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DOMINANCE STATUS AND LATITUDE ARE UNRELATED IN WINTERING DARK-EYED JUNCOS[1]

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Differential migration by the age and sex classes of a population produces latitudinal segregation during the non-breeding season in many species of birds (references in Ketterson and Nolan 1976). Dark-eyed Juncos (*Junco hyemalis*) wintering in the eastern United States exhibit differential migration, with post-hatching-year birds (hereafter adults) tending to winter south of hatching-year birds (hereafter young), and females south of males (Ketterson and Nolan 1976). Various proximal and evolutionary mechanisms have been proposed as the bases for such differential migrations, most notably: (1) body-size hypothesis—smaller individuals migrate greater distances because of their inability to survive harsh northern winters; (2) arrival-time hypothesis—sexual selection for early arrival at breeding grounds leads to shorter migrations in the territorial sex; and (3) dominance hypothesis—subordinate birds migrate greater distances because of competition with socially dominant birds (for details see Ketterson and Nolan 1976, Gauthreaux 1978, Myers 1981).

The dominance hypothesis predicts that individuals of subordinate age-sex classes should migrate farther from the breeding grounds. This has been substantiated in many differentially migrating species (e.g., juncos, Ketterson and Nolan 1976; waterfowl, Nichols and

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Haramis 1980; raptors, Kerlinger and Lein 1986). However, correlational studies such as those cited are not critical tests of the dominance hypothesis for most species, since alternative hypotheses based on size or sexual selection for early arrival at the breeding site also predict segregation by age-sex class (but see Belthoff and Gauthreaux 1991). In Dark-eyed Juncos, for example, males are the dominant sex, are larger than females, and establish breeding territories, so all of the hypotheses listed above would predict that males migrate less far than females.

The goal of our study was to determine whether dominance status within age-sex classes of Dark-eyed Juncos was related to the distance individuals migrated into the winter range. Although many determinants of dominance, such as size or plumage color, vary more between classes than within a class, flocks of juncos comprised of only a single class of birds form stable dominance hierarchies indistinguishable from those in mixed-class flocks (unpubl. data). In addition, in captive flocks there is no evidence that juncos interact only with individuals of other age-sex classes. Thus, although the dominance hypothesis (Gauthreaux 1978) refers specifically to segregation of different age and sex classes, individuals of the same age and sex that differ in dominance status would also be predicted to migrate different distances into the winter range. The advantage of testing the relationship between dominance and migration distance within age-sex classes is that the confounding effects of body-size, age, and sex are eliminated. Therefore, intra-class differences in wintering latitude are not easily explained by alternative explanations such as size-related survivorship or differential selection for arrival time.

Our experiment follows from those of Rogers et al. (1989), in which northern-wintering Dark-eyed Juncos were also pitted against southern-wintering individuals. We differed from Rogers et al. (1989) in that our subjects were tested as flocks in large, semi-natural enclosures, rather than as pairs in closely confined cages. The two wintering populations that we compared were separated by twice the distance of those in Rogers et al. (1989), representing over 50% of the entire winter latitudinal range of this species. Unlike Rogers et al. (1989), we tested dominance status at an aviary midway between the two latitudes of capture, to ensure that there was no prior residence effect (Cristol et al. 1990) for either group of birds.

METHODS

Juncos were captured at two wintering areas located 700 km apart: Kalamazoo Nature Center, near Kalamazoo, Michigan (42°N latitude: hereafter MI); and Percy Priest Wildlife Management Area, 25 km southeast of Nashville, Tennessee (36°N latitude; hereafter TN). Capture sites were baited with corn on 15 December 1988, approximately the end of autumn migration for juncos at these latitudes (Ketterson and Nolan 1976, 1985). We captured birds simultaneously at both locations with mist nets from 31 December 1988 through 2 January 1989.

Birds were aged by a combination of skull ossification (Ketterson and Nolan 1982), iris color (Yunick 1977), and outer rectrix shape (Pyle et al. 1987). Sex determination was by crown and body plumage (Ketterson and Nolan 1976). All morphometric data were gathered by D.A.C. Wing-length was measured as the length of the flattened wing chord (to nearest 1 mm). Birds were weighed on the night prior to flock establishment, and at the same hour on the night following the termination of behavioral observations (see below). At each weighing the deposits of subcutaneous fat were scored visually on an integer scale of 0–5 (Nolan and Ketterson 1983). The proportion of white on each of the outer four rectrices was scored visually on an integer scale of 1–10.

Birds were housed in groups in large flight cages for 0.5–2 days during the capture operation, and then transported by automobiles to Bloomington, Indiana on 2 January. Subjects were housed individually in small (28 × 28 × 20 cm), visually isolated cages until flock establishment. Flocks were tested in large (7 × 4 × 3 m) enclosures. All birds were provided with food and water ad lib. when behavioral data were not being gathered.

We tested eight flocks of six or eight juncos. Each flock consisted of three or four dyads of matched juncos. Each dyad was comprised of a MI and a TN junco of the same age class, sex, and wing-length (within 1 mm). Subjects were used in only one flock. Flocks 1, 2, 3, and 8 contained only young males; flock 5 contained only young females; flock 4 contained only adult males; flock 6 contained adult females with a pair of young females; and flock 7 contained two pairs of adult males and two pairs of young males. Flocks 1–4 (hereafter Group I) were established on 14 January and observed from 16–21 January. Flocks 5–8 (Group II) were established on 22 January and observed from 24–27 January.

All juncos were assigned randomly one of eight colors of plastic leg bands for identification. Observations were carried out from a blind adjacent to the test cage and lasted 0.5–1.5 hr. Food was removed from test enclosures for 0.5–2 hr prior to observation periods to increase rates of activity, and then food was provided at a single point source during observations. Social interactions occurred primarily, but not exclusively, at the food source. All displacements were scored as described in Cristol et al. (1990). Observations continued until all pairs of individuals within a flock had interacted at least five times; the average number of interactions per pair was 15.

Each junco interacted with all members of its flock. We used an arbitrary rule based on the binomial distribution to determine if one bird was dominant to an opponent (see Holberton et al. 1989). A bird was classified as dominant if it beat its opponent more times than expected by chance ($P < 0.10$). We then calculated a dominance score for each bird based on the number of flockmates dominated divided by the total number of flockmates. In three cases where birds did not meet our criterion for dominance over an opponent, 0.5 was added to the numerator of the dominance score of each member of the "tied" pair.

We used two-factor (capture site, group) analysis of variance to compare dominance scores. Wing-lengths, starting mass, and mass change during observations were compared using t-tests. Starting fat and tail-white scores, fat change during observations (as a percentage of starting fat), and tarsus lengths were compared using

TABLE 1. Morphometric comparisons ($\bar{x}$ ± SD) of Dark-eyed Juncos used as subjects from Tennessee (n = 29) and Michigan (n = 29).

	Tennessee	Michigan	Z	t	P
Tarsus (mm)	20.89 ± 0.59	20.95 ± 0.64	0.08		>0.9
Tail white (score)	2.04 ± 0.28	2.00 ± 0.26	0.47		>0.6
Wing-length (mm)	80.41 ± 2.77	80.55 ± 2.61		0.19	>0.8
Starting mass (g)	19.27 ± 1.39	19.52 ± 1.50		0.67	>0.5
Starting fat (score)	3.03 ± 0.64	3.26 ± 0.53	1.03		>0.3
Mass change (g)	0.43 ± 1.03	0.26 ± 1.09		0.60	>0.5
Fat change (%)	8.1 ± 2.6	1.0 ± 1.4	0.61		>0.5

non-parametric statistics (Mann-Whitney U). A significance level of $P < 0.05$ was used in all cases. All subjects were returned to sites of capture and released immediately following the experiment.

RESULTS AND DISCUSSION

TN juncos dominated MI juncos in 58 (55%) of 105 pairwise combinations (excluding 2 ties). The mean dominance score for TN birds did not differ significantly from that for MI birds (TN: $\bar{x}$ = 0.55, SD = 0.30; MI: $\bar{x}$ = 0.45, SD = 0.32; F = 1.49, df = 1, $P >$ 0.23). The pattern of dominance differences did not differ significantly between Groups I and II ($F_{\text{interaction}}$ = 0.12, df = 1, $P >$ 0.73).

MI and TN juncos did not differ significantly in tarsus length or amount of white in outer rectrices (Table 1). Because each TN subject was matched for wing-length with a MI subject there was no geographic difference in wing-length (Table 1). MI and TN subjects did not differ significantly in starting mass or fat, change in mass during observations, or change in fat score (Table 1). At neither site did those juncos used as subjects differ significantly in wing-length from those juncos captured but not used as subjects (Table 2).

The dominance hypothesis predicts that in a species whose breeding and wintering ranges are disjunct, such as the Dark-eyed Junco, dominant individuals should overwinter closest to the breeding range, or in the most favorable habitats (Gauthreaux 1978). Since differential migration of juncos results in population segregation by latitude in winter, the hypothesis would be supported if juncos wintering at a northern site tended to be dominant to those wintering at a more southern latitude. Our results, however, indicate that juncos wintering closer to the breeding range (MI) did not tend to dominate southern-wintering (TN) juncos of the same age class and sex. This suggests that dominance alone does not explain the maintenance of differential migration in Dark-eyed Juncos.

Several other interpretations of our results are conceivable. One possibility is that if MI birds tend to be longer-winged than TN birds, we might have inadvertantly biased the results by matching smaller-than-average MI birds with larger-than-average TN birds. Our within-sex comparison of subjects and non-subjects indicates that such a bias did not occur (Table 2). Further, no significant geographic variation in wing-lengths was found for any age-sex class in a much larger sample from the same two study sites (Nolan and Ketterson 1983).

Another possible view of these results is that although northern birds were not dominant to southern birds in our experiment, this was not an appropriate test of the dominance hypothesis because we tested dominance within age-sex classes of juncos, whereas the hypothesis attempts to explain only inter-class differences in migration distances. We feel that since social dominance is a phenomenon that operates at the level of interacting individuals, it could not be a mechanism for inter-class differences in migration behavior without also affecting the distribution of individuals within each class. Thus, if dominance interactions result in greater average migration distances for subordinate age-sex classes, the subordinate individuals within each age-sex class should also show a tendency to migrate farther than dominant individuals of the same class. Otherwise, one must postulate separate mechanisms for intra-class and inter-class variance in migration distance.

Rogers et al. (1989) performed an experiment similar to ours comparing juncos from northern (43°N) and southern (39°N) latitudes. They, too, found no tenden-

TABLE 2. Wing-length comparisons ($\bar{x}$ ± SD mm) for male and female Dark-eyed Juncos from Tennessee and Michigan. Those birds used as subjects in the experiment are compared with those not used as subjects.

	Subjects	Non-subjects	n	t	P
Tennessee					
Males	81.4 ± 1.8	80.9 ± 1.9	57	0.92	>0.3
Females	76.7 ± 2.7	76.9 ± 1.7	49	0.26	>0.7
Michigan					
Males	81.5 ± 1.5	80.8 ± 1.2	40	1.50	>0.1
Females	76.8 ± 2.7	77.8 ± 1.9	24	0.95	>0.3

cy for northern birds to dominate southern birds. In concluding that factors other than dominance must be important mechanisms in determining latitude of winter residence for juncos, Rogers et al. (1989) implicitly assumed that dominance is a temporally stable phenomenon that persists unchanged through migration and winter. If this assumption is valid, our experiment, and that of Rogers et al. (1989), are acceptable tests of the dominance hypothesis. However, if dominance status is affected by hunger or other transitory factors (as suggested by Cristol 1992), then site-dependent differences in food supply, competitor abundance, or climate could differentially alter the dominance status of juncos wintering at different latitudes. Studies on wild flocks during migration, in which the dispersal tendencies of dominants and subordinates could be compared, might be the only way to directly test whether dominance is a mechanism for differential migration. Even a direct test might be challenged on the grounds that dominance is an ultimate, rather than proximate, factor in shaping migration patterns. Clearly this is a difficult problem that must be approached with caution.

Southern-wintering juncos were not subordinate to conspecifics of the same age class, sex, and size wintering closer to the species breeding range. We found no evidence that social dominance is a mechanism responsible for variance in migration distances within classes of juncos. We suggest that the question of whether behavioral dominance is an important mechanism in differential migration of Dark-eyed Juncos and other animals should now be tested by direct observation of migrating groups, rather than further experiments with post-migration subjects.

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