not limit the breeding density of grouse. It is noteworthy that Stewart and Aldrich (1951), in their removal experiment, found that some species were not saturated. A single male ruffed grouse (*Bonasa umbellus*) shot on their experimental plot was not replaced. Similarly, Dorney (1960) removed 10 territorial male ruffed grouse from a 360-acre area in the spring. When the 10 were removed, two yearling males appeared on two of the territories. After the two replacements were removed, no others appeared. This result is in accord with our own and suggests that in these ruffed grouse, territorial males did not create a large surplus, and birds that were surplus were yearlings. Presumably, when 2 years of age, all surviving ruffed grouse join the breeding population.

In contrast to our results and those of Dorney, Jenkins *et al.* (1964) shot red grouse from 100 acres of moorland. Red grouse chicks are mature by August. In August, old and young cocks establish

territories and those that cannot, disperse (Watson and Jenkins, 1964b). They removed 14 males, and a month later 16 new males were on the original territories and two new territories. All the new males but two were less than a year of age. When the experiment was repeated in November the emptied territories remained empty. Clearly, there was a surplus of potential territory holders in August and most were newly mature males. The fact that no replacement occurred in November presumably means that all surplus males of this area were dead by this time.

The behaviour of female blue grouse is little understood. Stirling (1965) describes the reproductive behaviour of males and females in captivity. Hens in nature apparently behaved the same way in both sparse and dense populations. There is no evidence that hens on the breeding range are involved in any process of population control. The hens appear to be distributed more or less evenly among the males on the breeding range. What determines this distribution is unknown. Hens are apparently attracted to hooting males and this likely provides a mechanism for contact between the sexes. Very little antagonism was observed between hens. In our aviary, hens harassed others in the same pen and there was an increase in the level of their aggressiveness during the breeding season (Stirling, 1965). Hens have a variety of calls and wing sounds that are frequently heard in spring. Lack (1954) suggests that birds space themselves simply by avoiding areas of concentration. Perhaps hens space themselves over the breeding range by avoiding areas occupied by other hens.

Since virtually all hens on the summer range appear to breed this makes the territorial behaviour of males seem somewhat irrelevant to the limitation of population. In the red grouse and white-tailed ptarmigan (*Lagopus leucurus*), for example, hens without a male and territory apparently do not breed (Jenkins *et al.*, 1963; Choate, 1963). A shortage of territories might limit population and result in a surplus of males and females. At present, there is no evidence for a non-breeding surplus of hens of blue grouse, at least on the breeding range. The fact that virtually all hens were breeding supports the conclusion reached later that territorial behaviour in blue grouse functions to ensure successful reproduction.

It is possible that territorial behaviour or some form of interaction among grouse away from the breeding range affects the rate of death and dispersal so that autumn numbers are adjusted to those

observed in spring. Boag (1966) believes that a major part of the annual mortality among blue grouse he studied in Alberta occurred on the winter range and that this loss was important to numbers in spring. We are out of contact with our birds from early September to time of arrival on the breeding range. We may, therefore, miss the process of population regulation if it occurs during this time. Indeed, there may be in blue grouse a process comparable to that observed in autumn in the red grouse, and the song sparrow (*Melospiza melodia*) (Tompa, 1964). Since more young appear to go onto the winter range each year than join the population in the spring, we look for the regulation of population as a result of the death and dispersal of grouse from 4 months to approximately 1 year of age. This age class has a higher rate of disappearance than older birds. The cause of disappearance and control of population may be one or a combination of the following: some form of territorial behaviour, predation, and starvation.

Our present knowledge of the autumn and winter ecology of blue grouse permits little more than speculation that the process or processes of population regulation may occur on the winter range. In the autumn, blue grouse migrate into the coniferous forests of the mountains. We have found grouse in autumn and winter on open ridges in subalpine forest and in open alpine meadows with scattered clumps of conifers. While death and dispersal of young on the winter range may be important, a number of observations suggest that autumn and winter are not critical to blue grouse. Adults and yearlings have a high survival over winter, and come from the highlands in good weight (Simard, 1964). Winter range, as far as we know, is unlimited and has not changed. Apparently, the same winter range has supported the high and relatively low populations of grouse originating at Lower and Middle Quinsam Lakes.

The fact that striking changes in density of grouse have followed logging and fire on the lowlands also suggests that it is the summer ranges which are most important to numbers of grouse. Thus, differences in density of grouse and processes regulating density must be related in part to some aspect of the summer range, some change in the quality of stock, or both.

Boag (1963) shows a variation with age in the autumn diet of blue grouse and this may be related to the survival of young and old birds. The yearlings we have measured in good weight in spring may not be representative of those that have starved and

died in the winter. There may be inadequate food on the winter range with young grouse at a disadvantage as compared to old birds because of their smaller size and inexperience. Quality of summer range may affect the population density in spring by determining the condition, or physical quality as distinct from genetic quality, of chicks that go into the winter. A burn producing nutritious plants might produce high quality chicks while a poorer burn might result in chicks of poorer quality. Thus, chicks from a high quality burn might survive well on the winter range and result in an increased population in spring. Chicks from a poor quality burn may enter the winter in poor condition, and this and inadequate food may cause heavy loss and result in a stationary or decreased population in the next spring.

We know very little of the behaviour of blue grouse in autumn and winter. The males and hens with brood leave the breeding range at least a month apart and may winter separately as do rock ptarmigan (*L. mutus*) and willow ptarmigan (*L. lagopus*) (Weeden, 1964), and black grouse (*Lyrurus tetrix*) (Koskimies, 1957). The autumn migration appears to be a dispersal, so that members of a breeding population winter perhaps miles apart.

Grouse are reported to spend much time in winter, alone, without obvious display, and in a few trees (Hoffmann, 1956). We have found single males and groups of two to three males on winter range. King (pers. comm.) says that males winter separately from hens and young, and are usually found alone. Other authors have recorded flocks of grouse on the winter range (Beer, 1943, Caswell, 1954; in Wing, 1947).

These apparent breaks in social organization do not suggest contact in winter between birds of a particular breeding population that might determine their density in spring.

Perhaps there is important loss of young at the time of break-up of broods. Hens and their chicks would be related to a particular breeding population, although away from it, so that processes within the brood that affect the loss of young could be important to numbers in spring. The broods may break up in the autumn (Bendell, 1955a; Henderson, 1960; Wing *et al.*, 1944; Wing, 1947). However, King (pers. comm.) says that hens with brood move onto the winter range as intact family groups. This raises the possibility that interaction between hen and young in the winter and the quality of young produced from a particular summer range may be important to population regulation.

We have kept groups of blue grouse of both sexes together in our aviary over the winter months. Some birds are chased and killed by dominant cocks and hens (Stirling, 1965). This might happen on the winter range also, related or unrelated to food supply, and partly explain the relatively high rate of disappearance of young grouse.

According to Chitty (1960, 1964) animals from populations of different density and phase of growth might be expected to differ genetically and as a result show differences in aggressive behaviour, weight, and rates of birth, death, and dispersal. The sizes of territories that we have studied are more readily related to density than to characteristics of particular males. The same males have been observed on small territories in dense population and on larger territories in sparse population. Conversely, in sparse population, males held large territories when alone in an area. The same males lived on smaller territories when new males settled close to them. In both sparse and dense populations, in open vegetation at least, males tended to space themselves evenly over the breeding range. Hence, size of territory seems more a dependent of population density than an attribute of a particular male.

From Chitty's hypothesis, one consequence of aggressive behaviour is that some animals are excluded from holding territory and form a surplus that disperse and die. In our removal experiment we did not detect surplus adults and any replacement was by yearling males.

It would be presumptuous to suggest that we can measure the aggressiveness of grouse in the field without some objective test. However, we have observed grouse in dense and sparse populations and have not noted marked differences in fighting or other interaction between males or females that might indicate a different kind of individual in the populations. There is variation in the behaviour of grouse, but it cannot be related to density.

The genetic quality of stock should show itself in rates of birth and death, and body weight. Animals of a dense and declining population should have decreased birth rates, increased rates of death and dispersal, and a lighter body weight than animals of a sparse and expanding population. We cannot as yet make all these tests, but the birth and death rates of adult males, and the body weights of adults and yearlings, were virtually the same in the dense and later declining population at Lower Quinsam Lake, and in the sparse and expanding population at Middle Quinsam Lake (Bendell, 1955b; Simard, 1964). Hence, in terms of behaviour, rates of birth

and death, and body weight of adult and yearling males we cannot find support for the idea that regulation of breeding density was related to the genetic quality of grouse in the population.

Several important criticisms of our work should be mentioned. It may be argued that interaction early in the spring results in surplus males and females which do not appear on the breeding grounds. These males may have left the breeding range before we opened areas for them by shooting established birds. Also some males may have held territory for only a short time and then returned to the winter range. But we reject the contention that resident males were removed too late to permit potentially breeding adults to settle. As noted, all adults observed in spring can be assigned to territories. We do observe grouse that are non-breeding and off territory, but they are found in July and August when males are moving to the winter range.

In 1960, work began in March before grouse were found on the breeding range. In April and May, 11 adult males were shot on or near the removal plots. In 1959, 1961, and 1962, when shooting began in May, ten, two, and six adults, respectively, were taken from the same area. Thus, removing males a month earlier did not greatly increase the number shot. Moreover, in 1960, as compared to the other years, there was an increase of breeding adults on the reference plots and presumably on the removal area as well. This, rather than early shooting, is an explanation for the relatively large number of males taken in that year.

The behaviour of yearlings also suggests that the removal experiment would have revealed any surplus adult males. Some yearling males are surplus in that they hoot and occupy territory after resident males are removed. Replacement by hooting yearlings occurred throughout May and June. There was virtually no replacement of shot adults by adults. We would expect surplus adults to behave like replacement yearlings, at least through May, a time of peak reproductive activity. That this did not happen indicates all adult males were established on the breeding range from time of arrival.

Stewart and Aldrich (1951) and Hensley and Cope (1951) showed a surplus of a number of passeriforms in June and July in Michigan. If blue grouse are comparable, we should have detected surplus males at least to the end of May.

Arguments against missing a surplus population of hens on the breeding range have already been given. There was no apparent exodus of yearling hens early in spring, and virtually all hens bred.

Another criticism that might be made is that our reference and removal plots were not equally attractive to new males. If the reference plots were more attractive than the removal area, then, despite the presence of resident males, we might expect to find more new males on the reference plots. Males tend to occur on heights and in open vegetation (Bendell and Elliott, 1966). Hence, the removal area in very open vegetation and on a hill was probably more attractive to new males than the reference plots, which were on lowland and contained open and dense vegetation, which became more dense with the growth of planted fir. Hence, if this bias existed it tended to reveal surplus grouse rather than prevent their detection.

Another possible bias in the work was the effect of the different densities of vegetation on search. Hooting birds can be heard and found more or less equally in all types of cover but silent grouse are detected more easily in sparse vegetation than in dense. Search with dogs helps to overcome this bias, but numbers of silent grouse in dense vegetation were probably underestimated.

The intensity of search of an area was also probably biased by the presence of a hooting male. Once territorial males were located there was a tendency to go to these males to check them rather than to follow a uniform pattern of search. This gave more search of an area near a hooting male and hence greater likelihood of locating other grouse near it than elsewhere. None of these criticisms weaken our major conclusions for they are based on observations of hooting cocks.

If territorial behaviour on the breeding range does not function to regulate density then what other purpose or purposes might it serve in blue grouse? The functions attributed to territorial behaviour are reviewed by Hinde (1956). The present data suggest that in blue grouse, territorial behaviour functions mainly to bring the sexes together and provide conditions for successful mating. Territorial behaviour seems to provide undisputed area for the male to attract a mate, and to court and copulate successfully. As the theory would predict, hens are apparently attracted by territorial males. The behaviour of silent yearling males provides a natural experiment to show that successful mating depends upon having a territory.

In natural populations very few yearlings hold territory. Some yearling males become territorial when established males are killed. A non-territorial yearling was observed to display to a hen, and all yearlings on the breeding range appear to produce

sperm. In our aviary, yearlings mated to produce chicks. This was also observed by Wing (1951). Thus, yearling males apparently can breed, but we believe that without a territory in nature they cannot mate successfully.

We cannot say that silent yearling males did not mate with hens. However, there are data that infer this and therefore that a territory is essential to mating. Most lone hens in April and May were found on the territories of hooting males. Males observed to give a full sequence of courting behaviour were on their territories. Finally, territorial males reacted strongly to trespassing males and chased them away. It is most likely that the sound and visual display of the male are involved in the attraction and successful courting of females, or receptive females make themselves conspicuous. Yearling males may attempt courtship, but lacking undisputed use of area they are detected by a resident cock and quickly driven away. All this suggests that it is the territorial males that breed, and an important function of territory in the blue grouse is to provide the undisputed use of area for attracting hens and copulating with them. A number of authors have reached the same conclusion with a variety of birds (Hamerstrom, 1958; Lack, 1939; Nice, 1941; Pitelka, 1959; Stenger Weeden, 1965; Tinbergen, 1956; and others).

Yearling males are apparently attracted by hooting males to their territories. Yearling males when adult establish themselves on old territories or near hooting males. This relationship between young and old males may function to perpetuate the use of a particular part of the breeding range. It would seem advantageous in that yearling hens breed in their first year and commit themselves to a relatively small home range already containing a number of territorial males. Thus, a yearling male, by replacing an established male, or settling nearby, may more readily obtain a mate than if it pioneered the same kind of habitat but without previous breeding males. Eng (1959) concluded that drumming ruffed grouse attracted yearling males. Their behaviour in some respects is similar to that of a yearling blue grouse. Eng also discussed the possibility that the association between young and old grouse continued the use of a drumming site.

Some workers have suggested for the species they were studying that territorial behaviour functions to ensure an adequate supply of food for the adults and their young (Jenkins, 1963; Stenger, 1958; and others). We do not have quantitative measurements of the quantity and quality of

food in territories. However, general observations and the breeding behaviour of both sexes tend to dismiss this as an important function of territorial behaviour on the breeding range in blue grouse.

The males feed on a wide range of vegetation from herbs through shrubs to deciduous and coniferous trees, particularly the needles of Douglas-fir. The diet reflects roughly what is available on the range (Fowle, 1960). One study plot at Lower Quinsam Lake had been planted to Douglas-fir as had two study plots at Middle Quinsam Lake. The areas were comparable in density and age of fir, other structural features of the habitat, and species composition of the vegetation. While supply of food was apparently the same, territories were relatively small in the one population and large in the other. Clearly, size of territory was not related to the supply of food. Moreover, as the amount of vegetation on the study plots at Lower Quinsam Lake increased, size of territory also increased. The reverse would be expected if the extent of territory was related to the supply of food.

Hens and most yearling males are not territorial and occur on and off the territories of males, apparently without disadvantage in terms of weight and survival. Moreover, hens and hens with young may forage on and off territories. Since their movements cannot be related to the extent of territory of any one male, it is difficult to see how territorial behaviour can be related to the provision of food for hens or hens with brood. Hence, from the territorial behaviour of males and the movements of silent yearling males, hens, and hens with brood, there is no apparent relationship between food supply and territorial behaviour on the breeding range.

To some authors, the importance of territorial behaviour in the spacing of males and of females on nests is that maximum spacing of individuals might reduce the success of predators and slow the spread of disease. In blue grouse, non-territorial hens and yearling males have approximately the same mean annual death rate as adult territorial males. We would expect a greater death rate in territorial males because of their display. Indeed, in the remains found at a fox den in May, the ratio of adult males to females was 12:3 (Bendell, 1955c). However, the similarity of death rates in all birds beyond a year of age suggests that loss to predation is little affected by the territorial behaviour of the male. The nests of females are apparently spaced, however, and this may be important in reducing loss to predators (Murton and Isaacson, 1962).

It is difficult to see how the territorial behaviour of males might affect the spread of disease in blue grouse. Yearling males, hens, and hens with young range over a number of territories and so might spread an infection. When some parasites of blue grouse were studied (Bendell, 1955c), adults and yearlings of both sexes had comparable infestations, while those of chicks were of different kinds and intensities. This difference is explained by the age and diet of the chick rather than any effect of territorial behaviour.

The behaviour of the yearling male on the breeding range instigates several lines of discussion. Other workers on galliforms have observed that yearling males do not participate in breeding or are weak or late in the development of sexual behaviour (Lumsden, 1961; Dorney, 1960; Choate, 1963; Eng, 1959, 1963; and others). In blue grouse, the transient and non-breeding behaviour of yearling males is documented here and by a number of workers (Bendell, 1955a; Boag, 1964; Buss and Schottelius, 1954; Mussehl, 1960; and others). This behaviour may be explained by immaturity and domination by other males. Collias and Taber (1951) conclude that yearling pheasants (*Phasianus colchicus*) were dominated by adults. Bendell (1955a) and Simard (1964) in blue grouse, and Eng (1963) in sage grouse (*Centrocercus urophasianus*) show that the volume of testes of yearlings is about half that of adults through the sexual cycle, and this difference cannot be explained by differences in body weight. Since yearling sage grouse strut after the adults have left the booming ground this suggests that dominance by older birds is partly the reason for their lack of development.

Recently, Simard (1964) examined the testes of a large number of yearlings and adults on the breeding range. Yearling males go through the same stages of spermatogenesis as the adults but with a slower recrudescence, a faster regression, and a shorter period of production of sperm. All yearlings produce sperm and appear to be potential breeders. As noted, in our aviary and that of Wing (1951), yearlings copulate with hens that produce viable young. This suggests that most yearlings on the breeding range were dominated by territorial males. However, the testes of naturally territorial and replacement yearlings did not show testicular development greater than that of silent yearlings. Replacement yearlings were presumably not suppressed by other cocks. One replacement yearling male that was followed, hooted weakly, abandoned territory early in the year, and did not return to the

same territory in a subsequent year. These data suggest that the behaviour of the yearling male is also the result of immaturity. Hence, the behaviour of most yearling males on the breeding range is the result of domination by established males and immaturity.

A number of observations tend to support this conclusion. If some yearling males do not descend at all in their first year this cannot be explained by interaction, at least with adults on the breeding range. Moreover, apparently about the same proportion of yearling males migrated in spring into the dense and sparse populations. Since most yearling hens breed and are on the lowlands in good numbers, non-migratory yearling males are likely sexually immature. Then Simard (1964) found that testes of birds from 1 to 5 years of age tend to increase in size and amount of intertubular tissue. This suggests that sexual maturation may extend over a number of years. It seems likely that all male blue grouse are inherently sexually immature until nearly 2 years of age and possibly older. It follows that non-territorial and replacement yearlings are not surplus in the sense of unestablished and potentially breeding birds. Hence, there were no surplus individuals on the breeding ranges in spring.

While sexual immaturity explains the proximate cause of the behaviour of the yearling male it leaves the ultimate cause still unknown. Why should most yearling females breed in their first year while most yearling males do not? Part of the answer may be the habitat selection of grouse. Breeding grouse are committed to a habitat. By free-ranging a year, the yearling male may find a habitat and site for territory that is more to his advantage for subsequent mating than if he settled quickly on the breeding range in his first spring. Once established on a new area the hooting male would attract yearling hens to him. This idea could be tested by observing the occupancy of openings and slash burns in newly cut forest.

There are many reasons for research on the population ecology of animals. In general, we seek to understand how numbers of animals are determined in nature so that we may manipulate them to our purpose. If there are fundamental principles of population control, then work on one species may help our understanding of processes in all populations. The study of populations is of vital concern to us because of its implications for the continued supply of living resources, the prevention of spread of disease, and the control of our own numbers and distribution.

Besides the search for principles governing animal populations, there is often justification for the study of the animal in itself. Many forms of wildlife are spectacular and useful parts of our environment and we would be the poorer without them. It is fortunate when the study of a wildlife species yields data useful to management and adds to our general understanding of populations as well. The main concern of the foregoing sections was relating our findings to general theory. We now want to relate our findings to the management of blue grouse.

The outlook

The blue grouse is a distinctive element of the fauna of the West. It is as much a part of British Columbia as the mountains. In spring, the deep and mournful sound of the hooting male resonates among the hills and across the burns. The species and the environment in which it lives are enjoyed by all who have the senses to appreciate. As the records of the British Columbia Fish and Wildlife Branch show, the blue grouse has supplied thousands of hours of hunting pleasure and an enormous harvest of meat.

The blue grouse seems relatively secure as a species because it lives in subalpine and alpine forests and adjacent open habitats over vast areas. Since much of this land does not, as yet, have an alternative economic use, grouse habitat and therefore grouse are likely to remain for a long time.

On a local scale, populations of grouse come and go, and other than setting hunting regulations, nothing is done to manage them. This is remarkable because it is the local lowland populations that are used most easily and have yielded the largest harvests. For example, on opening day in 1950, 1,458 blue grouse were counted at a station for checking hunters and their bags near Campbell River. In 1960, 397 grouse were counted. In 1966, the first day of the season yielded but 53 birds. This decline is related to the regrowth of vegetation

over the area burned in the forest fire of 1938 and once famous for its production of wildlife. Despite the dramatic disappearance of blue grouse, most people show little concern over the loss of their sport or fail to see the obvious connection between forest succession and grouse. Moreover, as blue grouse disappear from the changing burns so does a whole community of enjoyable plants and animals.

Habitat requirements

Blue grouse require open areas for summer range. Some of the habitat requirements of the species are set out in this report and others are given by Bendell and Elliott (1966). What we have described as open habitat will support good populations of grouse. As the forest becomes dense, grouse populations decline to extinction. Natural forest succession from open to dense is swift on the lowlands over much of Vancouver Island. It is often hastened and made complete by the close planting of Douglas-fir. If openings were left in the forest, particularly on hills that males prefer for territory, then grouse and a variety of other wildlife would remain. This includes blacktail deer (*Odocoileus hemionus*), black bear (*Ursus americanus*), cougar (*Felis concolor*), and many warblers and finches among the birds. There would be viewpoints and ways through the forest. The present prospect is of an impenetrable monotony of Douglas-fir devoid of variety in plant and animal life.

Whether we have blue grouse or not depends upon what we do with the land. While forestry has priority on most of the lowlands of Vancouver Island, it seems reasonable that good forestry manages the land to produce wildlife as well as trees.

On some lands, the production of blue grouse and other wildlife might have top priority. Clearly, blue grouse in early stages of forest succession can reach extremely high densities over relatively small areas of summer range. Small areas will produce a useful crop of grouse and probably can be managed to do so indefinitely. Why burns that are in approximately the same stage of forest succession should differ by as much as tenfold in density of grouse is still largely unknown. When we have land that we can manage for blue grouse then we can experiment to learn why this is so.

Utilization

The blue grouse is easily observed on lowland ranges and offers one of the many spectacles of spring. Against the exciting backdrop of a burn in

vernal bloom, the colour and the behaviour of the male and the life of the hen with her young provide a memorable experience. It is hoped that some of the things we have observed and described will stimulate others to see and enjoy this bird and the places where it lives. To those who already have the good fortune to know it, our results may add depth to their understanding. In the autumn, the blue grouse is an excellent game bird and will provide good harvests.

A general problem is how to harvest animals to get maximum sustained yields without depleting their numbers. The objectives of this study did not include the examination of the over-all population dynamics of grouse. This is essential to an evaluation of the importance of hunting loss to population and will be treated in a later report. However, the results at hand and those in preparation permit some comment on the effects of hunting.

It is suggested at times that there should be a spring season on male blue grouse. This suggestion is based on the fact that almost the entire harvest of blue grouse on Vancouver Island is taken from the hens and young, and the argument that one male will fertilize a number of females. The escape of the cocks is due to their migration from the lowlands before the hunting season begins. It may be that some males could be harvested safely from April to August but we cannot say how many should be taken or what the effects might be. If they were shot in the same numbers as the hens and young, this loss would likely replace some natural mortality. As another possibility, there might be an increase in the survival of the young over winter to replace those males shot. Certainly, from our experience of shooting hooting males on the removal area and elsewhere, there is little difficulty in taking them from the open burns. When all adult males were taken from the removal area, the density of males in the next year was less than that of hooting males on the control plots. Apparently, at this extreme level of exploitation, the loss of breeding males is not quickly replaced. While some yearlings will replace hooting males that are removed, yearlings are not unlimited in number or expendable, as most join the breeding population when adult. Moreover, yearling males apparently are not as competent breeders as adults.

Although harvested males might be replaced, some consequences of killing males in the spring, or at any time of the year, on the reproductive success of the hens, should be considered. Our

work suggests that all males on the breeding range in spring are established members of the breeding population and that there are no surplus mature males available to replace those shot. Also, hens may be monogamous and we do not know if they will accept another male if their mate is killed. If males were shot in spring, hens might go unmated. Moreover, a disproportionate killing of males at any time might result in unproductive hens. Finally, yearling males are apparently attracted by territorial males and this may perpetuate the occupancy of a territory. It may be that hens are committed to the territory of a male and an empty territory will result in unmated hens. Thus, where hooting males are removed, the chances of their replacement and, in turn, the successful mating of hens, may be reduced. There is no evidence that a reduction in the number of breeding hens from any cause will result in improved survival to autumn of the young of hens with brood. Thus, should hens go unmated, production to autumn will be reduced. This will result in fewer birds in the bag and a smaller escapement that may become insufficient to replace natural mortality. Under these conditions a population will decline.

This is perhaps too cautious a view. Present data indicate hens are promiscuous and several hens may be fertilized by one male. Hence, killing of males at any time of the year should not affect productivity, and therefore a spring and summer harvest seems possible. If a spring and summer harvest of males were allowed, it should be studied carefully to measure changes in breeding stock and the production of young.

To the hunter, good management is the production of as many good quality birds as possible. There is a heavy loss of young from hatch to autumn and if this were reduced harvest would be increased. As noted, there is no evidence that loss to autumn is related to the density or behaviour of the parent stock. Hence the shooting of cocks or hens in spring will not increase the autumn population. The available data suggest the loss of young chicks is caused by some qualitative deficiency passed through the hen, predation on nests, and a number of miscellaneous factors (Zwickel and Bendell, 1967). With more knowledge we may be able to make up parental deficiencies to increase numbers by autumn. At present, the suppression of nest predators seems a possible form of management. On our areas these are short-tailed weasel (*Mustela erminea*), raccoon (*Procyon lotor*), and fox (*Vulpes fulva*).

Under present regulations, the harvest of blue grouse on Vancouver Island is taken from the hens and their young of both sexes. There is good evidence that present levels of harvest have little effect on populations of grouse. Seasons could be longer and bag limits more liberal. Available data suggest that there is a high and variable loss of young on the winter range. Moreover, usually more young survive into the autumn than are required to replace the annual loss of adults. The excess birds are expendable and may be harvested without affecting the level of the breeding population. Moreover, if a population is regulated, or returns to the same level each spring as a consequence of density-dependent mortality, excess young in autumn probably die on the winter range. Since these animals are doomed to die, any that are not harvested represent a waste as far as human utilization is concerned. The three populations of grouse that we have studied were apparently regulated by density-dependent loss of young on the winter range.

There is direct and indirect evidence that present levels of harvest have little effect on numbers of blue grouse. The return of bands from birds shot by hunters provides a direct measurement of the intensity of kill. From 1959 through 1963 and in 1966 we banded males, females, and chicks on the lowland at Middle Quinsam Lake. The numbers available to hunters and the percentage shot in each year are presented in Table 13.

In the table, the numbers of banded males and females available to the hunter were obtained from the number banded in a year plus the survivors from a previous year calculated at the rate of 72 per cent mean annual survival. The chicks represent only birds banded in each year. As might be expected, very few adult males (0.7 per cent) were shot by hunters. Approximately 5 per cent of the hens and chicks were shot each year. These calculations were checked by reckoning hunter kill only against birds actually checked as alive in a year. This treatment gave the same result. These data suggest that hunters shot a negligible percentage of the population at Middle Quinsam Lake. This result is comparable with a similar calculation of the percentage of birds harvested from the dense population at Lower Quinsam Lake (Bendell, 1955c).

There are two shortcomings to our estimate of the number of grouse killed by hunters. These are the lack of data on bands taken but not returned, and on number of banded grouse crippled or killed

TABLE 13 Number of banded grouse available to, and shot by, hunters at Middle Quinsam Lake, 1959 through 1966

Year	Males		Females		Chicks	
	Number banded	% shot	Number banded	% shot	Number banded	% shot
1959	31	0.0	27	11.1	2	0.0
1960	69	0.0	104	8.6	149	6.6
1961	84	2.4	123	6.5	65	3.1
1962	73	1.4	138	1.5	2	0.0
1963	63	0.0	131	5.2	6	0.0
1964	45	0.0	94	3.2	0	0.0
1965	33	0.0	67	3.0	0	0.0
1966	37	0.0	95	7.3	49	6.1
Totals	35	0.70	779	5.3	273	5.5

and not recovered. These statistics, if known, would probably increase the take of grouse. We believe we get a large percentage of the bands that are taken by hunters because of the concentrated nature of our banding, the examination of many grouse at checking stations, and the awareness of our study among local people.

Indirect evidence that loss to hunting has little effect on populations is provided by a comparison of the mean annual death rate of males and females and the sex ratio in spring. This assessment is valuable because it is not affected by the shortcomings in return of bands noted above. As shown, virtually all adult males escape the harvest while hens are shot. If hunting has a suppressive effect, then the death rate of males should be less than that of hens. Moreover, there should be uneven sex ratios on the lowlands in spring. From this report and elsewhere (Bendell, 1955c; Zwickel and Bendell, 1967) and from unpublished data, females have the same mean annual death rate as males (or the difference between them cannot be detected) and apparently equal numbers of males and females appear in spring. These data suggest hunting has little effect on population. We conclude from direct and indirect evidence that present levels of hunting have a negligible effect on the numbers of grouse. Mussehl (1960) reached the same conclusion from a study in Montana.

We can use our data on productivity and death rates to estimate a sustained yield of grouse. Hickey (1955) says that gallinaceous birds can safely withstand a hunting kill equivalent to about one half their annual mortality rate. In an average year, 50 per cent of the hens produce approximately three young into August. Hence, by autumn, the population has increased by approximately 40 per cent. If the population is to remain stable, there

must be a loss from autumn to autumn of this amount. The calculation gives a recommended harvest of approximately 20 per cent.

Another way to estimate a permissible yield takes into account the mean annual death rate of adults as well as the number of chicks alive in autumn. In an average year, as noted, 100 hens will produce 150 young. To maintain a stable population, enough young must survive the winter to replace an annual rate of loss of adults of 28 per cent. After replacements are set aside, approximately 30 per cent of the autumn population may be harvested. The calculation assumes that the young that are not shot have the same rate of death as adults.

Note that when calculated yields are compared with the actual harvest (Table 13) the yields are all higher. This suggests we should increase our harvests of blue grouse. The proposed harvests were calculated on production in an average year. The yield may be increased or decreased depending upon how many young survive to autumn.

It seems unlikely that populations of blue grouse could be seriously reduced by present methods of hunting. Approximately 86 per cent of the banded grouse taken by hunters were shot within 15 days of the opening of the season. This reflects the keenness of hunters and the disappearance of grouse from the lowland ranges. Cocks, and apparently some broodless hens as well, leave the open burns before the hunting season begins. Hence, a large segment of the population of grouse is not exposed to gunners. While present seasons on blue grouse run from September through November, many of the hens with brood probably have left the lowlands before a third of the season is over. Blue grouse are much more difficult to find in the mountains, let alone shoot, so that few are taken

from the uplands. Even on the open burns, as the density of vegetation increases grouse are concealed and less likely to be shot. The characteristics of blue grouse are such as to protect them from excessive exploitation.

Information and management

Practically all the data gathered on a species may at some time be used in its management. This information might be used to design research, or be applied in management directly. Some examples of the use of data from the present report in the design of research are as follows. A first step in management is to count the stock and this usually involves some sort of sampling. The finding that hooting males, and probably other grouse as well, tend to space themselves evenly over open and uniform habitat permits a choice of sampling methods that are applicable to this kind of distribution. As another example, it seems essential to understand the biology of grouse to know when and where to census them most accurately. Clearly, a determination of sex ratio when the hens are on the nest would be biased heavily in favour of the males which are much more conspicuous at this time. Similarly, a thorough knowledge of the time of upward migration in each year would seem essential to making counts of what birds were available for the harvest. As yet, no such study of autumn departure has been done.

- 1 Blue grouse (*Dendragapus obscurus fuliginosus*) were studied on their summer range to determine the importance of their behaviour to the regulation of numbers. Emphasis was placed on the territorial behaviour and population statistics of males. Relevant behaviour and population statistics of hens, hens with brood, and chicks were also examined.
- 2 We compared the behaviour of grouse in sparse and dense populations, and in cover that ranged from very dense to very open. The number of territorial males per acre in dense and sparse populations was approximately 0.44 and 0.13 and less, respectively. Resident males were shot to determine if they prevented the recruitment of new males to the breeding population.
- 3 Field work was done on Vancouver Island at Lower Quinsam Lake from 1950 through 1953 when population was dense, and 1957 through 1962 when population was sparse. Studies were also carried on at Middle Quinsam Lake from 1958 through 1962 with grouse in sparse population.
- 4 The study areas were in once-coniferous forest now logged and burned. The vegetation and other features of the burns were classified into habitats that could be related to the distribution of grouse. The following types of habitat were described: very open, open, dense, and very dense.
- 5 Males on the summer range did not regulate the breeding density of grouse. There was no evidence that the hens on the summer range were involved in a process of population control. Territorial behaviour in blue grouse functions mainly to provide the undisputed use of area where a male can attract a mate, court, and copulate successfully. The rate of death and dispersal of grouse from chicks (approximately 4 months of age) at the end of August to yearlings (approximately 11 months of age) in spring is high in comparison to older grouse. This loss of young might be part of the process of population regulation. The cause of disappearance of young grouse and regulation of population may be one or a combination of some form of interaction, predation, and starvation on the winter range.
- 6 The mean annual death rate of adult males (2 years and older) is 28 per cent, calculated on a sample of 125 birds. The mean annual death rate of yearling males is 27 per cent calculated on a sample of 22 birds. Adult and yearling hens appear to have the same rate of death as males. Death rates of adult and yearling grouse are constant with age and were the same in dense and sparse populations.
- 7 Breeding males appear to migrate directly to and

from their territories in spring and summer. In 1960, the first males arrived on the breeding range at Middle Quinsam Lake in the second half of March. The first females arrived about a week later than the males. Some cocks were on the lowlands approximately 1 week before hooting was heard. The build-up in numbers of both sexes was completed by the first half of May. Numbers of males were maintained until July; lone females through July. By August, most males and lone females had left the summer range. Hens with brood did not migrate until after August. In 1960 most breeding activity occurred between the middle of April and the end of June.

8 All adult males on the summer range appeared fully territorial. Virtually all territorial males in sparse and dense populations were adult. Some of the behaviour of territorial males is described and discussed. This includes hooting, wing fluttering, the courting display and call note to females, copulation, and fighting. It seems most likely that all territorial males were potentially breeding members of the population on the summer range. Males mate promiscuously, females probably do, but monandry or polyandry cannot be ruled out.

9 Breeding males establish a display and mating territory. They return to the same territory each year until presumed dead. The position and extent of territories were not related to vegetation and roads except that where vegetation was very dense, territories were located on the few open areas. Areas used as territories are attractive to other males. They include open areas and places of display and concealment. Hooting posts are usually on elevations.

10 Territorial males in very open and open cover in dense and sparse populations tended to space themselves evenly over the breeding range. In sparse population in very dense cover, the pattern of openings may have affected their local distribution. Groups of territorial males occurred over the breeding range. This clumping may be explained by the attractiveness of the habitat. Since male blue grouse defend areas and remain on them throughout the breeding season they show solitary rather than lek behaviour.

11 While fighting influences the dispersion of males, hooting and other auditory display alone may cause or at least maintain the spacing between them. Males appear to stimulate their neighbours to hoot, and hooting males are aware of other hooters. Males apparently learned a boundary between themselves and an adjacent male for one

breeding season at least.

12 The size of territory varied inversely with density. The area of territory is estimated to range approximately from 1 to 8 acres. The average size of territory in the dense population was estimated as 1.5 acres. In the sparse population the size of territory ranged between 5 and 11 acres. The available data did not show a relationship between size of territory and density of vegetation or age of male.

13 The size of territory was more variable in the sparse population because of the more variable movements of males. Apparently the limits of territory were better defined in the dense population. The movements of males on their territories may be related to the following: adjacent males, the pursuit of hens and intruding males, and requirements for display and routine activity.

14 It is estimated that approximately half the yearling males migrated to the summer range in the first year. This was apparently independent of density of grouse on the lowlands. Most yearling males on the burns were silent, moved widely, and were apparently attracted by hooting cocks. Most of these yearlings returned to the same general area of breeding range and established territory as adults.

The proportion of yearlings in the population of males at Middle Quinsam Lake was virtually the same from 1958 through 1962. There were relatively fewer yearling males in the dense population than in the sparse. It is calculated that 34-36 per cent of males in the sparse population at Middle Quinsam Lake were yearlings. A similar calculation gave 17 per cent yearlings among the males in the dense population at Lower Quinsam Lake.

The number of yearlings among the hooting males at Middle Quinsam Lake was 9 per cent. The number at Lower Quinsam Lake was approximately 1 per cent. The number of hooting yearlings was apparently related to density. Yearling males on the breeding range at Middle Quinsam Lake were of the following kind and estimated number: some established territories but were probably not as strongly territorial as, and left the breeding range earlier than, adults (11 per cent); others replaced territorial males that were shot (53 per cent); and still others moved over the burn as apparently non-breeding birds (36 per cent). The behaviour of most is explained by their inherent immaturity and domination by territorial males.

15 Some of the behaviour of females in spring is

described and discussed. This includes calls, flutter flight, defense display, and nesting behaviour. Hens were usually found singly and appeared more or less evenly spaced. Females lived on home ranges that overlapped, were larger than, and included several territories of males. Hens appeared to return to, and remain throughout the breeding season on, the same home range each year until presumed dead. Hens were attracted to territorial males, but there is no apparent relationship between particular females and males. The distribution of nests, incubating hens (as determined by clocker droppings), and hens with brood is not related to the territories of males. Hens with brood were usually found singly on the breeding range. They moved widely and in all directions over the burns.

16 Birth rate was high and constant from year to year. Virtually all the hens examined on the summer ranges were breeding. Clutch size was similar between adults and yearlings in different years, and in sparse and dense populations. Size of clutch in 36 nests was 6.22 ± 0.29 eggs (average and 95 per cent confidence limits). In the sparse population at Middle Quinsam Lake, yearling hens were not as successful as adult hens in rearing chicks.

The proportion of yearlings in the population of hens at Middle Quinsam Lake showed no significant variation from 1959 through 1962. There were fewer yearling hens in the dense population as compared to the sparse. The percentage of yearlings among the hens from April through June in the sparse population at Middle Quinsam Lake was 56 per cent, and in the dense population at Lower Quinsam Lake, 26 per cent.

Yearling hens appeared to outnumber yearling cocks on the breeding ranges by approximately 2:1. This is explained by the failure of approximately half the yearling males to migrate.

17 Data on the movement after August of 55 grouse were supplied by hunters who had shot banded birds. The autumnal migration of hens with brood from the study areas at Middle and Lower Quinsam Lakes apparently began after August and before September 15. Virtually all grouse headed in a westerly direction and 40 per cent travelled to the southwest, the most direct route to the mountains.

By September 15, approximately 65 per cent of the grouse (mostly hens with brood) were migrating at an estimated rate of approximately 2 miles per week. The average minimum distance moved by 28 grouse by September 15 was 3.6 miles with a

range of 1 to 10 miles.

The directions taken by grouse from the summer range suggest that lone hens, males, and hens with brood from a particular breeding population winter apart.

18 Local populations of blue grouse decline to extinction with the advance of forest succession. This decline is hastened by the rapid growth of planted Douglas-fir. Populations could be maintained or at least their decline postponed by making openings on summer range. The intensive stocking of logged and burned lowlands with Douglas-fir creates dense and monotonous forest with little variety in other plants and wildlife.

19 Blue grouse populations that we have studied were probably underharvested. We estimate that approximately 5 per cent of hens and young and approximately 1 per cent of males were shot each year. These estimates would be increased if we knew crippling loss and the number of bands taken but not reported. In the populations we have studied, a harvest of 20 to 30 per cent of populations in autumn might be taken without affecting numbers in spring. A spring and summer hunting season on males seems possible.

It is unlikely that killing by hunters could depress the numbers of grouse because of their migratory behaviour, an apparent density-dependent loss of young over the winter, and present methods of hunting.

20 All information on an animal may be useful eventually in its management. A main search is for factors that limit abundance and when these are identified manipulation of them will permit the best use of the species.

1 Le tétras sombre (*Dendragapus obscurus fuliginosus*) a fait l'objet d'une étude dans son territoire d'été en vue d'estimer l'importance de son comportement sur le nombre de sujets. La recherche a porté particulièrement sur le comportement territorial et le dénombrement des mâles, mais elle a aussi comporté l'étude des données statistiques ayant trait aux femelles, avec ou sans couvée, et à leurs petits.

2 On a observé le comportement du tétras au sein de populations clairsemées et de populations denses, dans un couvert allant de très dense à très clairsemé. Le nombre de mâles par acre de territoire s'est établi approximativement à 0.44 et à 0.13 ou moins, respectivement, pour les populations très denses et les populations éparses. On a abattu des mâles qui s'étaient constitué un territoire, afin de déterminer si d'autres mâles envahiraient leur territoire et chercheraient à s'accoupler.

3 Les travaux ont eu lieu dans l'île Vancouver, au lac Quinsam inférieur, de 1950 à 1953, alors que cette espèce y était en nombre, et de 1957 à 1962, alors qu'elle y était rare. D'autres recherches se sont déroulées au lac Quinsam central, de 1958 à 1962, au sein d'une population éparse.

4 Les territoires à l'étude ont consisté en une ancienne forêt de conifères qui a fait l'objet de coupes et de brûlages. Les brûlis sont classés, selon la végétation et d'autres caractéristiques, en habitats pouvant offrir un lien avec la répartition des tétras. On parle donc des quatre genres d'habitat suivants: très clairsemé, clairsemé, dense et très dense.

5 Dans le territoire d'été, ni le nombre de mâles ni leur comportement ont d'influence régulatrice sur la densité de nidification du tétras; par ailleurs, rien n'indique que les femelles exercent une telle influence. Le comportement territorial du tétras sombre mâle a surtout pour objet de délimiter et de défendre un certain territoire où il peut attirer la femelle, lui faire la cour et s'accoupler avec elle. En comparaison des oiseaux plus âgés, la mortalité et l'éparpillement des petits, d'environ 4 mois à la fin d'août jusqu'à l'âge d'environ 11 mois au printemps suivant, sont fort élevés; cette perte d'oisillons s'inscrit peut-être dans le mécanisme d'auto-régulation de l'espèce. Il se peut que la cause en soit l'un ou l'autre des facteurs suivants, seuls ou combinés: une certaine influence réciproque entre oiseaux, les ravages des prédateurs et le manque de pâture dans le territoire d'hiver.

6 Chez les mâles adultes (de 2 ans et plus), la mortalité annuelle s'établit en moyenne à 28 p. 100, selon l'observation de 125 sujets, et chez les mâles

d'un an, à 27 p. 100, selon l'observation de 22 sujets. Apparemment, la mortalité chez les femelles adultes et chez celles d'un an est à peu près la même que chez les mâles. Dans chaque cas, il s'agit d'un taux constant en fonction de l'âge et qui reste le même, aussi bien chez les populations très denses que chez les populations éparses.

7 Apparemment, les migrations des mâles reproducteurs au printemps et à l'été se font directement de l'un de leurs territoires à l'autre. En 1960, c'est après la mi-mars que les premiers mâles arrivèrent à l'aire de reproduction, au lac Quinsam central, suivis, une semaine plus tard, des premières femelles. Quelques mâles se trouvaient dans les basses terres à peu près une semaine avant que les premiers chants ne se fissent entendre. Vers la mi-mai, la colonie, mâles et femelles, est au complet. Les mâles demeurent dans l'aire de reproduction jusqu'en juillet; les femelles non accouplées, jusqu'à la fin de juillet. Vers le mois d'août, la plupart des mâles et des femelles non accouplées ont quitté le territoire d'été; d'autre part, les femelles avec couvée n'émigrent que passé le mois d'août. En 1960, l'accouplement s'est fait, en majeure partie, de la mi-avril à la fin de juin.

8 Dans le territoire d'été, tous les mâles adultes vivent constamment au sol, semble-t-il. Presque tous les mâles cantonnés, dans les populations tant éparses que denses, sont adultes. L'auteur décrit en partie le comportement du mâle dans son territoire d'été, notamment le chant d'amour, le battement d'ailes, la parade, le chant d'appel destiné aux femelles, l'accouplement et les combats entre mâles. Il est fort probable que tous les mâles cantonnés ont atteint la maturité sexuelle et peuvent s'accoupler. Le mâle s'accouple avec plusieurs femelles et la femelle est probablement polyandre; on ne saurait donc nier qu'il y ait des cas de monogamie, non plus que des cas de polyandrie.

9 Le mâle reproducteur se délimite un territoire pour la parade et l'accouplement, territoire auquel il revient chaque année jusqu'à sa mort présumée. La végétation et la proximité des routes ne semblent pas influencer sur le choix et l'étendue de ce territoire, sauf qu'aux endroits où la végétation était très dense, l'oiseau choisissait les quelques espaces à découvert qui s'y trouvaient. Le territoire choisi offre un certain attrait aux autres mâles; il se compose ordinairement d'un espace à découvert, d'une aire de parade et d'un couvert sous lequel l'oiseau peut se dissimuler. D'ordinaire, le mâle se perche sur une élévation pour chanter.

10 Quelle que soit la densité des populations, les

mâles cantonnés dans des espaces sans couvert ou presque ont tendance à se répartir uniformément dans l'aire de reproduction. Aux endroits à végétation très dense où les tétras sont peu nombreux, l'agencement des espaces à découvert semble influencer la répartition des mâles; des groupes de mâles cantonnés se forment dans l'aire de reproduction. Cette association de mâles s'explique probablement par l'attrait que leur offre ce genre d'habitat. Vu que le mâle défend le territoire qu'il s'est constitué, et qu'il y demeure pendant toute la saison de reproduction, il parade seul plutôt que de concert avec d'autres mâles.

11 Bien que les combats influent sur la dispersion des mâles, souvent le chant et d'autres cris suffisent à établir l'aire de parade et à en éloigner les intrus. Apparemment, le chant a un effet contagieux sur les autres mâles, mais le chanteur demeure toujours conscient de la présence d'autres mâles chanteurs autour de lui. Il semble que les mâles aient appris à se tenir à distance les uns des autres, du moins pour une saison de reproduction.

12 L'étendue du territoire varie inversement selon la densité de population; on estime qu'elle est à peu près de 1 à 8 acres. Elle est en moyenne de 1.5 acre dans les aires très peuplées, tandis qu'elle varie de 5 à 11 acres dans les aires peu peuplées. D'après les données recueillies, il n'existe aucun rapport entre l'étendue du territoire, la densité de la végétation et l'âge des mâles.

13 L'étendue du territoire est moins uniforme dans les aires peu peuplées, en raison des déplacements plus variables des mâles. Il semble que les limites des territoires soient mieux définies dans les aires très peuplées. Les déplacements des mâles dans leur territoire sont attribuables à l'une ou l'autre des raisons suivantes: voisinage d'autres mâles, poursuite des femelles et des intrus mâles, espace requis pour la parade et l'activité normale.

14 D'après l'auteur, la moitié, environ, des mâles d'un an émigrent à leur territoire d'été pendant la première année, quelle que soit la densité des populations de tétras dans les basses terres, semble-t-il. La plupart d'entre eux gardent le silence, se déplacent beaucoup dans les brûlis et sont apparemment fascinés par les mâles chanteurs. Une fois adultes, presque tous reviennent à la même aire de reproduction, où ils établissent leur propre territoire.

Chez les mâles du lac Quinsam central, la proportion de jeunes d'un an est restée plus ou moins la même de 1958 à 1962. Il y eut relativement moins de ces oiseaux dans les aires très peuplées que dans

les aires peu peuplées. Dans ces dernières, au lac Quinsam central, l'auteur estime que la proportion de mâles d'un an atteignait de 34 à 36 p. 100, en regard de 17 p. 100 dans les aires très peuplées du lac Quinsam inférieur.

La proportion de jeunes d'un an parmi les mâles chanteurs au lac Quinsam central s'est établie à 1 p. 100, environ. Il semble que le nombre de jeunes parmi les chanteurs soit fonction de la densité de la population. Dans l'aire de reproduction du lac Quinsam central, voici les observations faites au sujet des jeunes d'un an: certains se sont constitué un territoire (11 p. 100), mais ils n'y étaient probablement pas aussi attachés que les adultes, car ils ont quitté l'aire de reproduction avant eux; d'autres (53 p. 100) se sont substitués à des mâles cantonnés qui ont été abattus, et d'autres (36 p. 100), selon toute apparence des sujets non reproducteurs, se sont déplacés partout dans les brûlis. Dans la plupart des cas, ce comportement s'explique par l'absence de maturité du jeune oiseau et par la domination des mâles cantonnés.

15 Il est question aussi du comportement des femelles au printemps, notamment de leurs appels, de leur volètement, de leurs démonstrations de défense et de leurs actions au nid. Les femelles vivent seules en général et se répartissent plus ou moins uniformément dans tout le territoire. Elles aussi se constituent un territoire qui chevauche ceux de leurs voisines, qui est plus grand que ceux des mâles et s'étend au territoire de plusieurs mâles. Elles semblent garder le même territoire pendant toute l'époque de reproduction et y revenir chaque année jusqu'à leur mort présumée. Elles sont attirées par tous les mâles, mais ne semblent s'attacher à aucun d'entre eux en particulier. La répartition des nids, tant des femelles couveuses (déterminée par leurs fientes) que des femelles avec couvée, est sans rapport avec les territoires des mâles. En général, les femelles ayant des petits vivent seules dans l'aire de reproduction; elles se déplacent beaucoup et en tous sens dans les brûlis.

16 La natalité est élevée et se maintient constante d'une année à l'autre. Presque toutes les femelles observées dans les territoires d'été étaient reproductrices. Le nombre d'œufs par couvée était à peu près le même pour les femelles adultes et celles d'un an en différentes années, sans égard à la densité de population. La moyenne d'œufs dans 36 nids s'est établie à 6.22 ± 0.29 (limite de confiance de 95 p. 100). Dans les aires peu peuplées du lac Quinsam central, les femelles d'un an ont eu moins de succès que les adultes dans l'élevage des poussins.

De 1959 à 1962, la proportion d'oiseaux d'un an parmi les femelles au lac Quinsam central n'a pas sensiblement varié. Les populations denses comptaient moins de femelles d'un an que les populations éparses. Dans ces dernières, au lac Quinsam central, la proportion d'oiseaux d'un an parmi les femelles, d'avril à juin, inclusivement, s'est établie à 56 p. 100, en regard de 26 p. 100 dans les aires très peuplées du lac Quinsam inférieur.

Dans les aires de reproduction, le nombre de femelles d'un an est à peu près le double du nombre de mâles d'un an; la raison en est que la moitié, environ, des mâles d'un an n'émigrent pas aux territoires d'été.

17 Les données relatives aux déplacements de 55 tétras après le mois d'août proviennent de chasseurs qui ont abattu des spécimens bagués. Dans le cas des femelles avec couvée, il semble que la migration automnale des aires étudiées au lac Quinsam central et au lac Quinsam inférieur ait débuté après le mois d'août mais avant le 15 septembre. A peu près tous les tétras se sont envolés vers l'ouest; du nombre, 40 p. 100 ont bifurqué vers le sud-ouest, le chemin le plus court vers les montagnes.

Vers le 15 septembre, environ 65 p. 100 des tétras migrants (la plupart des femelles avec couvée) parcouraient une distance de quelque deux milles par semaine. A cette même date, on a constaté que le trajet parcouru par 28 tétras variait de 1 à 10 milles, s'établissant en moyenne à un minimum de 3.6 milles.

A en juger par les directions prises par les tétras à leur départ du territoire d'été, les femelles solitaires, les mâles et les femelles avec couvée d'une population reproductrice donnée hivernent à part.

18 Dans certaines aires, les populations de tétras sombres s'amenuisent au point d'être près de s'éteindre, en fonction de l'empiètement progressif des terrains boisés sur leur territoire. La croissance rapide du sapin de Douglas dans les plantations accélère cette diminution. On pourrait aider les populations actuelles à se maintenir ou, du moins, en retarder la raréfaction en pratiquant des éclaircies dans leur territoire d'été. Le reboisement intensif en sapin de Douglas des basses terres déboisées par des coupes et des incendies donne naissance à des boisés denses et homogènes, où la faune et la végétation sont peu variées.

19 Il est probable que les populations de tétras sombres que nous avons étudiées, sont peu décimées par les chasseurs. Ces derniers, d'après nos observations, abattent chaque année 5 p. 100 des jeunes et des femelles et 1 p. 100 des mâles, environ. Ces

chiffres seraient plus élevés si nous connaissions le nombre d'oiseaux qui meurent de leurs blessures et le nombre de spécimens bagués dont l'abattage n'est pas rapporté. Dans les populations que nous avons étudiées, une perte de sujets de 20 à 30 p. 100 à l'automne n'entraînerait pas une réduction sensible du nombre d'oiseaux de cette espèce au printemps. Il serait possible, apparemment, d'autoriser la chasse aux mâles au printemps et à l'été.

A en juger par les directions prises par les tétras à tétras, par la mortalité chez les petits en hiver, laquelle est apparemment fonction de la densité de la population, et par les modes actuels de la chasse au tétras, il est fort peu probable que l'activité des chasseurs contribuerait à abaisser sensiblement le nombre d'oiseaux de l'espèce.

20 En fin de compte, tous les renseignements recueillis à l'égard d'une espèce animale peuvent se révéler utiles à sa conservation. Il faut rechercher surtout les facteurs qui contribuent à la réduction numérique de l'espèce et, une fois ces facteurs bien établis, les adapter judicieusement afin de permettre l'emploi le plus sage de cette ressource faunique.

Literature cited

- Anthony, A. W. 1903.** Migration of Richardson's grouse. *Auk* 20:24-27.
- Armstrong, E. A. 1963.** A study of bird song. Oxford University Press, London.
- Bauer, R. 1962.** The ecology of blue grouse on a summer range in north-central Washington. M.Sc. Thesis, Washington State University.
- Beer, J. 1943.** Food habits of the blue grouse. *J. Wildl. Mgmt.* 7:32-44.
- Bendell, J. F. 1954.** A study of the life history and population dynamics of the blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway). Ph.D. Thesis, University of British Columbia.
- Bendell, J. F. 1955a.** Age, breeding behavior and migration of sooty grouse, *Dendragapus obscurus fuliginosus* (Ridgway). *Trans. N. Am. Wildl. Conf.* 20:367-381.
- Bendell, J. F. 1955b.** Age, molt and weight characteristics of blue grouse. *Condor* 57:354-361.
- Bendell, J. F. 1955c.** Disease as a control of a population of blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway). *Can. J. Zool.* 33:195-223.
- Bendell, J. F., and P. W. Elliott. 1966.** Habitat selection in blue grouse. *Condor* 68:431-446.
- Blackford, J. L. 1958.** Territoriality and breeding behavior of a population of blue grouse in Montana. *Condor* 60:145-158.
- Blackford, J. L. 1963.** Further observations on the breeding behavior of a blue grouse population in Montana. *Condor* 65:485-513.
- Boag, D. A. 1958.** Biology of the blue grouse of the Sheep River area. M.Sc. Thesis, University of Alberta.
- Boag, D. A. 1963.** Significance of location, year, sex, and age to the autumn diet of blue grouse. *J. Wildl. Mgmt.* 27:555-562.
- Boag, D. A. 1964.** A population study of blue grouse in southwest Alberta. Ph.D. Thesis, Washington State University.
- Boag, D. A. 1965.** Indicators of sex, age, and breeding phenology in blue grouse. *J. Wildl. Mgmt.* 29:103-108.
- Boag, D. A. 1966.** Population attributes of blue grouse in southwestern Alberta. *Can. J. Zool.* 44:799-814.
- Buss, I. O., and B. A. Schottelius. 1954.** Breeding age of blue grouse. *J. Wildl. Mgmt.* 18:137-138.
- Buss, I. O. 1960.** Blue grouse of Big Blue Buck Mountain. *Naturalist* 11:3-9.
- Carrick, W. H. 1963.** Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. *Proc. XIII Intern. Ornithol. Congr.* p. 740-753.
- Caswell, E. B. 1954.** A preliminary study on the life history and ecology of the blue grouse in west-central Idaho. M.Sc. Thesis, University of Idaho.
- Chitty, D. 1960.** Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38:100-113.
- Chitty, D. 1964.** Animal numbers and behaviour. *Fish and Wildlife: A memorial to W. J. K. Harkness.* Longmans, Don Mills, Ont. p. 41-53.
- Choate, T. S. 1963.** Habitat and population dynamics of white-tailed ptarmigan in Montana. *J. Wildl. Mgmt.* 27:684-699.
- Clark, P. J., and F. C. Evans. 1954.** Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- Collias, N. E., and R. D. Taber. 1951.** A field study of some grouping and dominance relations in ring-necked pheasants. *Condor* 53:265-275.
- Dorney, R. 1960.** Relation of weather, parasitic disease and hunting to Wisconsin ruffed grouse populations. *Wisc. Cons. Dept. Tech. Bull.* No. 20.
- Eng, R. L. 1959.** A study of the ecology of male ruffed grouse (*Bonasa umbellus* L.) on the Cloquet Forest Research Center, Minnesota. Ph.D. Thesis, University of Minnesota.
- Eng, R. L. 1963.** Observations on the breeding biology of male sage grouse. *J. Wildl. Mgmt.* 27:841-846.
- Errington, P. L. 1956.** Factors limiting higher vertebrate populations. *Science* 124:304-307.
- Farner, D. S. 1955.** Bird banding in the study of population dynamics. *In Recent studies in avian biology*, A. Wolfson, Ed. University Illinois Press, Urbana.
- Fowle, C. D. 1960.** A study of the blue grouse (*Dendragapus obscurus* (Say)) on Vancouver Island, British Columbia. *Can. J. Zool.* 38:701-713.
- Hamerstrom, F., and F. Hamerstrom. 1958.** Comparability of some social displays of grouse. *Proc. XII Intern. Ornithol. Congr.* p. 274-293.
- Henderson, U. B. 1960.** Blue grouse on summer range in north-central Washington. M.Sc. Thesis, Washington State University.
- Hensley, M. M., and J. B. Cope. 1951.** Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. *Auk* 68:483-493.
- Hickey, J. J. 1955.** Some American population research on gallinaceous birds. *In Recent studies in avian biology*, A. Wolfson, Ed. University of Illinois Press, Urbana.
- Hinde, R. A. 1956.** The biological significance of the territories of birds. *Ibis* 98:340-369.
- Hoffmann, R. S. 1956.** Observations on a sooty grouse population at Sage Hen Creek, California. *Condor* 58:321-337.
- Jenkins, D. 1961.** Social behaviour in the Partridge *Perdix perdix*. *Ibis* 103a:155-188.
- Jenkins, D. 1963.** Population control in red grouse (*Lagopus lagopus scoticus*). *Proc. XIII Intern. Ornithol. Congr.* p. 690-700.
- Jenkins, D., A. Watson, and G. R. Miller. 1963.** Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. *J. Anim. Ecol.* 32:317-376.
- Jenkins, D., A. Watson, and G. R. Miller. 1964a.** Predation and red grouse populations. *J. Appl. Ecol.* 1:183-195.
- Jenkins, D., A. Watson, and G. R. Miller. 1964b.** Current research on red grouse in Scotland. *Scottish Birds* 3:3-13.
- Kluyver, H. N., and L. Tinbergen. 1953.** Territory and the regulation of density in titmice. *Arch. Neerl. Zool.* 10:265-289.
- Koskimies, J. 1957.** Flocking behaviour in Capercaillie *Tetrao urogallus* (L.) and Blackgame, *Lyrurus tetrix* (L.). *Papers on Game Research* 18:1-31.
- Krajina, V. 1959.** Bioclimatic zones in British Columbia. University of British Columbia Bot. Ser. No. 1.
- Krebs, C. J. 1964.** The lemming cycle at Baker Lake, Northwest Territories during 1959-1962. *Arctic Inst. N. Am. Tech. Paper* No. 15.
- Lack, D. 1939.** The display of the blackcock. *British Birds* 32:290-303.
- Lack, D. 1954.** The natural regulation of animal numbers. Clarendon, Oxford.
- Lack, D. 1966.** Population studies of birds. Clarendon, Oxford.
- Leopold, A. 1933.** Game management. Charles Scribner's Sons, New York.
- Lumsden, H. 1961.** The display of the Capercaillie. *British Birds* 54:257-272.
- Murton, R. K., and A. J. Isaacson. 1962.** The functional basis of some behaviour in the woodpigeon *Columba palumbus*. *Ibis* 104:503-521.
- Mussehl, T. W. 1960.** Blue grouse production, movements, and populations in the Bridger Mountains, Montana. *J. Wildl. Mgmt.* 24:60-68.
- Nice, M. M. 1941.** The role of territory in bird life. *Am. Midland Nat.* 26:441-487.
- Odum, E. P., and E. J. Kuenzler. 1955.** Measurement of territory and home range size in birds. *Auk* 72:128-138.
- Pitelka, F. A. 1959.** Numbers, breeding schedule and territoriality in pectoral sandpipers of northern Alaska. *Condor* 61:233-264.
- Rowe, J. S. 1959.** Forest regions of Canada. *Bull. 123. For. Br. Dept. N. Aff. Natl. Res.* Queen's Printer, Ottawa.
- Simard, B. R. 1964.** The testicular cycle of blue grouse (*Dendragapus obscurus fuliginosus*) and its relation to age, breeding behaviour and migration. M.Sc. Thesis, University of British Columbia.
- Stenger, J. 1958.** Food habits and available food of ovenbirds in relation to territory size. *Auk* 75:335-346.
- Stenger Weeden, J., and J. B. Falls. 1959.** Differential responses of male ovenbirds to recorded songs of neighbouring and more distant individuals. *Auk* 76:343-351.
- Stenger, J., and J. B. Falls. 1959.** The utilized territory of the ovenbird. *Wilson Bull.* 71:125-140.
- Stenger Weeden, J. 1965.** Territorial behaviour of the tree sparrow. *Condor* 67:193-209.
- Stewart, R. E., and J. W. Aldrich. 1951.** Removal and repopulation of breeding birds in a spruce-fir forest community. *Auk* 68:471-482.
- Stirling, I. G. 1965.** Studies of the holding, behaviour and nutrition of captive blue grouse. M.Sc. Thesis, University of British Columbia.
- Stirling, I., and J. F. Bendell. 1966.** Census of blue grouse with a recorded call of a hen. *J. Wildl. Mgmt.* 30:184-187.
- Tinbergen, N. 1956.** On the functions of territory in gulls. *Ibis* 98:401-411.
- Tompa, F. S. 1964.** Factors determining the numbers of song sparrows, *Melospiza melodia* (Wilson), on Mandarte Island, British Columbia, Canada. *Acta zool. Fen.* 109.
- Watson, A. 1964.** Aggression and population regulation in red grouse. *Nature* 202:506-507.

Watson, A., and D. Jenkins. 1964. Notes on the behaviour of the red grouse. *British Birds* 57:137-170.

Weeden, R. B. 1964. Spatial separation of sexes in rock and willow ptarmigan in winter. *Auk* 81:534-541.

Wing, L., J. Beer, and W. Tidyman. 1944. Brood habits and growth of "blue grouse". *Auk* 61:426-440.

Wing, L. 1946. Drumming flight in the blue grouse and courtship characters of the tetraonidae. *Condor* 48:154-157.

Wing, L. 1947. Seasonal movements of the blue grouse. *Trans. N. Am. Wildl. Conf.* 12:504-511.

Wing, L. W. 1951. Practice of wildlife conservation. Wiley & Sons, New York.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Hafner, New York.

Zwickel, F. C. 1965. Early mortality and the numbers of blue grouse. Ph.D. Thesis, University of British Columbia.

Zwickel, F. C., and J. F. Bendell. 1967. Early mortality and the regulation of numbers in blue grouse. *Can. J. Zool.* In press.

Zwickel, F. C., and J. F. Bendell. 1967. A snare for capturing blue grouse. *J. Wildl. Mgmt.* In press.



Canadian Wildlife Service
Department of Indian Affairs and Northern Development
