A TELEMETRY STUDY OF DISPERSION AND BREEDING BIOLOGY
IN BLUE GROUSE

by

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B.Sc., University of British Columbia, 1963

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We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
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Department of **Zoology**

The University of British Columbia
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Date **Jan 23/68**
ABSTRACT

A general property of animal populations is their failure to continue increasing in number indefinitely, even when the habitat may contain enough resources to support more animals than are present at the time. Certain populations of blue grouse have expressed this property by failing to increase when the habitat has undergone changes that have produced striking increases in past cases. Other populations have expressed it by arresting their increase before the resources of the habitat were exhausted.

In blue grouse populations on Vancouver Island, adult mortality is constant and it is restricted recruitment that has held these populations stable in the periods they have been studied, even though sufficient young have been produced to support an increase.

The hypothesis that the behavior of territorial adult males affects the local occurrence of recruits and other grouse in general on the summer range was tested by studying dispersion during the breeding period.

Information on dispersion and social behavior were obtained from nine grouse fitted with miniature radio transmitters. Data from non-instrumented birds supplement this work.

The principal finding is that there was no evidence of social interaction causing females and immature males to occur in special places, and that no interaction of a sort that could affect recruitment occurs between blue grouse on their summer range. It is alternatively suggested that such behavior occurs in winter.

Other conclusions are that the onset of estrus induces hens to seek out and become localized near a mate, that several hens may seek out the
same mate, and that no lasting pair-bonds are formed. Each type of reproductive activity in blue grouse has a distinctive movement pattern, and perhaps movement rate, associated with it. Excepting for hens in estrus who briefly seek out mates, and some yearling males who are prevented by adults from remaining on territories, movements and local occurrence within the breeding range are unaffected by social interaction with other grouse.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>i</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>vii</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>PART 1  STUDIES OF DISPERSION</td>
<td>4</td>
</tr>
<tr>
<td>Movements prior to mating</td>
<td>4</td>
</tr>
<tr>
<td>Movements from pairing to incubation</td>
<td>8</td>
</tr>
<tr>
<td>Movements during incubation</td>
<td>10</td>
</tr>
<tr>
<td>Nest dispersion</td>
<td>11</td>
</tr>
<tr>
<td>Movements of hens after the hatch</td>
<td>12</td>
</tr>
<tr>
<td>Movements of unsuccessful hens</td>
<td>14</td>
</tr>
<tr>
<td>Migratory movements</td>
<td>15</td>
</tr>
<tr>
<td>Summary of Part I</td>
<td>18</td>
</tr>
<tr>
<td>PART II  BREEDING BIOLOGY</td>
<td>20</td>
</tr>
<tr>
<td>Pairing in blue grouse</td>
<td>20</td>
</tr>
<tr>
<td>Habitat use</td>
<td>21</td>
</tr>
<tr>
<td>Incubation behavior</td>
<td>23</td>
</tr>
<tr>
<td>The brood patch in an unmated hen</td>
<td>25</td>
</tr>
<tr>
<td>Comparative rates of travel</td>
<td>26</td>
</tr>
<tr>
<td>Very early juvenile mortality</td>
<td>28</td>
</tr>
<tr>
<td>Summary of Part II</td>
<td>30</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table I  Distances between adjacent nests and between nests and adjacent males  11

Table II  The use of plant associations and slope compared to their occurrence on the Comox Burn  22
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Movements of yearling male</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>Panel layout: Model LR-1 VHF Receiver</td>
<td>48</td>
</tr>
<tr>
<td>3</td>
<td>Block diagram: Model LR-1 VHF Receiver</td>
<td>49</td>
</tr>
<tr>
<td>4</td>
<td>Schematic: Pre-amp and first converter, Model LR-1 VHF Receiver</td>
<td>50</td>
</tr>
<tr>
<td>5</td>
<td>Schematic: Second converter/IF/Detector, Model LR-1 VHF Receiver</td>
<td>51</td>
</tr>
<tr>
<td>6</td>
<td>Schematic: Audio amplifier, Model LR-1 VHF Receiver</td>
<td>52</td>
</tr>
<tr>
<td>7</td>
<td>Schematic: Metering circuit and audio fitter, Model LR-1 VHF Receiver</td>
<td>53</td>
</tr>
<tr>
<td>8</td>
<td>Schematic: Power supply and battery charger, Model LR-1 VHF Receiver</td>
<td>54</td>
</tr>
<tr>
<td>9</td>
<td>Schematic: Transmitter, Model LT-1</td>
<td>55</td>
</tr>
<tr>
<td>10</td>
<td>Movements of yearling female 1760</td>
<td>76</td>
</tr>
<tr>
<td>11</td>
<td>Movements of unsuccessful yearling hen 1745</td>
<td>82</td>
</tr>
<tr>
<td>12</td>
<td>Movements of adult hen 1539</td>
<td>82</td>
</tr>
<tr>
<td>13</td>
<td>Positions of pre-hatch and post-hatch home ranges of two hens in 1964</td>
<td>87</td>
</tr>
<tr>
<td>14</td>
<td>Locations of feeding sites of nest hens 1834 and 1837</td>
<td>87</td>
</tr>
<tr>
<td>15</td>
<td>Movements of broodless yearling hen 1837</td>
<td>91</td>
</tr>
<tr>
<td>16</td>
<td>Movements of adult brood hen 1859</td>
<td>92</td>
</tr>
<tr>
<td>17</td>
<td>Path of travel of migrating brood hen 1894 and her chick 1865</td>
<td>95</td>
</tr>
</tbody>
</table>
Figure 18. Movements of brood hen 1894 and chick 1865 in the four days before they migrated.

Figure 19. Diagrams of habitat occupied by migrating hens and chicks.
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It would be unusual indeed to find a field study that did not owe much of its success to the contributions of people other than the author, and my study is not unusual at all this respect.

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INTRODUCTION

This study is part of some long-term research on the biology of blue grouse, *Dendragapus obscurus fuliginosus* (Ridgway), begun in 1944 and still continuing. The object of the most recent work (Bendell and Elliott, 1966; Bendell and Elliott, 1967; and Zwickel and Bendell, 1967) is to explain the distribution and abundance of blue grouse in nature.

The work described in the present paper was undertaken to discover how blue grouse, particularly females, are dispersed on the breeding range. A number of studies have shown that enforced dispersal in certain animal populations results from social interaction, and as a consequence, the number of individuals in those populations is also affected (Carrick, 1963; Hensley and Cope, 1951; Kluyver and Tinbergen, 1953; Stewart and Aldrich, 1951; and others). Changes in numbers in animal populations are partly due to changes in the rate of recruitment of new individuals, and Wynne-Edwards (1962) contends that restricted recruitment and special dispersion patterns are linked consequences of social interaction. Recruitment holds the key to changes in numbers of blue grouse which have a relatively constant rate of adult mortality (Zwickel and Bendell, 1967). In certain populations, the numbers of this grouse failed to increase even though many more young have been produced than were necessary to replace annual losses among the adults. Despite fluctuating production, the recruitment of young birds has been quite constant (Zwickel and Bendell, 1967). In other words, roughly the same numbers of new birds have joined the population each year, and this number has been just sufficient to replace adult losses and so keep the population size unchanged.
A central problem, then, is why are certain young birds able to join the population while the rest are not? If social interaction affects recruitment of new individuals, perhaps this interaction is revealed in part through the way blue grouse, particularly new recruits, are dispersed over the breeding range. Accordingly, I studied movements and behavior of blue grouse to see if there was any evidence of social interaction that had these effects.

I gave new recruits (yearling birds) and particularly females the most attention because these are the most likely candidates for the influence of adult male behavior, and also because previous information suggests that blue grouse are polygamous (Bendell, 1954), meaning that only non-breeding hens or declining numbers of hens can significantly reduce the production of new stock.

Movements were studied over the entire six-month period blue grouse are on the breeding range on Vancouver Island. The data collected permit me to re-examine some views about blue grouse dispersion made by Elliott (1965), who assembled several conclusions explaining local occurrence of different sex and age groups at different periods in the breeding season. Some of these conclusions appear in two other papers which are more accessible (Bendell and Elliott, 1966 and 1967), and I shall, whenever possible, refer to them rather than to Elliott (1965).

The major hypothesis of these authors that I tested states that females and yearling males are attracted to and grouped around territorial males. It is useful to select this specific idea for testing because, if it is true, it provides an avenue for interaction between grouse which could affect recruitment by dispersing some birds to positions outside the breeding
range or preventing them from engaging in breeding even if they are allowed to stay.

The work reported here was carried out from 1 May through 1 September 1964, and from 1 April through 9 October, 1966 on the east coast of Vancouver Island on 1000 acres of recently logged and burned forest known as the Comox Burn. This is an area of moderately sloping foothills well-dissected by small drainage courses. The original vegetation was Pacific Coast Mesothermal Forest (Krajina, 1965), and in 1964 - 1966 the area was in the pioneering stages of secondary succession after the fire, with most of the plants being herbs and shrubs less than three feet high.

A trained pointing dog was used to locate birds in 1964, but was found to be inadequate. A dog does not pick out certain birds; he scans any bird as he comes across it, meaning that a few scattered data are gathered from many birds without detailed knowledge of any. The better that individual birds are known, the better their behavior can be distinguished from that of others. Radio-telemetry was adopted in 1966, primarily to acquire many consecutive data on specific individuals. Moreover, telemetry permits certain data to be obtained at will, so that the observer is assured of being on hand to witness events which occur only at certain expected times. A few non-instrumented birds were known in sufficient detail to supplement the data from the radio-marked birds in several instances as noted in the text.

In 1966, nine blue grouse were fitted with miniature radio transmitters and followed with portable receivers (Table 1). One advantage of tracking grouse by telemetry is that large amounts of information other than that on locations are also collected. Where these additional data help explain dispersion they are included in PART I, otherwise they are assembled under
TABLE (1)
BLUE GROUSE INSTRUMENTED, 1966

<table>
<thead>
<tr>
<th>BIRD NO.</th>
<th>SEX</th>
<th>AGE</th>
<th>DATE</th>
<th>REPRODUCTIVE STATUS AND PERIOD OBSERVED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>♂</td>
<td>yearling</td>
<td></td>
<td>New recruit, non-territorial male, observed in period when territories were being established by breeding males.</td>
</tr>
<tr>
<td>2</td>
<td>♀</td>
<td>yearling</td>
<td></td>
<td>New recruit, successful breeder, observed from before she mated until she began to incubate.</td>
</tr>
<tr>
<td>3</td>
<td>♀</td>
<td>yearling</td>
<td></td>
<td>New recruit, unsuccessful breeder, observed prior to mating period, and into time when successful hens were incubating.</td>
</tr>
<tr>
<td>4</td>
<td>♀</td>
<td>adult</td>
<td></td>
<td>Returning resident, successful breeder, observed from before she mated until she began to incubate.</td>
</tr>
<tr>
<td>5</td>
<td>♀</td>
<td>yearling</td>
<td></td>
<td>New recruit, nesting hen, observed during last 17 days of incubation, and first two days after hatch.</td>
</tr>
<tr>
<td>6</td>
<td>♀</td>
<td>yearling</td>
<td></td>
<td>New recruit, nesting hen, observed during last 7 days of incubation and for a month after she lost her chicks to a predator.</td>
</tr>
<tr>
<td>7</td>
<td>♀</td>
<td>adult</td>
<td></td>
<td>Returning resident, brood hen, observed during her chicks’ second and third weeks of life.</td>
</tr>
<tr>
<td>8</td>
<td>♀</td>
<td>yearling</td>
<td></td>
<td>New recruit, observed for 1½ months in autumn, during migration.</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>juvenile</td>
<td></td>
<td>Chick of Hen 8, observed simultaneously with her.</td>
</tr>
</tbody>
</table>
appropriate headings in PART II.

The telemetry equipment and its use are fully described in Appendices I, II, and III. Each transmitter had a different frequency in the range 150.31 to 150.55 MHz, which allowed birds to be recognized individually. Most locations were obtained by triangulation from close range; each bird was also checked visually every three days or less. The equipment performed at least as well as that used in other studies (Marshall and Kupa, 1963; McEwen and Brown, 1966; and others), and there was no evidence that the transmitters affected the behavior or health of the birds. The fact that instrumented grouse mated, nested, brooded chicks, and underwent fall migration is a good indication that telemetry was a reliable technique for studying behavior.

PART I STUDIES OF DISPERSION

Movements Prior to Mating

If social interaction is to affect recruitment of new birds and production of young, the important events will occur prior to mating (copulation) in any given year. Since failing recruitment explains why certain populations have not increased, and since early mortality inadequately accounts for the numbers of potential recruits that disappear, the events from autumn to spring must explain these losses. It is reasonable to expect the spring months (April - May), when blue grouse descend to the breeding range and begin territorial behavior, to be the scene of these events, which could include the process of dispersion and social interaction
between members of the population. These two features occur simultaneously with a spring decline in breeding numbers is some species (Smith, 1967) and I felt it worthwhile to look for them in blue grouse. It was possible for me to observe the birds in early spring only once (April 1966).

I instrumented one yearling male and three females about ten days after the first birds appeared on the breeding range in late March 1966, or about a month before mating began. Although few birds were instrumented, the value of the data lies in the many observations giving detailed knowledge of each individual.

The yearling male was tracked for two weeks, a yearling female for three weeks, another for six, and an adult female for four. Detailed histories of these birds are presented in Appendix IV. I found each bird at least once, and usually two or three times a day. For analysis, their locations were plotted on maps and the distribution of these locations was tested against a random distribution. A polygon, drawn by connecting the peripheral locations of each bird, was divided into zones surrounding the activity centers of the territorial males nearby (Fig. 1). Territorial males perform most of their activities in a relatively small part of the whole area they frequent. They have places where calling ("hoots") and displaying are done regularly and where these males are found most of the time. These activity centers are the most meaningful places to mark the position of a territorial male, particularly in this study when adult males were not seen often enough to learn their precise territorial boundaries. Therefore activity centers served as points around which dispersion was measured.

The object of this procedure was to see if hens and yearling males kept significantly closer to adult males than would be expected from purely random
Figure 1: Movements of the Yearling Male

The solid line is the path of travel of the instrumented yearling male. The numbered points on the line are his consecutive radio-fixed locations. Numbered dots are the activity centers of territorial males. UB = unbanded territorial male. The zones used for analysis consist of the sets of concentric rings around these males. The sub-zones consist of the separate rings within the zones. The broken line encloses the area tested in the analysis of dispersion.
movements.

Apparently no such grouping occurred, because the observed distributions in the four instrumented birds did not differ significantly from those expected by chance: (yearling male--\(\chi^2 = 0.86, \text{d.f.} = 1, p > 0.05\); yearling female--\(\chi^2 = 0.72, \text{d.f.} = 1, p > 0.05\); adult female--\(\chi^2 = 1.18, \text{d.f.} = 1, p > 0.05\); yearling female--\(\chi^2 = 2.58, \text{d.f.} = 1, p > 0.05\)).

Because the occasional occurrence of other birds quite close to adult males could speak of attraction, a second test was run to see if the locations within the zones were grouped. Accordingly the zones were divided into four concentric sub-zones and the area of each sub-zone was calculated and summed (Fig. 1). The distributions over the sub-zones did not depart significantly from those expected by chance: (yearling male--\(\chi^2 = 1.21, \text{d.f.} = 3, p > 0.05\); yearling female--\(\chi^2 = 2.58, \text{d.f.} = 3, p > 0.05\); yearling female--\(\chi^2 = 2.97, \text{d.f.} = 3, p > 0.05\); adult female--\(\chi^2 = 2.57, \text{d.f.} = 3, p > 0.05\)).

According to these calculations, none of the instrumented birds were grouped near adult males, and together neither of the tests lend any support to the idea that adult males attract other birds.

In addition, none of the activities of these birds gave any evidence that they responded to territorial males in the pre-mating period. The yearling male was found nine times (21 percent of his radio-fixed locations) within 200 feet of activity centers, yet he did not remain there on any occasion and subsequent travel took him over four times this distance away from adult males. On three occasions, adult males were found very close to

(1) 200 feet approximates the boundary from the center of an average territory and I chose this distance as a measure to distinguish close from distant locations.
this yearling which showed no movement or activity that looked like a response to these males, even though they were almost certainly aware of each other's presence. The same was true of the hens, with one exception when a male courted and tried to mount the adult hen. She avoided his repeated advances and eventually flew away.

Contrary to the findings of Bendell and Elliott (1966), there was nothing about the behavior of these four radio-marked birds to indicate that they were attracted to adult males. All four passed through several territories during their travels. The average size of their home ranges, which were not mutually exclusive, was 47 acres with a range of 19 to 60. The movements of the yearling hens did not differ from those of the adult hen, or from those of the yearling male.

Movements from Pairing to Incubation

Mating must bring the sexes together. To find out how this occurred in hens that had been showing no reaction to males, I compared movements and activities in hens during and after mating with those before.

Two of the three hens instrumented before mating eventually nested; the third showed no reproductive activity at all. I continued observing all three daily; their detailed histories are given in Appendix IV.

One yearling hen ranged widely and moved randomly with respect to males until 5 May. On 5 May she was found less than 100 feet from the activity center of an adult male and from then until she began to incubate her movements spanned an area near him and 150 yards in diameter, less than one-sixth the extent of her former home range.
The adult hen began to limit her movements on 8 May, after I had observed a week of wide-ranging travel. From 8 May onward she frequented just one adult male, whereas before she had encompassed the territories of all three that were in the general area. Eighteen days after restricting her movements to the vicinity of this male, she began to incubate.

Both hens timed the change of reproductive activity and movements similarly. They started laying 12 days after restricting their movements, and since captive blue grouse started to lay a week after they copulated (Stirling, unpubl.), mating of the instrumented hens likely occurred within five days of their first localized movements. Nevertheless, how and where the hens conducted themselves during these five days was apparently independent of the male (except to copulate), since no lasting pair-bonds were formed (see PART II).

Without a lasting pair-bond with her mate, it seems safest to conclude that the hen restricts her movements initially by being attracted to him for copulation, and that her continued localization afterwards is due to something else, perhaps selection of a nest site, or simply a decline in the desire to travel.

The third instrumented hen did not nest and did not become localized like the others. She was still ranging widely by 15 June, when all but re-nesting hens were incubating. From this contrast between nesting and non-nesting hens I infer that estrus\(^1\) brings about a change in behavior; hens becoming localized and each restricting her movements near one male, likely

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(1) Estrus is a term used generally for mammals, but other authors (see references in Brander, 1967) have applied it to birds and I use it here to denote the period when a hen is receptive to males.
Movements during Incubation

Two hens were radio-tracked during part of their incubation periods to see where and how they went about daily feeding. Most of the behavior I observed is described in PART II.

I followed movements in one hen through the last 18 days she incubated, during which time she visited ten different sites for feeding. Her favorite ones were in a wet area about 150 feet from the nest, having succulent vegetation, while the others, totalling only one-quarter of all her feedings, were dry sites about the same distance from the nest but scattered in a wide arc in front of it. Use of the dry and wet sites had no consistent pattern and I could not relate the choices to any obvious factors. The duration of feedings and the rates at which feeding occurred were not correlated with feeding places, even though the ostensibly poorer sites might have been expected to require longer feeding.

Another yearling hen was also observed through most of the latter part of her incubation. She fed in fewer places (three), which she used more consistently; but, rather unexpectedly, I found she used relatively dry sites devoid of succulent herbage even though several moist sites were close by. Again, I could see no relationship between choice of feeding site, duration and rate of feeding, or environmental conditions, and together these points suggest that incubating hens had no trouble satisfying their requirements in any of the types of habitat that were available. It may also be true that the nest site is not selected for its proximity to prime feeding habitat.
Nest Dispersion

There are many territorial males who try to mate with several females but we do not know how many of these attempts succeed. It is important to our understanding of social structure in breeding populations of blue grouse to know whether certain males actually copulate with more hens than do others, for a strong selective advantage exists for them which could affect population processes in future generations. One can expect that some males do accomplish more matings because although the sex ratios are even (Zwickel and Bendell, 1967) most yearling males apparently do not mate while many yearling hens do, so that adult cocks must mate the yearling hens as well as the adults.

With evidence that hens nest close by their probable mates, I studied nest dispersion to discover where nests were placed in relation to each other and to the territorial males nearby. Without direct knowledge of polygamy our answer to the question, "do males share the hens or hoard them", requires that all nests in an area be found. This was achieved on a part (about 1/5) of the study area, by intensive search to locate nests themselves and to discover young broods from nests not found.

Seven nests were located and no broods less than a week old were found, other than from those nests. I am confident that the search was sufficient to have discovered all broods present, which means that all the nests in the area were likely found as well. Locations of nests were plotted on maps and distances were measured between adjacent nests and between the activity centers of the closest males.

By comparing Table 2 (a) with (b) we can see that every nest was
**TABLE II**

DISTANCES BETWEEN ADJACENT NESTS AND BETWEEN NESTS AND ADJACENT MALES

(a) **Nest to Nest**

<table>
<thead>
<tr>
<th>Nest (♀)#</th>
<th>Map Distance (Yards)</th>
<th>U.S. = 299 yards</th>
<th>S.E. = 110.09</th>
</tr>
</thead>
<tbody>
<tr>
<td>1163 and 960</td>
<td>286</td>
<td></td>
<td></td>
</tr>
<tr>
<td>UNID ♀ and 960</td>
<td>264</td>
<td></td>
<td></td>
</tr>
<tr>
<td>960 and 1142</td>
<td>176</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1121 and 933-A</td>
<td>396</td>
<td></td>
<td></td>
</tr>
<tr>
<td>933-A and 933-B</td>
<td>210</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1155 and 933-B</td>
<td>462</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) **Nest to Male**

<table>
<thead>
<tr>
<th>Nest (♀) to Male #</th>
<th>Map Distance (Yards)</th>
<th>U.S. = 122 yards</th>
<th>S.E. = 41.47</th>
</tr>
</thead>
<tbody>
<tr>
<td>1156 to 946</td>
<td>176</td>
<td></td>
<td></td>
</tr>
<tr>
<td>933-A to 764</td>
<td>110</td>
<td></td>
<td></td>
</tr>
<tr>
<td>933-B to 1764</td>
<td>88</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1121 to 943-A</td>
<td>88</td>
<td></td>
<td></td>
</tr>
<tr>
<td>960 to unbanded #1</td>
<td>110</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1142 to unbanded #1</td>
<td>88</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1163 to 1127</td>
<td>88</td>
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<tr>
<td>UNID ♀ to unbanded #1</td>
<td>187</td>
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</tbody>
</table>
placed closer to a male than it was to the closest adjacent nest. This is to be expected if hens nest near their mates. If this assumption is true, Table (1b) shows that certain males can mate with more than one hen (unbanded male no. 1 was the closest male to three different nests). We may conclude that several hens in estrus may submit to a single male and that they space themselves so their nests are nearer to him than to each other. Field-notes describe a few cases where active nests have been located less than 30 feet apart, so the tendency of nesting hens to avoid one another is not universal.

In general, dispersion of nesting hens may be viewed as groupings near territorial males. The males tend to be regularly spaced (Elliott, 1965) and one may mate with more hens than his neighbor.

Movements of Hens after the Hatch

(1) Leaving the nest.

I wished to study brood movements at the time the chicks first leave the nest, to see if broods made use of the areas the hen had used previously, especially her home range after she had mated and while she was incubating. An instrumented yearling hen left the nest with her chicks on the morning of 25 June 1966. Her movements in the first two days after the hatch were well away from the feeding areas she used most during incubation. Similar data on two non-instrumented hens make it apparent that broods do not necessarily use areas frequented by the hen prior to hatch. It follows then, that the pre-hatch home range is not selected for use by the brood, and the absence of this behavior suggests there is no advantage in it for young chicks.
Later brood movements.

Telemetry permitted the study of habitat use from day to day in a single brood. I could also compare brood movements with those of hens of other reproductive status, and observe the organization of the brood as the chicks grew older.

An adult brood hen was instrumented 26 July 1966 when her five chicks were a week old, and was tracked daily until they were three weeks old. All the chicks in this brood lived to at least 35 days of age, so their movements and activities can be described for future comparison with broods of high early mortality.

This brood showed marked habitat selection. Out of 40 observations free from disturbance by me, the brood was located in wet or moist spots 25 times (60 percent.). They returned directly to such habitat on three occasions when flushed out by me, and showed a tendency to go directly and quickly to similar habitat when one moist area was vacated. The summer of 1966 was dry, and by August the vegetation not in wet areas became visibly desiccated. Habitat selection is one way broods can avoid the effects of a drought.

The way the chicks spaced and conducted themselves did not change over the two weeks. When feeding undisturbed the most distant chicks were about 50 feet apart. I saw no particular pattern in the way they were dispersed around the hen and they showed no antagonism toward one another.

The behavior of the hen did change; she became tamer toward me as time passed, perhaps because she was less attentive to the chicks as they grew older, or simply because she was growing used to me. The chicks grew neither tamer nor wilder toward me up to three weeks of age.
I found them once feeding within 75 feet of two other broods. All three were grouped by themselves and no exchange of chicks occurred. Broods do mix and chicks occasionally switch hens and Bendell and Elliott (1967) conclude there was no intolerance between young birds. As far as I could tell, the radio-marked brood showed no reaction at all to the others near them.

In its pattern of movements, this brood resembled none of the hens of other reproductive status, for the hen and chicks did not roam continuously like anestrus hens nor did they become localized for longer periods like mated hens. This brood moved slowly and would remain for a few days in one favored area, then make longer, direct trips into others to their liking.

Movements of Unsuccessful Hens

Two kinds of unsuccessful hens were observed by telemetry in 1966. One described earlier that apparently failed to mate, continued travelling widely after other hens had become localized and had nested, and another had her chicks taken by a predator just after they hatched. Blue grouse can renest; even if the first nest is destroyed in the late stages of incubation, a second clutch can be started as soon as 14 days after loss of the first (Zwickel and Lance, 1965). The radio-marked yearling was in just this position as I followed her and was therefore of special interest as a potential renester. I tracked her for a month after her chicks were lost but she did not make another nest, and so can be compared with a hen that did renest in 1964.

Movements of the instrumented hen were tested against a random dis-
tribution and showed no significant departure from it \( \chi^2 = 0.75, \text{d.f.} = 1, p > .05; \) and \( \chi^2 = 2.15, \text{d.f.} = 3, p > .05 \) for the two tests described on pp. 5 - 7). In this respect she behaved the same as the pre-nesting (anestrus) hens. Other behavior also indicated she was not responsive to territorial males. It is unlikely she reverted to reproductive condition after 13 July when her transmitter failed, because records show there is no breeding activity this late, so I class her, then, not only as a broodless hen, but as one not about to resume reproductive activity.

The adult hen who renested in 1964 ranged widely for one week, then became localized in the same manner as other nesting hens, indicating that renesting hens cannot take advantage of the localization which occurs after the first mating and the first nest, but must repeat the sequence of physiological and behavior events from the beginning. This is likely because they are in anestrus when incubating and must revert to estrus before renesting can occur. The random wanderings of the non-renesting hen indicate she failed to return to estrus.

From evidence that broodless hens travelled faster than any others, Elliott (1965) concluded they migrated from the breeding range after nest or chick loss. Contrary to this, the broodless hen I followed by radio had not left the breeding range after a month, even though she did increase her rate and extent of travel.

**Migratory Movements**

It is well established that blue grouse migrate between summer and winter ranges, but except for a few early observations (Anthony, 1903; Bent,
1932; Wing, 1944 and Marshall, 1946), the modes and directions of travel, distances moved, habitats frequented, and social organization when migrating are all undocumented. Radio-telemetry was expected to make migration, at least in hens and chicks, more completely known.

Social organization during fall migration is particularly interesting, for while many hens return to the same summer range in following years, few of their chicks do. Autumn dispersal of young is known for many species (examples in Wynne-Edwards, 1962); breakup of broods in red grouse, *Lagopus scoticus*, (Jenkins, Watson, and Miller, 1963) and ruffed grouse, *Bonasa umbellus*, (Bump et al, 1947) occurs early in autumn, and migration seemed a likely time to expect it in blue grouse.

A yearling hen and one of her seven chicks were instrumented on the breeding range and followed for 42 days, during which they migrated. They stayed on the breeding range four days after instrumentation, then migrated steadily for six days (1 - 6 September 1966), and stayed in one place for a month afterward.

The hen and all her chicks stayed together for at least the first two days of migratory travel. I could see the birds only in the first two days. In the next four days of travel and for the month after, at least the radio-marked chick stayed with the hen, indicating that some broods may not disperse en route to the winter range and may remain together for some time after travel stops.

Three times during the first two days of migration I saw the brood walking in a closely gathered group, only about 20 feet across. I could not tell if the hen was in the lead.

No other birds were found with the migrating brood and of 39 blue
grouse located by dogs during search in the winter range, all were in broods or were lone adults, giving no evidence of either brood dispersal or flocking in autumn 1966.

The six days of migratory travel were highly oriented, for the birds followed a remarkably straight line. Their net deviation was only two degrees. The birds did not follow the easiest route along contours but travelled across them, and they made no effort to avoid dense vegetation.

As to what directed their travel, their movement was as rapid on overcast days as on sunny days except for short periods in the hot mid-afternoons of the latter when they apparently stopped to rest. They did not travel between full dark and 3:00 A.M. on a clear night with a full moon.

Although blue grouse have been known to fly during spring migration (Anthony, 1903), walking was the only method of travel I recorded, and though they encountered great topographic relief over short distances, for example, a small stream 1000 feet below the surrounding ridges, they walked the entire way across.

Six and one-half miles were covered in the six days, making the rate of travel about a mile a day. I watched them take six hours for continuous travel over a measured half-mile. The high rate of travel by itself is probably sufficient for one to distinguish migratory movements from any others.

Migration began abruptly and I could not identify a proximate stimulus. Instrumenting the birds likely had no effect since they did not start to migrate until four days later. Much of the vegetation on the breeding range was desiccated but the birds avoided it during these four days by using moist sites. Advancing age of chicks cannot explain their departure since other broods of greater age remained later on the breeding range, and photoperiodic
response is not a sufficient explanation either since the bulk of brood migration occurs earlier some years than others.

Although the instrumented birds themselves were not seen between 6 September and 9 October 1966, I sighted several others while searching in the same region. All were hens with chicks. This area comprises well-dissected ridges at 3000 - 4000 feet elevation, forming foothills to mountains of 6000 feet. Above 3500 feet the vegetation is in the Subalpine Mountain Hemlock Bioclimatic Zone (Krajina, 1965), with many openings within the tree canopy. These gross features are similar to those of winter range described by others (Marshall, 1946; Wing, 1944; King, in preparation) except that the habitats they described were at higher elevations.

Almost all the birds I saw were on the ground, while typical wintering behavior has them roosting in trees. Perhaps the birds I saw were not yet in full wintering behavior and they may later have moved to higher elevations, and in such case migration, at least in hens and chicks, may not be completed in one movement. Habitat which has some of the elements of true winter range may merely bring about a temporary halt.

King (in preparation) found only males among the adults in the winter habitat he studied and concluded that they lived separately from the hens in winter. I found no males other than chicks in the habitat I searched, which supports King's conclusion at least to mid-October.

Summary of PART I

None of the birds of varied reproductive status gave evidence of interaction with territorial males, except for estrus hens. Although the period
before mating is most important, the remainder also shows that males likely do not affect the local occurrence or numbers of other birds at any time.

According to Elliott (1965) hens and yearling males were grouped around regularly spaced territorial males until time of hatch. This pattern changed when broods appeared and moved randomly with respect to one another and to males, and broke down completely when males (and presumably also broodless hens) began to migrate.

Combining the conclusions I have presented above permits me to modify this account. Before mating, hens wander at random among the territorial males. Yearling males also wander randomly during this time. Hens coming into estrus abruptly change to localized movements near territorial males and mate shortly after. The hen stays near her mate while she lays her eggs and incubates them. Dispersion at this time may be viewed as groupings of mated hens around the adult males; the number of hens around each male is variable. Unmated (anestrus) hens and yearling males are still wandering randomly. After the hatch, broods move randomly with respect to males and each other, but may select the vegetation they frequent. Hens that lose their eggs or chicks, and do not renest join the anestrus hens and young males in unpatterned movement, but hens that renest repeat the original sequence of wide-ranging travel; which gives way to localized movements when the hen reverts to estrus.
Earlier I concluded that mating occurs within a week after localized movements begin in hens, and that apparently the only time the hen responds to the cock is when she is attracted to him in estrus. Lack (1940) groups the blue grouse with other birds wherein the sexes meet only briefly for copulation, but there is no direct evidence from field studies to attest to this. The proper evidence is hard to obtain because it requires that continuous attention be paid to a hen and cock suspected of being paired, to be sure that they are mating partners and that they remain together by behavioral response to one another.

In this study, continuous observation of the required extent was not practicable and we have to be satisfied with several shorter periods with gaps in between. Moreover, no copulations were seen and so mating between certain cocks and hens has to be inferred from the way the hen became localized near the male before she nested. Nevertheless sufficient observation was made on several hens to permit some conclusions.

One radio-marked hen was watched thirteen times between the time she localized her movements and the time she began to incubate. In many consecutive hours of observation she was never seen in the company of males, even though she mated during this time and made her nest less than 100 yards from two of them. Both these males hooted regularly from their activity centers but I never saw them approach her.

Another hen avoided the advances of the male closest to her even though
she began to lay only three days later and so had very likely mated before the encounter took place. In twenty-two observations in 1964 on three hens between the times they mated and incubated, no males were present. Although I could have missed occasions when males briefly accompanied any of these hens, it is certain no continuous pair-bonds existed. This leaves pairing in blue grouse as a brief event, likely occurring only at copulation as Lack (1940) suggested.

In dealing with mode of sexuality, Elliott (1965) called male blue grouse promiscuous because they try to mate with any hens they encounter. We cannot call hens promiscuous by the same criterion, for they fail to associate with more than one male, let alone attempt matings. Bendell (1954) said male blue grouse are polygamous, but polygamy is usually defined as lasting bonds between a male and several females (Lack, 1940). While certain males may mate with several females, the fact that pairing is only temporary makes promiscuity a better term for sexuality, in males at least. Females form a temporary link with just one mate, but because it is temporary, this link does not constitute monogamy in the usual sense, and perhaps a different term altogether is fitting for hens.

Habitat Use

The study of habitat use on the breeding range was subordinate to the study of movement and activity per se, and so the data on preferences are not as complete as they would have been if given priority. They are adequate, however, for one to see how some blue grouse used the plant associations and topographic types occurring on the breeding range. The objective here is to
see simply if certain habitats are preferred and to see how dispersion could be affected if some resources were in short supply.

Five grouse, each of different reproductive status, were followed by radio. The number of times each was found in certain vegetation and slope was compared to the availability of these features on the breeding range. This comparison is made in Table 2, which shows that of the five birds, only the brood hen appeared to select vegetation and topography. She was found 60 percent of the time in relatively rare wet depressions covering less than 10% of the study area, mostly stream courses containing succulent plants. Her choice of slopes less than 10° reflects the flatness of these depressions.

Plants in these places were visibly less desiccated than elsewhere during the dry summer of 1966. Choosing wet habitat by brood hens has been noted in other years by Bendell and Elliott (1966) and is apparently one way hens with chicks avoid the effects of a dry season. The fact that other birds fail to show this preference suggests this behavior benefits the chicks rather than the hen.

Bendell and Elliott (1966) showed that all blue grouse had preferences for certain types of structure in the vegetation, but these preferences could not express themselves on the Comox Burn because it did not have the variety of successional stages that occurred where these authors worked. The absence of habitat selection again suggests that all but the brood were able to satisfy their requirements anywhere on the Comox Burn. In this latter case the habitat did affect dispersion.
### Table III

The use of plant associations and slope compared to their occurrence on the Comox Burn

<table>
<thead>
<tr>
<th>BIRD NO.</th>
<th>FACTOR</th>
<th>NO. OBSERVATIONS</th>
<th>EXPECTED OCCURRENCE</th>
<th>OBSERVED OCCURRENCE</th>
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<td>Ad ♀</td>
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</tr>
<tr>
<td>1539</td>
<td></td>
<td></td>
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<td>13</td>
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</tr>
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<td></td>
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<td></td>
<td>Plant</td>
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<tr>
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<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Gaultheria = 6</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Anaphalis-</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Gaultheria = 10</td>
<td>6</td>
<td>&gt;.01</td>
</tr>
<tr>
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<td></td>
<td>Epilobium = 6</td>
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<tr>
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<td></td>
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<td></td>
<td>Other = 1</td>
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<tr>
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<th>EXPECTED OCCURRENCE</th>
<th>OBSERVED OCCURRENCE</th>
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<td></td>
<td></td>
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</table>

**Notes:**

1. $P$ is the probability a similar departure from the expected would occur by chance. The 1% level of acceptance was chosen (Chi$^2$ test) because of the relative inaccuracy of the areal coverage estimates for both slope and plant associations. Type I error is reduced by using the 1% level.

2. **OTHER** includes associations of infrequent occurrence (generally less than 5% areal coverage of the home range of each bird) and which were not visited by the birds.
Incubation Behavior

The movements of two incubating hens were described in PART 1, and radio-telemetry provided an opportunity to add to other knowledge of their behavior because this technique enables one to acquire information while concealed from the bird.

(a) Development of incubation behavior

One hen was observed during the days she laid eggs, as well as in the first part of her incubation period. On the evening prior to the first day she incubated, this hen fed for a half-hour only 60 feet from the nest. At dusk she abruptly ceased feeding and flew toward the nest but continued past it, roosting 200 feet away for the night. The next evening saw the procedure repeated except that she fed farther away and mounted the nest after her flight.

Her behavior on the evening before she incubated is striking. The only other examples known of spontaneous flight which terminates feeding and leads to roosting (on the nest) occur in incubating hens. Normally, in non-incubating hens, feeding movements (walking) merge directly into roosting. Perhaps behavior patterns of incubation develop gradually in blue grouse hens as the eggs are laid. The change from laying to incubating may be gradual, with each containing common elements of behavior (Palmer, 1949).

(b) Occurrence of feeding during incubation

Fragmentary data have shown that certain hens may feed at different times of the day, but knowledge of how consistent the feeding pattern of each hen is requires that incubating hens be observed continuously, which is hard to accomplish except by telemetry.
Two hens observed until their eggs hatched fed more consistently in the evening than in the morning. Neither hen fed on the days the eggs hatched, and hens likely remain on the nest at such a time to prevent exposing the wet chicks. These hens fed in all other evenings but only in half the mornings I kept watch.

In the evenings light intensity appeared to set off the start of feeding, these times being 20 to 45 minutes earlier under dark overcast skies. The start of feeding in the morning was less consistent, usually beginning just before dawn, but occasionally being delayed until mid-morning. I could not see what influenced the starting time of morning feedings. Neither bird fed twice in one morning. 

(c) Modes of travel

On most evenings (22/26; 85%), the hens I observed flew to and from their feeding places; less often they walked one way and flew the other. Walking was more common 5/9; 51%) in morning feedings, particularly those in mid-morning. By flying to and from feeding, the incubating hen avoids leading mammalian predators to the nest by scent trail. In daylight, a flying bird would likely attract more attention than one afoot, perhaps best explaining the tendency for hens to fly in the evening and walk in the morning.

(d) Behavior on the nest

Four hens were observed by radio while they incubated and two of these were observed visually as well, to see what variation existed among hens in their behavior on the nest.

Three of the four sat motionless on the nest, excepting just before they left to feed and just after they returned. At these times, the radio signal revealed they briefly shuffled about, perhaps adjusting themselves on
the eggs, and another distinctive radio signal revealed that the eggs were turned by the hen just after she returned from feeding. One of two hens observed until their eggs hatched did not turn her eggs after feeding on the last five days.

Signals from the other hen revealed that she was in continuous motion while she incubated, even to the day of hatch. I could not approach her undetected, and this made her become still. The movement signal returned as I withdrew. Thermocouple leads attached to the eggs of certain hens become coiled, showing that the eggs are turned continuously while being incubated (unpubl. data). The reason for this behavior is unknown. All seven eggs hatched but the chicks were taken by a predator before they left the nest. As nest destruction by predators seems the main reason certain hens produce no young (Zwickel, 1965), it would be interesting to note whether some of these variations in the hen's behavior on the nest can affect predation.

The Brood Patch in an Unmated Hen

Zwickel (1965) concluded that if a blue grouse hen had a brood patch she had mated and attempted to nest. Bailey (1952) found that brood patches formed in three stages in passerine birds: I, a stage of feather loss, where the down of the ventral apterium is molted several days before laying; II, a Vascularization Stage, where the skin begins to thicken and the blood vessels proliferate; and III, an Edematous Stage, with general edema and vascularization of the skin. Comparable stages occur in blue grouse that complete most of their incubation periods.

One instrumented hen I observed in 1966 failed to nest or mate, yet
had a brood patch like those of other hens usually considered to have bred. Close examination of this hen revealed no increased vascularization, edema, or thickening of the skin, suggesting that her brood patch was not complete and that blue grouse can achieve ventral feather loss without having mated. Therefore we need new criteria to distinguish an unmated hen from one who has mated but not nested, or one whose nest has failed early in the incubation period.

**Comparative Rates of Travel**

When grouse were located by radio several times a day, rates of travel were obtained by measuring distances moved and dividing by elapsed time. Two such rates were sought from the data for 1966: comparative daily rates of travel among individuals, and rates of travel for parts of the day. One object of this was to see if certain birds travelled faster than others of different reproductive status so that each could be classed by rate of travel alone.

Rates for three parts of the day (dawn to 10:30 A.M.; 10:30 A.M. to 6:00 P.M.; and 6:00 P.M. to dusk) were compared for three birds by analysis of variance. For any one bird, these rates were similar for all parts of the day. Larger samples might reveal differences, for other data show that blue grouse are more active at certain times of day (Bendell, 1955).

The data were pooled to give daily rates for each bird. Average rates for 27 measurements were:

- **Yearling male:** 60.3 feet per hour  S.E. 23.75
- **Broodless yearling hen:** 49.1 feet per hour  S.E. 18.21
Adult brood hen: 29.1 feet per hour. S.E. 7.05

These rates were compared by analysis of variance and were significant at the five percent level of acceptance (F = 3.65; d.f. = 2,26), although the New Multiple Range Test (Steele and Torrie, 1966) failed to identify which rates differed from the others.

Elliott (1965) found among females that lone hens prior to mating travelled most slowly, then brood hens, with broodless hens being the fastest. Elliott thought his pre-mating hens travelled slowest because they localized themselves near territorial males. As I have pointed out earlier, this is very likely the case from mating onward but not before. The greater the number of measurements taken from the period when most hens are mated or nesting, the slower the average rate of travel. My observations on mated hens were too few for statistical analysis but several times I found them staying still for lengthy periods and their rates of travel are probably slower than those of any hens not on the nest.

The fastest rate Elliott obtained, 78 feet per day for broodless hens, was far slower than any of mine. I suggest he got these low values because he could only obtain infrequent measurements, and therefore could not know the total distance covered by his birds in the meantime. In following birds by telemetry one can see that actual travel is much longer than a straight line between points a day or more apart.

Aside from these differences, the rates I obtained are in general agreement with what one might expect from other information. Brood hens are encumbered with chicks which travel slowly, especially when young. Broodless hens and non-territorial males tend to travel faster since they have fairly extensive home ranges.
Among hens at least, rates of travel may be promising means of identifying their reproductive status, but measurements from several more birds will be required for statistical safety.

**Very Early Juvenile Mortality**

Average brood size is consistently smaller than average clutch size, even when the chicks are only a week old, and from this, Zwickel (1965) concluded that some very early losses occur even before the major mortality period, 7 - 14 days of age. I observed an instrumented hen as she left the nest with her newly-hatched young, an excellent opportunity to see if any were lost at this time.

Of the three chicks that hatched, only two were present after five hours and 100 feet from the nest. Neither I nor an experienced dog could find the missing chick. A second case of very early mortality was a chick from another brood less than 24 hours old, found with 3/4 inch of yolk sac protruding from its abdomen. This chick, also from a yearling hen, was very weak, scarcely able to move from the nest, unable to keep up with its brood mates, and would have died shortly.

These cases show that some very early mortality does occur when chicks first leave the nest, a time when malformations which reduce a chick's ability to travel first take effect.

**SUMMARY OF PART II**

(1) The pair-bond in blue grouse is brief, likely occurring only at copulation.
Sexuality in males is promiscuous; hens form a transitory bond with one male only.

(2) Of a yearling male and several females, only a brood hen showed any habitat preference, choosing wet depressions containing succulent vegetation.

(3) Incubation behavior in hens may develop gradually as the eggs are laid.

(4) Incubating hens feed consistently in the evening and less often in the morning.

(5) The hen does not leave the nest the day the eggs hatch.

(6) An unmated hen developed the first stage of a brood patch, meaning that ventral feather loss is not sufficient to distinguish mated from unmated hens.

(7) Incubating hens travel the most slowly with mated hens next, then brood hens, lone hens, and migrating hens.

(8) Some very early juvenile mortality occurs when malformed chicks try to leave the nest.
DISCUSSION

Criticisms of the Data

(1) Variability

The most obvious weakness of the data obtained from the instrumented grouse is that only a few individuals are represented and these may be atypical—a danger that can be surmounted only by obtaining larger samples. Nevertheless, the conclusions I have drawn from these birds are answerable to empirical test; the most fundamental being whether my observations can be repeated.

(2) Incomplete coverage

Since I have drawn these conclusions from only part of each phase of the birds' breeding activity, it is possible that key events have been missed which would negate what I have said. While telemetry allowed more continuous observation and greater detail than permitted by other methods, several scattered birds cannot be watched simultaneously. Brief but significant events can be missed. The problems in expanding the coverage are obvious.

(3) Artifact

There is the possibility of artifact induced by the telemetry technique, but all the present evidence is to the contrary.

(4) Analysis of dispersion

Did my method of analysis prejudice the conclusion that hens and yearling males are not attracted to territorial males? I used activity centers as reference points around which to measure dispersion, and concluded that hens and yearling males were found no more often near activity centers than
in areas farther away. One argument against this method is that it is not sensitive enough to identify groupings of birds. For example, birds some distance away from an activity center may have been within the territory boundaries of adult males and should have been considered grouped near these males. Then perhaps enough would have been so grouped to have shown non-random distribution. I do not think such an error exists in my method, because locations of birds grouped in any area will show non-random distribution, no matter where that area lies in reference to a given point.

There are exceptions to this. By chance, territorial area could have been divided evenly among the divisions (zones and sub-zones) I used for analysis; then bird locations grouped on territories but distributed randomly within them would have also been spread randomly over my divisions. This could falsely discredit the hypothesis of attraction. However, in reality, most of the area of territories is near the activity centers (Bendell and Elliott, 1967), so that chance distribution of territorial area evenly over my divisions is unlikely. Moreover, birds that were attracted to adult males would not likely move randomly over the territories of these males, and since territory boundaries are ill-defined at best, it is often arbitrary to place locations of these birds inside or outside these limits. These reasons make it improbable that preference for territories falsely resembled random distribution in my analysis.

Contrary Evidence

Although I have concluded that yearling males fail to show attraction to territorial adults, other evidence shows that the two can interact. For
example, if the occupant of a territory is shot he is often replaced by a yearling within a few days (Bendell and Elliott, 1967). These yearlings, which formerly showed no reproductive activity, become localized like adults and begin to sing and display. These authors conclude that the territory holder can keep most yearlings off his territory while at the same time attracting them to him. As a result of this one expects yearlings to show non-random dispersion, perhaps grouping themselves along the territory boundary or at a certain distance from the activity center of the territorial occupant, ready to supplant him. This is what Bendell and Elliott (1967) claim occurs.

If I am correct in saying no attraction to males occurs, how can the response of yearlings to removal of adults be explained? I suggest that yearlings do not necessarily move toward the objects that attract them, particularly if the presence or behavior of adult males is sufficient to neutralize that attraction. Yearlings may be attracted by acceptable habitat for territories and not by the occupants of territories. Another way of putting it is to say that an adult male neutralizes the attraction his territory has, and yearlings do not respond to this attraction unless the adult disappears.

I would stress that these ideas can explain the dispersion of yearling males only. Limited evidence suggests that hens vacate an area when males are removed (Zwickel, 1965) and so a certain number of males may be necessary for females to occupy an area, even though once on it, hens ignore males except to copulate with them.

The hypothesis that adult males attract other grouse (Elliott, 1965; and Bendell and Elliott, 1966 and 1967) is supported by data which are, I believe, suspect. These data were of three kinds:
(1) The distribution of locations where hens and yearling males were found was compared to a set of points placed randomly over the breeding range. The grouse were closer to territorial males than were the random points.

(2) The numbers of hens and yearling males found on territories occupied by adult males exceeded the number found on vacant territories (vacant sites occupied by adult males in previous years).

(3) The numbers of hens found on plots where territorial males had been removed were fewer than on plots where territorial occupants were untouched. Numbers of yearling males remained unchanged.

These results were likely prejudiced by an artifact of method. The study plots were searched repeatedly to find hens and yearling males; however Bendell and Elliott themselves mentioned (1967, p. 62) that observers spent a disproportionate amount of time searching near territorial males, increasing the chance of finding other grouse there than elsewhere. This would make it appear that these birds were grouped near territorial males.

Procedure (2) had another problem; it was a natural experiment lacking an essential control. The vacant territories were useless for comparison with ones occupied by adult males because these vacant territories may have been unsuitable for any grouse, hens, adult males, and yearling males alike. To serve as proper controls, vacant territories must be known to be acceptable to adult males at least.

The third procedure treated hens separately from yearling males. According to the hypothesis that adult males attract yearlings, the numbers
of yearling males should be reduced when adults are removed from an area. Fewer yearlings means fewer new adults the next year. Despite the fact that the numbers of new males did not decline the next year, Elliott did not consider this as evidence against the hypothesis. Even without contrary evidence, these faults weaken the case for attraction.

Elliott did consider the parallel experiment involving hens as a test of the attraction hypothesis. Here the prediction that removal of males would leave fewer hens in the pre-nesting period was borne out by the results.

How can these results showing attraction of hens be reconciled with mine showing none? I have already pointed out that males may be required for females to occupy an area, so that removal of males would mean that females disappear also. Certain information suggests that blue grouse choose open vegetation because it allows them to communicate easily (Elliott, 1965). I suggest that anestrus hens, once in an area, move at random with respect to males as long as they are in range of communication with them. Very low densities of males may mean that communication is lost and hens leave the area.

Comparing the dispersion of hens to that of yearling males on a breeding range occupied also by territorial adult males, we can say that although the patterns of the two groups are similar, the patterns have different influences. Hens require territorial males before they will reside in an otherwise suitable area, while yearling males need the area only. Once on such an area the hens ignore the territorial males and travel about at random, but yearling males travel randomly because adult males usually prevent them from becoming localized on territories of their own.
Blue Grouse Compared to Other Tetraonids

(1) Ruffed grouse

Brander (1966 and 1967), using radio telemetry, concluded that ruffed grouse (Bonasa umbellus) hens and yearling males were repeatedly attracted to various drumming adult males. I tend to agree with Brander's conclusions, but not with his confidence in them or his reasons for making them. While we can grant that each hen that eventually nested must have been attracted at least once, the data do not permit us to distinguish this event from the other times hens passed near adult males. Three conditions will identify movements resulting from attraction from those that do not: spatial association must be (a) prolonged near one or more males, or (b) if not prolonged, then movements from male to male must be non-random and directed from one male to the next, or (c) the distribution of places where hens and yearling males are found must depart from a non-random distribution. The direction of departure would be toward clumping with adult males. Since Brander's data do not appear to meet these conditions, there is no reason to be sure that his hens or yearling male were attracted (except copulating hens) simply because they frequently passed near drumming cocks. The fact that hens in estrus occupied home ranges nearer males than when in anestrus is to me better evidence that cocks can influence hens' movements. If this is true, then ruffed grouse and blue grouse hens behave essentially the same in estrus, except that the former may be promiscuous while the latter appear to visit one male only.

(2) Spruce grouse (Canachites canadensis)

Stoneberg (1967) thought each pre-nesting female occupied a home range coinciding with that of an adult male, but his observations were too few to
tell if the male and hen were paired, except in one hen who lost her chicks and was later seen several times with a male not her original mate. If this is generally the case it is quite opposite from that in blue grouse; pre-nesting hens and broodless hens alike.

Immature spruce grouse males show movements localized around an activity center. They make journeys away from the center and a limited number of observations suggest they use these trips to seek out adult males (Ellison, 1967). Therefore while yearling blue grouse males appear to locate themselves independently of other birds, those of spruce grouse may become established in the population through interaction with adults.

These differences are quite distinct and provide some evidence that the social systems of blue and spruce grouse differ fundamentally and that the two genera are not closely related.

(3) Ptarmigan

Ptarmigan (Lagopus) differ from the other grouse in having a lasting pair-bond coupled with a tendency to localize themselves on territories, beginning at one year of age (Weeden, 1963; and Choate, 1953). Here the males have ample opportunity to control the numbers of hens present, and indeed certain males may have one hen, others two (Weeden, 1963).

(4) The lek or prairie grouse

In general, the sexes flock separately prior to the breeding period. The males, including yearlings in some species (e.g. Pedioecetes), take up territories which are grouped on a display ground, and the hens come to them only to copulate (Lack, 1940). Blue grouse hens behave similarly, but yearling males differ in that they participate infrequently in breeding behavior.
Significance of Dispersion to Habitat Selection in Blue Grouse

The idea that yearling males are attracted by suitable habitat alone finds support in studies of habitat selection done by Bendell and Elliott (1966). Attraction to suitable habitat is of adaptive value to coastal blue grouse which often respond to forest clearings by increasing in number. Such clearings are often transitory and individuals equipped to locate them rapidly and settle in them will have a selective advantage. Blue grouse, particularly adult males, show a strong tendency to return to the same breeding range each year once they have settled in it. Elliott (1965) suggests the tendency of blue grouse to disperse widely between their first and second summers facilitates exploitation of new habitat. I would suggest further that because yearling males disperse independently of other birds they are free to exercise their habitat preferences, so achieving the same end. If yearling males settle in suitable habitat and behave as normal territory-holders, they may make that habitat suitable for hens as well and so a new population is established.

Dispersion and the Numbers of Blue Grouse

I have applied the preceding pages to the general social system in blue grouse. The specific problem we seek to explain is why certain potential recruits join the populations of blue grouse present on the summer range while others do not. Individuals that fail to join suffer two fates: they die, or they go elsewhere. Dispersal does not necessarily exclude
death, but dispersal per se specifically concerns us here and it means essentially that individuals that fail to join the population live in different places from those that succeed; their pattern of distribution no matter where they are differs from those that succeed; or both.

Tinbergen (1957) sees dispersion as a product of intraspecific interaction, and Wynne-Edwards (1962) contends this interaction sorts animals into those that become part of the population and those that become surplus. Surplus animals can be identified by their deferential treatment at the hands of breeding birds, either by retreating from contact with breeders, or by showing a particular manner of life that is a direct consequence of unsuccessful encounters with them. Wynne-Edwards selects dispersion, or the pattern of local occurrence as an especially significant consequence of social interaction, but the important point is that social interaction is a necessary condition to explain it. As far as blue grouse are concerned, we know that the recruits that add to the population are dispersed differently from those that do not, simply because the successful ones are present on the breeding range while the others are not, but there is no evidence to show that interaction occurring on the breeding range is involved in the dispersion of either group. To repeat the conclusions of p. 6, I saw no evidence that social interaction with adult males could explain the way females and yearling males were dispersed on the summer range, and the absence of any contrary evidence makes it appear that the dispersion of hens and yearling males has no specific pattern beyond that affected by habitat preferences. Therefore it is hard to see how intraspecific interaction on the breeding range can affect recruitment either. A similar conclusion was reached by Bendeli and Elliott (1967), who found no evidence that the territorial behavior of adult males produced
a surplus of other males or females.

Although it is most reasonable to expect that the response shown by many blue grouse to a change in the summer range will be explained by events occurring in the summer, lack of evidence that such events occur then increases the likelihood that they happen in winter. I would like to propose one avenue through which winter events may affect summer numbers. The young of the year appear to remain with the hen as she migrates to the winter range. As well, the fact that we find adult males only by themselves means they probably live separately from the hens and young. This evidence suggests that hens and chicks form a separate social unit in the fall. There is no such organization when the birds return to the breeding range next spring, therefore this unit must break down some time between fall and spring. Concomitantly, the chicks (the potential recruits) of both sexes disappear at a faster rate than do the mature hens. These young birds also disperse widely, since few banded on the breeding range return to it as yearlings, while most yearlings that do appear are unbanded (Elliott, 1965).

Considering the accumulating evidence that dispersal is a consequence of intraspecific hostility, I suggest that intolerance between members of the hen-chick social unit in winter affects the dispersal of many young and is necessary to regulate recruitment to the breeding population next spring. This sort of process occurs in red grouse (Lagopus scoticus) during a period of display and territorial behavior on the breeding grounds in autumn, only here adult males participate as well as females (Jenkins, Watson, and Miller, 1963). The location may differ between red grouse and blue grouse but the process and its effects may be much the same.

With so little known about blue grouse in winter it is hard to be
more specific. A more specific hypothesis will have to await further knowledge of the natural history of the birds during this period, but at this point the problem becomes more complex, for if the process of regulation occurs in one place and the effects of the process occur in another, separated by months as well as miles, we have to satisfy the requirements for a carry-over of information from one place to the other. If coastal blue grouse adjust in winter to changes in the summer range, summer assessment of that range must be retained for implementation in winter in the adjustment process. It is simpler to assume that blue grouse assess or retain nothing of the sort, and that the process of population regulation occurs independently of conditions on the summer range. If this hypothesis is true, and population processes in blue grouse are determined during winter, then if any environment influences these processes it will be the environment on the winter range that does so, not that of the summer or breeding range. The only effect the summer range would have on breeding numbers is, then, to prevent the localized establishment of enlarged breeding populations if the summer habitat is too densely vegetated or otherwise unsuitable to the birds. It follows also that summer ranges which could support increased breeding populations might fail to entertain them through no fault of their own, and that the simultaneous occurrence of an increase in breeding stock with the availability of suitable breeding range to handle the increase is merely coincidence, totally fortuitous for grouse and sportsman alike.
LITERATURE CITED


King, D. A., in preparation. The ecology of blue grouse on their winter range.


APPENDIX I - DESIGN SPECIFICATIONS OF TELEMETRY EQUIPMENT

This equipment was constructed from extensive modifications to the design of similar apparatus described by Marshall and Kupa (1963). The modifications were of two types: design changes and substitution of improved components.

Description of Receiver: The VHF Receiver is a narrow-band, crystal-controlled receiver, capable of operation on any one of 24 channels in the 140 - 160 MHz VHF band. The receiver is basically a dual conversion superheterodyne type with amplitude modulation (AM) detector, audio amplifiers and extensive metering facilities.

The incoming signal between 140 and 160 MHz is amplified and then mixed with the third harmonic of the first crystal local-oscillator to produce the first IF output of 6 MHz, nominal. This IF is amplified and passed to the second mixer for conversion to the second IF of 455 kHz. The second local oscillator consists of up to 24 switch-selected crystals. Channel selection is thus achieved at the second mixer; the first stages serve as pre-amplifiers and convertors.

The signal is amplified by two 455 kHz stages and is detected by diode rectifiers. The derived audio is then passed through the volume control to the Audio Amplifier and thence to the headphones and metering circuit. By appropriate switching, the meter indicates (1) Battery condition, (2) Audio Output, (3) Signal Level.

Certain applications may require the monitoring of an unmodulated signal. For such cases, a "beat frequency oscillator" (BFO) is provided to produce an audio note when an unmodulated signal is received.

Other controls permit one to adjust the set for optimum reception under
most conditions.

The entire receiver is powered by 12 - 1.25 volt, rechargeable Nickel-Cadmium batteries at an operating voltage of 15v. A recharging network is provided to permit recharging from a 12-volt car battery.

The major portions of the LR-1 receiver were assembled from modules manufactured by International Crystal Manufacturing Co. Inc. of Oklahoma, U.S.A. These modules were extensively modified. The modules incorporated were Model Nos. TRC-5B, TRB-1 and TRA-2.

PERFORMANCE SPECIFICATIONS

Model: VHF Receiver

Number of Channels: 24 maximum

Useable Frequency Range: Any 1MHz span in range 140 - 160 MHz

Channels Equipped:
(Serial 1)
1. 150.310 MHz
2. .340
3. .370
4. .400
5. .430
6. .460
7. .490
8. .520
9. .550
10. .355
11. .325
12. .430
13. 150.550
14. .385
15. .475
16. .415
17. 
18. 
19. 
20. 
21. 
22. 
23. 
24. 

Bandwidth: 5 kHz @ - 6 db
10 kHz @ - 20 db

Sensitivity: 0.05 μv at threshold
(Sensitivity control at maximum)

"Peaking" Tuning Range: ± 4 kHz

BFO Tuning Range: ± 5 kHz
Power Source: 15 vdc, battery
Current Consumption: 40 ma. @ 15 v.
Size: $3\frac{1}{2}'' \times 5\frac{1}{2}'' \times 9''$ high
Weight: 9 lbs. 4 oz. not including carrying bag.
FIG. 2.

Panel Layout
Model LR-1 VHF Receiver

24 Channel Selector Sw.

Meter
0-50 Arbitrary Units.

Turns BFO 'On'
(For Beat Note)

R.F. \( \frac{1}{P} \), 150MHz (BNC)

Any Headphones.

Connect to 12V Battery to Charge.
(Main Sw. Must Be 'Off')

Main On-Off Switch.

Depress to Test Battery Condition.
(Reading \( \frac{3}{3} \) = Volts)

Tune For Strongest Signal.
Set To Max.
Unless Signal is Very Strong.

Sensitivity

Tuning

Volume

BFO Pitch

BFO Meter Filter

Meter Gain

Restricts Audio Response When 'On!'
Adjust Both For Optimum Meter Reading.
Adjust For Loudest Pitch.

Up - Audio Level
Down - Carrier

Connect (For Beatt Note)
FIG. 3  BLOCK DIAGRAM

MODEL  LR-1  VHF RECEIVER

CLIENT  UBC, DEPT. OF ZOOLOGY

FILE  18-05

DATE  MARCH 1967

DRAWN BY  [Signature]

NATIONAL ELECTROLAB ASSOCIATES LIMITED
FIG. 5  
Schematic

2nd Converter/AF/Defector

Client: UBC Dept. of Zoology
File: 18-05
Date: March 67

Drawn by: [Signature]

NATIONAL ELECTROLAB ASSOCIATES LIMITED
Fig. 6
Schematic Audio Amplifier Model LR-1 VHF Receiver.

Q12

Q10

NOTE
16. 750 ohm output
17. 750 ohm output
19. 50 ohm input
20. Ground
21. 50 ohm input
22. 100,000 ohm input high side
23. 100,000 ohm input ground side
24. -15 VDC
25. +15 VDC / GROUND
26. 3.2 ohm output
27. 3.2 ohm output

NATIONAL ELECTROLA3 ASSOCIATES LIMITED
NOTE
D1, 2, 3, 4 are IN4001

FIG. 8 SCHEMATIC
Power Supply 
Battery Charger

<table>
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<th>UBC Dept Of Zoology</th>
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<td>DRAWN BY</td>
<td>L. Ingram</td>
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NATIONAL ELECTROLAB ASSOCIATES LIMITED
FIG. 9  TRANSMITTER MODEL LT-1
Department of Zoology
University of British Columbia

SCHEMATIC DIAGRAM

Components List

- $Y_1$: 150.31 to 150.55 MHz Crystal
- $C_1$: 1000 pf.
- $C_2$: 1000 pf.
- $C_3$: 1 to 9 pf. Trimmer
- $C_4$: 4.7 pf.
- $C_5$: 15 pf.
- $C_6$: 1 to 9 pf. Trimmer
- $R_1$: 100 K ohm
- $R_2$: 1 K ohm
- $L_1$: .22 mH
- $L_2$: .080 nh.
- $Q_1$: Transistor Fairchild 2N3563

File: 18-508  October 1965
**DESCRIPTION OF TRANSMITTER**

**Tuning Range:** 130 to 160 mc/s, depending on the crystal. The transmitter described in this application has been optimized for use at 150 mc/s.

**Emission:** Continuous wave

**Power Output:** 1 milliwatt maximum

**Input Impedance:** Designed for use with a ship antenna

**Transmitter duty cycle:** Continuous

**TEST RESULTS**

**Power Output:** The measured power output of the transmitter when adjusted for a 50Ω load was 0.6 milliwatts.

**Frequency Stability:**

A. Under temperature variations of 0° C to ±45° C the variation in frequency was less than ±1 kc.

B. The variation of frequency for battery voltages varying from 100% to 90% was less than ±.5kc.

**Spurious Emission:** The strongest spurious emission was the second harmonic, which was measured as 28 db below fundamental. Other harmonics were not measurable.

**OTHER TEST RESULTS**

Because the antenna is coupled directly to the transmitter oscillator, a variation in frequency occurs with movement of the antenna and the bird, see Appendix III. This change in frequency permits the operator of the receiving station to deduce the nature of the movement of the bird through the variations in signal frequency. The maximum measured variation in frequency is less than ±4 kc.
METHOD OF OPERATION: RECEIVER

1. Turn main switch to ON.

2. Test receiver battery condition by depressing BATT. TEST. Meter should indicate 15 v. or more when read as n/3.

3. Connect hand antenna and headphones.

4. Set SENSITIVITY control to maximum, TUNING and BFO PITCH to median position, METER GAIN to minimum and VOLUME to suit.

5. Set toggle switches as follows: BFO—on; METER—on; FILTER—off.

6. Set CHANNEL SELECTOR to desired channel.

7. Sweep hand antenna 360° with elements horizontally oriented. Repeat with elements vertically oriented.

8. Adjust PITCH and TUNING as required to bring signal onto audio scale.

9. When signal tone is head in headphones, adjust TUNING for strongest signal and adjust BFO for loudest pitch.

10. Adjust METER GAIN to bring needle onto scale.

11. Repeat antenna sweeping with elements oriented to give strongest signal and sharpest peak signal, either in the headphones, on the meter, or both. The position of the antenna at loudest signal is the directional azimuth.

12. Readjusting TUNING and BFO PITCH may accentuate the signal peak. The peak volume may not change but the arc covered by the peak signal should decrease to make the directional azimuth more accurate.

13. Weak signals with peaks that are difficult to identify may be more accurately read on the meter.

14. When the signal is very strong, overloading the receiver may be prevented by reducing SENSITIVITY. METER GAIN and SENSITIVITY controls should be set to prevent the meter needle from going beyond the upper end of the scale.
15. The accuracy of directional azimuths at very close range may be improved by reducing SENSITIVITY and VOLUME to settings just exceeding audio threshold.

FURTHER AIDS TO OPERATION

1. RECEIVING WEAK SIGNALS

Search for very weak signals is aided by presetting the receiver controls to peak tuning positions. These positions for each channel can be learned from previous trials. The high stability of the receiver maintains peak tuning positions between trials.

2. MALFUNCTIONS

Failure to detect a signal can stem from several sources:

(a) transmitter out of range
(b) transmitter malfunctioning or transmitter battery exhausted
(c) receiver malfunctioning
   i. break in antenna connections or co-axial conductor
   ii. break in head phones, conductor, or connector
   iii. internal receiver malfunction
(d) receiver batteries discharged below 13 v.
(e) transmitter detuned beyond reception frequency (rarely occurs)
(f) signal shielded by metal or electric sources near receiver or transmitter
(g) external interference on or close to selected channel frequency may be blocking signal reception.

When no signal can be received, these potential causes should be tested systematically:
(1) make several attempts from different sites to bring transmitter into range
(2) try to receive a signal from another channel to make certain the other channels are functioning normally
(3) move receiver from shielding sources
(4) wait for external interference to cease
(5) allow time for bird to move; attenuated signal will revert to normal when transmitter antenna is freed from obstructions or from local shielding.

If signals can be received on other channels and steps (3), (4) and (5) do not restore the missing signal, the cause is likely (a) or (b). If signals cannot be received on any channel the cause may be a mechanical fault in the receiving apparatus (steps 6 to 3).

(6) test for earphone malfunction: receiver background noise will not be heard with a faulty headset. Be sure BFO is on and FILTER is off.
(7) test for antenna malfunction: hold receiver antenna close to running automobile. Radio noise from electrical system will register as audio static if antenna is normal
(8) internal receiver malfunction: if preceding steps do not identify the fault the receiver should be examined for internal malfunction.

SPECIAL CONDITIONS OF FIELD USE:
SIGNAL REFLECTION

In ground dwelling birds, triangulation is the principal method of position finding. Accurate directional azimuths are of vital importance. Reflection of the VHF signal is the main source of erroneous azimuths and is
the most frequent reception problem encountered. Reflected signals may occur in combination with normal ones or they may be the only signals received. Since reflected signals seldom occur on the same bearing as the true direction it is important to be able to identify them to save being misled. In most cases the strength of reflected signals equals that of normal ones so that signal strength alone is not sufficient for identity. Width of signal peak is usually greater than in normal signals, and reflected signals cannot be sharpened by tuning. The normal or true signal then can be distinguished from one or more reflected ones by its greater initial sharpness or its capacity for improved sharpness through tuning.

The sources of reflected signals are many. Topographic features such as gully sides, high ridges, or intervening hills were most frequently responsible for reflections encountered in this study. Bedrock which outcrops or is near the surface can reflect signals as badly as terrain, particularly if the rock has a high metal content. Free metal and electrical energy can be as reflecting as topography. At close range they are exceedingly great reflecting agents. Of lesser influence are water bodies and vegetation.

In all cases the procedure in dealing with reflected signals consists of repeating the triangulation bearings from several locations. The source of the true signal will not change but the apparent sources of reflected signals will not be fixed geographically. Most reflecting or shielding agents can be simply avoided if the receiver operator moves away from them. Triangulated positions should not be relied upon for accuracy until several sharply peaked azimuths are obtained and agree in point of intercept.
ANTENNA ORIENTATION

Orientation of the hand antenna can reveal some features of the position of the transmitter. Signal transmission along a straight line is prevented by structures between transmitter and receiver which block out the horizontally propagated radio-waves. The signal is usually weak or absent when the hand antenna is held with elements parallel to the ground. With elements vertical a better signal is usually received. In this position the unimpeded waves propagated in or near the vertical plane are received. When the signal is received as well or better on horizontal than on vertical the transmitter and receiver are separated by free space. When received best on vertical the signal source is almost always separated from the receiver by topographical obstacles.

SWEEPING PATH OF THE ANTENNA

The hand antenna is normally swept in an arc parallel to the ground. This yields azimuths that can be oriented by compass. When triangulation places the signal source on a steep or high hillside, sweeping perpendicular to the ground and through the triangulation point often yields the elevation of the signal source as well.

RECEIVING FROM VEHICLES

Signals can be received from automobiles with little loss of strength providing the antenna is outside and as far from the car body as possible. Care must be taken to avoid signal reflection and the car engine must be turned off.

Reception from fixed-wing aircraft was attempted twice without success. Despite shielding of the plane's electrical system no signals could be received from distances as close as 300 feet directly overhead. Probably the
antenna was not extended far enough to avoid the shielding influence of the metal fuselage and wings. Schladweiler (pers. comm.) has achieved successful reception from a helicopter at distances up to one mile.

WEATHER

The telemetry equipment described in this appendix was used in the field at temperatures from +26°F to +94°F. No changes in function were observed at any temperature. I have used similar equipment (see Appendix ) at -20°F with no change in function. However the receiver was kept warm between periods of use and no period exceeded one hour so that the temperature of the receiver likely did not fall to the ambient temperature.

A considerable degree of temperature control in the transmitter is achieved by placing as much of it as possible under the bird's plumage. The battery and harness can be totally concealed with the contour feathers. Approximately two-thirds of the transmitter can be covered. This includes the portion containing the crystal oscillator which is sensitive to temperature. Harness tubing which shatters at -20°F when naked, remains pliable on free-ranging birds at that temperature. Maintaining stable transmitter temperatures is important since current draw increases with temperature. Normal body movements and preening by the birds aid the process of concealing the transmitter in the plumage after instrumentation.

Leaks from precipitation can cause short circuits. For this reason the transmitters used in this study were coated with silicone rubber to aid waterproofing. The receiver was protected from rainfall by a carrying bag. Precipitation did not affect transmitter function in this study, nor did it alter signal transmission.
APPENDIX II - FIELD PERFORMANCE - VHF TRACKING SYSTEM

This section describes field performance of the radio-tracking apparatus used in this study. The purpose of recording characters of performance under field conditions is to fully describe this method of data collection, to present a summary of the various kinds of information I obtained from the apparatus, and to compare its performance to other similar equipment.

Evaluating a radio-tracking system can consist of answering two main questions: does the apparatus perform its designed tasks as well as expected; is it consistent and accurate in function? Secondly, has it any special features which allow uses other than the principal one? I have had the opportunity to use three different sets of tracking equipment designed for the same general purpose. I had little opportunity to measure much of the quantitative performance of these three sets. Most of the discussion is qualitative. Nevertheless some features differed sufficiently to permit easy comparison, particularly between the set used to gather biological data in this study, and the other two sets.

One set was built for field use in this study, but it did not perform well enough to gather biological data. I call it SET I. A second set, SET II, was like that described by Marshall and Kupa (1963). It was in current use in Montana, U.S.A. in 1966 (see McEwen and Brown, 1966) and I used it in the field while in Montana in January and February of that year. SET III refers to the equipment used extensively in this study.

CHARACTERISTICS OF SET I

Frequency: Fixed, crystal-controlled in the 72.020 - 72.200 MHz band on even 20 kHz spacing.
Signal: Pulsed continuous wave

Pulse rate: 40 per minute

Pulse duration: 8 milliseconds

Power supply: 9 volt, 600 milliamp-hour cells (Mallory 1604 dry cells, or equivalent)

Power output: 75 milliwatt pulse

Transmitter weights: 55 to 65 grams

(including harness and battery)

Transmitter antenna: Toroid, formed into a circular neck loop.

Transmitter dimensions: 1.00 x 3.50 x 0.72 inches (including battery which was incorporated into the transmitter packet).

Field performance: Use of this equipment did not progress past the trial stage. Maximum range of 540 yards was obtained in one trial over flat terrain, but direction-finding capacity was highly inaccurate and this equipment was rejected as unsuitable.

CHARACTERISTICS OF SET II

Frequency: Fixed, crystal-controlled in the 151 MHz band, with even 15 kHz spacing between channels.

Signal: Continuous wave, continuous emission.

Power supply: 1.4 volt, 800 milliamp hour mercury cells; Eveready 401 or Mallory Hg 401-T or equivalent.

Power output: 1 milliwatt maximum

Transmitter weights: Approximately 25 grams including harness and battery.

Transmitter antenna: 13 inch whip of .015 inch-diameter tempered steel wire.

Transmitter dimensions: 1.50 x .30 x .50 inches (excluding battery which is housed separately from transmitter packet).
Field performance: Maximum observed range approximately three miles. Transmitter life to more than 100 days (usual range 30 - 60 days). Accuracy of directional azimuths--<5° error.

CHARACTERISTICS OF SET III

Frequency: Fixed, crystal-controlled in band from 150.31 to 150.55 MHz with even 15 kHz spacing between channels.

Signal: Continuous wave, continuous emission.

Power supply: 1.4 volt, 800 milliamp hour mercury cells (Eveready 401, Mallory Hg 401-T2 or equivalent.

Power output: 1 milliwatt maximum

Transmitter weights: Approximately 25 grams including harness and battery.

Transmitter antenna: 13 inch whip of .015 inch-diameter tempered "Elgalloy" steel wire.

Transmitter dimensions: 1.50 x .30 x .50 inches (excludes battery which is housed separately).

Field performance: Maximum observed range approximately 4½ miles. Transmitter life to at least 50 days, average 30 (likely reduced by overheating some cells during instrumentation of birds). Accuracy of directional azimuths--<5° error.

Most of the discussion will center on set III as it was used most extensively by me, and since it is new and has not been described elsewhere.

As a general rule, radio-tracking apparatus consists of two self-contained parts, the transmitter and the receiver. A strong signal which is relatively unaffected by the external environment does not require an elaborate receiving apparatus to monitor it. Such a signal is possible when there are few restrictions placed on the size and shape of the transmitter. A complex transmitter with a relatively simple receiver is used in most radio transmission, and
this model was followed in the design of set I. This set was a compromise between miniaturization and complexity in the transmitter. A high degree of control or "shaping" of the outgoing signal was attempted to surmount the effects of topography and the animal itself on signal transmission. The receiver was small, less than half as large as those of sets II and III, and had only two tuning controls; signal-to-noise ratio, and volume. This design failed because the signal did not override environmental effects, and the transmitter was too large for the birds to carry.

There is another good reason why the transmitter should be kept simple, and that is the expense of loss or malfunction. In many cases a troublesome transmitter cannot be rectified by the receiver operator since the transmitter must be working properly in the first place in order for one to find the bird that wears it. The smaller transmitters are, the better they suit the animal, and small transmitters, usually being simple, are more expendable if they are damaged, cease functioning, or are carried out of range.

The receiver, then, should be the complex half of the system. One of the main successes of sets II and III is the high degree of control in the receiver over the characteristics of the incoming signal.

Set I also differed from the other two in having a pulsed signal tuned to a directional null. A pulsed signal has the advantage of lower current draw, giving longer battery life. Counterbalancing this is the need for more components to "shape" the signal. More components require greater voltage and a bulkier power source. As well, no information is sent during the "off" phase of a pulsed signal. A directional null means the receiver operator cannot tune the signal when it is highly distorted or very weak, such as at long range. When a signal is weak, one desires a maximum of it to work with.
With the signal tuned to a null the operator cannot distinguish between a correct directional null and one from signal malfunction or interference. Moreover, with null tuning, a very weak signal drops below auditory range when approaching the null azimuth sooner than it does when strong. A continuous emission signal is "on" at all times and the operator can distinguish rapid changes in signal character. He can adjust the receiver for changes in signal as soon as they happen.

A continuously emitted signal from a whip antenna attenuates as the whip flexes. Attenuation, a slight change in frequency, alters the pitch of the signal. Patterns of pitch change can be distinguished for several modes of flexing in the antenna. These occur in response to activities by the instrumented animal. When one knows an animal's type of activity he can adjust the tracking procedure accordingly. For example, he can "hear" a distant bird fly and anticipate seeing it. Activity can be monitored from a distance, when the animal is screened by vegetation, or when it is well to keep the animal unaware of the observer.

Set I had a frequency of 75 MHz, Sets II and III had 151 and 150 MHz respectively. The lower frequencies travel out of depressions and over obstacles better but are more subject to reflection and shielding. This means one may hear a signal of lower frequency but not be able to fix its source. Despite the superiority of 150 and 151 MHz, shielding and reflection of the signal were the biggest problems in reception on Vancouver Island in 1966.

The higher frequencies have the advantage of requiring shorter antennas. To maximize the ratio of signal strength to power consumption in the transmitter and to maximize signal gain, the size of the transmitting and receiving antennas is crucial.

1Signal gain is the proportion of the available incoming signal which is utilized in reception.
receiving antennas should be a function of signal wave length. A 13 inch whip 0.015 inches in diameter has good flexing action and is close to a one-quarter wave length function of 150 - 151 MHz. The lower frequencies have greater wave length functions. Then the transmitting antenna is too long for a whip and is usually incorporated into a body or neck loop which cannot transmit information about behavior. The ratio of output to consumption is lower in loop antennas, requiring a larger battery or a sacrifice of transmission life. Useful design requires as much life as possible without sacrificing signal strength. Grouse are relatively small animals and all these reasons make the 150 - 151 MHz range suitable for them.

Frequency similarly affects receiving antennas. The portable yagi used with sets II and III has a driven (distal) element 38 inches long and a reflecting (proximal) element 42 inches long. It is easy to carry and use in all but the thickest vegetation. Again the lower frequencies require larger elements which make the antenna clumsy to use.

Briefly, set I was rejected for field use for three reasons:

(i) its large complex transmitter could not be carried by blue grouse
(ii) the frequency of 75 MHz had many disadvantages
(iii) not considering (i) and (ii), the apparatus performed improperly.

I could not compared the performance of sets II and III side by side. I used set II at Highwood, Montana, U.S.A. in January and February, 1966, through the cooperation of Mr. R. L. Brown of the State of Montana Fish and Game Department. One adult male sharptail grouse Pediocetes phasianellus was radio tracked daily during a wide range of normal activities, in several types of weather, and over many kinds of terrain. This equipment performed perfectly from +40°F to -20°F and over as much as one foot of snow. This weather had no noticeable
effect on any phase of telemetry I witnessed or performed. Beside weather, the
biggest difference between Highwood and the Comox Burn (where set III was used)
was topography. The Highwood area was flatter, less dissected, and had no logs,
stumps or trees to shield radio signals. Consequently longer signals could be
received at Highwood. In other respects Highwood and the Comox Burn were
similar.

I saw no gross differences in performance of the two sets of equipment.
Direction-finding was quite accurate, with less than 5° error in each set.
Signals were comparably affected by free metal, rock outcrop, and topography.
Schladweiler and Mussehl (1965) using set II equipment reported that signals
originating behind a ridge follow a path of least resistance and appear to come
from the end of the ridge. I observed this effect several times with set III.

Brown (pers. comm.) has received signals from three miles with set II.
This was over flat ground. Ranges of set III varied considerably with the
environment. Six transmitters did not differ appreciably in range. A maximum
range of 4½ miles was recorded for two of them. The intervening distance was
free space for both, except at the sources where minor relief and vegetation
may have been partially screening the signals. The maximum capable range
exceeds 4½ miles but is still unknown empirically. On the Comox Burn few
ranges over one-half mile were recorded. There were always obstructions between
the instrumented birds and the receiver at distances beyond one-quarter mile.

Repeated observations showed that range was restricted mainly by
shielding of the signal at its source. A large dog or stump next to the
instrumented bird and in direct line between bird and receiver could shield the
signal 100% at distances as close as 100 yards. A signal from the bottom of a
60 foot gully could not be heard in an adjacent gully 200 feet away. Signal
strength also dropped with increasing distance, but distance was a lesser influence than local shielding. A 50% reduction in distance seldom produced a proportionate increase in signal strength unless shielding also decreased.

The more efficient the equipment is to operate the faster radio-tracking becomes. Set III was more efficient than set II. The former requires less retuning during reception to maintain a peak signal. The peak signal was usually found at the same settings of the controls in set III, even when it was switched off or moved between trials. Less work for tuning means accurate azimuths are found faster and more attention can be given to monitoring information about behavior.

Transmitters of set II also varied more than in set III. Some had shorter ranges and gave poorer behavior signals than others. Restricted range is a significant fault when the instrumented animals move long distances in a short time. Behavior signals are difficult to interpret when change in pitch is slight. Certain transmitters of set II attenuate less than others and give poorer behavior information. On the other hand transmitters which attenuate greatly are more susceptible to detuning when the antenna strikes obstacles. Severe detuning can deflect the signal frequency away from the range of reception. Each transmitter must be a compromise of signal stability for reception and signal attenuation for behavior. Set III transmitters all gave good behavior signals and seldom detuned.
Behavior information is a no-cost bonus to the main function of radio-tracking when transmitters are fitted with whip antennas that attenuate the signal when the animal moves.

Signal attenuation causes recognizable patterns of change in pitch. The patterns correspond to distinctive types of movement by the animal. The operator learns the signals while watching the animal and then can monitor a repertoire of activities while he is concealed.

Thirteen activities could be identified this way.

(a) feeding pecks - heard as a sharp pitch deflection or several in succession; often followed by oscillatory deflections which rapidly damp out.

(b) walking - an irregular series of pitch deflections. Rate and degree of deflections correspond to speed of travel.

(c) stopping travel - a brief but distinctive series of damping pitch oscillations occurs when the animal stops moving. The series is more pronounced when travel has been rapid.

(d) active flight - a rapid series of oscillations, each induced by a wing beat.

(e) gliding flight - the pitch appears to "tremble". The signal is produced by the antenna trailing in the air as the bird glides.

The total flight signal in blue grouse consists of active flight at take-off, followed by gliding (when most of the distance is covered) and another active phase (braking at landing).

(f) predator crouch - a sharp pitch change followed by a steady signal.
This signal occurs when the bird first sights a predator (or the
observer) and is caused by the bird suddenly crouching.

(g) brood hen cluck - a short series of staccato pitch deflections
corresponding to jerks of the body with each cluck to call the
chicks.

(h) incubating hen movement - observed in one nest hen that moved
continuously (except when alarmed) during incubation. The signal
pitch wandered continuously and fairly rapidly in an unsystematic
pattern.

(i) hopping onto log - a sharp pitch deflection followed by damping
oscillations. It is usually interspersed with the walking signal
and is often difficult to distinguish from feeding pecks except
that the latter usually occur several at a time.

(j) antenna striking obstructions - sharp pitch changes as the signal
detunes with antenna contact. The signal sounds much like (h)
except that the pitch change is greater, damping oscillations are
also heard, and the walking signal is interspersed.

(k) roosting or resting signal - usually a steady tone, however wind
may move the antenna causing slight pitch deflections.

(l) respiration signal - produced differently from the other signals.
It is the result of attenuation by body capacitance when the space
between transmitter and body changes size with each respiration.
At each inspiration the body expands against the transmitter harness,
decreasing the intervening space and lowering the pitch. Expiration
restores the pitch to normal.

(m) turning of eggs by incubating hen - heard as a brief series of
erratic pitch deflections a short while after the hen mounts
the nest after feeding. The signal sounds much like subdued
feeding pecks.

Other activity signals will be identified with further study. I in-
strumented no territorial males but hooting by these males should produce a
distinctive signal as should any activity involving a distinctive movement.
APPENDIX IV - HISTORIES OF INSTRUMENTED BIRDS

The history of each radio-marked bird is repeated here individually, and in more detail. The data are presented descriptively; discussions and interpretation are confined to the main body of the thesis.

Yearling Male 1759

This yearling cock was instrumented in the pre-mating period and his movements were followed daily for two weeks (10 - 22 April 1966), starting about ten days after the first birds appeared on the breeding range. Notes were kept of the activities of other grouse, particularly territorial males. Locations 1, 11 - 13, 24, 26, 28, and 37 were all within 200 feet of activity centers of territorial males, yet no prolonged stays occurred and subsequent travel took this bird over four times this distance away from adult males (locations 2 - 10, 14 - 23, 29 - 36, 38 - 42). When the bird was within 200 feet of an activity center, extended observations were made of short-range movement and behavior. In most cases this was done by telemetry without him being aware of my presence. On none of these occasions did this bird show any directional movement or any activity that could be related to the adjacent activity center or the territory holder. Slow to moderately rapid walking was the most common activity (14 of 42 occasions), and feeding was interspersed with walking in about half of these. Roosting was the second most common activity (combined day and night roosting; 12 occasions). Ten of the remaining records were discarded, as the bird was reacting toward the observer. On only three occasions were other grouse detected within certain communication range of 1759. All
three involved territorial adults and in no instance did any of the birds respond to one another, even though they almost certainly knew the other birds were there.

The instrumented yearling male passed within 200 feet of the activity centers of nine different adults, and passed near three of these a second time. This home range was not restricted to the area around one or two males, but encompassed several. This home range was one-third mile in diameter, greatly exceeding the size of the largest territories, 10 acres, recorded by Elliott (1965).

**Yearling Female 1760**

This hen was captured and instrumented 15 April 1966, and observed daily until 26 May when the transmitter failed. Briefly, the history of this hen was as follows: wide-ranging movement until 5 May; abrupt decrease in range of movements after 5 May; began incubating seven eggs 23 May; transmitter dead 26 May; nest destroyed shortly after 26 May, and hen not seen again in 1966.

The movements of 1760 are shown in fig.(10). The pattern of movements was distinctly bimodal. From 15 April to 5 May (locations 1 - 26) her range spanned the territories of six different males and was approximately one-half mile wide in greatest extent. From 5 May onward (locations 26 - 40) the two most distant locations were only 150 yards apart and overlapped only two activity centers of adult males.

The activities of this hen gave no evidence of response to the eight territorial males within her range of pre-nesting travels, except on 5 May when
Fig. 10. MOVEMENTS OF YEARLING FEMALE 1760.

Note: Open circles with numbers represent activity centers of territorial males.
when her movements changed. Positions 4 - 6, 10 - 11, 19 - 21, 22, and 24 - 26 were all within 200 feet of male activity centers. In all cases but the last she moved on and showed no decrease in distance moved or in rate of movement. Locations 24 - 26 fell on 5 May after which restricted movements occurred and if this restriction results from the onset of estrus and response to advertising males, then 1760 likely mated with male 1114 about this time.

Before 5 May, roosting was the most frequent activity noted (combined day and night roosting; 16 of 38 observations). Walking was next most frequent (8 of 38). Most movement was very slow and feeding was frequently interspersed. On eleven occasions the bird showed some reaction to me, and these records were discarded.

During eight observations from one to three hooting males were within 200 feet of 1760. On 20 April, male 1114 was hooting approximately 125 yards away from his activity center. Female 1760 was less than 100 feet from him. She showed only slight changes in position over one and one-half hours of observation. By nightfall she had moved past 1114's activity center and the next day continued travelling away from him. Her activities and movements were monitored at length twice during 20 April. Two hooting males (1114 and one other) were within 200 yards of her during the morning observation period and three were present in the evening. These three continued hooting well into full dark and very likely were stimulated by the presence of the instrumented female. I could find no evidence of any response either positive or negative on her part. Male 1184 and one other hooted nearby when the hen was at location 17 on 28 April. Male 1114 hooted at her while in his territory and she was at point 23 on 4 May. There was no observable response in either case during extended watches.
In summary, yearling female 1760 gave no evidence of attraction to territorial males and her movements were not restricted to the area around any particular male until 5 May, when she came into estrus. After 5 May, this hen was followed through mating and onto the nest. The transmitter failed after she had incubated for three days. Twenty observations were made from mating onward. Thirteen of these preceded incubation, and six of the seven during incubation were made while the hen was on the nest (location 40 in fig. 10).

The period during incubation can be compared with that before. Incubation began 23 May. Five observations were made in the two days immediately preceding incubation, in which the hen was at the nest site or less than 150 feet from it. At least one egg was laid during this time. Thus incubation commenced no more than two days after the last egg was laid. By backdating from the start of incubation at a laying rate of 1.5 eggs/day (Standing, 1960) for a seven egg clutch we can put the start of laying at about 18 May. Since it is unlikely that mating occurred before 5 May, a maximum of about 13 days separated mating and laying.

Locations 26 - 40 (fig. 10) record the movements of female 1760 prior to incubation. The most distant (26 and 36) are about 280 feet apart. All are within 150 feet of the nest site. As seen from the map, distances between successive positions are short. The typical rate of movement was slow; one observation period two hours long saw a total movement of 70 feet. Thirteen observations found the bird motionless, and slow movements with lengthy pauses were recorded in five others. Extensive feeding occurred in two of these.

One evening feeding sequence was observed. This is of interest because it was similar to that shown by incubating hens. Female 1760 was located only
60 feet from her nest at dusk on 22 May, the evening before incubation began. She fed steadily for 30 minutes, then flew past the nest site and landed 200 feet from it. After remaining motionless for 10 minutes she moved slightly and roosted for the night.

Evening feeding during incubation was recorded on May 25 (location 41 fig. (10)). She was located off the nest and slightly uphill from it. She ceased feeding abruptly and flew back to the nest. Darkness prevented seeing how close to the nest she landed, but she walked rapidly for only five seconds before settling on the eggs, so could not have been much more than 20 feet away.

These two feeding sequences were similar in that both featured steady feeding abruptly terminated by a flight of about 150 yards. Night roosting followed closely after the end of the pre-incubation flight and the hen mounted the nest almost immediately after the flight in incubation. Normally, in non-incubating hens, feeding movements (walking) merge directly into day or night roosting. If 1760 is a typical example of other hens about to nest, the general pattern of feeding behavior during incubation may be begun before incubation actually occurs. Not all aspects were comparable since the feeding sites were not the same and the roosting site was well away from the nest, but the similarities observed were unique. It is possible that behavior patterns of incubation develop gradually during laying and that transition from laying to incubation may contain common elements of behavior. It would be of interest in this context to maintain close observation of a laying hen to see if the time on the nest increased at each laying.

In summary, lengths and rates of pre-incubation movement in 1760 were less than those prior to mating. The widest diameter of her pre-incubation home
range was only one-sixth that of her pre-mating home range. Her nest was located approximately in the center of the pre-incubation home range and several locations observed near the nest site revealed a tendency for the hen to remain close by. The abrupt change from wide-ranging movements without reproductive behavior to restricted movements wherein nesting follows closely on mating, may indicate that the general area of the nest is determined by the general location of mating which is in turn determined by who she mates with.

**Adult Female 1539**

This hen was captured and banded as a chick in 1964, was not seen in 1965, and was instrumented on 2 May 1966, about three weeks after the first hens arrived on the breeding range. She did not nest until 26 May. Her movements are shown in fig. (12). No striking bimodal pattern of movement os evident even though this bird eventually nested. However, because she built her nest on the far side of a deep river gorge, most radio observations had to be made across this obstacle and from a distance. Short-range movements were indistinguishable at this range, but the radio-bearings that were obtained showed her movements to be grouped around point 11. This point was identified by triangulation from close range. Long movements prior to incubation could have been detected, though not accurately measured, but none are known to have occurred and I conclude that 1539, like yearling 1760, restricted herself before incubating, to a limited area. Additionally, 1539 spent some time before incubating, on the near side of the river (points 12 - 16) and her movements-then were shorter than those before 8 May (when she first localized herself near point 11). Points 12 - 16 were grouped directly across
the gorge from the nest site (17). She began to incubate 26 May, but as she was not observed at length, none of her trips across the river were observed between 20 May and 25 May when she would have been going across to lay. Nevertheless the grouping of points 12 - 16 speaks of a tendency to localize herself near the nest even though she was across the river from it.

Map positions 1 - 10, then, are positions plotted from her movements prior to mating (estimating this by backdating to have occurred while she was on the far side of the river between May 8 and 20). Although fewer in number than for the other hens, they were treated similarly. Her movement pattern did not differ from a randomly determined one.

The observed activities of female 1539 at points 1 - 10 in fig. (12) fail to support a positive response to territorial males. One sequence of behavior is especially worthy of note. A territorial male hooted about 40 feet from the hen while she was at location 6 on 5 May. He was almost 150 yards away from his activity center. I watched these birds for three hours until noon. For 1½ hours the hen moved very slowly and sporadically while feeding steadily. The male hooted steadily and advanced about 25 feet toward her during this time. In the next ¾ hour the male followed and courted the hen in five sequences of display accompanied by precopulatory calls and attempts at mounting. At each attempt the hen adopted a crouching posture described for subordinate Chukar partridge (Alectoris chukar) by Stokes (1963), and ran from the male. About 30 seconds after his last advance she flew 250 yards and roosted in a tree. The male continued hooting where he stood. The birds stayed where they were for another 1½ hours, until I left. An almost identical sequence was repeated on 19 May. Clearly this female was not receptive to these accosting males and strongly avoided them. This was the only type of reaction other than
FIG. 11. MOVEMENTS OF UNSUCCESSFUL YEARLING HEN 1745.

FIG. 12. MOVEMENTS OF ADULT HEN 1539.
none at all that I was able to see involving females prior to mating. It agrees with the random pattern of movements and suggests that females are simply not sufficiently interested for mating at this time.

To summarize, adult female 1539 exhibited random movements with respect to males while she was in anestrus, and her avoidance of soliciting males affirms the suggestion that random travel is a consequence of the anestrus state.

**Yearling Female 1745**

This hen was captured and instrumented on 2 May 1966, and observed regularly until 25 May when the transmitter ceased functioning (fig. (11); locations 1 - 30). She was found four more times (points 32 - 34) by our dogs after radio contact was lost. This hen had not mated as of her last sighting on 15 June. By this time incubation had begun in all but renests, so I consider that 1745 did not mate in 1966.

If a bimodal movement pattern is a characteristic of successful hens only, then it should be absent in non-breeders. 1745's movements did not change with time (data on p. ).

Again records were made of activities during each observation. In 8 of 35 observations a total of 11 males were found within 200 feet of the hen. Seven of these were hooting males and on one occasion two displayed to her, one only 10 feet away. I watched one hour from cover. The hen remained motionless for all but 30 seconds of the hour and gave no evidence of response to the males who gradually withdrew and stopped hooting. By 1045 the next morning she had moved 275 yards to point 20; thus these males did not manage to keep her nearby. On two other occasions hooting males were found within 200 feet of the hen and
she did not respond. However, these times there was a chance she was aware of me.

Walking (fast or slow rates were equally common) was the most frequent activity (18 observations). Feeding was detected only three times. 1745 was observed feeding fewer times than the successful hens and her rates of movement were generally faster. These differences may be part of activity characteristic of unsuccessful hens.

By comparing 1745 to the successful hens, we can see that the most obvious difference was that she did not show a change of movement pattern with time. But it is in the pre-mating period that differences identifying unsuccessful hens should be formed. Her movement, except possibly rate, did not differ from the successful hens and, as well, even hens that later mate show no movement or dispersion early on that foretells of their potential reproductive activity. Therefore I do not believe that factors responsible for differences in female reproductive success manifest themselves in movement phenomena prior to mating, at least not in dispersion relative to males.

Yearling Nest Hen 1834

This very tame hen was captured by hand while incubating. Her movements and behavior were observed during 17 days of incubation and one day of brooding before the transmitter failed (7 - 25 June 1966). Fig. (14) shows the location of the nest and her different feeding sites (numbers 1 - 10). Some sites were used more frequently than others. Forty-seven observations were made while the hen was on the nest. Sites 2, 3, 4, 5, 7, and 9 were all contained in an area approximately 200 feet across. It was a wet spot with succulent herbaceous
vegetation. This area received 13 of the feeding visits observed for 1834 during incubation, and was usually reached and vacated by direct flight. The bird also flew to and from sites 6 and 8. Site 1 was reached by walking with a return flight, while for 10 the hen walked both ways. All but site 1 and one visit each to 3, 9, and 10 were evening feedings. The hen left the nest to feed each evening but the last, the one before she left the nest with her chicks. Drying takes from 12 to 24 hours in chicks hatched in incubators and this hen remained entirely on the nest the last day, probably to dry the chicks.

Six observations were made in the early morning and continuing until noon. 1834 left the nest to feed on four of these mornings. She failed to leave once during mid-incubation and on the last morning. Of the four mornings she left, two involved mid-morning departures in full daylight. She did not feed at dawn on these days. The other two mornings she left at dawn and did not leave again until that evening.

Modes of travel were inconsistent. In one mid-morning feeding the hen walked off the nest and flew back; in the other she walked both ways. In one dawn feeding she flew both ways; in the other she walked back (I did not see how she left the nest). Comparing morning and evening feedings, the latter were more consistent in mode of travel to and from feeding site. Evening feedings involved flights both ways in all but one case. Evening feedings were consistent in occurrence; morning feedings less so.

Evening feedings were coordinated with light intensity. Accurate light measurements were unavailable but general field records revealed consistently earlier feeding on overcast evenings; from 20 to 45 minutes earlier than on clear evenings. Duration of evening feedings were also consistent; between 7 and 10 minutes in 13 of the 16 observations. The range was 7 to 60 minutes.
There was no consistent relation between weather and length of feeding, although warm, clear evenings generally had brief feeding periods. The longest period occurred on a cool overcast evening when the eggs would likely lose heat more rapidly. Duration of feeding also appeared unrelated to the length of previous periods.

Intensity of feeding varied unsystematically also. Time and rate of feeding could not be correlated with feeding site even though the ostensibly poorer sites 1, 6, 8, and 10 might have been expected to require longer feeding.

The eggs of all birds are turned in the nest during incubation. A distinctive radio signal was received from 1834 two or three minutes after remounting the nest from feeding. Visual confirmation could not be had without disturbing the bird but I suggest this signal represented egg-turning (see Appendix III) by its time of occurrence and consistency. The signal was absent the five evenings previous to hatch, indicating that egg-turning ceases toward the end of the incubation period.

Several visual observations were made of 1834 during her feeding periods. In cases where she flew to the feeding site, she walked four or five feet away from the nest, paused, and surveyed her surroundings before taking wing. The return flight was followed by a similar reconnaissance before walking back onto the nest.

After remaining on the nest the last day of incubation, 1834 left with her chicks on the morning of 25 June. Of the three chicks that hatched (three infertile eggs) only two were present after five hours and 100 feet from the nest. Initial movement of the brood was away from the areas most used by the hen during incubation.

In summary, data on 1834 showed her to have no consistent pattern of
Fig. 13. Positions of pre-hatch and post-hatch homeranges of hens 933 and 960; 1964.

Note: Numbers in brackets refer to the number of times a hen was found after the hatch, inside her pre-hatch homerange. Hen 933 had two nests in 1964; homerange B is that of her second nest (the first was destroyed).

Fig. 14. Locations of feeding sites of nest hens 1834 and 1837; in 1966.
incubation feeding sites, modes of travel, feeding rates or durations. Evening feeding was consistent in occurrence and timed by light intensity. The post-mating home range is not selected for use as a brood range. The movements of two non-instrumented brood hens affirmed this (fig. 15).

**Yearling Nest Hen 1837**

Captured on the nest on 8 June 1966, her 19th day of incubation, this hen was much less docile than 1834. Nevertheless she went back on the nest in only 33 minutes. I observed her through the rest of incubation, destruction of the nest by a predator, and into the broodless period.

The locations of 1837 during incubation and the first day after nest destruction are shown in fig. (14). She was observed 21 times on the nest. Location 1 was a feeding site used twice, #3 was used once, and #2, four times. The observations while feeding are fewer than for 1834, but sufficient to permit comparison. I made three early morning observations on 1837. She fed for 32 minutes from 4.50 a.m. on 14 June, flying back to the nest. She failed to leave during six consecutive hours on the morning of 9 June and five consecutive hours on 13 June.

Six observations were made in the evening. She left the nest in four of these. One of the other two was the day of hatch, the other the 20th day of incubation. Location two was the site of most of her feedings. It was a relatively dry site compared to the favorite feeding area of 1834. Location three, also a dry site, had one evening feeding. Moist sites were available at similar distances from the nest but were apparently not chosen. The mode of departure from the nest was not recorded. In all but one instance she returned
by flying.

Radio signals from the nest revealed that 1837 was in continuous motion most of the time she incubated, even to the end. By contrast, 1834 was motionless except for egg-turning. Movements signals from 1837 varied unsystematically and resembled only the egg-turning signal (Appendix III). The resemblance was only approximate however, and the egg-turning signal itself could be distinguished several times in the same context as in 1834. I attempted to match the movement signal with a visual assessment of her activity but the nest was placed so that I could not approach without being seen. My approach brought about a characteristic response in the signal. Pitch deflection declined in amplitude as I drew near, presumably when the hen first became aware of me. When I was close enough to see her the signal was steady and she motionless. My retreat caused the reversed to occur. I conclude this signal represents constant motion on the nest.

The nest of 1837 was destroyed by an unknown predator on 15 June at dusk. The chicks had hatched by this time as told by typical shells nearby. The hen escaped unharmed but search with a dog produced no chicks. She roosted for the night at location 1 (fig. 15), only 130 feet from the nest. At dawn the next morning she was found feeding at location 2, very near the site of most of her feeding in incubation. Locations 2 - 6 represent her path of travel the rest of the day. Subsequent movements led her well away from her incubation home range.

Summarizing her movements to time of hatch, yearling hen 1837 agreed generally with 1834 in consistent evening feeding and less frequent morning feeding. Contrary to 1834 she fed at drier sites with less succulent vegetation than available elsewhere. 1837 was in constant motion on the nest. The result
may be that certain hens turn their eggs continuously during incubation and for the entire incubation period. After nest destruction 1837 remained near her incubation feeding site for one day but moved well away thereafter.

Her movements were recorded for 28 more days until the transmitter failed. Fifty-five observations were made while she was broodless (fig. (15)). It is immediately apparent that she did not leave the breeding range, contrary to Elliott's (1965) conclusions. 1837 did increase her rate and extent of travel but made no migratory movements in the month of observation.

As to the possibility of renesting, her movements showed none of the localization coincident with mating and nesting in 1760 and 1539 in 1966, or 933 who renested in 1964. It is unlikely she reverted to reproductive condition after 13 July when the transmitter failed. A clutch of average size dated from a mating then would not hatch until 19 August at the earliest. In a sample of 144 nests, Zwickel (1965) found none hatched later than the week beginning 6 August. 1837 can be classed not only as a broodless hen, but one not inclined to resume reproductive behavior.

The distribution of her observation points was treated as with the pre-nesting hens described on pp. 3 - 4. The areas around territorial males received no more visits than would be expected by random movement. In this respect, broodless hen 1837 behaved no differently than pre-mating (anestrus) hens.

Brood Hen 1859

Detailed brood movements were studied by radio telemetry in adult female 1859, instrumented 26 July 1966 when her five chicks were a week old. Fig. (16)
FIG. 15. POST-HATCH MOVEMENTS OF BROODLESS YEARLING FEMALE 1837.
FIG. 16. MOVEMENTS OF ADULT BROOD HEN 1859.

Note: Locations 18, 19, 21, 25, 26, 28, 29, 30, 31, 32, 33, 36, 37, and 39 are all clustered with the others in stream course A.
Broken line: stream course.
shows her movements to when the chicks were three weeks old.

Locations 9, 10, 12, 14, 15, 16 - 19, 21, 25, 26, 29 - 33, 37, 39 - 42, 47, and 49 were all in wet depressions with succulent vegetation. Locations 2, 5, 6, 22 - 24, 27, 28, and 48 were all outside such depressions and in each case the birds reached there as a direct result of my presence. Out of 40 observations free from disturbance, the brood was located in wet spots 25 times (60%). Such habitat occupied less than 10% of the study area, so this brood showed a rather strong preference for it. The brood returned to such habitat on three occasions when flushed out by me, and successive locations show her tendency to go directly and quickly to similar habitat when she vacated one favored area (i.e., series 12 - 16, 39 - 42, 47 -49).

The spacing of the chicks and some aspects of their behavior were noted. When undisturbed the brood was spread over an area approximately 50 feet across. No precise measurements were taken but this distance was rather consistent and did not change over the two weeks of observation. The chicks appeared randomly dispersed with respect to each other and the hen. No antagonism was seen between broodmates, although concealing vegetation hindered my watching. The hen's behavior changed with time. Initially she flushed readily and displayed strongly to me. Two weeks later she would remain motionless as I moved close to her, providing no chicks were flushed en route. Flushing distances of the chicks did not change with age (up to three weeks).

This brood was found on one occasion feeding within 75 feet of two others (location 47, fig.(16)). All three were grouped by themselves and no exchange of chicks occurred. Brood 1859 showed no intolerance of the others.

The movement of brood 1859 bore no resemblance to hens of other reproductive status. It did not roam continuously like lone anestrus hens nor did
it become localized for long period like hens from mating through nesting. Fig. (16) shows that average daily movements were short but that long trips do occur.

Migrating Birds: Brood Hen 1894 and her Chick 1865

Yearling brood hen 1894 and one of her seven chicks were instrumented on the breeding range and followed by radio for 42 days during the autumnal migration. I was able to keep a visual check on this brood for the first seven days only.

The travels of 1894 and 1865 are presented in figs. (17) and (18). Fig. (18) covers the period before migration began. Locations 12 and 13 are the first two points obtained during migration. The point marked "start" in fig. (17) corresponds to 13 in fig. (18). Migration began on 1 September and ceased 6 September 1966. Forty-one observations were obtained in this period. From these, six accurate locations were plotted. Many others less precise were not plotted, however none of these indicated departure from the line of travel. Nine records were made between 7 September and 9 October. These showed that the hen and instrumented chick remained in the area marked "end" in fig. (17). This area was difficult to traverse and several attempts to get close-in fixes with visual corroboration failed. Therefore although telemetry showed that the instrumented chick remained with the hen during this time I cannot be certain of his broodmates.

On three occasions during the first two days of migration I saw the brood walking. They were closely gathered; only about 20 feet across the group. I could not tell if the hen was in the lead. If the entire brood behaved as
FIG. 17. PATH OF TRAVEL OF MIGRATING BROOD HEN 1894 AND HER CHICK 1865.

A.

COASTAL WESTERN HEMLOCK FOREST

Note: Below 2500 ft.: forest removed (logged).
Above 3500 ft.: Subalpine Mountain Hemlock forest.

B.
FIG. 18. MOVEMENTS OF BROOD HEN 1894 AND CHICK 1865 IN THE FOUR DAYS BEFORE THEY MIGRATED.
the instrumented chick, the chicks remained with the hen throughout the travel period and while the hen remained relatively localized in the month that followed. At least some broods, then, do not disperse en route to the winter range and may remain with the hen for a time after travel stops.

Fig. (17) shows that the migrating brood travelled in a remarkably straight line. One change in direction of 8° was recorded. This was followed a day later by a change of 10° in the opposite direction, returning the path of travel within two degrees of its original bearing. The birds did not follow the easiest or shortest route along contours, but travelled across contours. Dense climax forest could have been avoided by a deviation of \( \frac{1}{2} \) mile on days three and four but none was made. I conclude that fall migration in blue grouse broods is oriented travel along a straight line and that the course is not affected by recognizable features of vegetation or topography.

The orientation mechanism is unknown. Travel proceeded at approximately the same rate on overcast days and sunny days except for short stationary periods in the hot mid-afternoons of the latter. No travel occurred between full dark and 3:00 a.m. on a clear night with a full moon.

No other birds were found with the migrating brood, and of 39 blue grouse located by dogs during search on the winter range, all broods were alone and only two adults were seen together. There was no evidence of flocking in 1966.

Fig. (18) shows the movements of this brood during the four days between instrumentation and migration. Movement toward the winter range began abruptly. I could not identify a proximate stimulus. Instrumentation likely had no effect since migration did not begin until the four days had elapsed. The desiccated vegetation at this time is not a sufficient explanation either,
since the brood frequented succulent vegetation near free water (locations 1 - 5) and near moist areas (6 - 9) during three of the four days. Neither is age of the chicks an adequate answer since three broods of greater age than the radio-marked brood (71 days on 1 September) remained later on the breeding area. Since other evidence shows that the bulk of brood migration occurs earlier some years than others, the photoperiod is not a sufficient explanation either, at least for hens and chicks.

The way these birds travelled is of interest. Anthony (1903) described gliding flights from ridge to ridge during spring migration; the birds walking between flights. Neither 1894 or 1865 flew at all. Extended observation on 3 and 4 September, when they passed the crest of a ridge at 2800 feet and then crossed a river gorge at 1700 feet, revealed the entire distance was covered on foot.

During the six days of travel, the brood moved 4.5 airline miles; but because of many changes in elevation, the actual distance was about 6.5 miles. Rate of travel then was about one mile in a 24 hour day. Subtracting nighttime (about 11 hours at this latitude and season) makes the actual coverage a mile in 13 hours. This was corroborated when I observed continuous travel of six hours over a measured half-mile. Therefore the full daylight period was required at this rate to cover the observed daily distance. There are then, no prolonged stops during daylight hours. A mile a day is much faster than any rates previously quoted for blue grouse travel and may be sufficient to distinguish migration movements from any others.

Although the instrumented birds were not seen between 6 September and 9 October, several others were sighted in the same region and vegetation type. The habitat comprises well dissected ridges at 3000 - 4500 feet forming foot-
Fig. 19. Diagrams of habitat occupied by migrating hens and chicks.

A: Habitat Profile: Relative Heights of Rock Outcrop and Vegetation

B: Plan View: Forest 66%; Rock Outcrop 33%
hills to mountains of 5500 - 6000 feet. Above 3500 feet the vegetation is of the Subalpine Mountain Hemlock Bioclimatic Zone (Krajina, 1964). There is much rock outcrop. The microtopography and vegetation are shown diagramatically in fig. (19). Similar habitat structure has been described for wintering blue grouse by several authors (Marshall, 1946; Wing, 1944, King, 1964; and others) although elevations were typically higher than those reported here. The birds I saw were almost all on the ground. If true wintering behavior consists of prolonged free-roosting as reported by the above authors, then these hens and chicks were not yet in that phase.

True winter range may well lie at higher elevations. In such case, fall migration, at least in hens and chicks, may not be completed in one movement. Reaching habitat which approximates true winter range may merely bring about a temporary halt.

No males other than juveniles were found in the habitat I searched, which supports King's (in preparation) conclusion that the sexes (in adults) live separately in winter.