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BEHAVIORAL DIFFERENCES OF FEMALE SPRUCE GROUSE UNDERTAKING SHORT AND LONG MIGRATIONS

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ABSTRACT.—Movements by 93 radio-tagged Spruce Grouse (*Dendragapus canadensis*) between winter and summer ranges in southwestern Alberta were compared between sex and age classes. A bird's movement from the range occupied during its first winter to its first potential breeding area was considered to be the spring phase of dispersal. Subsequent movements between the breeding and wintering areas were classed as migratory movements. The similarity between spring dispersal and migration distances within a sex, and the site fidelity of adult females to the range occupied during their first winter, support the suggestion that migratory movements in Spruce Grouse retrace their first spring dispersal movement made when about nine months old. Proportionally more females than males moved long distances. Among adult females, short-distance migrants (moving <2 km) were more variable than long-distance migrants in the timing of migratory movements. Additionally, short-distance migrants associated less with other adult females, especially other short-distance migrants, in winter flocks than did long-distance migrants. The behavioral differences may reflect the proximal causes producing each type of migration/dispersal.

Like many other Tetraoninae, Spruce Grouse (*Dendragapus canadensis*) migrate between winter and summer ranges (Herzog and Keppie 1980). The distance and direction of migration vary among individuals, as does the timing of movement, and the behavior of migrating birds. The migration of adults has been suggested to be a retracing of movements made during their spring phase of dispersal as yearlings, when about nine months old (Herzog and Keppie 1980). Dispersal, as described by Keppie (1975), is divided into fall and spring phases separated by a winter period during which relatively little movement occurs. Movement during these phases encompasses overall dispersal movement from the place of hatching to the first potential breeding area. Some ultimate consequences of such dispersal (increased gene flow, colonization of suitable habitats, population regulation) have been reviewed by Gaines and McClenaghan (1980), Greenwood and Harvey (1982), and Swingland and Greenwood (1983).

If migratory behavior in adult Spruce Grouse is dependent upon their spring dispersal as yearlings, proximate causes of dispersal, such as inheritance (Myers and Krebs 1971) and intraspecific aggression (Herzog and Boag 1977, 1978; Alway and Boag 1979; Keppie 1979), may also influence subsequent patterns of migration. This study examines behavioral data from radio-tracked females exhibiting short and long-distance migratory movements. Although males also migrate, long-distance migrations are less frequent (Herzog and Keppie 1980), which makes studying them difficult.

Long-distance migrations by female Spruce Grouse are predictable in consistency of direction and in rate of movement (Herzog and Keppie 1980). This suggests a relatively fixed behavioral pattern in these birds which may differ from those shown by females moving over short distances. Likewise, the possibility that some young birds select wintering areas where the potential for successful breeding the following spring is high (Alway and Boag 1979), suggests that differences in dispersal, and hence migration, may be related to behavioral differences shown during the preceding winter. Since timing of migrations may be an important aspect of female behavior associated with dispersal and subsequently migration, and since Spruce Grouse commonly flock in winter (Ellison 1973, Keppie 1975), both were examined and compared for females migrating short and long distances.

METHODS

Spruce Grouse were radio-tracked in 1974–1975, 1977, and 1982–1984 near the R. B. Miller Biological Station, 27 km west of Turner Valley, Alberta (50°39′N, 114°39′W). The main Gorge Creek study area consisted of 555 ha of forest dominated by lodgepole pine (*Pinus contorta*), with scattered clumps of white spruce (*Picea glauca*) and poplar (*Populus* spp.).

Birds were noosed (Zwickel and Bendell 1967), individually marked with colored leg bands, and harnessed with radio transmitters. Radio-tagged birds were tracked with a hand-held yagi antenna and receiver. Locations were plotted using a large grid system superimposed

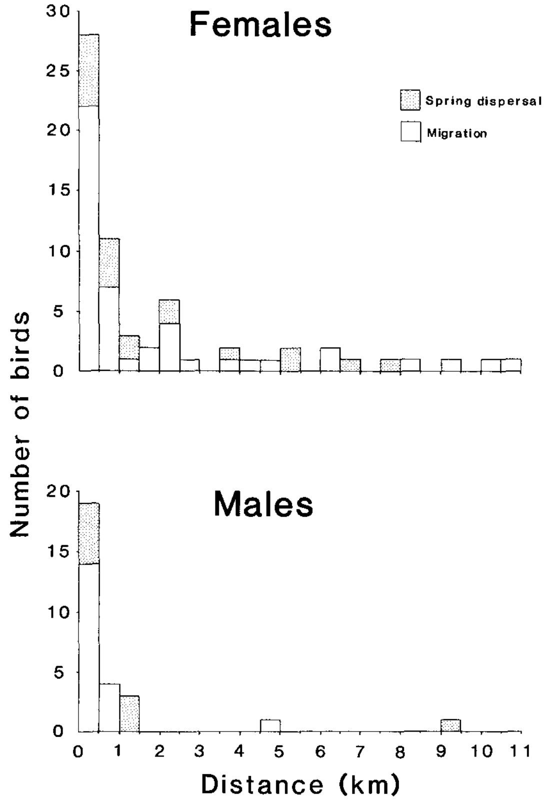

FIGURE 1. Distribution of spring dispersal and migratory distances for radio-tracked female ($n = 65$) and male ($n = 28$) Spruce Grouse at Gorge Creek, Alberta.

on air photos. To help eliminate the potential biases inherent in typical censusing techniques, I used only behavioral data obtained from radio-tagged birds.

Grouse were classed as juveniles (<6 months), yearlings (6–15 months), or adults (>15 months). Designation of seasons was based on aspects of behavior, such as movement and dispersion within a season (Herzog and Boag 1978), and timing of migration and dispersal movements (Herzog and Keppie 1980), and were as follows: Winter (15 October–31 March); and Summer: (15 May–15 August). These designations, with up to two months between them, enabled me to avoid confusion between early and late movements, either dispersal or migration, and normal daily movements within summer or winter ranges.

Spring dispersal distances were estimated by measuring the distance between the median locations (calculated from all sightings) of a bird on its first winter range and subsequent breeding range. Distances migrated were estimated by measuring the distance between the median location of summer and winter ranges as adults. A distance of 2 km, which is about one-sixth of the maximum migratory distance recorded, was used to separate long and short migrations. This was a natural dividing point in the skewed distribution of distances described (Fig. 1). Distances falling in the tail of the skewed distribution were classed as long-distance migrations. The 2-km separation point approaches the distance used by Herzog and Keppie (1980) to separate "residents" from "migrants," the equivalent of short-distance and long-distance migrants, respectively. Herzog and Keppie's classification is inappropriate because many of their "resident" birds actually undertook seasonal migrations inside the boundaries of the study area.

The timing of migration was estimated for radio-tagged birds that were tracked frequently. Dates of migration were based on their (1) last day on wintering range, (2) first day on breeding range, (3) last day on breeding range, and (4) first day on wintering range. This method uses two dates for each movement (numbers 1 and 2 for spring migration and numbers 3 and 4 for fall migration). I compared the timing of these movements in long-distance and short-distance migrants. Because of the difficulty in differentiating between normal daily movement and short-distance migration, I excluded birds migrating <400 m when analyzing the timing of migration (400 m was chosen because it was the radius of the maximum home range occupied by an individual bird of any sex during any season recorded by Herzog and Boag 1978). In comparing dates (and distances), median values were used to reduce the statistical influence of outlier points.

Social behavior in winter was analyzed by examining the composition and stability of flocks. Any association of two or more birds,

TABLE 1. Median dates of departure from and arrival on summer and winter ranges for radio-tracked migrating female Spruce Grouse at Gorge Creek, Alberta.

Category	Short migrations			Long migrations			Overall median
	n	Median	Range	n	Median	Range	
Last sighting on winter range	5	17 Apr.	19 Mar.–8 May	8	26 Apr.	16 Apr.–11 May	25 Apr.
First sighting on summer range	5	19 Apr.	1 Apr.–11 May	7	27 Apr.	23 Apr.–16 May	26 Apr.
Last sighting on summer range	6	11 Oct.[a]	3 Aug.–18 Dec.	6	12 Sept.	30 Aug.–13 Oct.	13 Sept.
First sighting on winter range	9	31 Aug.[a]	19 July–23 Sept.	7	27 Sept.	9 Sept.–16 Oct.	23 Sept.

[a] Because of frequent reverse migratory trips, the last sighting on the summer range is later than the first sighting on the winter range.

TABLE 2. Associations among adult female Spruce Grouse in winter flocks at Gorge Creek, Alberta (percent in parentheses).

Category of migrant	Number of female sightings	No. in flocks[a]	No. in flocks with birds other than adult females	No. in flocks with other adult females
Long distance	157	73 (46.5)	44 (28.0)	54 (34.4)
Short distance	419	147 (35.1)	121 (28.9)	45 (10.7)
P[b]		<0.05	>0.50	<0.001

[a] Some flocks contained both adult females and non-adult females.
[b] Chi-square contingency table.

with a maximum nearest-neighbor distance of 50 m, was considered a flock. Although a maximum nearest-neighbor distance of 18 m was used by Ellison (1973), awareness among individuals in this area (Nugent and Boag 1982) warranted the larger 50-m distance. Grouse seen in the same flock during consecutive sightings (maximum time of three days between sightings) were considered part of a stable flock. Because many of the areas adjacent to the Gorge Creek study area consisted of slightly different grouse densities and habitat types, I analyzed only flocking data obtained on the main study area.

RESULTS

DISTANCES OF MOVEMENT

Females were recorded moving up to about 11 km during spring dispersal and migration, and males up to 10 km (Fig. 1). The relative number of birds moving >2 km during spring dispersal did not differ from that migrating, either for males or females ($P > 0.50$; Chi-square contingency table). The similarity between spring dispersal and migratory distances for each sex is expected if the latter merely retraces a bird's first spring dispersal movement. An examination of females' fidelity to a winter range showed that of 30 birds (15 short-distance and 15 long-distance migrants) observed during their first winter as juveniles/yearlings and again in subsequent winter(s) as adults, only one had a winter range as an adult more than 500 m away from its first winter range (950 m). The median distance between successive winter ranges of an individual female was 154 m. Because spring dispersal movements are apparently retraced as subsequent migrations, they were combined for comparing male and female movements. Females moved >2 km significantly more frequently than males ($P < 0.01$; Chi-square contingency table).

TIMING OF MIGRATION

The dates of migration for females undertaking long or short migrations were not significantly different (Table 1). However, long-distance migrants deviated significantly less from the overall median dates of movement ($P = 0.005$; Klotz test for equal variances).

Some of the variability in the timing of short migrations (<2 km) appeared to reflect repeated migratory trips during a single season. For example, some females moved to their winter range, returned to summer range, and finally moved back to winter range, all during a single fall season. This type of movement was found in 15 females during this study. All but one were short-distance migrants. The one exception was a female that moved 2.15 km, only marginally greater than the separation point between long and short migration (2 km). Although repeat migratory trips would probably be more difficult for long-distance migrants to make, because of the longer distances moved, none of the long-distance migrants (apart from the above exception) reversed its direction during a migratory movement, even for a single day.

WINTER FLOCKING

Long-distance migrants flocked with other birds significantly more than did short-distance migrants (Table 2). The difference appeared to reflect their association with other adult females as opposed to flocking in general. For example, migrants of both categories flocked equally with birds other than adult females. A more detailed examination of flocks containing more than one female, showed that long- and short-distance migrants flocked equally with long-distance migrants (Table 3). However, adult females that were short-distance migrants associated significantly less

TABLE 3. Associations among adult female Spruce Grouse in winter flocks at Gorge Creek, Alberta in relation to their migratory status (percent in parentheses).

Category of migrant	Number of flocks containing females[a]	No. in flocks containing short-distance migrants	No. in flocks containing long-distance migrants
Long distance	54	31 (57.4)	32 (59.3)
Short distance	45	16 (35.6)	31 (68.9)
P[b]		<0.05	>0.10

[a] Some flocks contained both short-distance and long-distance migrants.
[b] Chi-square contingency table.

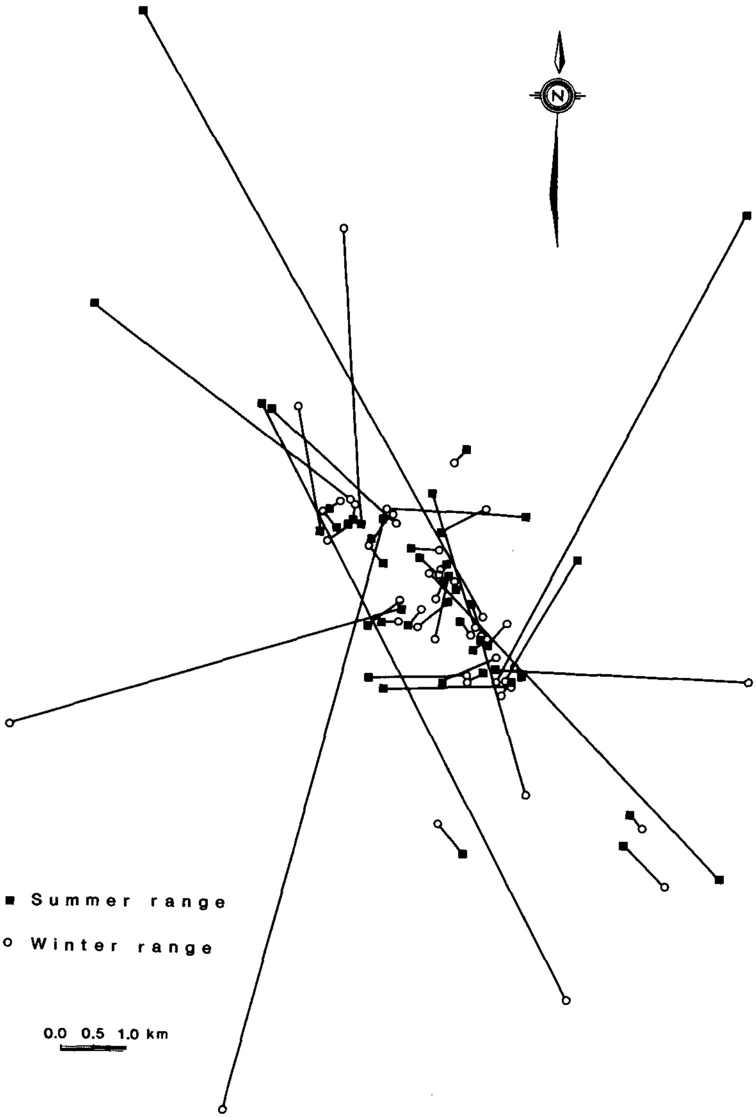

FIGURE 2. Directions and distances of straight-line migratory paths between the median locations of winter and summer ranges for radio-tracked female Spruce Grouse near Gorge Creek, Alberta.

often with other short-distance migrants than did long-distance migrants.

Results were similar when the composition of stable flocks was examined. Short-distance migrants were less common in stable flocks than expected, based on their frequency of occurrence in the population ($P < 0.05$; Chi-square contingency table). Additionally, stable flocks with two more long-distance migrants appeared to be more common (seven recorded) than flocks with two or more short-distance migrants (two recorded). Furthermore, stable flocks with two or more adult females present were of greater duration when composed of long-distance migrants ($\bar{x} = 6.6$ days) than short-distance migrants ($\bar{x} = 3.0$ days). This occurred despite the fact that short-distance migrants outnumbered long-distance ones by approximately 2:1 in the Gorge Creek population.

DISCUSSION

These results show that distances covered during the spring phase of dispersal and subsequent migration are similar, thus supporting Herzog and Keppie's (1980) suggestion that migration may be a retracing of the preceding spring dispersal movement. This suggestion is also supported by the high degree of site fidelity of birds to their first wintering area, to which they return after making a spring dispersal movement, as well as to their first breeding area (Herzog and Keppie 1980). These observations imply that the spring dispersal movement is an important event in the life history of individual Spruce Grouse. Factors that influence how far a yearling will disperse in spring may also influence its subsequent migratory behavior.

Since most females apparently breed during their first spring, they may be forced to move from winter range to find a vacant territory (Herzog and Boag 1977, 1978; Boag et al. 1979; Nugent and Boag 1982). Differences in the timing of migration may reflect different proximal reasons for the original dispersal movements. For example, intrasexual interactions may be responsible for the movements observed in short-distance migrants, as well as in short-distance dispersers. Since vacant areas are filled over time (Nugent and Boag 1982), such intrasexual interactions could explain the variation in the timing of dispersal and migration in these short-distance migrants. Although this study did not show a direct relationship between aggressive interactions and migration distance, it appeared to indicate that the migratory patterns of short-distance migrants are not as fixed as those of long-distance migrants. Intrasexual interactions, however, are unlikely to force a bird to move over 10 km in a straight line, as occurs in some long-distance migrants. Moreover, long-distance migrants do not make this movement in response to the lack of suitable habitat because many birds commonly move through habitats used by others and thus are apparently suitable (Fig. 2). Additionally, some Spruce Grouse spend both the winter and breeding seasons on the same areas (Herzog and Keppie 1980), which suggests that selection of separate habitats in each season is not a major factor evoking long movements. The apparently random direction of migratory movements ($P > 0.50$; Mann-Whitney U-test) also seems to rule out the importance of broad habitat differences in influencing long movements, such as with the seasonal changes in elevation and habitat reported for Blue Grouse, *Dendragapus obscurus* (Anthony 1903, Marshall 1946, Wing 1947, Bendell 1955, Mussehl 1960, Zwickel et al. 1968).

If some birds are looking for a place to breed during their first winter (Alway and Boag 1979), they may display more spatial separation with respect to other potential breeders: a behavior similar to the territorial behavior that grouse display in spring (Herzog and Boag 1977, 1978). If such spatial separation in the winter is important among potential breeders, it should be more prevalent among short-distance dispersers/migrants. Not only did short-distance migrants flock less than long-distance migrants, they also flocked less with other adult female Spruce Grouse. Additionally, in flocks containing females, short-distance migrants were seen significantly less with other short-distance migrants than were long-distance migrants. Since both categories of migrants were found on the same area and in the same general habitat, I see no obvious habitat-related reason why they should differ in their relative flocking tendencies. Furthermore, the median distance moved of 0.33 km for short-distance migrants suggests that they may not remain entirely on their summer territories during the winter and, hence, they are probably available for flocking with other females. Since the two categories of migrants are essentially equally represented in flocks with non-females, I suggest that short-distance migrants do not avoid flocking in general, but avoid other females, and especially other short-distance migrants. The result of such intrasexual avoidance may be that short-distance migrants are spatially separated in the winter. Additionally, the lack of intrasexual avoidance by long-distance migrants may indicate that they are not immediate competitors for space in which to breed.

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RECENT PUBLICATIONS

The birds of the Republic of Panamá (4 vols.).—Alexander Wetmore (coauthored with Roger F. Pasquier and Storrs L. Olson in Part 4). 1981–1984. Smithsonian Institution Press, Washington, DC. Vol. 1—483 p., $25.00; Vol. 2—605 p., $25.00; Vol. 3—631 p., $25.00; Vol. 4—670 p., $29.95. The late Dr. Wetmore began his studies in Panamá in 1944 and continued them annually for at least 22 years. The first three parts of his treatise on the country's avifauna were published in 1965, 1968, and 1972 by the Smithsonian Institution in its *Miscellaneous Collections* series. Of the remainder, he had prepared accounts for almost all of the "ten-primaried oscines" when failing health overtook him. S. Dillon Ripley then persuaded Storrs Olson to handle the identification of specimens and systematic decisions, and Roger Pasquier to compile the species accounts and descriptions for the rest of the species. With the work completed, the Smithsonian Press reprinted the first three volumes to make them all available and in hardcover.

Four thick volumes were needed to provide comprehensive treatment for Panamá's extraordinarily rich avifauna. Nearly 900 species have been reported there, a country that is smaller than South Carolina. Volume 1 spans tinamous through skimmers, 2: pigeons—woodpeckers, 3: woodcreepers—sharpbills, and 4: swallows—finches. Each family is introduced by a brief general statement, followed, where necessary, with a key to the species that have been recorded in Panamá. Species accounts include description, critical measurements, status and distribution, and observations on habits and ecology. For birds that are represented by more than one subspecies, each form is treated separately, giving its characters, measurements, and other information.

The volumes are illustrated with color painting frontispieces by Walter A. Weber (Vols. 1–3) and Guy Tudor (Vol. 4) and pen-and-ink drawings by both artists. An appendix in Volume 4 gives information about birds that belong to families treated in the preceding volumes and that have been found in Panamá since those books were first published. Each volume carries an index.

This monumental work is a fitting capstone to Wetmore's oeuvre, already distinguished by its wide range of subjects and importance of its contributions, not to mention its sheer quantity. For completing it, and at a standard equal to that of the first three volumes, great thanks are due Pasquier, Olson, and their collaborators. The book constitutes a major reference for any future studies of neotropical ornithology. Owing to the clearing of forests, it is also, sadly, the record of a birdlife that has been seriously altered since Wetmore first knew it.

Birds of Rio Grande do Sul, Brazil. Part 1. Rheidae through Furnariidae.—William Belton. 1984. Bulletin of the American Museum of Natural History, Vol. 178, Article 4. 268 p. Paper cover. $17.10. Source: Librarian, American Museum of Natural History, Central Partk West at 79th Street, New York City, NY 10024. Rio Grande do Sul, the southernmost state of Brazil, contains Atlantic beaches, rolling or hilly grasslands, areas of chaco-type terrain, riverine tropical forests, and forested coastal mountains. Thanks to this diversity of habitats, the region (slightly larger than Colorado) has a total avifauna of 586 species, most of which can or do breed there. Copious information about these birds is given in this monograph, the first attempt at a comprehensive survey of the avifauna of the state. The report is based on extensive fieldwork by Belton, a U.S. diplomat stationed in Brazil and subsequently living there in retirement. In addition to taking and meticulously filing notes, he collected and measured specimens, and made tape recordings of voices. To this base are added observations by other workers and data from other specimens in museum collections. Preceding the species accounts are a description of the region (illustrated with good photographs), an analysis of the avifauna, a history of ornithological investigation there, and a number of suggestions for conservation action and ornithological studies. The species accounts treat distribution and status, voice, breeding data, etc., and are furnished with unusually large, clear range maps. Detailed, thorough, and well put together, this work is an important contribution to the ornithology of eastern subtropical and temperate South America. It will be completed with publication of the second part, which will give species accounts from the Formicariidae through the Corvidae. Birders in the region need not lug these volumes, but instead can use Belton's pocket guide (noted in Condor 86:442).