

VARIATION IN ALTITUDINAL MIGRATION, WINTER SEGREGATION, AND SITE TENACITY IN TWO SUBSPECIES OF DARK-EYED JUNCOS IN THE SOUTHERN APPALACHIANS

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ABSTRACT.—We studied altitudinal migration of Dark-eyed Juncos (*Junco hyemalis*) over 5 yr in the Great Smoky Mountains to test hypotheses concerning ecological determinants of winter distribution and distance traveled in migration. We individually marked 1,832 juncos belonging to two subspecies that occur together in winter in the foothills: Carolina Juncos (*J. h. carolinensis*) that breed in high-elevation spruce-fir forests locally and Northern Juncos (*J. h. hyemalis*) that are latitudinal migrants.

Carolina Juncos spend the winter at higher elevations than Northern Juncos. Above 600 m elevation in the drainage that formed the study area, juncos were 76% Carolinas in winter on average. Carolina Juncos show winter assortment by sex across altitudes that parallels latitudinal assortment found among Northern Juncos by Ketterson and Nolan (1976, 1983). Most Carolinas wintering above 600 m elevation and within 20 km of ridgeline breeding habitats were males (77%). Farther downslope most juncos were Northerns (83%) and most Carolinas were females (80%). Some males are resident year-round in the breeding habitat, while others migrate through the entire altitudinal range. Differential altitudinal migration by the sexes of Carolina Juncos and altitudinal segregation of the two races in winter were variable between years; smaller and competitively subordinate classes of juncos were better represented at higher elevations in a milder winter. This variation and the patterns of survival and ranging revealed by recapture data were consistent with the hypothesis that social dominance in competition for food significantly affects winter distribution.

Migration and choice of wintering ground in this system are flexible responses that are probably malleable by pressures created by behavioral interactions with other birds in competition for winter food and breeding territories as well as by physiological constraints. Although three hypotheses developed in studies of latitudinal migration predict the basic patterns of winter assortment by subspecies, sex, and size, the balance of selective forces is likely different for these altitudinal migrants. *Received 14 August 1984, accepted 17 April 1985.*

SEASONAL movements of animals in response to changing environmental conditions are of widespread importance in structuring natural communities. Understanding the maintenance of migratory systems requires knowledge of the proximate ecological and physiological factors that prompt seasonal movement and determine the degree of movement (Dingle 1980, Keast and Morton 1980, Myers 1981, Gauthreaux 1982, Ketterson and Nolan 1983). Undoubtedly, escaping the frigid temperatures and relative food scarcity of high-latitude winters is the major impetus to most autumnal avian migration, and broad indicators of ecological conditions (e.g. temperature and daylength) trigger physiological responses resulting in migration (Rowan 1925, Wolfson 1942, Farner 1955, Berthold 1975, Meier and Fivizzani 1980). However, migratory effort (distance migrated) often varies considerably within a population, suggesting that

adjustments are made by individuals that may be sensitive to variable costs and benefits of migration. In some populations, migratory effort varies among age and sex classes of individuals, and this results in geographic segregation across the winter range (Nice 1937; Lack 1944; King et al. 1965; Ketterson and Nolan 1976, 1983; Mueller et al. 1977; Myers 1981). Such variation raises questions concerning ecological and behavioral constraints determining migratory effort.

Altitudinal migrations by Carolina Juncos (*Junco hyemalis carolinensis*), the southern Appalachian subspecies of Dark-eyed Junco (*J. h. hyemalis*), provide an opportunity to study variability of seasonal movements. These Carolina Juncos breed in high-altitude coniferous forests of the southern Appalachian Mountains; in winter they retreat to lower altitudes and form large flocks with Northern Juncos (*J. h.*

hyemalis), latitudinal migrants that have returned from breeding in Canada and the northern United States (Miller 1941, Stupka 1963, Rabenold 1978). Altitudinal zonation of climates and habitats provides a vertical array within a few kilometers comparable to that encountered in thousands of kilometers of latitudinal travel. We ask whether patterns of variability in migratory effort in this system are parallel to those of latitudinal migrants, and we address three hypotheses formulated in the study of latitudinal migration: (1) physiological tolerances that vary systematically within and between populations produce patterns of variation in migratory effort and geographical segregation (Calder 1974; Ketterson and Nolan 1976, 1983); (2) behavioral differences among individuals concerning dominance in competition for resources in winter produce patterns of variation in migratory effort (Lack 1966; Fretwell 1969; Ketterson and Nolan 1976, 1983; Gauthreaux 1978); and (3) competition in the breeding season for territories and mates contributes to the advantage of residency in and proximity to the breeding habitat, thereby contributing to variation in migratory effort (Kluyver and Tinbergen 1953; von Haartman 1968; Ketterson and Nolan 1976, 1983; Myers 1981).

All of the above hypotheses predict that Carolina Juncos will winter at higher altitudes than Northerns and that female Carolinas will migrate farther downslope than males. Hypotheses (1) and (2) predict year-to-year shifts in distribution with changes in temperature or food availability. Only hypothesis (3) explicitly predicts nonmigration by some individuals. Social dominance of hypothesis (2) could also result in variability in ranging and survival on the winter ground. To assess the hypotheses, we investigated patterns of differential and partial migration among Carolina Juncos, altitudinal distribution in winter of the two races of juncos, distributions of sizes of individuals with altitude in winter among Carolina Juncos, and patterns of site tenacity in winter and summer. We draw these patterns from a 5-yr study of 1,832 individually marked juncos of both subspecies in a river drainage of the Great Smoky Mountains. A wide range of seasonal responses is shown in the local population, from year-round residency in the breeding habitat by some males to migration far downslope to warmer habitats by others.

STUDY AREA AND METHODS

Carolina Juncos occur throughout the southern Appalachian Mountains from Georgia to West Virginia. They breed in high-altitude forests, generally above 1,200 m elevation, dominated by red spruce (*Picea rubens*) and Fraser's fir (*Abies fraseri*) or by spruce, hemlock (*Tsuga canadensis*), and northern hardwoods such as yellow birch (*Betula lutea*) and American beech (*Fagus grandifolia*). They breed on territories defended by mated pairs packed as densely as 30 in 10 ha, nesting on or near the ground beginning in April. In October, most Carolina Juncos retreat downslope below 1,000 m elevation to winter in the considerably warmer climates of southern hardwood forests and clearings. However, some individuals remain in the spruce-fir forests of the highest ridges (up to 2,025 m on Clingman's Dome in the Great Smoky Mountains), enduring frigid temperatures, high winds, and prolonged snow cover. During the winter in the low valleys, Carolina Juncos mingle in large flocks of up to 100 individuals with Northern Juncos. Beginning in early March in some years, Carolina Juncos that wintered in the low elevations move back into the high-elevation breeding habitat (Miller 1941; Tanner 1958; Hostetter 1961; Stupka 1963; Rabenold 1978, 1984; Kendigh and Fawver 1981; pers. obs.).

In 1979 we began a study of juncos in the Oconaluftee River valley of the Great Smoky Mountains National Park in North Carolina. Within park boundaries, this drainage flows from spruce-fir forest at Indian Gap (IG; elevation 1,607 m) southeast to the park entrance (PE), a distance of 19 km (elevation 610 m), at the edge of the town of Cherokee (Fig. 1). From 1980 to 1984 we captured and banded 1,832 Dark-eyed Juncos of both races at 22 sites along this 1,000-m elevational gradient and at 4 sites outside the park boundary (UN and RE in Fig. 1; 22 km from IG).

As attested by their flora, the upper elevations of the study area have essentially a Canadian climate. Newfound Gap, in the lower part of the Carolina Juncos' breeding range at 1,538 m elevation, has an average January temperature of -2.7°C , while the town of Cullowhee (24 km from the main study area) at 668 m has a mean January temperature of $+4.7^{\circ}\text{C}$. Daily minimum temperatures do not diverge as much as maxima [data from National Oceanic and Atmospheric Administration (NOAA) and National Park Service]. Prolonged snow cover and high winds undoubtedly make winter in the breeding habitat even more stressful, but detailed climatological data are not available. The winter of 1980–1981 was colder than the winter of 1981–1982. Using data from Oconaluftee (620 m elevation) and Newfound Gap (1,538 m) within the study area, mean January temperatures were lower in 1981 than 1982 at both high and low elevations (-5.7°C vs. -2.3°C for Newfound Gap, -1.3°C vs. -0.1°C for Oconaluftee; National Park Service data). In addition, the temperature at New-

found Gap remained below freezing on 20 days in January of 1981 but only 10 days in January 1982. For 7 weather stations at low elevations within 30 km of Oconaluftee, temperatures were 2.7°C colder in January and 4.2°C colder in February of 1981 compared with 1982. January and February of 1981 were 4–7°C colder than average in this area (NOAA data).

Methods.—We made 6 winter banding trips to the study area in 5 yr: 16 days in March 1980, 17 days in January–February 1981, 12 days in March 1981, 18 days in January 1982, 10 days in March 1982, and 18 days in January–February 1984. We also performed censuses in the breeding habitat in 1980 (17 days in May–June), 1981 (10 days in June), 1982 (10 days in June), 1983 (5 days in June), and 1984 (10 days in July). For winter banding, we set up large ground-level feeders stocked with millet 2–4 months before banding began. We have no indication that birds caught at these feeders were a nonrandom sample of the population, but some bias in captures remains a possibility (e.g. Weatherhead and Greenwood 1981). Because of the paucity of other sparrows in the area, we attracted few birds other than juncos. Two feeders at each site were separated by 200–400 m at the following elevations: UN, RE, PE, and BC sites at 610 m; OC at 640 m; TS and HU at 685 m; SM at 730 m; KE at 850 m; BF at 1,220 m; LG at 1,520 m; and IG at 1,610 m (see Fig. 1). The last three sites fell within the breeding habitat of Carolina Juncos. Spring censuses were done most intensively within a 2-km radius of Indian Gap (IG) and Luftee Gap (LG) but also were performed in 1980 and 1981 along a trail between Clingman's Dome and Peck's Corner—a linear distance of 20 km (Fig. 1)—using playbacks of recorded junco vocalizations.

We captured juncos with mist nets and walk-in Potter traps at the feeding stations. We roughly standardized our efforts by visiting each site twice during each trip with nets and traps. Success in capturing birds varied widely depending on weather conditions; cold snowy days sometimes produced 100 captures within a day at low elevations, while warm, clear days could pass without a single capture. We gave each Carolina Junco an individually unique set of colored plastic leg bands, measured its wing-chord length, and recorded the amount of white coloration in the outer tail feathers (rectrices). Northern Juncos were banded only with numbered aluminum U.S. Fish and Wildlife Service bands. In 1980 and 1984 we also weighed all birds to the nearest 0.5 g with a hand-held 50-g Pesola scale. The two subspecies are easily distinguishable in the hand by beak color, plumage, and size (Chapman 1932, Miller 1941, Peterson 1947). We have never seen a junco that we would call a Northern in the breeding season in the Smokies, nor have we seen juncos we would call Carolinas in Indiana in winter. We were unable to age birds in midwinter because skull ossification seemed complete by January. We kept records of all recap-

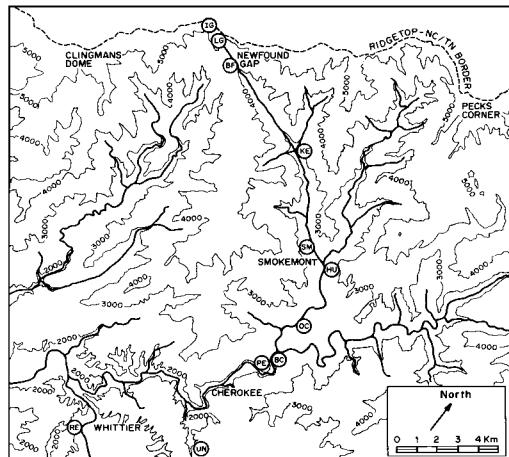


Fig. 1. Topographic representation of the study area in the Great Smoky Mountains National Park, North Carolina. Light solid lines with numbers represent 1,000-ft contour intervals. Dark solid lines are major streams; study sites (letters within circles) are arranged along the Oconaluftee River, which flows from Newfound Gap (at top) through the town of Cherokee, North Carolina (at bottom). The highest site—1,607 m elevation at Indian Gap (IG)—occurs at the top of the ridge along the North Carolina-Tennessee border.

tures and resightings of marked birds for both subspecies over the years, and a chronological record each day. Because our primary objective in this phase of the study was to sample winter distributions, we usually netted at a site until 75% of the birds captured at the end of a visit were marked.

Carolina Juncos are very subtly sexually dimorphic in size and plumage, and this dimorphism differs from that of the Northern Junco in that males are more similar to females in plumage except for the tail (Miller 1941, this study). We have developed criteria for sexing these birds from a reference set of individuals caught mainly during the breeding season (see Appendix 1).

RESULTS

Altitudinal variation in winter density.—Both Northern and Carolina juncos are more abundant in the study area in winter below 850 m than above. Relatively few individuals spend the winter in the breeding habitat (roughly above 1,200 m). It has not been uncommon to mark over 100 individuals at a single site within 2 weeks at the lower elevations; no more than 24 have been marked at high-elevation sites with the same effort. Over the 4 winters

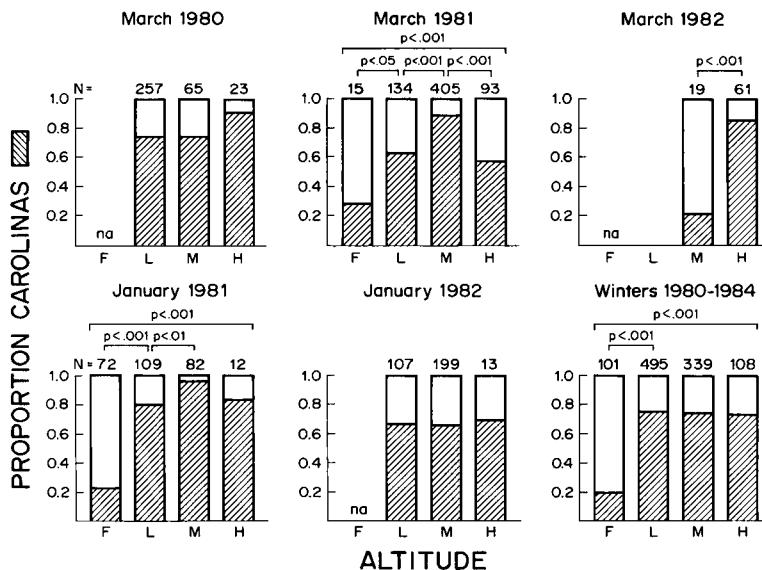


Fig. 2. Patterns of subspecies distribution with altitude during different banding visits. Each histogram depicts proportions of the two subspecies found at particular time at each of four altitudinal classes of sites: F = far from breeding habitat at low elevation (sites UN and RE); L = low elevation within 20 km of breeding habitat (PE, BC, and OC at 610–640 m); M = middle elevations (HU, SM, and KE at 685–850 m); and H = high elevation within breeding habitat (BF, LG, and IG at 1,220–1,610 m). Values at tops of bars are sample sizes of birds caught; significance levels of comparisons indicated by brackets result from Chi-square tests. Data are pooled from March 1980, January 1981, January 1982, and January 1984 (not shown separately) to produce the "all winters" analysis on the bottom right (see text for explanation). "na" indicates no attempt made at those sites at that time.

we averaged 72 ± 42 birds marked at each site per winter below 850 m but only 14 ± 10 at high-elevation sites.

Using the Jolly-Seber mark-recapture estimator of total population size (Caughley 1977), January populations averaged 170 ± 101 below 750 m (SM, HU, OC, and PE) and 15 ± 7 in the breeding habitat above 1,500 m (LG and IG). These calculations indicate that on average we banded only about half of the birds visiting feeders at low-elevation sites but nearly all those at high elevations. Breeding habitat is a small area compared to wintering habitat, so that a small proportion of the junco population spends the winter in the high-altitude breeding habitat; the majority probably winter more than 10 km from the breeding habitat at elevations from 600 to 800 m.

Winter distribution of subspecies.—Winter flocks within 20 km of breeding habitat were composed mostly of Carolina Juncos. In the Oconaluftee drainage within park boundaries, 76% (1,257) of the 1,654 juncos we banded in January and March were Carolinas (Fig. 2), al-

though the composition varied somewhat from year to year. In January 1981, 87% were Carolinas ($n = 203$), while in January 1982 at the same sites, the figure was 66% ($n = 319$, $P < 0.001$, χ^2 test; Fig. 2). As previously shown, the winter of 1982 was milder than that of 1981. Birds visited feeders less frequently in 1982, and although we have no quantitative estimates, natural food abundance seemed higher in that year. Outside of park boundaries, farther than 20 km from breeding habitat, wintering juncos were mostly Northernns: 83% ($n = 97$) in January of 1981 and 1984 at UN and RE sites. At our highest sites, within the breeding habitat, few Northern Juncos occurred in winter [32 of 108 birds (30%) in the winters of 1980–1984 at sites BF, LG, and IG; Fig. 2].

Timing of spring migration varied from year to year. In March 1980, the density and stability of Carolina Junco populations suggested that the birds were still settled on their winter ranges. On the same calendar dates in 1981, movement among low-elevation sites was relatively high, as we detected individuals mov-

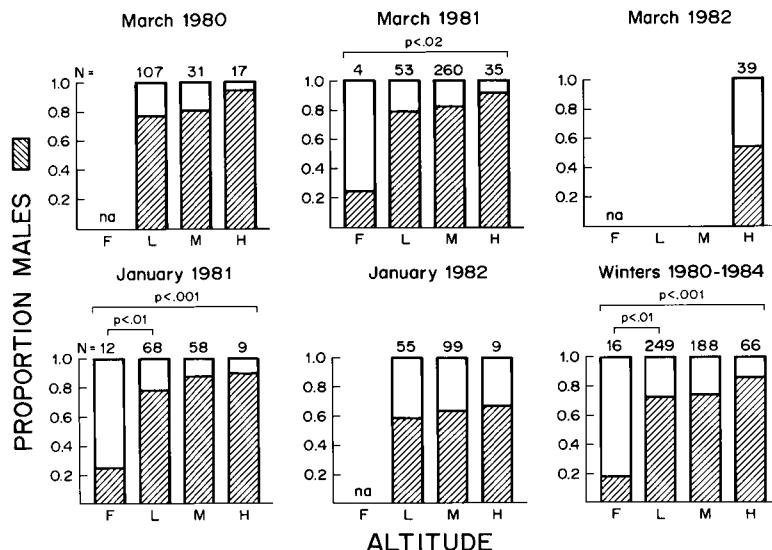


Fig. 3. Patterns of distribution of the sexes of Carolina Juncos with altitude during different banding visits. Each histogram depicts the sex ratio found at a particular time at each of four altitudinal classes of sites: F = far at low elevation; L = low-elevation; M = middle-elevation; and H = high-elevation (see Fig. 2). Values at tops of bars are sample sizes; significance levels of comparisons indicated by brackets result from Chi-square tests. Data are pooled from March 1980, January 1981, January 1982, and January 1984 to produce the "all winters" analysis on the bottom right.

ing several kilometers up- and downslope within 24 h. Also, many unmarked birds were singing territorial songs at high-elevation sites where the few overwintering birds had been marked in January. We even detected a banded migrant establishing a breeding territory near IG; this bird wintered at the lowest elevation near PE and was found on the same breeding territory again in June. In spite of the obvious return of Carolinas to the high altitudes at this time, we also captured many Northerns there (Fig. 2), although we have never found one in the Smokies in summer. In the warmer year of 1982, altitudinal migration was nearly complete in March when we arrived. Few birds were at the low elevations, and the Northern Juncos were mostly gone from the high elevations as well (Fig. 2). In 3 yr at the same calendar time (2–16 March) we witnessed a range of states in the study population from stability on the winter grounds (1980) to beginning migration (1981) to nearly complete evacuation of the winter range (1982).

An altitudinal gradient in subspecies composition of junco populations was apparent in January 1981, when we sampled the sites farthest from breeding habitat (Fig. 2). Even with-

in park boundaries, comparing low- (610–640 m) and middle-elevation (685–730 m) sites, we found significant altitudinal differences in the proportion of juncos that were Carolinas (80% vs. 96%; $P < 0.01$, χ^2 test; Fig. 2). We found no such differences in January 1982 when the winter was milder. Northern Juncos were better represented in the drainage overall in this winter than before, as shown above.

Pooling data from March 1980 (because no hint of incipient migration was seen) with the January data of 1981, 1982, and 1984, an average view of the relative winter distribution of the two subspecies can be formed (Fig. 2, bottom right). Carolina Juncos predominated in this drainage in winter, mostly staying within 20 km of breeding habitat. Northern Juncos were more abundant at greater distances from the mountaintops.

Sex-specific migratory effort in Carolina Juncos.—We captured and sexed 896 Carolina Juncos in the Oconaluftee drainage above 610 m, in January and March visits in the 4 yr; 687 (77%) were male. In the breeding habitat, we sexed 149 Carolinas in the nonbreeding season; 122 (82%) were male. Excluding March data of 1981 and 1982, when return migration to the

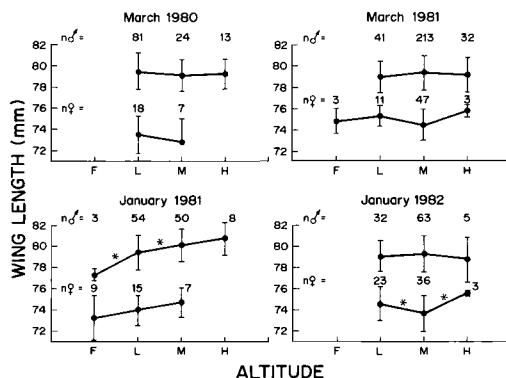


Fig. 4. Patterns of size distribution with altitude among Carolina Juncos, separated by sex. Each set of values records mean size (\pm SD) and sample size for measurements made during one trip at sites differing in altitude and distance from breeding habitat (altitude codes as in Fig. 2). Asterisks indicate significant differences ($P < 0.05$, t -tests) in mean sizes between sites.

breeding habitat was underway, 56 of 66 Carolinas sexed during winter in high-elevation breeding habitat were male (85%). Very few females appear to spend the winter in breeding habitat. At sites outside the park boundary (RE and UN), distances of 22 km, females outnumbered males in winter: of 20 Carolinas sexed, 16 (80%) were female (Fig. 3).

As shown for subspecies composition, the composition of Carolina Junco populations by sex at a particular altitude can vary significantly from year to year. In the cold January of 1981, 83% ($n = 135$ sexed) of Carolina Juncos were male in the Oconaluftee drainage while in the milder January of 1982, at the same sites, only 63% ($n = 163$) were male ($P < 0.001$, χ^2 test). This difference was apparent even at the highest elevations (Fig. 3).

Carolina Juncos moving first into the summer range were mainly males. Of 35 Carolinas sexed at LG and IG in March 1981, 32 (91%) were males—a composition indistinguishable from the winter sex ratio. Densities of birds (Jolly-Seber estimates averaged 35 ± 12 birds at each site—3 times the winter values), the arrival of a bird banded 20 km downslope in the previous winter, and the resurgence of territorial male singing strongly indicated the beginning of breeding territory establishment. In contrast, on the same calendar dates in 1982 the winter grounds already had been abandoned

and females had arrived in sufficient numbers in the breeding habitat to produce a nearly 1:1 sex ratio—18 of 39 sexed birds were female at IG and LG. This arrival of females in the first week of March was fully 6 weeks before the earliest recorded egg-laying of Carolina Juncos (Tanner 1958, Stupka 1963).

In summary, sex ratios of Carolina Juncos in winter were very biased toward males within 20 km of breeding habitat (above 610 m elevation) in the Oconaluftee drainage. Farther away, the ratio was female-biased (Fig. 3, bottom right). Assuming no radical departure from a population sex ratio of 1:1, this indicates longer-distance altitudinal migration by females. Almost all birds resident in the breeding habitat were males. Sex ratio in the study area was variable on an annual basis, probably because of environmental variability.

Altitudinal distribution of sizes during winter.—Carolina Juncos are larger than Northerns, and males of both subspecies are larger than females (Chapman 1932, Miller 1941, Ketterson and Nolan 1976, pers. obs.). Because Carolinas winter higher than Northerns and male Carolinas winter higher than females, there is a general trend for larger birds to spend the winter at higher altitudes than smaller birds. Wing chord is a good predictor of body mass in many small birds (Connell et al. 1960, Helms et al. 1967, Nolan and Ketterson 1983). For a sample of 200 Carolina Juncos caught in the winter of 1980, wing chord (unflattened) and body mass were positively correlated ($P < 0.001$, ANOVA; see Appendix 2). We therefore used wing chord as a measure of body size. Overall, there was no strong trend in size distribution with altitude within the sexes of Carolina Juncos (Fig. 4). During only one capture interval, the cold January of 1981, did Carolina Juncos possibly assort by size. At this time, male wing chords at the distant sites averaged 77.3 ± 0.2 mm SD ($n = 3$), at low sites 79.4 ± 1.6 mm ($n = 54$), at middle sites 80.1 ± 1.6 mm ($n = 50$), and at high-elevation sites 80.8 ± 1.6 mm ($n = 8$; Fig. 4). However, analysis of variance showed no significant pattern for either sex in any year.

Patterns of winter site tenacity and ranging: mark-recapture data.—We recaptured hundreds of previously marked individuals. From 1,279 Carolina Juncos banded in the nonbreeding season, 538 recaptures resulted (counting multiple recaptures of the same individual). Only 41 recaptures of 38 individuals occurred at sites

TABLE 1. Site tenacity of Northern (N) and Carolina (C) juncos.

Time scale	Number banded with potential for recapture ^a	Number recaptured at same site	Significance of N-C difference in proportion recaptured (χ^2 test)
A. Within March 1981	382 C 105 N	205 C (54%) 35 N (33%)	$P < 0.001$
B. January–March 1981	183 C 82 N	85 C (46%) 8 N (10%)	$P < 0.001$
C. Within winter months*	542 C 212 N	87 C; 61 (70%) same feeder 37 N; 23 (62%) same feeder	NS

* See text for explanation.

other than the banding site, but 30 of these recaptures were of birds caught during March 1981 when migration was beginning and winter ranges apparently were breaking down. On a finer temporal scale, 729 Carolinas were banded in March 1980, January 1981, and January 1982, and 89 were recaptured at a later date in the same month. Only 2 of these were recaptured at a different site (sites average 2 km apart) and only 26 of the remaining 87 birds (30%) were captured at the other paired feeder within the same site (average 300 m distant). Carolina Juncos did not seem to wander extensively on the winter ground, although our ability to detect movement away from a site was very limited.

Recapture data are most extensive for 1981 and allow a comparative assessment of site tenacity of the two subspecies within and between months. The crudest analysis pools all recaptures in 1981 of birds banded in that year. We banded 565 Carolina Juncos and 187 Northern Juncos in January–March 1981 at times when a subsequent visit to that site made recapture there possible; we recaptured 290 Carolinas (51%) and only 43 Northerns (23%; $P < 0.001$, χ^2 test). This measure of site tenacity cannot distinguish mortality from emigration from the site, but it suggests either that Carolinas survive better than Northerns or (if mortality could be assumed negligible in the span of a few weeks) that Carolinas have more localized movements in winter at these sites. Considering only mark-recapture data within March 1981—a time when migration upslope seemed to be starting—Carolinas banded at an initial visit to a site were more likely than Northerns to be recaptured later (Table 1A). If we consider only January–February banding and March recapture in 1981, isolating between-month site

tenacity on the winter ground, Carolinas again appeared to have greater site tenacity (Table 1B). Although migration had just begun in 1981, it is possible that the apparently low site tenacity of Northerns simply reflects the beginning of migratory movement in March. To allow potential separation of mortality from ranging patterns or emigration on the winter ground, we can focus on recaptured birds (survivors) and ask what tendency they show to wander from the location of first banding. Within the winter months of March 1980 and January of 1981, 1982, and 1984, Carolinas were as likely as Northerns to be recaptured and as likely to be recaptured at the feeder opposite the one where they originally were caught (Table 1C); we detected no difference between Carolinas and Northerns in probability of recapture or in ranging.

Carolina males and females differed slightly in site tenacity. Females banded in March 1981 were as likely as males to be recaptured in the same month at the site where originally banded (Table 2A). Females banded in January–February 1981 were as likely as males to be recaptured at the same site in March (Table 2B). However, considering only recaptured survivors, females were more likely than males to move in winter months between paired feeders at the site where they were banded (Table 2C). This pattern held even when only low-elevation sites were considered. While female and male Carolina survivorship may be similar on the winter ground, males probably have smaller ranges than females.

To compare Carolina Junco site tenacity at different elevations, we used the Jolly-Seber mark-recapture analysis that produces a value p , which is an index of the probability of an individual surviving and not emigrating be-

TABLE 2. Site tenacity of male (M) and female (F) Carolina Juncos.

Time scale	Number banded with potential for recapture ^a	Number recaptured at same site	Significance of M-F difference in proportion recaptured (χ^2 test)
A. Within March 1981	223 M	123 M (55%)	NS
	45 F	27 F (60%)	
B. January–March 1981	117 M	59 M (50%)	NS
	32 F	12 F (38%)	
C. Within winter months ^a	313 M	56 M; 45 (80%) same feeder	$P < 0.05$
	94 F	31 F; 16 (52%) same feeder	

^a See text for explanation.

tween captures. We were unable to use this calculation in other analyses because of insufficient sample sizes for female Carolinas and for Northerns. The value of p , in spite of its description, has an indefinite maximum (Caughey 1977). Calculating p for the interval January–March in 1981 and 1982, we found that for sites where samples were sufficient to permit the calculation, values were consistently higher for the high-elevation sites (Table 3). It is possible, however, that low-elevation values were depressed by the beginning of migration in 1981. We detected no difference in movement between feeders for males at high and low elevations, nor any pattern of site-tenacity variation among males of different sizes.

Site fidelity between years and seasonal movement.—Individual Carolina Juncos return faithfully to particular ranges in both summer and winter after migratory absences. However, we are not confident that our censuses are exhaustive and so will not attempt to estimate survival. In winter of 1981, 1982, and 1984 we recaptured 66 individuals that had been marked the winter before. Fifty-two (79%) of these were recaptured at the same site where originally banded, while only 14 were recaptured at different sites. Among these 14, 6 had returned to sites higher than previously and 8 were lower. All of the 21 birds banded in winter in breeding habitat that were recaptured in a successive winter were recaptured at the site of banding (Table 4A). During breeding-season censuses, we resighted 29 Carolina Juncos that were censused in the previous summer. In all cases but one, birds were located on the same breeding territory as in the previous year (24 males, 5 females; Table 4B). The one bird that changed territories between summers was female; she had moved approximately 6 km. Each summer

we have censused extensively around Indian Gap, Luftee Gap, and Newfound Gap; in 1981 we censused an estimated 510 birds between Clingman's Dome and Peck's Corner using playbacks of territorial song. This census technique was much more effective for males than for females, although we often recorded pairs of birds responding together. It is not likely that the apparently high breeding territory fidelity is an artifact of censusing only where birds had been found before.

Some Carolina Juncos are clearly site-attached, year-round residents in the breeding habitat; these birds are nearly all males. Only 9 females (of 55 Carolinas—16%) were captured in January within the breeding habitat, and although 3 of these were recaptured at the same sites the following March, none were seen in the breeding season. However, of 15 males banded in breeding habitat in January of 1981 and 1982, all were recaptured at the same site in March. Over 5 yr we have banded 164 Carolina Juncos in the breeding habitat in January or March, and 57 of these have been resighted in the breeding season. All resightings have

TABLE 3. Site tenacity of Carolina Juncos at high and low elevations, measured by Jolly-Seber p (tendency to survive without emigration) for January–March 1981 and 1982. The difference between high- and low-elevation values is significant at $P = 0.03$, Mann-Whitney U -test.

Low-elevation sites	Jolly-Seber p	High-elevation Sites	Jolly-Seber p
PE81	0.36	LG81	1.25
OC81	0.83	IG81	1.13
HU81	0.74	LG82	6.71
SM81	0.93	IG82	1.25

TABLE 4. Site fidelity of Carolina Juncos between years and between seasons.

Time scale	Number recaptured or resighted		Number at same site as previously
A. Winter-winter	66	All elevations	52
	21	Breeding habitat	21
B. Summer-summer	24	Males	24
	5	Females	4
C. Winter-summer	57	Breeding habitat	57

been within 200 m of the original banding site (Table 4C). This pattern, combined with the extremely high site fidelity of birds during and between winters and summers, indicates that males wintering in the spruce-fir forests are in fact permanent residents on year-round ranges. To illustrate, 10 males have been captured and seen at the same locations near Indian Gap for two successive years, summers and winters.

In contrast to these individuals resident in the breeding habitat, we located 6 breeding males that had traversed the length of the Oconaluftee drainage in the course of spring migration. In 1981, between Indian Gap and Peck's Corner along the crest of the ridge, we found birds that had been banded at each of the major low-elevation sites during the previous winter (PE, BC, OC, HU, and SM). Distances traveled between winter and summer ranged from 19 to 10 km. Clearly, a range of individual tactics exists, from year-round residency on a small range in the breeding habitat to seasonal migration that encompasses the full extent of the population's range.

DISCUSSION

Dark-eyed Juncos in this study showed a clear pattern of altitudinal assortment in winter that is similar to geographical assortment by latitudinal migrants: male Carolina Juncos winter higher and nearer the breeding habitat than females. In addition, members of the Carolina subspecies winter higher than Northern Juncos. Moreover, these patterns are flexible since composition of wintering junco populations at a particular altitude by subspecies, sex, and size is variable from one year to the next, apparently depending on environmental conditions.

The variability in seasonal timing of spring migration that we have witnessed over 3 yr establishes that this facet of an individual's mi-

gratory response is not strictly controlled by simple photoperiod response or an inexorable endogenous clock. Carolina Juncos are not extreme "instinct migrants" (Berthold 1975). Behavior of individuals varies widely even within categories of subspecies, sex, and size; some large male Carolinas are resident in the breeding habitat and some migrate considerable distances. Site tenacity of individuals varies among subspecies and sex classes, suggesting different survival or ranging behavior on the winter grounds. These results establish the likelihood that migratory effort and choice of wintering site are flexible, adaptive individual responses; we may reasonably proceed to consider in turn the three subsidiary hypotheses given at the outset concerning possible competitive and physiological determinants of migratory effort.

Does physiology determine migratory effort?—Larger-bodied birds should be better able to withstand the stress of cold temperatures and food shortage that are more likely at high altitudes (Kendeigh 1969a, b; Calder 1974; Calder and King 1974; Carey et al. 1978; Weathers 1980). Laboratory studies have shown that male White-crowned Sparrows (*Zonotrichia leucophrys*) can endure cold and fasting for longer periods than the smaller females, and the argument has been made that this difference contributes to differential migration and patterns of male-biased sex ratios at high latitudes in winter in some migratory species (Ketterson and Nolan 1976, 1978; Ketterson and King 1977; Dolbeer 1982). However, male and female Dark-eyed Juncos do not differ significantly in rate of overnight weight loss (Ketterson and Nolan 1978) or in fasting endurance (Stuebe and Ketterson 1982). Furthermore, among latitudinally migrating juncos, although males winter north of females, no size pattern is evident among males and smaller juveniles that winter north of same-sex adults (Nolan and Ketterson 1983).

Among Carolina Juncos, some evidence is consistent with the physiological hypothesis. Since Carolina Juncos are dimorphic, differential migration results in larger-bodied birds at higher elevations. In a harsh winter (1981), smaller Northerns and female Carolinas were more poorly represented at middle altitudes. However, there was only a weak suggestion of segregation by size with altitude among Carolina males. The fact that probability of recapture was indistinguishable in this study between male and female Carolinas, and between males of different sizes, argues that once birds settled onto the winter range, body size did not subsequently lead to differential mortality. Patterns of size assortment by Carolina Juncos on the winter range likely result mainly from differential migration of the sexes rather than differential mortality of smaller birds. However, characteristics other than hardiness can vary with size, most notably aggressive dominance. A clear evaluation of the hypothesis that physiological tolerances determine migratory effort and are responsible for assortment of size, sex, and subspecies classes on the winter ground will not be possible until measurements of physiological condition are made while controlling for other factors.

Does social dominance determine migratory effort?—Larger individuals are dominant over smaller in contests for food in many studies of passerine aggressive interactions, and in dimorphic species males are generally dominant over females (Thompson 1960; Fretwell 1969; Ketterson and Nolan 1976; Balph 1977, 1979; Baker and Fox 1978; Gauthreaux 1978, 1982; Ketterson 1979). In preliminary aviary studies we have found that male Carolina Juncos are clearly dominant over females and that Carolinas, even females, are dominant over Northerns regardless of size (Wiedenmann and Rabenold in prep.). Other studies also have found patterns of interracial dominance in juncos and measurable effects on feeding efficiency (Millikan et al. 1985). Because interracial and intersexual dominance patterns can cut across size categories, and because we found size rank does not correlate well with dominance rank, predictions of the physiological hypothesis can be decoupled from those of the social dominance hypothesis.

Aggressive dominance in competition for food probably can produce survival advantages, especially if dominants directly parasit-

ize the food-finding abilities of subordinates (Baker and Fox 1978, Kikkawa 1980, Smith et al. 1980, Baker et al. 1981, Barnard and Sibley 1981, Pulliam and Millikan 1982, Czikeli 1983). We have also studied the effects of dominance on diet among Northern Juncos in aviaries and found that subordinates in flocks feed less efficiently and on poorer-quality foods than do dominants; subordinates in flocks shift their diets away from preferences established in isolation (Langen and Rabenold in prep.). Clearly, there are regular patterns in dominance interactions among juncos, and social dominance has strong potential for affecting the energy budgets of individuals.

Given the background available from studies on aggressive behavior in juncos, one would predict that if food limitation were the most important stress factor associated with wintering at high altitudes, then male Carolinas would be better able to compete for scarce food and females would do better to migrate. Avoidance of competition with dominant males has been proposed to explain the longer-distance migrations of female juncos that migrate latitudinally (Balph 1975, Ketterson and Nolan 1976). Aggressive interactions between males and females in competition for food could force subordinate females to leave the breeding habitat in the autumn, create a centrifugal effect in flock structure, and perhaps ultimately force females to range more widely in search of food on the winter ground.

Results of this study are consistent with the hypothesis that competition with males favors longer-distance migration by females. Most female Carolina Juncos migrate well away from the breeding habitat to areas where their principal competitors are subordinate Northern Juncos. Female Carolinas and Northerns were more common in the male Carolina-dominated Oconaluftee drainage in the mild winter of 1982 than in the harsher winter of 1981. Milder conditions in that year could have ameliorated competition between dominant Carolina males and subordinate females and Northerns. However, temperature data alone cannot conclusively indicate the strength of potential competitive effects; abundance of food is probably important as well. It is also plausible that reduced cold stress simply allowed smaller juncos to winter at higher altitudes or dominants to use feeding stations less, regardless of competitive interactions.

Recapture data also point to the potential importance of competitive interactions organized by social dominance in structuring winter populations. Probability of recapture was indistinguishable for male and female Carolinas in 1981, suggesting equal survivorship. Equal minimum survivorship also was found for the sexes of wintering Northern Juncos in Indiana and South Carolina by Ketterson and Nolan (1982). However, in our study female Carolinas seemed to have larger ranges on the winter ground than males, which is consistent with the possibility that competition with males makes females peripheral members of flocks and affects their movements. Our data suggest that Northern Juncos might have either lower survival or larger ranges in winter on the study area. This could be due to their smaller body size and consequent physiological frailty or to competitive inferiority to Carolinas. Clearly, more detailed study of winter ranges and agonistic behavior is required to adequately test the possibility that social dominance structures junco populations.

Does competition for breeding site determine migratory effort?—If large Carolina males are dominant over all other classes of juncos in the Oconaluftee drainage, and if there are few competitors of other species, why should they remain in the breeding habitat over winter? Remaining on a familiar area could enhance survival, or permanent residency could enhance reproductive success (Ketterson and Nolan 1976, 1983; Myers 1981). In the latter case, perseverance on one's breeding territory year-round could be considered an extension of reproductive effort if it enhances mate attraction or hastens breeding and so allows multiple clutches. Ample observational and experimental evidence suggests that prior occupancy is an advantage in aggressive conflicts (Waser and Wiley 1979, Wiley 1982, Yasukawa and Bick 1983). Males already entrenched on territories early in spring may have an advantage in mate attraction and pair formation because of their enhanced ability to defend their territories (Gauthreaux 1982). This is especially plausible because female Carolinas arrive so early in the spring, apparently on the heels of early male returnees, more than a month before egg-laying begins.

Studies of sex differences in dispersal by young birds have found males less likely than females to move far from the natal area (Baker

and Mewaldt 1978, Greenwood et al. 1979, Greenwood 1980). In addition, males are more likely to return each breeding season to the same territory (Berndt and Sternberg 1969, Harvey et al. 1979). As territory founders and defenders, males generally may be under selective pressure to remain as near as possible to places where they are likely to breed in order to reap the benefits of site-dependent dominance. In this light, residency within a flexible migratory system is analogous to natal philopatry and site fidelity in nonmigratory species. Early territory establishment could give resident males a head start in breeding, and this helps explain one end of the range of variable migratory tactics in this population, one not easily explained by other hypotheses.

CONCLUSIONS

It is difficult to rank the predictive power of multiple hypotheses that have coincident major predictions. The main patterns detected in this study—sex and subspecies assortment on the winter ground—are consistent with all three hypotheses considered. Moreover, interpretation of such naturally occurring patterns is plagued by a common problem: if the explanatory perspective is one of adaptation, then one expects the patterns to be the result of past adjustments that erase traces of the pressures that produced them (Connell 1980). In spite of these problems of interpretation, the variability we observed in the basic patterns of migration and choice of winter grounds does allow a glimpse of underlying mechanism. The range of behaviors found in this study is not plausibly explained by physiology or winter dominance alone. The most likely benefits to males resident in the high-altitude breeding habitat are ones of prior occupancy of territory and a head start on breeding.

The two major alternatives to the winter-competition hypothesis are of doubtful application in this system, although more work clearly is needed. Physiological studies by Ketterson and Nolan (1978) and Stuebe and Ketterson (1982), and study of size assortment by Nolan and Ketterson (1983), have cast doubt upon whether differential migration can be explained by size-related tolerance of cold and food deprivation in juncos. In this study, the absence of altitudinal size assortment within Carolina Junco sexes weakens this argument

further. Studies by Myers (1981) of shorebird migration, in which the major hypotheses are more separable, support the plausibility of the early-arrival hypothesis. Applied to altitudinal migration in Carolina Juncos, however, this hypothesis seems a more reasonable explanation for residency by some males than for segregation of migrants by sex. Male and female Carolina Juncos wintering outside the breeding habitat are separated by no more than 20 km; compensating for this extra distance in spring migration would require only a few hours' earlier departure. We know that considerable movement within the winter range immediately precedes return to breeding habitat. In addition, the early-arrival hypothesis does not predict year-to-year shifts in winter assortment, as seen in this study. The hypothesis that behavioral dominance in winter leads to differential migration and subspecies assortment seems the strongest single explanatory scheme for this system, in part because of the support from other studies of the potential impact of agonistic interactions.

The flexibility demonstrated by these altitudinal migrants in timing of migration and altitude of wintering, along with patterns of site tenacity, argues that migration in this system is a facultative character, malleable by pressures created by interactions among individuals (see also Terrill and Ohmart 1984). More detailed study is needed of the relationship among agonistic competitive interactions, movement patterns, survival, and reproductive success. In this small-scale migration system, operating over a wide range of climates and habitats compressed into a small geographical area, patterns of differential migration resemble those of latitudinal systems. Ketterson and Nolan (1983), in their comprehensive review of differential migration, proposed that patterns in latitudinally migrating juncos are best explained by a balance among distance-determined costs of migration, benefits of early return to the breeding ground, and competition between age-sex classes. Our study is the first to test these ideas with altitudinal migrants. For Carolina Juncos, the short distances separating males and females makes it likely that energetic costs of migratory travel and effects of wintering ground on time of return will be relatively less important, and competitive effects more important, than for long-distance migrants. In this study, additional patterns of par-

tial migration of males, yearly variability of assortment, segregation of local and long-distance migrants, and trends in site tenacity in a marked population help us to begin testing corollaries of the major hypotheses concerning the ecological and behavioral determinants of migratory effort.

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APPENDIX 1

To create a reference set for determining the extent of sexual dimorphism in the study population, we captured 80 Carolina Juncos (52 males and 28 females), usually near active nests; 24 of these were captured in winter and laparotomized. The sexes are easily distinguishable in the hand when in breeding condition because only the male shows a pronounced cloacal swelling and only the female has a highly vascularized, defeathered brood patch on the abdomen (Wolfson 1952, Hostetter 1961). We confirmed this with laparotomy in 14 cases but discontinued the procedure because the pattern of female-only incubation and associated morphological differences were so clear. In 16 cases, we were able to capture members of both sexes attending a nest, presumably mated pairs; in each case, the bird with the brood patch (female) had shorter wings and less white in the tail than the bird with the cloacal swelling (male). We estimated, to tenths, the number of feathers on each side of the tail that were white, summing across the parts of feathers that were not completely white. The white outer-tail feathers are used in aggressive territorial displays and in courtship, in which the tail is conspicuously fanned. Females generally do not perform this display.

Using our reference set of 80 birds, females averaged 73.9 ± 1.6 mm SD wing length (unflattened chord) and 2.0 ± 0.2 white tail feathers per side, while males averaged 78.6 ± 1.7 mm wing length and 2.6 ± 0.2 white tail feathers per side (Fig. 5). From this set we developed the following sexing criteria for use in the nonbreeding season: male = 77

mm wing chord or larger with 2.3 or more white tail feathers per side, female = 76 mm wing chord or smaller with 2.2 or fewer white tail feathers per side. These cutoffs fall near one standard deviation from the mean value for each sex. If an individual classified as one sex by chord but the other sex by tail, it was removed from analysis of sex differences in migration. For the 80 birds of known sex, these criteria produced no errors in sexing but failed to classify 11 birds (14%). The sex ratio of classified birds is then 62% male, while the sex ratio of the entire sample is 65% male. For example, 5 males had wings long enough to satisfy the male criterion but too little white in the tail. Discriminate function analysis (DFA) was not more effective than the above criteria when applied to the reference set. Although DFA showed that both variables were important in separating the two classes, overlap between the sexes was as great as we found by applying the simple chord and tail criteria. For our entire data set of 1,341 Carolina Juncos, we dropped 25% from some of the analyses because they were not clearly classifiable as male or female. Because omission from the analysis probably is balanced for the two sexes (as in the reference sample), similar proportions of birds are omitted at different sites, and the probability of incorrect sexing is near zero, this procedure results in a conservative estimate of sex ratios at different sites.

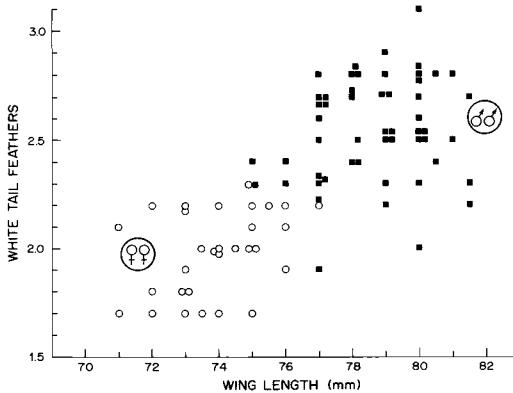


Fig. 5. Wing length (mm, unflattened chord) and number of white outer rectrices per side in Carolina Juncos of known sex (30 females, 52 males). Sexing criteria for nonbreeding birds were based on this reference set (see text).

APPENDIX 2

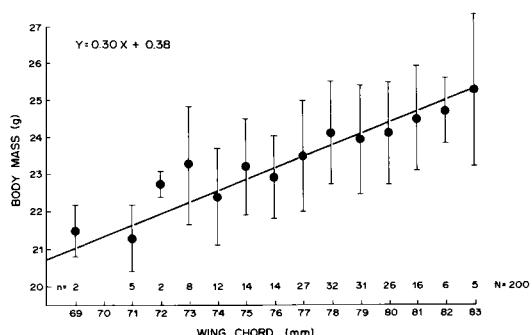


Fig. 6. The relationship between wing chord (unflattened) and body mass (\pm SD) for a sample of Carolina Juncos caught 2–15 March 1980. Analysis of variance revealed a significant relationship ($P < 0.001$, $r^2 = 0.87$). Climatic conditions varied from snowy and cold to warm and clear, undoubtedly contributing to variance in fat deposition.