

SOCIAL ORGANIZATION, MOVEMENTS, AND HOME RANGES OF BLUE GROUSE IN FALL AND WINTER

JAMES E. HINES¹

ABSTRACT.—Social organization, movements, and home ranges of Blue Grouse (*Dendragapus obscurus*) were investigated on Hardwicke Island, British Columbia from 1979 to 1982. Most broods disbanded by the end of September, and young grouse did not associate with their mothers or siblings in winter. The tendency to form flocks was lowest in fall. Grouping increased gradually until midwinter and then declined until spring. Approximately half of the grouse observed during winter were in groups that usually consisted of 2 or 3 birds ($\bar{x} = 2.9 \pm 0.1$ [SE], $N = 210$). Daily movements were usually small during winter (median = 69 m) and home ranges averaged 16.8 ± 2.3 ha ($N = 21$). Although Blue Grouse did not show the strong segregation of sexes found in some other tetraonines, birds most frequently associated with individuals of their own sex and age. The partial segregation of grouse by sex and age may have resulted because females wintered at lower elevations than males and juveniles migrated longer distances than adults. Segregation of sexes of other species of grouse may be explained by a similar mechanism. Flock formation is most frequent in species of grouse that winter in open areas and less frequent in species that winter in forests. Received 20 Sept. 1985, accepted 18 Feb. 1986.

Studies of the social organization of grouse and other birds have usually emphasized the breeding season, with mating systems drawing particular attention (Wiley 1974, Wittenberger 1978, Oring 1982). The nonbreeding season is thought to be a critical period for mortality in avian populations (Lack 1954, 1966; Bendell 1972; Fretwell 1972), and selective pressures during fall and winter may be important in shaping the overall patterns of avian sociality.

During winter, many species of grouse tend to form single sex flocks. A possible proximate explanation for this segregation is that the sexes migrate different distances or prefer different kinds of habitats and hence are not in contact with each other during winter (Koskimies 1957, Weeden 1964, Irving et al. 1967, Hoffman and Braun 1977, and others). Other possibilities are that males and females avoid each other or that members of the same sex are attracted to each other (de Vos 1983). The relative importance of any of these factors in determining the fall and winter sociality of grouse has received little attention, as winter studies are seldom undertaken and it is difficult to identify different sex and age classes in the field.

From 1979 through 1982, I studied Blue Grouse (*Dendragapus obscu-*

¹ Dept. Zoology, Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada. (Present address: Wildlife Management Division, Dept. Renewable Resources, Yellowknife, Northwest Territories X1A 2L9, Canada.)

rus) wintering on Hardwicke Island, British Columbia, Canada. Here, I describe groupings, movements, and home ranges of grouse during fall and winter. These data are then compared with those for other grouse in an attempt to identify (1) ecological conditions that lead to flocking and (2) factors that influence segregation of the sexes during winter.

STUDY AREA AND METHODS

Hardwicke Island (50°28'N, 125°50'W) is in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). Much of the 77-km² island has been logged or burned in the past 100 years and has a variety of successional stages. Breeding densities of coastal Blue Grouse reach peak numbers in openings created by logging or fire, but plant succession occurs rapidly in such openings and, about 20 years after disturbance, dense coniferous cover again prevails, herbaceous cover decreases, and numbers of Blue Grouse decline (Zwickel and Bendell 1972, Niederleitner 1982). On Hardwicke Island, most Blue Grouse wintered in early seral stages or mature forest and generally avoided dense, second-growth forests (Hines 1986).

General methods used in studies of coastal Blue Grouse were described by Zwickel and Bendell (1967a) and Zwickel (1982). From late April until late August, a 464-ha study area consisting mainly of early successional stages (<15 years in age) was searched by census crews consisting of 2 or 3 people. Grouse were located with pointing dogs, captured with noosing poles (Zwickel and Bendell 1967b), and individually marked with colored legbands. In late summer and fall 1979–81, 235 juvenile grouse were equipped with radio packages similar to those described by Brander (1968). Most marked grouse observed in the present study were captured originally on the breeding range.

Fall and winter field work was conducted over much of the island from 1 September until 31 March in 1979–80 and 1981–82 and from 1 September until 12 December in 1980. Radio-marked grouse were located with a portable receiver and yagi antenna; grouse without radios were found with a pointing dog. For many sightings of both radioed and nonradioed grouse, the surrounding area was searched thoroughly with a dog to determine if other grouse were present. Grouse found in tall trees or without the aid of a dog were omitted from analyses of fall and winter groupings as the presence or absence of other birds usually could not be determined under these conditions.

A bird was considered alone if no other grouse was found within a 10-m radius. Although this criterion was somewhat arbitrary, increasing the distance to 50 m would not appreciably change the results as grouse were seldom found within 11–50 m of each other. I believe the definition was appropriate because visibility in winter habitat was usually restricted to distances of 10 m or less and I found no evidence that grouse communicated vocally over long distances. Sightings of 2 or more individuals were said to be “flocks,” “groups,” or “aggregations.” Although these terms are used interchangeably, it is not certain if the groups were true flocks in the sense of being cohesive social units. Given the relatively low densities of grouse on winter range, however, the probability of finding 2 birds within 10 m of each other was exceedingly low and “flocks” were probably more than coincidental or random associations.

In winter, the sex of Blue Grouse was readily determined in the field as males and females differ markedly in size and plumage. The body size and plumage of a juvenile is similar to that of an older bird of the same sex, and age could be determined only when a grouse was captured or identified by colored legbands. Grouse were classified as juveniles (i.e., hatched in the previous summer; <11 months in age) or adults (i.e., all older birds). Sample sizes were not sufficient to allow subdivision of the data into adult and yearling categories.

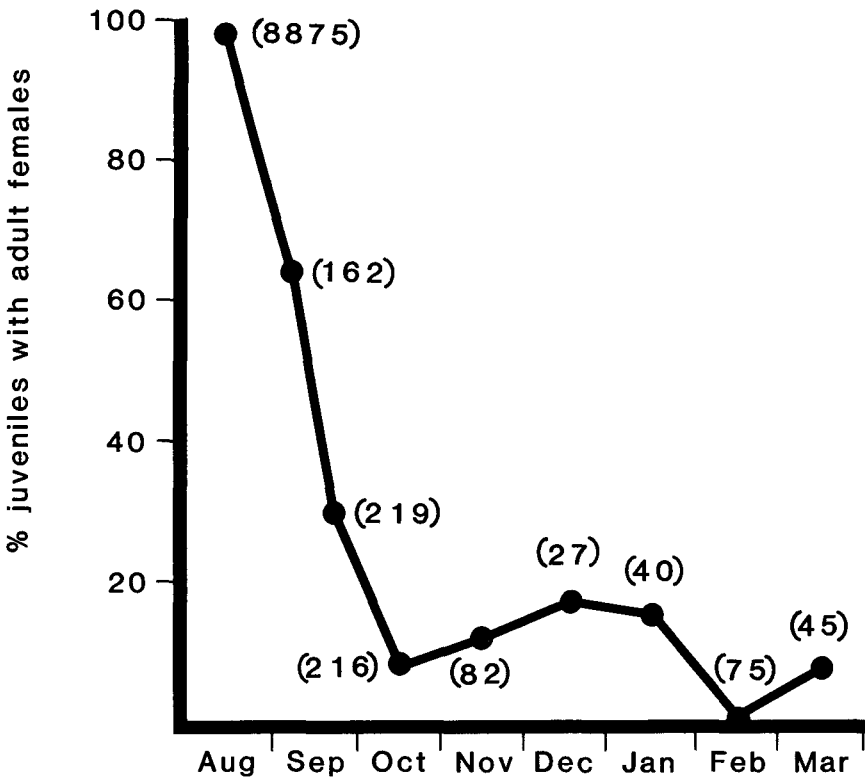


FIG. 1. The proportion of juvenile Blue Grouse observed with adult females during fall and winter on Hardwicke Island, British Columbia. Sample sizes are in parentheses.

When juveniles were individually identified during fall and winter, I attempted to determine if they were with their mothers or siblings. For this purpose, the probable mother of a juvenile was defined as the female with which the juvenile was first sighted in summer. Juveniles having the same probable mother were treated as siblings.

Minimum daily movements and home range sizes of radio-tagged grouse were measured. Daily movement was defined as the straight-line distance between the location of an individual on one day and its location on the following day. Home range size, the total area used by an animal during winter, was determined by the minimum area method (Mohr 1947) for grouse that had settled on winter range and were located 10 or more times after 1 November (but before the time they migrated in spring).

Statistical analyses involved comparisons of frequencies with contingency tables followed by pairwise contrasts (Brown 1974) when the overall χ^2 value was significant ($P < 0.05$).

RESULTS

Brood break-up.—Virtually all juveniles sighted in July and early August were in broods associated with older females. By late August, some

broods had started to disband, and by the end of September most juveniles had separated from adult females (Fig. 1). Because of brood break-up, only a small sample of juveniles whose mothers were known were found together in fall and winter. In September, 49% of these juveniles were found with siblings ($N = 49$). After 1 October, no juveniles were found with either brothers or sisters ($N = 73$). Thus, brood break-up likely was completed by 1 October.

Formation of fall and winter flocks.—The tendency for grouse to aggregate decreased throughout fall and was low in November for both males and females (Fig. 2). The decline in flocking was likely a function of brood break-up. After November, flocking again increased and peaked in January and February. In late February–early March, the number of grouse in flocks declined as older males returned to breeding areas. For example, 54% of 406 males were found in aggregations between 1 October and 1 March but only 18% of 160 males sighted in March were in groups ($P < 0.01$). In April, 22% of the males ($N = 373$) and 36% of the females ($N = 148$) observed during census of the main study area, were with other grouse. The latter figure likely overestimated the proportion of females in groups because the census crew concentrated on territorial males early in spring, and many of the females recorded were with these territorial males. In April 1982, I intensively searched a 50-ha plot as part of a study of movements and spatial relationships of female grouse and found 10 of 57 females (18%) with other grouse. This is probably a better indicator of the gregariousness of females during April.

Seasonal trends in flock size followed a pattern similar to the above data (Fig. 2). Flocks were relatively small in November but increased in size until January and then declined. Flocks sighted after brood break-up (i.e., after 1 October) consisted of 2–15 birds and averaged 2.9 ± 0.1 [SE] ($N = 210$). Two was the most common group size (Fig. 3).

The tendency to join flocks varied somewhat among sex and age classes. From 1 October (after the end of brood break-up) until the time of spring migration (beginning approximately 1 March for males, and 1 April for females), 46% of 127 adult males, 38% of 112 adult females, 57% of 170 juvenile males, and 55% of 267 juvenile females were found in groups. The proportion of grouse found in groups differed significantly among sex and age classes ($P < 0.01$); the only significant pairwise comparison ($P < 0.05$) indicated that adult females were less apt to be found in groups than were juvenile males or females.

Overall, 54% of the males ($N = 406$) and 51% of the females ($N = 495$) observed between the time of brood break-up and spring migration were in groups. (Grouse of known sex but unknown age were also included in these samples.) If data for both sexes were pooled, and sightings of birds

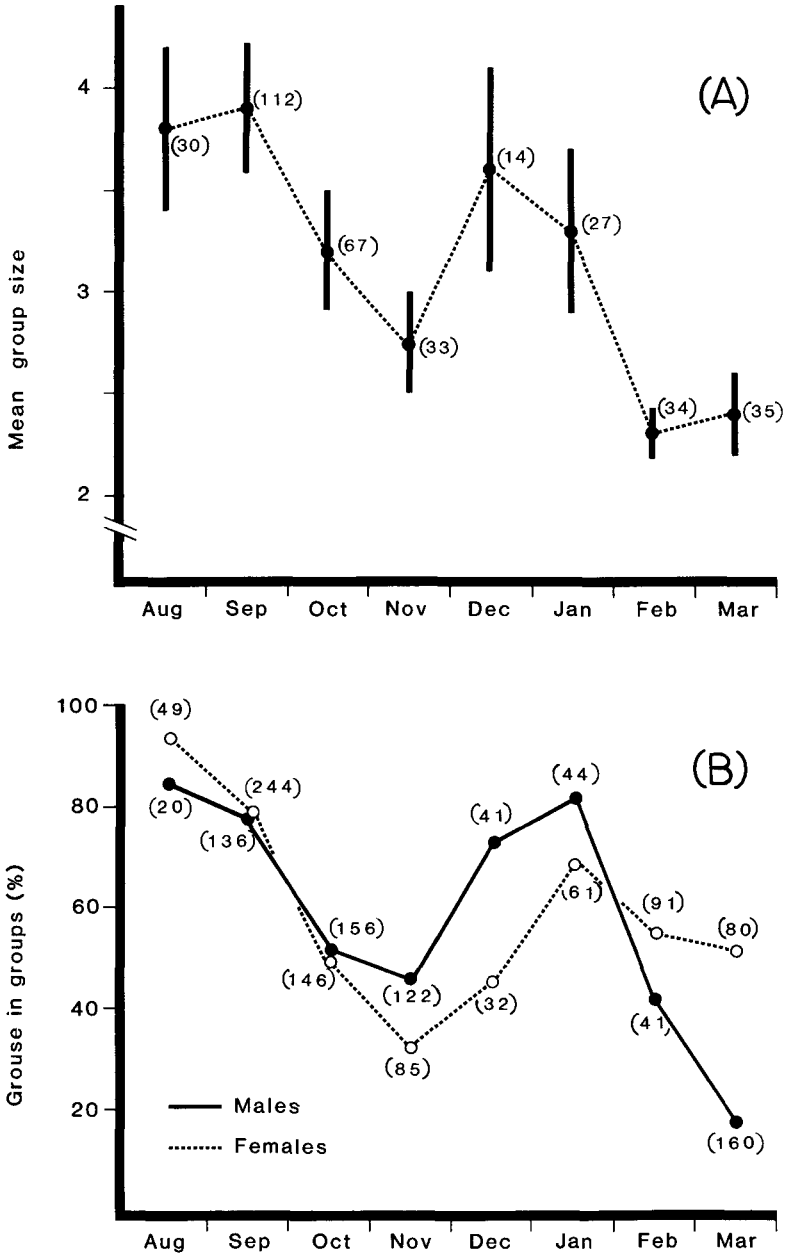


FIG. 2. The average size \pm SE of flocks during fall and winter (A) and the proportion of all grouse found in flocks (B).

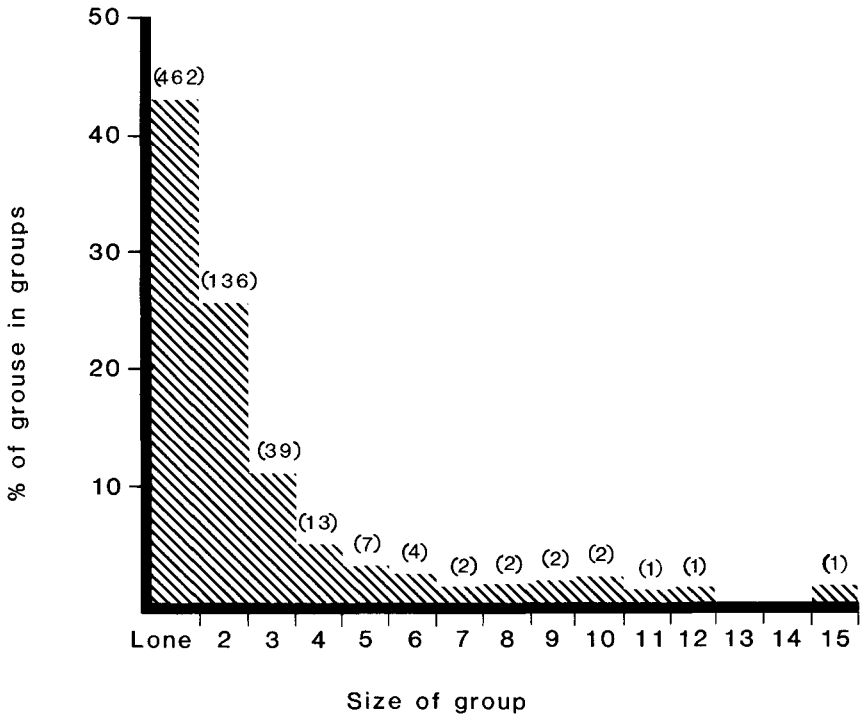


FIG. 3. Frequency distribution of flock sizes of Blue Grouse between 1 October and the time of spring migration. The number of flocks of each size are indicated in parentheses.

of unknown sex added to the sample, an estimated 52% of the grouse were in groups ($N = 1029$).

Associations among different sex and age classes.—Grouse associated most frequently with individuals of their own sex and age class, although some degree of association among all sex and age classes was found. For example, 68% of all adult males found in groups were associated with at least one other adult male, whereas only 15% were associated with adult females, 24% with juvenile males, and 9% with juvenile females (Table 1). Adult females flocked less with members of their own sex and age than did any of the other sex and age classes.

Daily movements and home range size.—Daily movements of radio-marked grouse were greatest in late summer and decreased during fall; they remained low but stable throughout winter (Fig. 4). Daily movements varied from 0 to over 600 m, but the median for the period lasting from 1 October until spring migration was only 69 m, indicating that short daily movements were typical (Fig. 5).

TABLE 1
ASSOCIATIONS BETWEEN BLUE GROUSE OF DIFFERENT SEX AND AGE ON HARDWICKE ISLAND, 1 OCTOBER TO 31 MARCH (DATA INCLUDE ONLY GROUSE SEEN IN FLOCKS)

| Age | Sex | (N) | % in flocks with | | | |
|--------------|---------|-----|------------------|---------------|----------------|------------------|
| | | | Adult males | Adult females | Juvenile males | Juvenile females |
| Adult | Males | 66 | 68.2 | 15.2 | 24.2 | 9.1 |
| Adult | Females | 43 | 23.3 | 23.3 | 18.6 | 30.2 |
| Juvenile | Males | 98 | 15.3 | 16.3 | 73.5 | 50.0 |
| Juvenile | Females | 148 | 6.8 | 12.2 | 28.4 | 73.7 |
| | | | Males | Females | | |
| All males* | | 247 | 80.6 | 53.4 | | |
| All females* | | 251 | 41.0 | 76.1 | | |

* Analysis includes 83 males and 60 females of unknown age.

Sizes of winter home ranges were determined for 18 radio-tagged juvenile females, 2 juvenile males, and 1 adult female. Home ranges during winter varied in size from 3.0 to 42.5 ha and averaged 16.8 ± 2.3 ha ($N = 21$). In many instances, overlap of home ranges was substantial (Fig. 6). Only radio-marked grouse on part of the island are shown in Fig. 6 and, as many other grouse resided in this area, home range overlap was undoubtedly more extensive than indicated.

DISCUSSION

Winter was a time of relatively low mobility for Blue Grouse on Hardwicke Island. Daily movements of < 100 m were most frequent, and home ranges averaged 16.8 ha for a 4–5 month period. Grouse were most often found alone or in small groups of 2 or 3 in late fall and winter, and the data suggest that winter associations of juveniles were comprised of non-siblings.

Immediately after brood break-up, the tendency to form flocks was low, but rates of aggregation gradually increased until midwinter then declined until spring. The cause of increased flocking in midwinter is not certain; it may reflect the concentration of birds in areas of suitable habitat or increased sociability. Similar trends in winter flocking occur in Ruffed Grouse (*Bonasa umbellus*) (Doerr et al. 1974), Black Grouse (*Tetrao tetrix*) (Hanson and Soikkeli 1984), and Capercaillie (*Tetrao urogallus*) (Pulliainen 1981). Doerr et al. (1974) suggested that decreases in feeding aggregations of Ruffed Grouse from January through March occurred when males became socially intolerant of each other and more attached

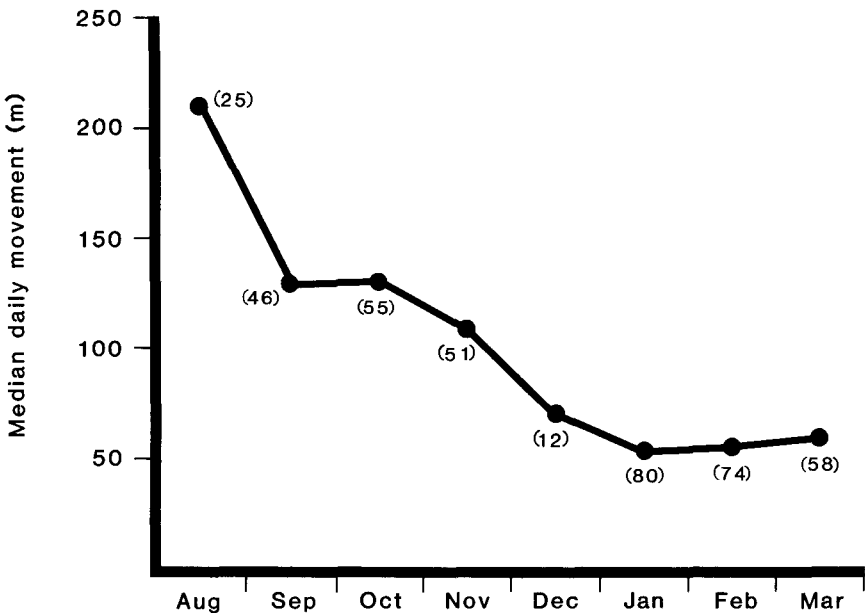


FIG. 4. Seasonal changes in daily movements (m) of radio-marked grouse. Sample sizes are in parentheses.

to their territories. This was likely true for Blue Grouse on Hardwicke Island as well, because there were proportionally fewer males in late winter flocks than in earlier groupings. Final dissolution of winter flocks occurred when females returned to breeding range.

Although Blue Grouse associated most frequently with individuals of their own sex and age, they did not show as strong a tendency to segregate by sex as do some other species of grouse. Data from studies of migration and winter habitat use by Blue Grouse (Hines 1986) suggest 2 factors that may have contributed to the partial segregation of grouse by sex and age. First, females wintered at lower elevations than males and the 2 sexes were separated somewhat because of this. Second, juveniles wintered farther from breeding range than adults, thereby bringing about partial segregation of the age classes. Given that both migration distances and the elevations at which the different sex and age classes wintered were somewhat variable (Hines 1986), the segregation of sex and age classes was incomplete. Data for other species of North American grouse support the view that segregation of the sexes is influenced by migration (Table 2). Segregation occurs most frequently when one sex winters closer to the breeding range (e.g., Sage Grouse [*Centrocercus urophasianus*], White-

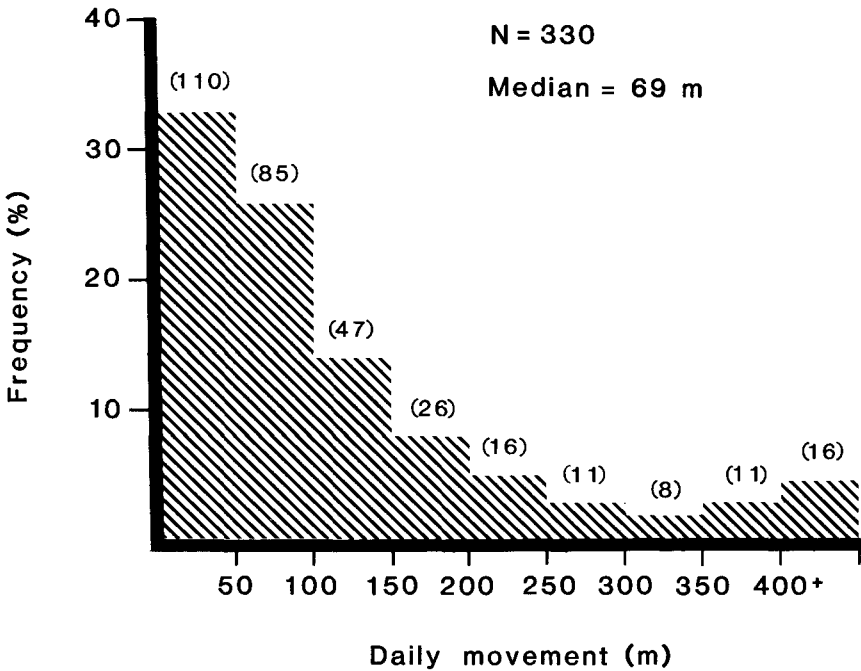


FIG. 5. Frequency distribution of daily movements (m) of radio-marked Blue Grouse during fall and winter. Sample sizes are indicated above the histogram.

tailed Ptarmigan [*Lagopus leucurus*], Sharp-tailed Grouse [*Tympanuchus phasianellus*], and formation of mixed flocks is more common in species that show little evidence of differential migration of the sexes (e.g., Blue Grouse on Hardwicke Island, Spruce Grouse [*D. canadensis*] in Alaska, Ruffed Grouse).

The question of why certain sex and age classes associate with each other was considered above, but this does not explain why there is such a range in gregariousness among species. To address the latter question, data on fall and winter groupings of Blue Grouse and other North American Tetraoninae were summarized with regard to typical and maximum flock size and winter habitat (Table 2). Although not all information was available for each species, species wintering in more open habitats seem to form large flocks (e.g., Sage Grouse, White-tailed Ptarmigan, Sharp-tailed Grouse), whereas species wintering in forested areas live solitarily or in small flocks (e.g., Ruffed Grouse, Blue Grouse, Spruce Grouse).

There are at least three ultimate or evolutionary pressures on animals to live in groups outside the breeding season (Alexander 1974, Wilson

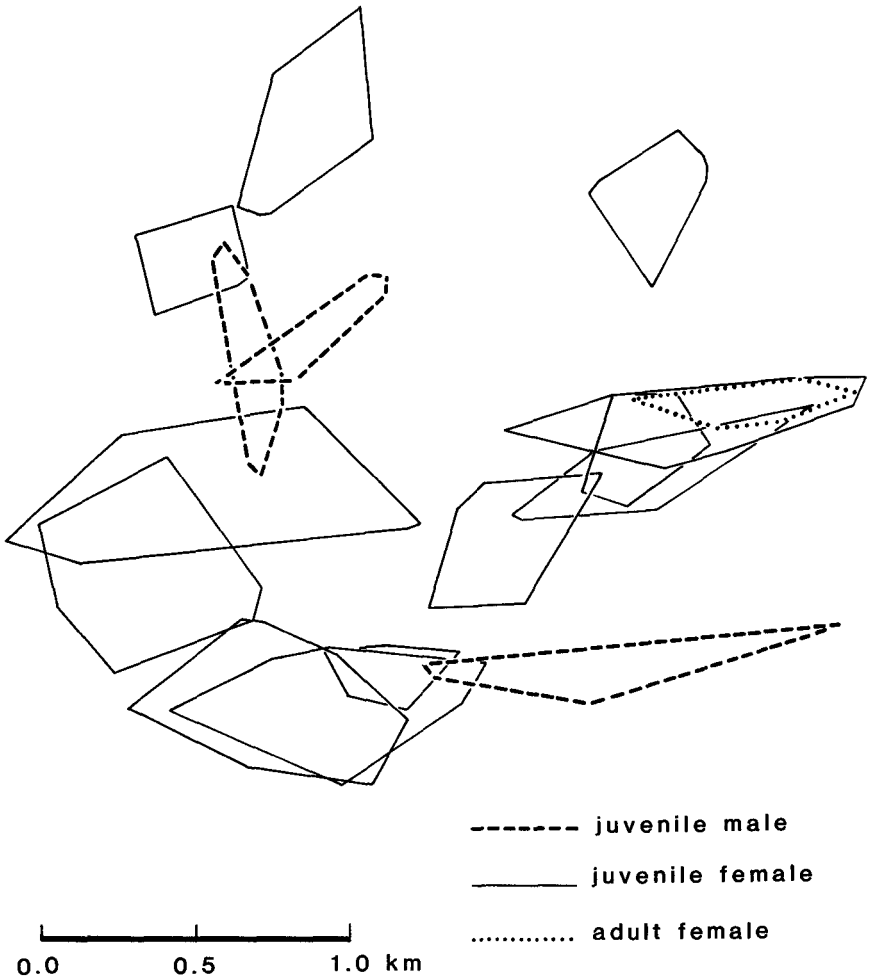


FIG. 6. Overlap of home ranges of 16 radio-marked Blue Grouse on part of Hardwicke Island, British Columbia during the winter of 1981-82.

1975, Pulliam and Millikan 1982, Madison 1984). By joining a group, an individual may (1) increase its chance of avoiding predators or (2) find and exploit a food resource more efficiently. In addition, individuals may aggregate in certain areas because (3) resources essential for survival are clumped in distribution and are not easily defended (Pulliam and Millikan 1982). The literature on grouse provides little information bearing on point (3)—it is not known if essential resources are more clumped in open

TABLE 2
FACTORS ASSOCIATED WITH FALL AND WINTER FLOCKING OF NORTH AMERICAN GROUSE

| Species | Location | Lone grouse | Typical flock size | Maximum flock size | Segregation of sexes | Winter habitat | Differential migration | Source |
|------------------------|------------------|-------------|--------------------|--------------------|----------------------|---------------------|------------------------|-------------------------------------|
| Sage Grouse | Colorado | Infrequent | <50 | 100+ | Yes | Sagebrush-grassland | Yes | Beck (1977) |
| Sage Grouse | Idaho | | <50 | 300 | Yes | Sagebrush | | Dalke et al. (1963) |
| White-tailed Ptarmigan | Colorado | Infrequent | <25 | 80+ | Yes | Alpine willow | Yes | Hoffman and Braun (1975, 1977) |
| Willow Ptarmigan | Alaska | Infrequent | | | Yes | Willow | Yes | Weeden (1964), Irving et al. (1967) |
| Rock Ptarmigan | Alaska | Infrequent | <20 | 100 | Yes | Willow | Yes | Weeden (1964) |
| Spruce Grouse | Alaska | Frequent | 2-4 | 15 | No | Coniferous forest | No? | Ellison (1973) |
| Sharp-tailed Grouse | Saskatchewan | | 5-10 | | Yes | Aspen parkland | Yes | Schmidt (1980) |
| Sharp-tailed Grouse | Wisconsin | | | 200 | Yes | Brushy areas | Yes | Hamerstrom and Hamerstrom (1951) |
| Blue Grouse | British Columbia | Frequent | 2 | 4 | Yes | Coniferous forest | Yes | King (1971) |
| Blue Grouse | British Columbia | Frequent | 2-3 | 15 | Moderate | Coniferous forest | No | This study |
| Ruffed Grouse | Alberta | Frequent | 2-3 | 9 | No | Aspen forest | No? | Doerr et al. (1974) |
| Ruffed Grouse | Saskatchewan | Frequent | 2 | 8 | | Deciduous forest | | Hines (1984) |

than forested areas. Instances of starvation seldom have been reported for grouse (e.g., McGowan 1969), suggesting that the need to exploit a food resource optimally is not the cause of tetraonine sociality. Predation, however, is a frequent cause of death for grouse (Jenkins et al. 1964, Gullion and Marshall 1968, Rusch and Keith 1971). Thus, flocking may be an antipredator response used by grouse inhabiting open areas. Comparisons of the distribution and abundance of resources, and assessments of the relative merits of flocking for maximizing feeding or avoiding predators in open vs forested habitats, and interactions among these variables are needed to resolve this issue.

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