MIGRATION IN A LOCAL POPULATION OF SPRUCE GROUSE

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ABSTRACT.—Migration of Spruce Grouse was observed in southwestern Alberta from 1970 to 1975 in a population of grouse that included both migratory and resident birds. Migrants comprised 39% of this population; these individuals migrated each year regardless of weather conditions. Migration occurred from mid-February to late May and from early September to mid-December. More females than males were migratory and females migrated longer distances. Distance between breeding and wintering sites ranged from 0.5 to 9.5 km.

Survival and reproductive success was similar for migrant and resident grouse during the study. Migration was generally related to the dispersal history of birds as yearlings. Yearlings that dispersed in spring tended to establish migratory patterns by returning to winter sites used as juveniles. Why these birds did not remain on summer areas for the winter, as did resident Spruce Grouse, is uncertain. The quality of winter habitat may be an important factor in establishment of migration; further investigation is required to determine the qualitative aspects of the breeding and wintering habitat of Spruce Grouse.

Migration has been reported for some species of the Tetraonidae, most notably Blue Grouse (*Dendragapus obscurus*; Anthony 1903, Marshall 1946, Wing 1947, Bendell 1955, Zwickel et al. 1968) and North American ptarmigan (*Lagopus* spp.; Weeden 1964, Irving et al. 1967, Hoffman and Braun 1975). Sage Grouse (*Centrocercus urophasianus*) undertake long seasonal movements but only in certain regions (Dalke et al. 1963, Eng and Schladweiler 1972, Wallestad 1975, Beck 1977). Sharp-tailed Grouse (*Pedioecetes phasianellus*) and Greater Prairie Chicken (*Tympanuchus cupido*) may travel long distances (Hamerstrom 1949, Hamerstrom and Hamerstrom 1951) although such movements occur only sporadically and have been difficult to document. Most reports suggest that changes in diet or food availability during winter may cause such movements, yet evidence is lacking.

This paper is the first report of migration in Spruce Grouse (*Canachites canadensis*). Observations were made during studies of population size and movements of this species in southwestern Alberta (Keppie 1975, Herzog 1977). We report the proportion of a local population that was migratory, evaluate characteristics of seasonal travel, and investigate a possible relationship between the occurrence of migration and earlier dispersal of young birds.

STUDY AREA AND METHODS

Studies were conducted in the eastern foothills of the Rocky Mountains from May 1970 through September 1973 (Keppie 1979), April through October 1974, and February through December 1975 (Herzog and Boag 1978). The main study area encompassed 555 ha adjacent to Gorge Creek (50°39'N, 114°39'W), 27 km west of Turner Valley, Alberta. Forest cover was predominantly lodgepole pine (*Pinus contorta*) with scattered clumps of white spruce (*Picea glauca*) and poplar (*Populus* spp.). The study area was contiguous with habitat suitable for grouse except for a 1-km wide area along the east side.

Grouse were censused regularly on the primary study area with the aid of pointing dogs. Birds were captured with extendable snare poles (Zwickel and Bendell 1967) and individually marked with colored leg bands. Essentially all birds (95%) were marked. Grouse were separated into three age-classes: juvenile (0–9 months of age; from hatching until 1 April), yearlings (9–21 months), and adults (greater than 21 months). Thus, yearlings were birds entering their first breeding season and were distinguishable from adults by tail feather patterns (Zwickel and Martinsen 1967) and shape of primaries until 14 months of age. Monthly we searched outside the main study area to obtain additional observations of migratory birds and distances they had travelled. Four migratory females were also radio-marked and monitored in 1975, using techniques described by Herzog (1979). Minimum daily movements were the distances between initial sightings on successive days. Contingency and goodness of fit chi-square tests, *t*-tests, *G*-tests and rank tests (Sokal and

Rohlf 1969) were used to evaluate statistical differences.

DEFINITIONS

We distinguished between dispersal and migration. "Dispersal" was the movement by juveniles in autumn from brood range to winter range and/or in spring, as yearlings, from winter range to breeding range. Thus, dispersal ended at 10 to 13 months of age as birds established breeding areas for the first time. Individuals undertaking these movements, emigration and immigration from and to the study area, are termed "dispersers."

We define "migration" as the movement between separate breeding and wintering areas by birds older than 14 months of age. Migrants were present in the study area only in summer (summer migrant) or only in autumn and winter (winter migrant). Conversely, residents were grouse that remained on the study area throughout the year. Residents included both local birds that had not emigrated as juveniles or yearlings and birds that remained sedentary after immigrating their first breeding season.

RESULTS

POPULATION STRUCTURE

The Gorge Creek study area was used by Spruce Grouse as summer and winter habitat. Of those birds living on the area, only a portion (61%) were resident throughout the year; 39% were migrants (Table 1). An additional 24 birds of uncertain status (transients) observed infrequently were omitted from this analysis. Some of these individuals were probably migrants, as they passed through the area at the time of migration, presumably enroute to summer and winter areas outside the study area. Thus the proportion of migrants in the local population was a minimal estimate. Significantly more females than males were migratory ($\chi^2 = 17.04$, $P < 0.001$). Most of the migrants were present only during winter, 72% (13/18) of the males and 76% (35/46) of the females. The major impact of migration on the study area population, therefore, was a net influx of birds for the winter. During summer, these migrants occupied breeding ranges outside the study area, whereas other migrants (summer) entered the area in spring and joined the resident cohort for the breeding period. Migrants were thus observed on the study area for only a few months each year (winter or summer) for at least two successive years. The complete

TABLE 1. Frequency of migrant and resident Spruce Grouse censused throughout the year at Gorge Creek, southwestern Alberta, 1970–1973.

	Males	Females	Total
Migrants	18 (22)[a]	46 (55)	64 (39)
Residents	63 (78)	38 (45)	101 (61)
Total	81	84	165[b]

[a] Percent of total birds in parentheses.
[b] Excludes an additional 24 "transients."

seasonal absence of certain migrants was confirmed by radio-tracking (Herzog 1977).

TIMING OF MIGRATION

Spring and autumn migration occurred over several months each year. Departure and arrival dates were only approximate because of the census methods we used. We estimate, however, only a 7- to 10-day discrepancy between our estimates and the actual dates. Migrants present in winter left our study area for other breeding ranges between 13 February and 11 May. No differences in timing were recorded for birds of different ages. Males migrated earlier than females (rank test, $U = 425$, $P < 0.001$): median dates for final sightings were 1 March for 11 males and 11 April for 40 females. Our last record for a male that only wintered on the study area was 19 March, at which time only 10% (4/40) of the females had departed. Sixty-three percent (25/40) of final sightings of females occurred between 8 and 25 April.

Arrival of migratory males for the summer (n = 3) coincided with the departure of males present only in winter (n = 11, rank test, $U = 29$, $P < 0.05$). All migrant females arriving for the summer (n = 17), however, were first observed between 28 April and 30 May (median date 15 May), after the departure of most winter migrants (median date 11 April, n = 40, rank test, $U = 672$, $P < 0.001$). Arrival of summer-only females coincided with the emigration of overwintered juveniles and immigration of new yearlings of both sexes to the study area (Keppie 1975, Herzog 1977).

Autumn migration occurred between 17 August and 31 December. Two males departed from the study area on 18 October and 12 November whereas the median date for males arriving for winter was 24 October (n = 14). The median date for females (n = 17) leaving the study area was 23 September, compared to 14 October (n = 53) for those returning for winter (rank test, $Z = 4.01$, $P < 0.001$). Eleven (79%) of the 14 arrival dates of males in autumn occurred af-

TABLE 2. Distances between summer and winter sites and direction from the study area to winter ranges used by Spruce Grouse in southwestern Alberta, 1970–1975.

Bird	Sex	Distance (km)[a]	Direction (summer to winter)
1[b]	F	5.7	NW
2[b]	F	2.6	NW
3[b]	F	5.4	W
4	F	2.2	SW
5	F	7.0	S
6[b]	F	2.0	NE
7	F	1.3	S
8	F	8.9	N
9	F	9.5	W
10	M	1.5	E
11	M	0.5	SW
12	M	1.9	W
13	M	3.0	NW

[a] Straight-line distance.
[b] Denotes a bird that was radio-marked.

TABLE 3. Dispersal histories of migrant and resident Spruce Grouse (sexes combined) based on juvenile grouse of known fate hatched in 1970, 1971, and 1974; southwestern Alberta.

Dispersal history	Number of grouse		
	Migrate	Do not migrate[a]	Total
Did not disperse[b]	0 (0)[c]	21 (100)	21
Immigrated in autumn[d]	0 (0)	15 (100)	15
Emigrated in spring[b]	14 (67)	7 (33)	21
Dispersed in autumn and spring[b]	19 (59)	13 (41)	32

[a] Birds represented in rows 1 and 2 (n = 36) became residents. Those of rows 3 and 4 (n = 20) did not return to the study area; they either died after emigration or became resident elsewhere.
[b] Raised on the study area.
[c] Percent of total birds in parentheses.
[d] Raised outside the study area.

ter the female median arrival date, thus males may settle on their winter ranges somewhat later than females.

FEATURES OF TRAVEL

Spruce Grouse travelled variable distances during migration and a preferred direction was not evident (Table 2). Mean straight-line distance travelled by migratory females and males differed, 5.0 km ± 1.0 SE, (n = 9) and 1.7 ± 0.5 km, (n = 4), respectively ($t = 5.3$, $P < 0.01$). Daily travel by radio-marked females during spring and autumn migration was strikingly directional (Herzog 1977). By using a test for randomness, which required a minimum of six travel locations (Anje 1968), we determined that autumn migration of Female 1 (Table 2) was highly directional ($A = 465$, $P < 0.05$). This was the only radio-marked female for which we had obtained the required number of locations for this test. Topographic features did not influence significantly the direction of travel because radio-marked females directly crossed ravines and ridgetops as Lance (1970) noted for Blue Grouse. Two females monitored during both spring and autumn migration selected the same routes during both seasons.

Mean daily distance travelled by radio-marked migrant females during spring was 1.2 ± 0.2 km (n = 7); mean daily distance in autumn was similar, 1.4 ± 0.2 km (n = 11). These rates of travel greatly exceeded ($t = 4.8$, $P < 0.01$) daily movements of radio-marked resident females which were 0.11 ± 0.02 km (n = 21) in spring and 0.15 ± 0.02 km (n = 29) in autumn. During the week before the onset of spring migration, however, mean daily movements of radio-marked migrant females were significantly less than those of radio-marked resident females (0.05 ± 0.01 km, n = 14 vs. 0.1 ± 0.01 km, n = 36, $t = 2.12$, $P < 0.05$).

Most travel by radio-marked females during spring and autumn migration appeared to occur during early morning as birds had moved beyond radio-tracking range by mid-morning. On three occasions when activity of these females was monitored before sunrise, movement began at daybreak. The signal was abrupt and rapid, indicating flight, and radio contact with the bird was quickly lost. We recorded only short distances between mid-morning and evening locations (0.1 ± 0.03 km, n = 4) so birds may have mostly rested and fed in the afternoon. Radio-marked females were observed to travel alone in spring and autumn; those followed during autumn migration had not raised broods. Generally, migrant females that raised broods during summer moved after brood break-up and apparently migrated alone. Two brood females, however, presumably left the area with their intact brood (17 August), and four migrant females arrived on the study area with juveniles, at which time both the female and young exhibited typical brood behavior.

SURVIVAL AND REPRODUCTION

We compared migrant and resident Spruce Grouse to determine how survival and reproductive success differed between them. Only adult grouse were used for survival calculations (1970–1973) in order to exclude possible mortality of yearlings during dispersal. No difference existed ($P > 0.05$) in survival between sexes for either migrants or residents; hence, data for both sexes were combined. Annual survival of migrants (75%) was not significantly less ($\chi^2 = 1.64$,
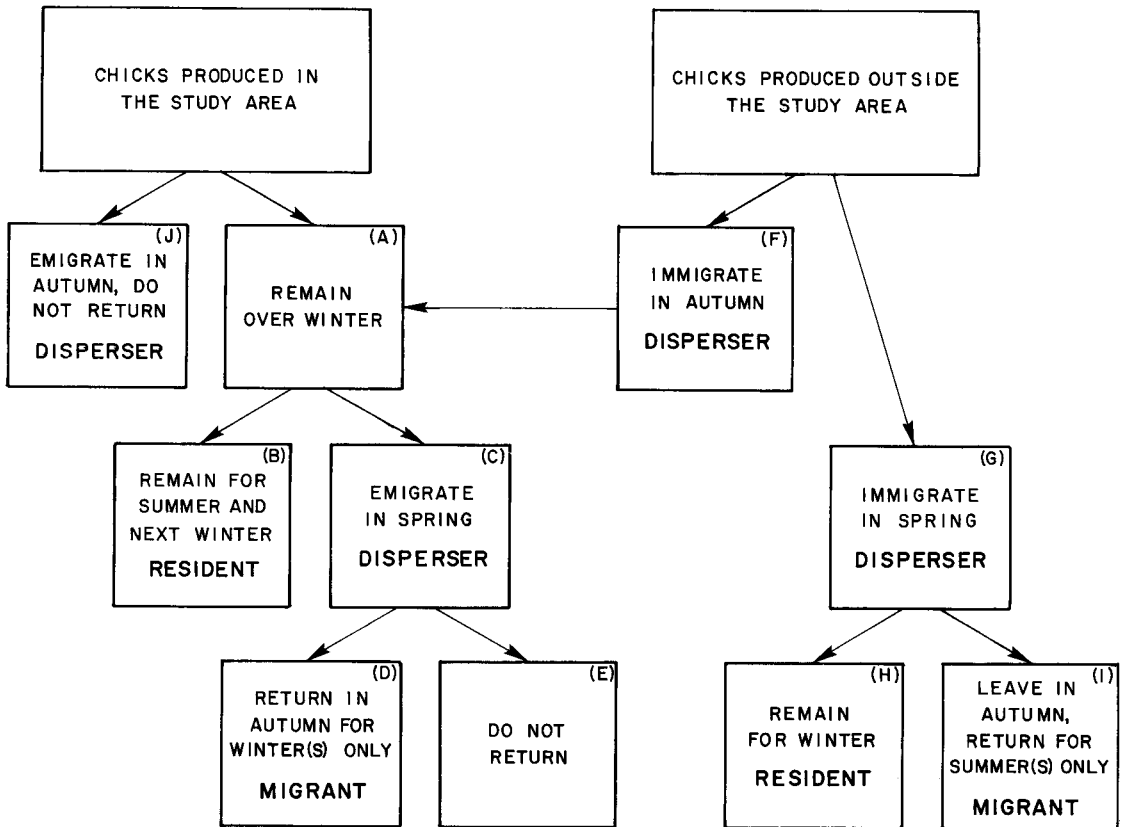
FIGURE 1.   Flow diagram of the development of Spruce Grouse migration from dispersal history. All types have occurred in southwestern Alberta, 1970–1975. Letters identifying boxes are used in the text.

$P > 0.05$) than survival of residents (83%). Twenty-six percent (31/118) of the females on the study area at breeding time (1970–1973) were migrants. Minimum proportions of migrant and resident females breeding (observed either on a nest, with a brood patch, or with a brood) were 68% (21/31) and 78% (68/87), respectively ($\chi^2 = 0.84$, $P > 0.05$). Similarly, the proportion of migrants with broods (55%, 17/31) was not different ($\chi^2 = 1.43$, $P > 0.05$) from that of residents (40%, 35/87). Resident females, however, contributed substantially more to total annual production than did migrant females; among 118 females tallied over four breeding periods (1970–1973), 74% were resident and they produced 67% (35/52) of the broods.

ACTIVITY OF MIGRANTS ON BREEDING RANGE

Male and female Spruce Grouse returned to the same small area each spring and autumn, showing strong fidelity to a specific locality (Keppie and Herzog, unpubl. data). During the period of spring migration, resident adults of both sexes were territorial and maintained exclusive areas (Herzog and

Boag 1978). Migrants returning in the spring quickly re-established territories adjacent to known neighbors. The best evidence of this process was from a female that returned to an area where all resident females were radio-marked. Her territory was vacant even though it was bounded on three sides by those of other adult females. Daily movements of radio-marked migrant females in the first week after arrival on breeding ranges were not different from those of resident females during this time (81 ± 12 m, n = 14 vs. 112 ± 17 m, n = 30, $t = 1.1$, $P > 0.05$). Four migrant females readily responded with aggressive calling to a playback of female calls soon after their arrival in spring and thus indicated their territorial status in similar fashion to that of residents (Herzog and Boag 1977).

MIGRATION AND DISPERSAL

Because not all adult grouse were migratory, we speculated that migration might be affected by an individual's dispersal history. Thus, we classified juveniles of known fate (resident or migrant) from 1970, 1971 and 1974 into four categories: did not disperse;

immigrate in autumn; emigrate in spring; disperse in spring and autumn (Table 3). No differences existed between sexes in the proportions migrating ($G = 1.0$, $P > 0.05$); therefore, data on both sexes were combined. The number of migrants and residents used in these analyses was less than the total number of birds on the study area (Table 1) because the dispersal history of adults present at the start of the study was unknown. The various pathways of dispersal by juvenile grouse leading to occupation of wintering and breeding sites as migrants or residents are presented in Figure 1.

Overall, migration frequencies were not independent of dispersal history (4×2 contingency, Table 3, $G = 33.9$, $P < 0.001$). Forty-two juveniles born on the study area also overwintered there (Box A, Fig. 1). Fifty percent (21/42) of these birds did not disperse in spring (Table 3); all subsequently became residents (Box B, Fig. 1), hence, not migrating after their yearling summer. Of the 21 locally raised juveniles that overwintered and then dispersed in spring (Box C, Fig. 1), 67% became migrants and returned for the next winter (Table 3; Box D, Fig. 1). The other 33% did not return to the study area (Table 3; $\chi^2 = 0.8$, $P > 0.05$) and presumably either died or became residents outside the study area (Box E, Fig. 1). Nearly all juveniles (95%, 76/80, 1970–1972) produced on the study area that dispersed in autumn did not return as yearlings (Box J, Fig. 1); four which did were only seen as transients.

Forty-seven juveniles immigrated to the study area in autumn (Box F, Fig. 1), remained over winter (Box A, Fig. 1) and were subsequently of known fate. Thirty-two of these birds dispersed a second time the next spring (Box 3, Fig. 1); 59% (19/32, Table 3) became migrants, returning to winter on the study area (Box D, Fig. 1). The remaining 41% did not return to the study area (Table 3; Box E, Fig. 1). The frequency of migration (59%) of juveniles raised outside the study area that dispersed again in spring did not differ ($\chi^2 = 1.1$, $P > 0.05$) from the frequency of migration (67%) of juveniles raised in the study area. Therefore, an important variable in the development of migration was the timing of dispersal; 62% (33/53) of the cohorts that emigrated in spring also became migrants, with little difference ($P > 0.05$) between whether they had been produced inside or outside of the study area. In contrast, autumn dispersal alone did not appear related to migration; autumn immigrants that did not emigrate

subsequently in spring always became residents (Table 3, Box B, Fig. 1). The difference between the frequency of migration for birds that dispersed only in autumn (immigrants, 0%, 0/15) versus only in spring (locally raised, 67%, 14/21) was significant ($G = 11.7$, $P < 0.001$).

Information on the migratory fate of spring immigrants to the study area (Box G, Fig. 1) contradicts our previous results. We expected that these individuals, counterparts of spring emigrants from our area, would show a high rate of migration similar to emigrants. However, 68% (13/19) of spring immigrants did not return to former winter areas but became residents on the study area following their yearling summer (Box H, Fig. 1). The remaining six immigrants migrated off the study area for winter (Box I, Fig. 1). The difference between the frequency of migration among spring immigrants (32%, 6/19) and spring emigrants (62%, 33/53) was significant ($\chi^2 = 4.1$, $P < 0.05$).

DISCUSSION

Other reports of grouse migration have indicated that entire local populations undertake seasonal movements except, perhaps, in years of mild weather when some birds remain on summer ranges (Dalke et al. 1963, Weeden 1964, Hoffman and Braun 1975, Beck 1977, Herzog 1980). Only part of the Spruce Grouse population we studied was migratory each year even with major differences in weather patterns (i.e., timing of permanent snow cover, snow depth and loss of snow cover in spring) that have been reported to be significant by other workers. Travel during migration appeared uninterrupted by weather conditions and indeed some individuals began moving during the winter. Given the time span over which migration was initiated, it also seemed unlikely that weather patterns had much influence on the start of migration.

Spruce Grouse did not change their status (migrant or resident) with age during the time limits of our study. Thus, migration in this population appeared to be an example of partial migration (Baker 1978), and results fit Baker's familiar-area hypothesis (p. 515) since adults began to migrate in their second autumn (as yearlings) via calculated movements to a winter area they had known as juveniles. According to Baker's summary, partial-migrant species should exhibit migrant:non-migrant ratios that are less for males than females; our results (Table 1) show such a relationship (0.3 for males and

1.2 for females). Bellrose (1972:238–239) listed a diverse range of species as partial migrants and he conveyed the common view that partial migration probably represents an initial step away from a permanent resident to a totally migratory species. We cannot comment on Spruce Grouse in this regard but note that this species is also partially migratory in New Brunswick (Keppie, unpubl. data).

Migrants of both sexes presumably left winter ranges early enough to allow sufficient time for establishment of spring territories. The amount of time needed for establishment appears to be short, as migrants quickly asserted their dominance in areas of past breeding, with territorial behavior being similar to resident birds (Herzog and Boag 1978). Migrating male Spruce Grouse arrived on breeding ranges earlier than females, similar to Blue Grouse (Bendell and Elliott 1967, Zwickel 1972). Thus, Spruce Grouse also illustrate Baker's "category *a*" of removal migrants (1978:323–328), one characteristic of which is earlier migration of males than females. Baker (1978) attributed earlier migration of males to a greater investment in establishment and defense of a breeding area and he used selected passerines for support. For Spruce Grouse, however, there is no evidence that females invest any less energy than males into acquisition of a breeding area given their territorial intrasexual activity (Herzog and Boag 1977, 1978). We found, nevertheless, that male Spruce Grouse began advertising breeding territories approximately 6 to 7 weeks before the estimated median date for first egg laying (Keppie and Herzog, unpubl. data) versus two to three weeks for females.

We hypothesize that migration in Spruce Grouse is a consequence of dispersal to a breeding site in spring. The difference between sexes in proportion of migratory individuals (females > males) paralleled the greater rates of dispersal by females (Keppie 1979) and could reflect the different reproductive habits of yearlings. Most yearling females probably breed (Keppie 1975, Herzog 1977); dispersal pressures appear relatively strong and serve to reduce winter concentrations of females. After dispersal in spring, yearling females establish exclusive breeding areas similar to adults (Herzog and Boag 1978). Conversely, although we lack direct evidence of non-breeding in yearling males, generally they display infrequently and occupy large areas adjacent to territorial adults (Herzog and Boag 1978). Delayed

breeding among yearling males (Wittenberger 1978) could mean that there is in effect less pressure to emigrate in spring from winter sites and thus may account for the low proportion of male migrants. As competition for breeding space appears to be a proximate factor causing the emigration of yearlings of both sexes (Herzog and Boag 1978), territoriality could be the indirect, but initial cause of migration.

We do not believe that migration, as we have analyzed it, affects the actual selection of a breeding site by Spruce Grouse because it begins only after a yearling has established its life-long breeding location. We detected no significant differences between breeding success of migrants and residents. Proper analyses, however, probably require knowledge of life-time reproductive output and early detection of non-breeding individuals.

The primary question remains: why should a yearling, after settling in a general area and often breeding in a very localized territory in summer, have returned (migrated) in autumn to the site of its previous winter? Perhaps good quality winter habitat was spatially restricted; home ranges and daily movements were minimal in winter and birds were concentrated in certain areas. Total density of grouse in winter was at least as great as that in summer. If the high degree of overwinter survival recorded for this local population (Keppie 1979) reflects the condition of the study area habitat, migration may have conferred an increased probability of survival to some individuals as hypothesized by Baker (1978). Possibly spring immigrants that subsequently stayed for winter (not conforming to our hypothesis) also did so because the study area was premium habitat. Therefore, we speculate that migration depends on initial dispersal as a yearling to breeding habitat, which in turn is unsuitable wintering habitat. This assumes that yearlings assess breeding range for winter features learned as juveniles. We did not measure food resources or other qualitative habitat characteristics necessary to test these speculations. The fact that summer ranges of migrants were used at least partially by other birds in winter also appears contrary to our ideas on the establishment of migration. Marked birds should be followed throughout the year to determine if individual seasonal ranges of migrants differ in quality (e.g., nutrition, structure) and whether ranges of resident grouse exhibit seasonal variations similar to those of migrants.

Dispersal of animals may be genetically influenced (e.g., Myers and Krebs 1971) and we question whether migration is an inherited trait in a species such as Spruce Grouse, which exhibits partial migration. The appearance of this trait would initially require the occurrence of spring dispersal. One analysis would be a test between the rate of juvenile emigration in spring and subsequent proportion of migratory individuals of the same cohort. We documented a substantial difference in emigration rates between two spring seasons (Keppie 1979), but although the subsequent proportion of migrants was greater for the cohort with higher emigration, the difference was not significant. Mortality of potential migrants may have weakened the comparison and we predict that with sufficient years of data, high years of spring emigration will be followed by high proportions of migrants in those cohorts.

ACKNOWLEDGMENTS

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