DIFFERENTIAL MIGRATION OF BLUE GROUSE IN COLORADO

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ABSTRACT.—We examined migration of adult Blue Grouse (*Dendragapus obscurus*) in north-central Colorado by radio tracking 13 males and 19 females. Elevational changes associated with movements to winter areas were greater for males (median = 488 m, range = 183–671 m) than females (median = 122 m, range = −61–760 m). Males (median = 10.5 km, range = 1.0–29.4 km) also moved farther than females (median = 1.0 km, range = 0.1–28.0 km), resulting in partial segregation of sexes during winter. Directional orientation of movements to wintering areas was nonrandom for long-distance (>3 km) migrants. Median elevational change (122 m) and distance (0.6 km) between the first-winter and first-breeding areas for seven juvenile females were similar to movements of adult females. Males (median = 7 July) departed breeding areas earlier than females (median = 11 August), but arrived (median = 14 October) on winter areas about the same time as females (median = 23 October). Both sexes exhibited fidelity to winter areas. The average distance between winter locations ranged from 94 to 312 m (median = 135 m) for 11 radio-marked adults, suggesting Blue Grouse were sedentary on their winter ranges. *Received 3 October 1991, accepted 21 February 1992.*

BLUE GROUSE (*Dendragapus obscurus*) move less than 1 km (Hoffmann 1956) to greater than 40 km (Boag 1966) between seasonal ranges. They breed in open coniferous, aspen (*Populus* spp.), and mountain-shrub habitats, but are restricted to coniferous forests during winter (reviewed by Schroeder 1984). Although frequently reported as migrating to higher elevations for winter (Marshall 1946, Wing 1947, Bendell 1955), some populations reside at the same area year around (Hoffmann 1956), or move to lower elevations for winter (Rogers 1968). The spatial relationship between habitats used for breeding and wintering appears to partially explain why Blue Grouse move up, down, or not at all between seasonal ranges (Zwickel and Bendell 1972).

Early efforts to document migratory patterns of Blue Grouse were based on band recoveries (Mussehl 1960, Boag 1966, Bendell and Elliott 1967, Zwickel et al. 1968). These efforts failed to document movements to winter areas because band recoveries were primarily from birds harvested by hunters in the autumn. Furthermore, most recoveries were from adult females and juveniles and did not detect possible differential migration between sexes, a commonly

recorded behavior among other species in the Tetraoninae (Seiskari 1962, Hoffman and Braun 1975, Schroeder 1985). Partial or complete separation of sexes during the winter has been documented for Blue Grouse (Marshall 1946, King 1971, Hines 1986), and appears to be related to migration patterns. Segregation of sexes for other grouse has been attributed to longer movements by females (Seiskari 1962, Weeden 1964, Hoffman and Braun 1975).

We monitored migration of Blue Grouse from 1981 to 1985 in conjunction with investigations of habitat use, food selection, and nutritional ecology during the winter in Colorado (Cade and Hoffman 1990, Remington 1990). Here, we report distances traveled, elevational changes, directional orientation, and chronology associated with migration. We test the hypothesis that distances and elevational changes between breeding and winter areas are equivalent for adult males and adult females. Movements and sex segregation on winter ranges and fidelity to winter areas are discussed as they relate to migration.

STUDY AREA AND METHODS

Blue Grouse were captured, banded, and radio-marked at Green Mountain (GM; 39°53′N, 106°20′W) and Whiteley Peak (WP; 40°18′N, 106°29′W), two distinct mountains located about 42 km apart in Middle Park, north-central Colorado. Elevations ranged from 2,390 to 2,863 m at GM and 2,500 to 3,075 m at WP.

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Both areas supported breeding and wintering Blue Grouse and included portions of the sagebrush (*Artemisia* spp.), quaking aspen (*P. tremuloides*), and Douglas fir (*Pseudotsuga menziesii*) vegetation types (Cade and Hoffman 1990). Low-elevation areas surrounding the study areas were predominantly sagebrush and hay meadows. Adjacent mountain ridges were forested with pure and mixed stands of quaking aspen, lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas fir. Timberline was from 3,350 to 3,500 m elevation.

Grouse were found by using tape-recorded calls (Stirling and Bendell 1966), by using trained pointing dogs (March–November), and by searching without calls or dogs (December–March). We captured 204 birds (GM = 60, WP = 144) with noose poles (Zwickel and Bendell 1967) between April 1981 and March 1985. Captured birds were classified to age and sex (Hoffman 1985), and marked with unique combinations of colored leg bands. Two age classes were recognized for analyses: juveniles (≤9 months) and adults (>9 months). Whenever possible, males were classified as territorial or nonterritorial (Bendell and Elliott 1967) and females as successful (hatched >1 egg), unsuccessful (nested but hatched 0 eggs), or nonbreeding (no known nest attempt).

Twenty-two males (20 adult, 2 juvenile) and 45 females (35 adult, 10 juvenile) were equipped with solar capacitor-assisted or lithium-battery-powered transmitters attached with a backpack harness (Brander 1968) or poncho collar (Amstrup 1980). We used a three-element Yagi antenna and portable receiver to locate radio-marked birds from the ground; each bird was located visually. Locations were recorded to the nearest 50 m as Universal Transverse Mercator (UTM) coordinates. Birds that remained on study areas were located at least once every two weeks. Birds that left study areas were located less frequently, depending on how far they moved and how accessible they were during winter.

Winter was defined as November through March. Winter areas of individual birds were delineated from locations (≥6) in conifer forests during this period. Breeding areas were defined by locations (≥4) from early April to mid-June for males, and late April to late June for females. We had fewer locations for some grouse that moved long distances to winter in remote areas. Numerous seasonal locations were not necessary to define long-distance migrations because movements between seasonal ranges were longer, were more unidirectional, and occurred at a faster rate of travel than movements within a seasonal range (Lance 1970, Sopuck 1979).

We defined migration distances for individual birds as the distance between bivariate medians of locations (*X* and *Y* UTM coordinates) at breeding and winter areas. Bivariate medians were computed following Berry et al. (1984). Elevational change was computed

as the difference between median elevations in breeding and winter areas. Multiresponse permutation procedures (MRPP; Biondini et al. 1988, Mielke 1991) were used to test null hypotheses of no distributional differences between sexes, season of capture, and study areas. We used Euclidean distances for MRPP statistics because of greater power to detect central tendency and dispersion differences between skewed distributions than statistics based on squared differences (Biondini et al. 1988). Medians and within-group statistics (average Euclidean distances) from MRPP were examined to determine whether differences were in central tendency or dispersion. Univariate and bivariate tests (distance and elevation change) were performed. Bivariate data were standardized by average Euclidean distance to remove effects of different measurement scales. Rao's spacing test for uniform, circular distributions was used to test for nonrandom directional orientation of movements (Bergin 1991).

Movements on winter areas were quantified by two Euclidean distance measures from MRPP: (1) average distance between all possible pairs of locations; and (2) average distance between sequential (ordered by date) locations. This approach avoids assumptions associated with bounding an area to estimate home range (White and Garrott 1990:177–178) and provides a distribution-free method for testing whether successive locations of an individual are serially independent (Mielke 1991). When grouse were located a number of times within a two-week period, we used only the first location in computations. Average distance measures describing winter areas were compared between sexes using MRPP.

Sex ratios in winter flocks (≥2 birds within 50 m) were tested for equality by using a permutation test for matched pairs based on a Euclidean distance statistic (Biondini et al. 1988, Mielke 1991). Each flock in which birds were identified to sex was considered a replicate. We used exact 2 × 2 chi-square contingency analyses (Berry and Mielke 1987) to test whether radio-marked adult males and females were found more frequently in flocks of the same sex versus flocks of both sexes. All statistical tests were made with the BLOSSOM software available from the National Ecology Research Center, U.S. Fish and Wildlife Service, Fort Collins, Colorado (Slauson et al. 1991. User manual for BLOSSOM statistical software. U.S. Fish and Wildl. Serv., Natl. Ecol. Res. Ctr. Unpubl. report).

Results

Movements.—Thirty-two radio-marked adult Blue Grouse were tracked from breeding to wintering (*n* = 21) or wintering to breeding areas (*n* = 11). Eight of 13 males and 6 of 19 females were followed in both spring and autumn migrations. Incomplete movements (not used in statistical analyses) were obtained for an adult
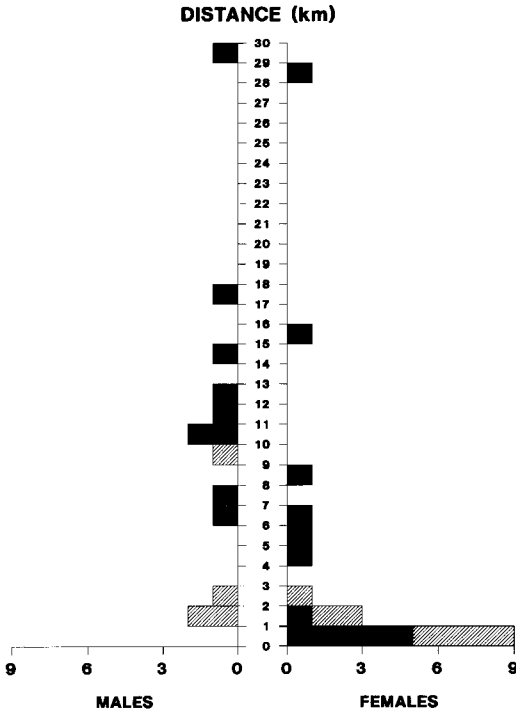
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DISTANCE (km)

Fig. 1. Distances between breeding and winter areas for 13 adult male and 19 adult female Blue Grouse radio-marked in spring (solid bars) and winter (hatched bars) at Green Mountain and Whiteley Peak, Colorado.

male that moved 7.0 km from GM before being harvested by a hunter in September and for an adult female that moved 12.0 km from WP before radio contact was lost in October. Twenty-one radio-marked adults (6 males, 15 females) provided no movement data because of death ($n = 15$) or loss of radio signal ($n = 6$). Radio-tracking success was independent of sex (exact 2×2 chi-square contingency test, $P = 0.400$). Movements of birds did not differ between study areas (males, $P = 0.881$; females, $P = 0.379$).

Males moved farther and gained more elevation than females ($P < 0.001$). The median distance moved was 10.5 km for males and 1.0 km for females (Fig. 1). Ten of 63 adult females and only 1 of 38 adult males banded in the spring were observed in the winter on the study areas, providing additional evidence that more females than males moved short distances (<3 km). The median elevational change between breeding and winter areas was 488 m for males and 122 m for females (Fig. 2). Elevation change varied less for males (average Euclidian dis-
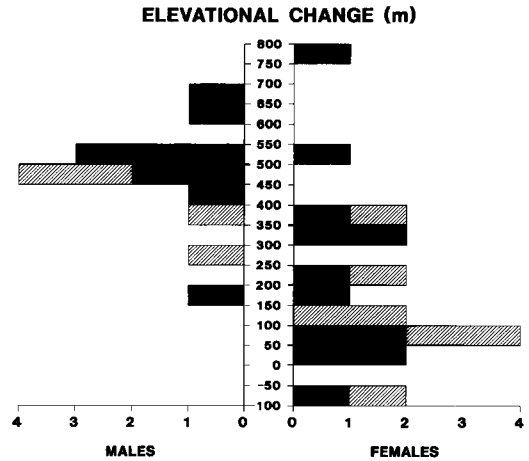
ELEVATIONAL CHANGE (m)

Fig. 2. Elevational changes between breeding and winter areas for 13 adult male and 19 adult female Blue Grouse radio-marked in spring (solid bars) and winter (hatched bars) at Green Mountain and Whiteley Peak, Colorado.

tance = 146 m) than for females (230 m). Long-distance migrants wintered at higher elevations ($n = 15$, median elevation = 3,160 m, range = 2,736–3,374 m) than birds that wintered on study areas ($n = 17$, median elevation = 2,865 m, range = 2,500–2,987 m; $P < 0.001$). Departing birds moved south and northeast ($n = 7$) from GM ($P = 0.001$) and east ($n = 8$) from WP ($P < 0.001$).

Males ($P = 0.006$) and females ($P = 0.052$) marked in winter moved shorter distances than those marked in spring. Consequently, we compared sexes by season of capture (Figs. 1 and 2). Spring-marked males ($n = 9$) moved farther and gained more elevation ($P = 0.003$) than spring-marked females ($n = 12$), whereas winter-marked males ($n = 4$) moved similar distances ($P = 0.182$) but gained more elevation ($P = 0.012$) than winter marked females ($n = 7$). Movements of spring-marked birds did not differ between study areas (males, $P = 0.651$; females, $P = 0.282$). A similar comparison was not made for winter-marked birds due to small sample sizes at GM.

Seven juvenile females were tracked from their first winter to first breeding areas. The median distance moved (0.6 km, range = 0.1–5.4 km) and elevational change (122 m, range = 0–360 m) did not differ ($P = 0.510$) from those of adult females marked in winter.

Timing of movements.—Eleven males abandoned breeding territories between 24 June and 27 July (median = 7 July). Five males located

every two weeks after leaving breeding areas traveled 2.6 to 13.9 km (median = 11.4 km) to summer areas, where they moved less than 0.5 km between successive locations from July through September, and then moved 0.9 to 4.5 km (median = 1.8 km) to winter areas. Three nonterritorial males left the breeding range in early July. Unlike territorial males, they made movements greater than 2 km between successive locations through summer. All radio-marked males occupied conifer forests after leaving breeding ranges, but did not arrive at the area where they wintered until early October to mid-November ($n = 10$, median = 14 October).

Females that wintered off study areas left later ($n = 6$, median = 11 August) than males, but departure dates were more variable (25 May–25 September). Successful females left later than unsuccessful or nonbreeding females. Most females (15/20) occupied vegetation types other than conifer forests during July through September. Females arrived at winter areas in early October to mid-November ($n = 16$, median = 23 October).

Winter home ranges and fidelity to winter areas.— We located 11 birds every two weeks throughout winter of which 5 made serially dependent ($P < 0.10$) movements (Table 1). The average distances among sequential locations did not differ ($P = 0.406$) between adult males (median = 148 m) and adult females (median = 127 m).

Five adult males and five adult females followed for two consecutive winters were found less than 0.4 km from where they wintered the previous year. Locations of four banded adult females observed in consecutive winters were separated by less than 0.3 km. Two adult females wintered 0.1 and 0.9 km from where they wintered as juveniles.

Sex composition in winter.—Excluding radio-marked birds, 57% of 205 grouse identified to sex (49 were unknown) at WP and 61% of 56 identified to sex (94 were unknown) at GM were females. Flocks with both sexes (50/69 at WP; 10/23 at GM) or females only (19/69 at WP; 12/23 at GM) were encountered most often. More females than males (median difference of 1 at WP and 2 at GM) were identified in flocks at both areas ($P < 0.001$). All four radio-marked adult males and 6 of 11 radio-marked adult females wintering on study areas were located a majority of time in flocks with both sexes (exact 2 × 2 chi-square, $P = 0.231$).

TABLE 1. Average distances for all sequential locations (by date) and for all pairwise locations for biweekly surveys of Blue Grouse during November through March, Middle Park, Colorado, 1981 to 1984.

Bird no.	n	Sequential distances (m)	All possible distances (m)	Serial agreement[a]	
				R	P
Adult males					
305	8	116	123	0.05	0.359
385	10	148	141	−0.05	0.605
397	8	154	163	−0.06	0.306
Adult females					
162	12	120	135	0.12	0.159
317	11	135	175	0.23	0.077
201	10	94	97	0.03	0.399
299	8	98	391	0.75	0.010
306	10	312	291	−0.07	0.691
359	12	109	144	0.25	0.028
367	11	195	359	0.46	0.004
371	5	152	300	0.49	0.029

[a] Serial agreement = 1 − (average sequential distance/average of all possible pairwise distances); P evaluated in multiresponse sequence procedure (Mielke 1991).

DISCUSSION

Movements of Blue Grouse between breeding and winter ranges are best described as an altitudinal (Marshall 1946, Wing 1947, Bendell 1955), seasonal, return migration (Baker 1978). Distances traveled varied among individuals from the same breeding population, but were within the range suggested by other studies (Mussehl 1960, Bendell and Elliott 1967, Zwickel et al. 1968, Hines 1987). The altitudinal change associated with migration was a function of the proximity of seasonal habitats; open habitats used for breeding occurred at lower elevations than conifer forests used in winter.

Populations occupying less than 10 km² of breeding range at GM and WP during April through July were occupying greater than 400 km² of winter range during November through March. Long-distance movements to winter areas were in directions that followed major ridges and avoided crossing extensive sagebrush rangelands. Birds did not necessarily move in the direction of nearest winter habitat. Zwickel et al. (1968) reported that Blue Grouse in north-central Washington bypassed suitable winter range during fall migration and dispersed over an area some 25 times as large as the breeding range where banded.

Blue Grouse can be characterized as differential, partial migrants, following terminology

of Terrill and Able (1988), because there were short- and long-distance migrants within the same population. Most short-distance migrants were females that were year-around residents of our study areas. These birds did not occupy the same seasonal ranges or habitat types throughout the year and, therefore, were not considered nonmigratory (Baker 1978). Short- and long-distance migrants have been observed in Spruce Grouse (*D. canadensis*) populations, but females moved greater distances than males (Herzog and Keppie 1980, Schroeder 1985).

Lower-elevation winter range that overlaps breeding range may be limited. Thus, in accordance with frequency-dependent selection theory (Lundberg 1987), it may be advantageous for many grouse to move longer distances to more abundant winter range at higher elevations. However, this theory does not account for differential migration of sexes. Longer movements by males are not due to lack of suitable winter habitat for males near breeding areas. Douglas fir stands used by 17 territorial males in spring were used by other males in winter. Males and females were observed in the same stands and trees in winter (Cade and Hoffman 1990), and fed in similar size and species of conifers (Remington 1990).

Three hypotheses have been advanced to explain differential migration of sexes in birds (Myers 1981, Gauthreaux 1982, Ketterson and Nolan 1983, Smith and Nilsson 1987). According to the "dominance hypothesis," if one sex is dominant in intersexual competition for resources during the nonbreeding season, the subordinate sex should move farther to obtain requisite resources. We do not know whether male Blue Grouse are dominant over females. However, assuming body size predicts dominance hierarchies in birds (Gauthreaux 1982, Smith and Nilsson 1987), female Blue Grouse, which weigh 26 to 30% less than males (Boag 1965), should move farther, which is inconsistent with our observations.

The "body-size hypothesis" suggests that if individuals of one sex are smaller and, consequently, less likely to survive harsh winters, members of this sex should migrate to milder climates. This hypothesis can be considered as being consistent with our observations and those of Hines (1987) in that females tended to winter at lower elevations where weather conditions presumably were less severe. Both male and female Blue Grouse appear to be well adapted

to cold climates (Pekins et al. 1992), and major climatic differences would be necessary to afford any advantages for females to winter at lower elevations. We doubt such differences existed over the altitudinal range where males and females occurred during winter. Furthermore, the mechanism proposed to maintain size-related variation in migration is differential fasting endurance during severe winter storms when food is temporarily unavailable (Ketterson and Nolan 1983). We doubt that food is ever unavailable to Blue Grouse during winter storms because they feed on conifer needles, which are not subject to burial by snow as are many other food sources.

The "arrival-time hypothesis" suggests that if one sex experiences greater intrasexual competition for breeding territories or mates, members of this sex should winter closer to breeding areas to arrive earlier. For Blue Grouse, this hypothesis would predict shorter migrations for males, because males arrive on breeding areas several weeks earlier than females (Bendell and Elliott 1967, Zwickel and Bendell 1972, Jamieson and Zwickel 1983). However, the assumption that early arrival of males indicates competition on breeding ranges is greater among males (Jamieson and Zwickel 1983) than among females (Hannon et al. 1982, Bergerud and Butler 1985) may be misleading.

Yearling (9–15 months old) male Blue Grouse rarely acquire territories and are not believed to breed (Jamieson and Zwickel 1983, Jamieson 1985, Lewis and Jamieson 1987). Prior experience and living long enough to occupy vacancies created by deaths of territorial adults probably are more important in territory establishment than early arrival on breeding range. In contrast, yearling females frequently nest and compete for space among adult females (Hannon et al. 1982, Bergerud and Butler 1985). Therefore, early arrival on the breeding range may have greater benefits for yearling females than yearling males. Juvenile females that winter where breeding and winter range overlap may have an advantage in acquiring nest sites as yearlings. They would be exposed to territorial males sooner and would have earlier opportunities to acquire space among adult females than juveniles that wintered farther away.

Constraints on movements during summer differ between sexes, with males having the least to gain by remaining near breeding areas. Densities of grouse increase on breeding range dur-

ing June and July as juveniles are added to the population, and habitat quality decreases due to desiccation of herbaceous vegetation. Losses to predation may increase as density of birds increases (Taylor 1976, Bergerud and Butler 1985). Therefore, it may be advantageous for some birds to move elsewhere, provided suitable habitat exists and the costs of getting there are not prohibitive (Ketterson and Nolan 1983). Plant phenology is delayed at higher elevations and lush herbaceous vegetation develops in subalpine forests coincident with desiccation at lower elevations. Since male Blue Grouse provide no parental care for chicks (Bendell and Elliott 1967), they can leave breeding ranges. Females have greater parental investment in their offspring and, initially, must remain on breeding ranges to allow chicks to obtain sufficient invertebrate foods. As chicks mature and shift to a herbaceous diet (King and Bendell 1982), females become less constrained to breeding ranges and some leave.

Most females, including those without broods, remained in aspen or mountain-shrub habitats throughout summer. The few found in conifer habitats during summer did not winter at those locations. Males were found exclusively in conifer habitats after leaving breeding range, but they used different areas in summer than in winter. Previous studies (Marshall 1946, Bendell and Elliott 1967, Zwickel et al. 1968) have assumed that males and unsuccessful females arrived on winter areas during late summer or early fall. Our findings suggest that male Blue Grouse occupy spatially distinct summer and winter areas, and do not arrive on winter areas until mid-October, about the same time as females.

We agree with the conclusions of Hines (1986) that Blue Grouse are relatively sedentary during winter and that there is only partial segregation of sexes on winter ranges. However, we found no evidence to suggest birds associated with individuals of the same sex as reported by Hines (1986).

Our results are incomplete in that access problems prevented us from intensively monitoring grouse that wintered at high elevations in subalpine forests (Cade and Hoffman 1990). We also recognize that our findings may only pertain to areas where breeding and winter ranges overlap. Males and females may make similar movements or females may move farther than males where seasonal ranges do not

overlap. Movements by adult females appear to be a retracing of their first winter to breeding area movement, a pattern documented for Spruce Grouse (Herzog and Keppie 1980, Schroeder 1985). However, understanding how migration patterns are established requires additional information on movements of birds as juveniles and yearlings relative to movements as adults.

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