

MOVEMENTS OF BLUE GROUSE ON THE SUMMER RANGE

A. N. LANCE¹

Department of Zoology
University of British Columbia
Vancouver, British Columbia
Canada

This study, part of a long-term research program begun in 1944 (Bendell and Elliott 1966, 1967), was done to find how Blue Grouse (*Dendragapus obscuras*) are spaced on the breeding range, and to relate dispersion to population regulation. In the populations studied, breeding numbers failed to increase, even though each previous autumn many more young than necessary were available to replace the relatively constant losses among adults over the winter (Zwicker and Bendell 1967). Despite fluctuating production, constant recruitment of young birds has equalled constant mortality among old birds, resulting in stable breeding populations.

We do not know the mechanism which allows certain young birds to join the breeding population while the rest disappear. I studied the dispersion, movements, and behavior of Blue Grouse on the summer range to see if there was any evidence of social interaction that might affect recruitment. I concentrated on year-old birds because these are the new recruits to the population.

Movements were studied over the entire six months when Blue Grouse were on the breeding range in 1966, and for four months in 1964. The work was in part a test of the contention of Elliott (1965) and Bendell and Elliott (1966, 1967) that females and yearling males are attracted to territorial males. If this is true, interaction between the attracted grouse and territorial males could conceivably affect recruitment by dispersing some birds to places outside the breeding range, or by relegating them to certain parts of the breeding range where their life expectancy would be less, or where they would be prevented from breeding even if they remained alive.

STUDY AREA, METHODS, AND ANALYSIS

The work was done 1 May–1 September 1964 and 1 April–9 October 1966 on the east coast of Vancouver Island near Courtenay, B.C. The area was 1000 acres of recently logged and burned forest called the Comox Burn, and consisted of moderately sloping foothills well-dissected by small streams (Zwicker 1965). 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 a fire in September 1961. Most of the plants were herbs and shrubs less than 1 m high.

A trained dog was used to find birds in 1964. However, a dog scents any bird as he comes across it, so that scattered data are gathered from many birds but no detailed consecutive knowledge about any. I used radio-telemetry in 1966 to overcome this and to permit me to witness events occurring only at certain expected times. A few birds without transmitters were known in sufficient detail to supplement these data. Most birds were individually recognizable from leg-bands affixed during this and previous studies.

I also observed the birds directly by watching their activities after the radio-location was made, particularly in cases where an adult male was visible, calling, or otherwise known to be nearby. I did this to look for direct evidence of interaction and to see if the behavior of the birds changed after such encounters.

In 1966 nine Blue Grouse were fitted with miniature radio transmitters and followed with portable receivers. The telemetry equipment was made in Vancouver, Canada. Its design and performance were similar to those of equipment used in other studies (e.g., Marshall and Kupa 1963; Brander 1967). Full details are given elsewhere (Lance 1967), along with detailed histories of each radio-marked bird. Each transmitter had a different frequency in the range of 150.31–150.55 MHz, which allowed birds to be recognized individually. I located each radio-marked bird at least once, and usually two or three times, a day. Most locations were obtained by triangulation from close range, but each bird was also checked visually at least every three days. Transmitters fitted with flexible whip antennas gave information on behavior as well as on locations. These additional data help explain dispersion by aiding direct observation. There was no evidence that the transmitters affected the birds' behavior or health. Grouse with transmitters mated, nested, brooded chicks, and migrated in the fall.

Radio-location gave a series of points showing the places traversed by each bird in its daily movements. These locations were plotted on maps, and the distribution of each bird's points was tested against the hypothesis that they were scattered at random. I was most interested in determining whether the points for each hen or yearling male were related to the positions of territorial adult males. I therefore divided the home ranges of the radio-marked birds into sections which could be identified according to their nearness to these territorial males.

The home range of each radio-marked bird was a polygon, drawn by connecting that bird's peripheral locations; the polygon was divided into circular zones of 80-m radius surrounding the activity centers of the

¹ Present address: The Nature Conservancy, Blackhall, Banchory, Kincardineshire, Scotland.

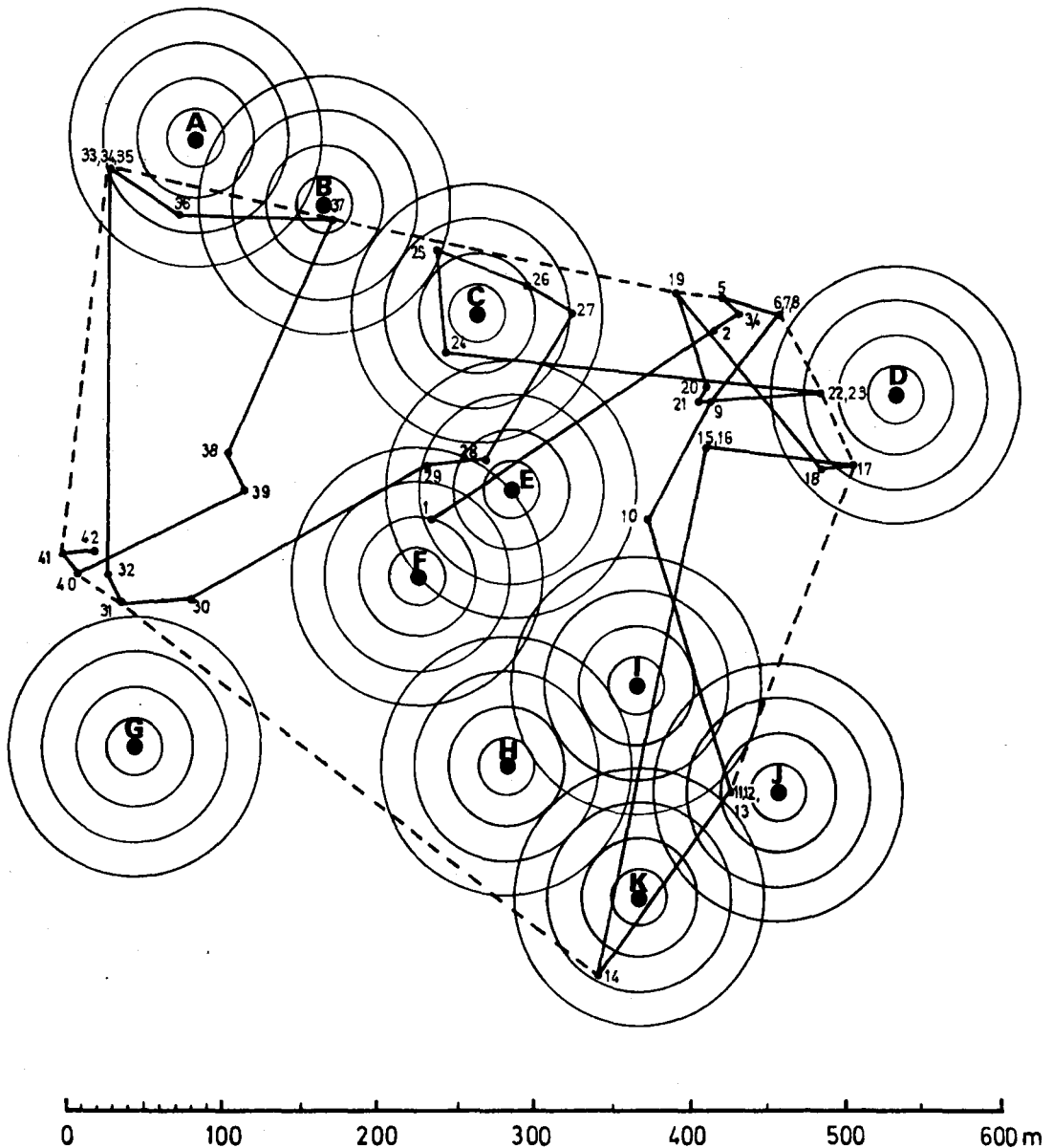


FIGURE 1. Movements of a yearling male Blue Grouse. The solid line is the path of travel of the radio-marked yearling male, and the numbered dots on the line are his consecutive radio-fixed locations. Lettered dots are the activity centers of territorial males. The zones used for analysis consist of the sets of concentric rings around the activity centers; sub-zones consist of the separate rings within the zones. The broken line encloses the area tested in the analysis of dispersion. Many more territorial males than shown occurred outside the broken line; however, the figure includes only those males whose circumscribed zones overlapped the polygon formed by the broken line.

territorial males nearby (fig. 1). Activity centers were the most meaningful places to mark the positions of territorial males, because of the difficulty in fixing the exact locations of territory boundaries (see Discussion). Activity centers are more easily determined since territorial males are seen most often in a small part of their home range, especially at places where they call ("hoot") and display regularly. The approximate mean distance between the activity center and the peripheral locations of territorial males was 60 m. Eighty meters, the radius of zones of analysis, encompass ground next to the territories where other

grouse might position themselves if they were attracted to territorial males, yet prevented from entering the territory itself. The analysis included each territorial male whose 80-m zone overlapped the home range of any radio-marked bird.

Two chi square analyses were performed on each distribution of points obtained by telemetry. The first test compared the proportion of points inside and outside the zones with the proportion expected by chance according to the area occupied by the zones; it was designed to see if hens and yearling males avoided or kept significantly closer to adult

males than would be expected with purely random movements. The second analysis compared the distribution of points within four concentric sub-areas inside the zones, the sub-areas being arranged at varying distances from the activity centers (fig. 1). This second test examined the question of attraction in more detail, using the locations nearer the activity centers.

RESULTS

MOVEMENTS PRIOR TO MATING

Social interaction and dispersion occur simultaneously with a spring decline in breeding numbers in some species of birds (e.g., Smith 1967). Since limited recruitment explains why certain breeding populations of Blue Grouse have not increased, and since the death of chicks in summer cannot fully account for the numbers of potential recruits that disappear, these losses must occur between autumn and spring. The work described here examines the possibility that such losses occur during the spring months (March–May) when Blue Grouse descend to the breeding range and begin territorial behavior. I was able to observe behavior in early spring only in 1966.

I put radios on one yearling male and three females about 10 days after the first birds appeared on the breeding range in late March 1966, about a month before mating began. The yearling male was tracked for two weeks, one yearling female for three weeks, another for six, and an adult female for four. The locations for each bird were analyzed for their distribution in relation to territorial males, using the first test described in the previous section. Apparently no grouping near territorial males occurred. According to this series of tests on zoned versus non-zoned areas (fig. 1) the observed distributions of the four birds with transmitters did not differ significantly from the distributions expected by chance (with 1 *df*, $\chi^2 = 0.86$ for the yearling male, 0.72 and 2.58 for the two yearling females, and 1.18 for the adult female, $P > 0.05$ in each case).

The second series of tests involved smaller concentric sub-zones, and was performed because the occasional occurrence of hens or yearling males close to adult males could suggest attraction. Again, the distributions over the sub-zones did not depart significantly from those expected by chance ($\chi^2 = 2.58$ for the yearling male, 2.58 and 2.97 for the two yearling females, and 2.57 for the adult female, $P > 0.05$ in each case). According to these calculations, none of the radio-marked birds was consistently located near adult males and

none of the statistical tests support the idea that adult males attract other birds.

Furthermore, none of the activities of the birds wearing radios gave any direct evidence that they were responding to territorial males in the pre-mating period. The yearling male was found 18 times (43 per cent of his radio-fixed locations) within 60 m of activity centers, yet he did not remain there on any occasion. On three of these occasions, adult males were found very close to this yearling, but at no time did the yearling show 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, except that on one occasion a male courted and tried to mount the adult hen, but she avoided his advances and eventually flew away. In no other instance did the behavior of a bird with a radio change after it was in contact with or close to a territorial male, and in no case did the area frequented or the range or rate of movements appear to change after such an encounter.

In summary, there were no indications that any of these four radio-marked birds either avoided or was attracted to territorial males in the period before mating.

MOVEMENTS FROM PAIRING TO INCUBATION

I compared movements and activities of hens during and after mating with those before, when hens had been showing no reaction to males. Of the three hens fitted with radios before mating, two eventually nested but the third showed no reproductive activity.

One yearling hen ranged widely and moved randomly with respect to males until 5 May, when she was found less than 30 m from the activity center of an adult male, and remained near him from then until she began to incubate. During this period the area she covered was only 140 m in greatest diameter, less than one-sixth the extent of her former home range.

The adult hen began to limit her movements on 8 May, after travelling widely the previous week. From 8 May onward she frequented one adult male, whereas previously her movements had encompassed the territories of the three adult males in that general area. Eighteen days after restricting her movements she began to incubate. The third radio-marked hen did not nest and was still ranging widely on 15 June when all but re-nesting hens were incubating.

Both hens that nested began laying eight days after restricting their movements. Cap-

tive Blue Grouse start to lay about a week after they copulate (Stirling, unpubl. data). If the same is true of wild birds, the hens with radios mated within a day or two of their first localized movements, which in turn suggests that a hen in estrus probably first restricts her movements when attracted to a male for copulation.

This latter point depends partly on evidence that Blue Grouse do not form a permanent pair-bond. Lack (1940) groups the Blue Grouse with birds in which the sexes meet only briefly for copulation, but I believe the following account is the first evidence of this from field studies. One radio-marked hen was watched 13 times from her first localized movements until the time she began incubating. In these periods, totaling 9 hr of observation, she was never seen in the company of males, even though she apparently mated during this time and nested less than 100 m from two males. Both males hooted regularly from their activity centers, but I never saw them approach her, or her them.

Another hen avoided the advances of a nearby male, even though she began to lay only three days later and had possibly mated with him a few days before this courtship encounter took place. In 22 observations in 1964 of 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 five hens, certainly no continuous pair-bonds existed. This evidence suggests strongly that pairing in Blue Grouse is a brief event which occurs only at copulation, as Lack (1940) suggested.

Yearling males and hens in estrus may be attracted to the general habitat in the territory of an adult male, rather than to the male himself. Since there is no lasting pair-bond, the continued localization of the hen after copulation may also be due to something other than a response to her mate, such as the selection of a nest-site.

NEST DISPERSION

Many territorial males try to mate with several females. How many of these attempts succeed is unknown, but some males probably do mate with more than one hen. The evidence indicates that, although sex-ratios appear even (Zwicker and Bendell 1967), most yearling males apparently do not mate but many yearling hens do. Thus adult cocks probably mate with yearling hens as well as adult hens.

As I had evidence that hens nest near their

TABLE 1. Distances between adjacent nests, and between nests and adjacent male Blue Grouse.

Map Distance (m)	
Nest to nest	
A to B	262
C to B	240
B to D	162
E to F	363
F to G	193
H to G	424
\bar{x}	274
SE	101.00
Nest to male	
A to 5	81
B to 1	101
C to 1	172
D to 1	81
E to 4	81
F to 2	101
G to 2	81
H to 3	161
\bar{x}	112
SE	38.04

probable mates, I tried to discover where nests were placed in relation to each other and to nearby territorial males. Since there is no direct evidence of polygamy, the number of hens mated by each male can only be estimated from the total number of nests occurring near him. The total number of males in the area examined (approximately 200 acres, one-fifth of the study area) was about nine; six well-known territory-holders plus an estimated three yearlings (estimated from an adult:yearling ratio of 2:1; Zwicker and Bendell 1967).

Eight nests were found in the area occupied by the six territorial males (close to the estimated population of hens, and there is no evidence that the actual number of hens differed greatly from this estimate). No broods less than a week old were found from other than these nests, and there is no other evidence of hens present that did not nest or whose nests were not found. Therefore, even allowing for the possibility of one or two nests overlooked despite intensive search, the eight nests found were probably a high proportion, if not actually all, that were made in the area. Locations of nests were plotted on maps, and distances were measured between adjacent nests, and between nests and the activity centers of the closest males (table 1).

Of the six territorial males, one (not listed in table 1) had no nests found near him, three had one nest, one had two, and one had three,

indicating that males may mate more than one hen, and that some may mate more hens than others. Every nest was placed closer to a male than to the nearest adjacent nest, as expected if a hen does nest near her mate. These measurements suggest that hens nesting around a male tend to avoid one another, although nests have been found elsewhere as close as 10 m apart. The dispersion of nesting hens may be viewed, then, as groupings near territorial males, which in turn tend to be regularly spaced (Elliott 1965).

MOVEMENTS OF UNSUCCESSFUL HENS

Two kinds of unsuccessful hens were observed by telemetry in 1966. The hen mentioned above, which apparently failed to mate, continued traveling widely after other hens had become localized and had nested. Another had her chicks taken by a predator just after they hatched. Renesting can occur in Blue Grouse within approximately 14 days after a first clutch is destroyed in the late stages of incubation (Zwickel and Lance 1965). This is known from a hen (without a radio) that renested after her first nest was destroyed near or during the period of hatching in 1964. The radio-marked hen that lost her newly-hatched chicks was therefore of interest as a potential renester, and her movements can be compared with those of the hen that did renest in 1964.

All indications were that the radio-marked hen did not renest. Her movements during the month after nest loss were tested for evidence of attraction to territorial males, and showed no significant departure from random travel in relation to the position of these males (χ^2 for the 80-m zone test = 0.75, and for the sub-zones test = 2.15; $P > 0.05$, with 1 and 3 *df*, respectively). In this respect she behaved like a pre-nesting (anestrus) hen. Direct observation of her behavior also indicated she was not responsive to territorial males. It is unlikely that she reverted to reproductive condition after July 13 when her transmitter failed (previous records show there is no breeding activity this late). She may be classified, then, not only as a broodless hen, but one not inclined to resume reproductive activity.

In contrast, the hen without a radio, which did renest in 1964, ranged widely for a week after loss of the first nest, then became localized in the same manner as other nesting hens and laid her second clutch.

From evidence that broodless hens traveled faster than any others, Elliott (1965) concluded that they migrated from the breeding

range after losing their nests or chicks. Contrary to this, the broodless hen that I followed by radio had not left the breeding range after a month, although she did increase her rate and extent of travel.

MOVEMENTS DURING MIGRATION

Social organization during migration to the winter range could be important to population processes, 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 (Wynne-Edwards 1962). Broods of Red Grouse, *Lagopus l. scoticus* (Jenkins, Watson, and Miller 1963), and Ruffed Grouse, *Bonasa umbellus* (Bump et al. 1947), break up early in autumn. Some broods of Blue Grouse may break up in the early stages of fall migration (Wing et al. 1944; Zwickel et al. 1968; and others). Other broods may remain intact until reaching the winter range (King in Bendell and Elliott 1967).

A yearling hen and one of her seven chicks were fitted with radios on the breeding range in late August 1966 and followed for 42 days. Migration began abruptly but I could not identify a proximate stimulus. Putting radios on the birds probably had no effect, as they did not start to migrate until four days later. They traveled steadily for six days (1-6 September), and stayed in one place for a month afterward.

In the six days 2.5 km were covered, making the rate of travel about 1800 m per day. I watched them take 6 hr for continuous travel over a measured 800 m. The high rate of travel itself is probably sufficient to distinguish migratory movements from any others.

The hen and all her chicks stayed together for at least the first two days of migratory travel. In the next four days and for a month after, telemetry revealed that at least the radio-marked chick stayed with the hen. Of 39 Blue Grouse located by dogs in adjacent areas at this time, all were in broods or were lone adults, giving no evidence of either brood dispersal or flocking in autumn 1966.

Migratory travel by this brood was highly oriented. The birds followed a remarkably straight line; the direction of travel on the last day differed by only two degrees from the direction on the first day. They did not follow the easiest route along contours, but traveled across them, and they did not avoid dense vegetation or rough terrain. Although Blue Grouse have been known to fly considerable distances during migration (Anthony 1903),

walking was the only method of travel I recorded, even though the birds encountered considerable topographic relief. They moved as fast on overcast as on sunny days, except for short periods on hot sunny mid-afternoons when they sat motionless. No movement was observed to occur at night.

Following their six days of travel, the radio-marked brood remained relatively stationary in an area of well-dissected ridges at 900–1200 m elevation, forming foothills to mountains of 1800 m. Above 1050 m the vegetation is in the Subalpine Mountain Hemlock Zone (Krajina 1965), with many openings in the tree canopy. This area was similar to winter ranges described by others (Marshall 1946; Wing 1947; King, unpubl. MS) except that the habitats they described were at higher elevations. Moreover, all the birds I saw were on the ground, whereas their typical wintering behavior is to roost in trees. Probably these birds were not yet in full wintering behavior and they may have moved later to higher elevations. In this case, migration by some birds may not be completed in one movement. Habitat that has some of the ingredients of true winter range may merely cause a temporary halt. However, Zwickel et al. (1968) recovered young grouse on a number of occasions in midwinter from the Interior Douglas Fir Zone of Washington State, relatively closer to the breeding range than is the Mountain Hemlock Zone of British Columbia.

King (unpubl. MS) found only males on the winter range that he studied and concluded that they lived separately from the hens in winter. I found only hens and juveniles in the lower elevations that I searched, which supports this conclusion at least through autumn.

LIMITATIONS OF THE STUDY

The findings from the present study are affected by small samples, weaknesses in their analysis, and the nature of the data. Conclusions drawn from these few individuals are necessarily tentative and must rest on their repeatability and whether they survive testing when applied in future work. Telemetry allowed more continuous observation and greater detail than other methods, but several scattered birds cannot be watched simultaneously. The record on any one bird, although improved, is still incomplete, and brief but significant events can still be missed.

Another possibility is that the birds carrying transmitters may have behaved abnormally. A

controlled test was not possible, but the health and activity of the radio-marked birds indicated no adverse effects.

There is little evidence that the relevant consequences of interaction occurred in the few days before my intensive observations began. When Blue Grouse occupy the breeding range in spring, territorial males are silent at first, begin calling only after a few days, and do not reach the peak of this behavior for two or three weeks (Bendell and Elliott 1967). Limited evidence also suggests that, in some years at least, the hens appear later than the adult males (Bendell 1955). Thus the type of behavior thought likely to affect recruitment is low in intensity at first, and cannot in any case affect hens if they are not yet present. The first hens were not seen on the Comox Burn until a week after the first males arrived in 1966.

Use of activity centers in analyzing dispersion might be questioned. One would expect most interactions involving territorial males to occur either at the activity centers where most calling and displaying is done or at the territory boundary. Bendell and Elliott (1967) plotted territory boundaries by connecting the peripheral locations of adult males, but territorial males are found less often at the periphery than near the activity center. Connecting the peripheral locations indicates the home range but not necessarily the territory boundary. Moreover, males do not patrol specific boundaries, so there is really no adequate evidence for a firm geographical limit, particularly in a sparse population such as on the Comox Burn from 1964 to 1966. Therefore one cannot be certain whether the locations of other grouse fall inside or outside the territories, or are adjacent to them, or well away from the edges.

In addition, encounters between Blue Grouse are seen too infrequently to calculate their most common sites of occurrence. Activity centers are the most useful points of reference for the analysis of dispersion because consistent use and advertisement there by adult males makes these sites readily recognizable.

The data have certain inherent weaknesses regardless of sample sizes and analysis. The conclusion that the movements of the radio-marked birds were unaffected by adult males is based on negative evidence. Although I believe that the possibility is remote, I could have missed relevant observations by looking at the wrong factors or at the wrong times. Nor can I deny categorically that the oc-

casional movements directed toward adult males did not actually stem from attraction. Hens and non-territorial males might have responded to adult males by behavioral means not yet detected or understood, and without developing any special patterns of dispersion.

During this study, dispersion was assumed to serve as an indicator of social interaction that was capable of affecting recruitment. Wynne-Edwards (1962) points out that where social interaction sorts a population into successful recruits and surplus individuals, the result is commonly reflected in dispersion patterns. However, although interaction would be unlikely to affect numbers without also altering dispersion, interaction could conceivably alter dispersion without necessarily affecting numbers. For instance, rather than being relegated to a completely different area, subordinate individuals might remain in the same area as successful recruits but with a different pattern of dispersion. The important point to determine is whether or not subordinate individuals manage to join the population, regardless of their dispersion pattern. The yearling grouse present on the summer range can be considered members of the population, so their interactions with adult males may bear no relation to processes affecting recruitment.

DISCUSSION

The main objective of this work was to look for evidence of social interaction on the summer range that could explain why certain potential recruits join the breeding population while others do not. Elliott (1965) and Bendell and Elliott (1966, 1967) concluded that adult males attract other Blue Grouse. Even though they found no evidence of surplus individuals excluded from the population, attraction of other birds to adult males is a type of behavior which still might affect recruitment. However, biases in their methods (Bendell and Elliott 1967:62) could have erroneously suggested that yearling males and hens were grouped near adult males, and lack of controls in some of their experiments makes it impossible to determine whether attraction, if it occurred, was to the habitat of the territory or to the adult male. The present study indicates that no attraction occurs. I believe there is no firm evidence for attraction to occupied territories, and thus no evidence that adult males interact with other grouse by this means to affect recruitment.

Another process through which recruitment could be effected is that of yearling males

taking over territories after the adults are removed (Bendell and Elliott 1966, 1967). This suggests that territories are attractive when unoccupied, and that the presence of adult males may neutralize the attraction their territories otherwise have. This appears, however, to have no effect on the recruitment of yearlings to the breeding population. Yearling males apparently suffer the same rate of annual mortality as adults, and during the next year show the same fidelity to the breeding range as adults (Zwickel and Bendell 1967). Thus the yearlings present can be considered already members of the population, even though few breed until they are adult (Simard 1964). The effect of adults on yearlings appears to be merely a part of the means whereby adults can breed without interference from other birds (Bendell and Elliott 1967).

For similar reasons, the recruitment of hens is apparently unaffected by encounters with adult males. Hens in estrus respond to males briefly, to copulate with them, but this interaction probably serves no more than to accomplish copulation itself. Although the argument is not entirely conclusive, the absence of convincing contrary evidence suggests that, excepting hens during mating and nesting, the dispersion of hens and yearling males has no pattern beyond that of habitat preferences, and that social interaction in summer has no direct effect on population numbers. I agree with Bendell and Elliott (1967) that territorial behavior and the interactions between adult males and other grouse on the breeding range may serve only to organize and accomplish breeding. Regulation of recruitment apparently takes place before any of the birds arrive on the summer range.

SUMMARY

Dispersion, movements, and social behavior were studied in nine Blue Grouse fitted with miniature radio-transmitters, and in other individuals marked with leg-bands. The object was to test the hypothesis that the behavior of territorial adult males affects the local occurrence of recruits and other grouse on the summer range.

The principal conclusions are that adult males do not cause females and immature males to occur only in certain places on the breeding range, and that the movements of other birds are largely unaffected by adult males. The single exception seems to be that hens in estrus are briefly attracted to adult males for copulation, and nest near their probable mates. Apparently no interaction

directly affecting recruitment occurs on the summer range. Alternatively, recruitment and population size may be regulated away from the breeding range, during fall and winter, although this period was not studied.

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