

Does dominance determine how far dark-eyed juncos, *Junco hyemalis*, migrate into their winter range?

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Abstract. The behavioural dominance hypothesis suggests that differential migration among individuals of a species of bird is due solely to social interactions that force subordinate individuals (often a class, e.g. female or young birds) to migrate farther into the winter range than dominant individuals (often a class, e.g. male or old birds). Here, this hypothesis was tested with two experiments. In the first experiment, the prediction was tested that dominance acts within a sex–age class and influences migration distance. The outcomes of interactions within dyads of dark-eyed juncos, *Junco hyemalis*, were observed. Each dyad consisted of a junco caught in winter in Michigan matched with another of the same sex–age class caught in Indiana, which is situated farther south and therefore farther into the winter range of this species. Michigan birds were dominant in only half of the experimental dyads (21 of 41 dyads), which is inconsistent with the prediction of the dominance model. In the second experiment the prediction was tested that members of a sex–age class that migrates farther into the winter range should be subordinate to members of a different class that migrates a shorter distance. Young males that wintered in Michigan were pitted against old males that wintered in Indiana. In 19 of 25 dyads, the more southern-wintering old males were dominant, which also is counter to the prediction of the dominance hypothesis. These results indicate, at the very least, that in migratory *J. h. hyemalis*, dominance does not play as important a role in determining latitude of winter residence as has been suggested.

Migration is one form of behaviour by which animals that breed at temperate latitudes may escape the rigours of winter. Differential migration in temperate-breeding birds occurs when individuals of the same species, but different sex–age classes, migrate varying distances into the wintering grounds. Differential migration of sex–age classes has been found in a wide variety of avian species (reviewed by Ketterson & Nolan 1976, 1983, 1985; Myers 1981; Gauthreaux 1982). In general, females and young overwinter farther into the wintering range than males and adults.

Various hypotheses have been advanced to explain such intraspecific variation in avian migration (for review see Gauthreaux 1982; Ketterson & Nolan 1983). The behavioural dominance hypothesis (Gauthreaux 1978, 1982) states that in social competition for resources, the sex–age classes experience unequal success because they differ in

social dominance status. According to the hypothesis, if resources on the breeding grounds are inadequate for an extended period such as a winter season, then dominant birds will travel only as far into the winter range as is necessary to find sufficient food, and subordinate birds will move farther in order to avoid competition with the dominant birds. The result predicted by the hypothesis is a linear relationship between potential dominance status and distance migrated into the winter range. No studies to date have directly tested this prediction of the dominance hypothesis.

In this study, we apply the dominance model to a bird species in which individuals migrate north to south between virtually non-overlapping breeding and wintering ranges, and settle for the winter over a considerable band of latitudes. In this situation, the model asserts that individuals wintering at latitudes closer to the breeding range should be dominant over those wintering at greater distances. While the entire distance migrated by any individual typically cannot be known merely from its winter location, because its breeding origin is unknown, the distance migrated into the winter range can be measured. In species with non-

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overlapping seasonal ranges, only this distance (and not the actual distance migrated) has the potential to determine with which conspecifics an individual will overwinter. Therefore it is the distance that is critical to the dominance hypothesis (Gauthreaux 1978, 1982).

Our experimental subject, the dark-eyed junco, *Junco h. hyemalis*, is a migratory bird species that breeds principally in Canada and spends the winter southward in southern Ontario and most of the eastern United States (Bent 1968); the breeding and wintering ranges overlap only slightly. Juncos are gregarious during winter, and, when in flocks, males tend to dominate females and old birds tend to dominate young birds (Balph 1977; Baker & Fox 1978; Ketterson 1979a). On average, males winter north of females (Ketterson & Nolan 1976, 1979) and young of the year winter north of adults of the same sex (Ketterson & Nolan 1983, 1985).

In the first of two experiments, we tested the prediction that in dyads of juncos of the same sex-age class, the member from the more northern wintering site should dominate the member from the more southern site. The second experiment tested the same prediction by measuring inter-class differences in social dominance. Even though old males dominate young males when they are members of the same population (see above), the dominance hypothesis would predict that the opposite would be true of young males that winter north of old males. We therefore determined dominance status in junco dyads each consisting of a northern-wintering young male and a southern-wintering old male. Because previous studies (Ketterson & Nolan 1982, 1983) have shown some annual variation in the age structure of winter populations of juncos at various latitudes, we sampled age structure in the winter of the second experiment in order to learn whether we were performing the experiment in a normal or an aberrant year.

METHODS

Experimental Junco Populations

In the junco, fall migration ends by approximately 1 December throughout eastern North America (Ketterson & Nolan 1976, 1985), and thereafter populations are considered stable until approximately 1 March, when spring migration begins (Ketterson & Nolan 1976, 1985; but see Terrill 1987,

who proposes that facultative migration may occur in mid-winter if feeding conditions deteriorate). All birds used in the present study were selected from two winter populations, one near Bloomington, Indiana (39°N latitude) and one 350 km northward, near Kalamazoo, Michigan (42°N latitude). Michigan (MI) experimental birds were captured at the Kalamazoo Nature Center, a large nature preserve including extensive forest edge habitat occupied by wintering juncos. Indiana (IN) juncos were taken from similar habitat at two locations.

Experiment 1

This experiment addressed the question of whether dominance determines the winter site in juncos of the same sex and age.

Capture dates

Birds were caught in two winters, as follows. In 1984–1985, birds were captured on 15–19 December 1984 (young males and young females in Indiana), 15–25 February 1985 (old males in Indiana), and 20–22 December 1984 (old males, young males, young females in Michigan). In 1985–1986, birds were captured on 1–11 January 1986 (young females in Indiana) and 6–10 January 1986 (young females in Michigan). Old females are uncommon as far north as Michigan and Indiana and were not included in the experiment.

Sex and age determination

Birds were sexed on the basis of plumage traits and wing length, after Ketterson & Nolan (1976). Two age categories are recognizable in this species; young juncos are those hatched the preceding breeding season, old juncos are in at least their second winter. Age determination by inspection of skull ossification is reliable until approximately 1 January (Ketterson & Nolan 1982), and we relied on this character until that date. Thereafter we used a combination of plumage traits, wing length and eye colour that has proved 93% accurate (Ketterson & Nolan 1982).

Dyad establishment and housing conditions

After capture and until determination of dominance status, juncos from different winter populations were kept visually isolated in two large separate aviaries at Bloomington, Indiana. Food and water were provided ad libitum, population densities were moderate, and free flight in the aviaries was possible.

Table 1. Aspects of individual junco dyads including number of displacements and number of avoidances (experiment 1)

| Type of dyad | Dyad number | Winner | No. of displacements | No. of avoidances | Wing length (mm) Winner-loser | Body mass (g) Winner-loser | Fat class Winner-loser |
|------------------------------------|-------------|----------|----------------------|-------------------|----------------------------------|-------------------------------|---------------------------|
| Young males | | | | | | | |
| | 1 | Michigan | 15 | 0 | 0 | -0.2 | 0 |
| | 2 | Michigan | 11 | 0 | 0 | -0.6 | 0 |
| | 3 | Michigan | 15 | 0 | 0 | 1.1 | -0.5 |
| | 4 | Indiana | 15 | 0 | -1 | 0.8 | — |
| | 5 | Michigan | 4 | 3 | 0 | -1.5 | — |
| | 6 | Indiana | 24 | 13 | 0 | 2.5 | 1.0 |
| | 7 | Michigan | 16 | 0 | 0 | -2.5 | -1.5 |
| | 8 | Indiana | 14 | 7 | 0 | 0 | -1.0 |
| | 9 | Indiana | 21 | 5 | 0 | -1.0 | 0 |
| | 10 | Michigan | 19 | 4 | 0 | -0.9 | -1.0 |
| | 11 | Indiana | 21 | 5 | 1 | -0.6 | 0.5 |
| | 12 | Indiana | 19 | 8 | 0 | 1.3 | 0.5 |
| | 13 | Indiana | 20 | 8 | 0 | 0.1 | 0.5 |
| | 14 | Michigan | 14 | 3 | 0 | 1.8 | 0 |
| | 15 | Michigan | 15 | 3 | 0 | -0.8 | -1.5 |
| | 16 | Indiana | 20 | 2 | -1 | -0.1 | 0.5 |
| Winner-loser ($\bar{X} \pm 1$ SE) | | | | | 0.06 \pm 0.11 | 0.04 \pm 0.32 | -0.18 \pm 0.22 |
| Young females | | | | | | | |
| | 1 | Michigan | 19 | 0 | 0 | -0.4 | 0 |
| | 2 | Michigan | 15 | 0 | 0 | 1.3 | 0 |
| | 3 | Michigan | 16 | 0 | 0 | 0.4 | 0 |
| | 4 | Michigan | 19 | 7 | 0 | 0 | 1.0 |
| | 5 | Michigan | 15 | 0 | 0 | 1.8 | 0 |
| | 6 | Michigan | 20 | 2 | 0 | -1.0 | 0.5 |
| | 7 | Indiana | 25 | 0 | 0 | 2.0 | 0.5 |
| | 8 | Indiana | 5 | 1 | 0 | 2.5 | 1.0 |
| | 9 | Indiana | 15 | 5 | 0 | 0.7 | 1.0 |
| | 10 | Michigan | 27 | 6 | 0 | -1.3 | -0.5 |
| | 11 | Michigan | 12 | 1 | 1 | -1.7 | -0.5 |
| | 12 | Indiana | 20 | 0 | 0 | -1.1 | 0 |
| | 13 | Indiana | 15 | 3 | 0 | 1.0 | 0 |
| | 14 | Michigan | 69 | 1 | 0 | -0.5 | -0.5 |
| | 15 | Michigan | 3 | 0 | 1 | 2.2 | 0 |
| | 16 | Indiana | 15 | 0 | 0 | -0.5 | -0.5 |
| | 17 | Indiana | 12 | 0 | -1 | 0.9 | -1.0 |
| | 18 | Indiana | 16 | 5 | -1 | -0.9 | -1.0 |
| | 19 | Michigan | 9 | 0 | -1 | 0.8 | 1.0 |
| | 20 | Michigan | 13 | 0 | 1 | 0.2 | -0.5 |
| | 21 | Michigan | 7 | 0 | 1 | 0.1 | 0.5 |
| Winner-loser ($\bar{X} \pm 1$ SE) | | | | | 0.05 \pm 0.13 | 0.31 \pm 0.27 | 0.07 \pm 0.13 |
| Old males | | | | | | | |
| | 1 | Indiana | 15 | 2 | 1 | -4.2 | -1.0 |
| | 2 | Indiana | 15 | 1 | -1 | -1.0 | -0.5 |
| | 3 | Indiana | 15 | 1 | 0 | 1.5 | 0.5 |
| | 4 | Indiana | 15 | 0 | 1 | 0.7 | 0 |
| Winner-loser ($\bar{X} \pm 1$ SE) | | | | | 0.25 \pm 0.55 | -0.75 \pm 1.46 | -0.25 \pm 0.37 |

The quantity winner-loser refers to the difference between, for example, the wing lengths of the contest winner and loser; such quantities are also shown for body mass and fat class. Average (± 1 SE) winner-loser values are indicated for separate age-sex classes.

Table II. Aspects of individual junco dyads including number of displacements and number of avoidances (experiment 2)*

| Young males versus old males | | | | | | |
|------------------------------------|----------|----------------------|-------------------|----------------------------------|-------------------------------|---------------------------|
| Dyad number | Winner | No. of displacements | No. of avoidances | Wing length (mm) Winner-loser | Body mass (g) Winner-loser | Fat class Winner-loser |
| 1 | Indiana | 12 | 2 | 3 | — | — |
| 2 | Michigan | 31 | 0 | 3 | — | — |
| 3 | Indiana | 7 | 1 | 2 | — | — |
| 4 | Indiana | 7 | 1 | 4 | — | — |
| 5 | Indiana | 15 | 18 | 0 | — | — |
| 6 | Indiana | 15 | 0 | 0 | — | — |
| 7 | Indiana | 21 | 8 | 2 | — | — |
| 8 | Indiana | 19 | 0 | 3 | — | — |
| 9 | Indiana | 17 | 4 | 3 | — | — |
| 10 | Indiana | 16 | 0 | 0 | — | — |
| 11 | Indiana | 15 | 4 | 6 | — | — |
| 12 | Michigan | 16 | 2 | 2 | — | — |
| 13 | Indiana | 17 | 2 | 3 | 0 | 0.5 |
| 14 | Indiana | 38 | 1 | 2 | 0.2 | -0.5 |
| 15 | Indiana | 15 | 5 | -1 | -1.2 | 0 |
| 16 | Michigan | 11 | 5 | -1 | -3.4 | -0.5 |
| 17 | Michigan | 26 | 1 | -2 | 1.3 | 0.5 |
| 18 | Indiana | 7 | 4 | 2 | -1.5 | -1.0 |
| 19 | Indiana | 14 | 4 | 4 | 0.1 | -1.0 |
| 20 | Michigan | 16 | 0 | -1 | -0.7 | 1.0 |
| 21 | Indiana | 15 | 0 | 4 | -0.8 | -1.0 |
| 22 | Michigan | 34 | 6 | -4 | 1.7 | 0.5 |
| 23 | Indiana | 24 | 1 | — | 0.1 | — |
| 24 | Indiana | 15 | 3 | 3 | 0.5 | 1.0 |
| 25 | Indiana | 20 | 4 | 1 | 0.6 | 0.5 |
| Winner-loser ($\bar{X} \pm 1$ SE) | | | | 1.70 \pm 0.48 | -0.24 \pm 0.37 | 0 |

* For a complete explanation, see Table I.

To form dyads, MI juncos were paired with IN juncos of the same age, sex, wing length (flattened wing, nearest 1.0 mm) and body mass (Pesola scale, nearest 0.1 g), as measured at the time of pairing. These factors were held constant because they have been shown to be correlated with dominance status in this species (Fretwell 1969; Balph 1977; Baker & Fox 1978; Ketterson 1979a). Thus, members of dyads were similar in all but one important respect: they terminated their fall migration at winter latitudes that were 350 km apart. We emphasize that there is no geographical variation in wing length (a general measure of body size, discussed by James 1970) within sex-age classes among winter populations of this species (Nolan & Ketterson 1983). Therefore, when we matched members of dyads for wing length, we did not eliminate naturally occurring geographical variation in size. Finally, by pairing birds of similar visible subcuta-

neous fat class (determined on a scale of 0-5, after Helms & Drury 1960; Nolan & Ketterson 1983) we attempted to control for the influence of stored energy on the motivation to feed in captivity at the time dyads were caged and dominance status was established. In sum, our direct control allowed a clear focus on the factor of major concern: chosen latitude of winter residence.

During observations, dyads were housed separately in cages (0.6 \times 0.6 \times 0.6 m) made of black plastic (back, bottom, two sides) and hardware cloth (front and top). Individual dyads could hear but not see dyads in other cages. Two parallel perches, 0.2 m apart and 0.3 m high, extended from the back of each cage. Ten (1984-1985) and 14 (1985-1986) identical cages allowed observation of several dyads at once. White millet and cracked corn, scattered over the entire cage floor, and water (snow in cold conditions) were provided ad libitum

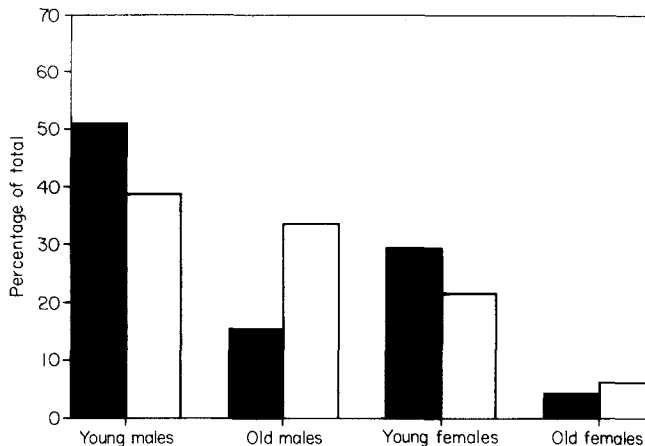


Figure 1. Relative abundances of the four junco age-sex classes at Kalamazoo, Michigan (■, 42°N, $N=255$) and Bloomington, Indiana (□, 39°N, $N=485$) in December-early January 1985-1986. Absolute frequencies of males were: MI = 130 young, 39 old; IN = 187 young, 163 old. A test of the 2×2 contingency table (MI, IN versus young, old juncos) for males was highly significant ($\chi^2 = 26.47$, $df = 1$, $P < 0.001$), indicating that old males, on average, selected a more southerly latitude for overwintering than young males.

at all times. A constant light regime (1984-1985: incandescent bulbs in a windowless room) of light:dark 9:15-h or a natural light regime (1985-1986: cages held outdoors) was provided. The experimental cages were on the second floor of an unheated building in 1984-1985 and just outside the building in 1985-1986; thus experimental birds experienced natural temperature fluctuations typical of southern Indiana in winter.

Criteria used to determine dominance status

We defined two categories of behaviour that indicated dominance of one member of a dyad over the other. Displacement consisted of a direct attack upon one bird by the other, which always resulted in rapid retreat by the attacked bird and occupation of its space by the attacker. Conflicts of this type occurred most often over food and perches but occasionally arose over water or snow. Avoidance, a more subtle behaviour, involved clear movement by one bird away from the other as the latter moved about the cage. Almost all avoidances occurred when one bird was feeding and hopped in the general direction of the second bird, also feeding, which moved aside.

A bird seen to displace its cagemate 15 times was classified as dominant. In a few cases (11 of 41 dyads) displacements were uncommon (fewer than 15) and we relied upon avoidances as well as displacements to make our determinations. We emphasize, however, that we observed no reversals

in either displacement or avoidance behaviour in any dyad in this experiment (or in the one to follow), suggesting highly stable dominance relations between dyad members. This is in accordance with previous studies on this species (Balph 1979; Ketterson 1979a).

Dyad members were introduced simultaneously into the observation cages in order to control for a possible effect of prior residence (Balph 1979; Yasukawa & Bick 1983). A total of 10 cages was used at once to house dyads, so it was necessary to determine dominance status in successive shifts in order to accumulate sample size. Groups of 10 or fewer dyads were established on 30 December 1984 (five of young males and five of young females), 9 January 1985 (six of young males and three of young females), 15 January 1985 (five of young males and five of young females), 26 February 1985 (four of old males), and 14 March 1986 (eight of young females). Observation began 1-8 days after establishment (32/41 dyads were first observed after at least 2 days had passed, and the mean was 3.6 days) and continued until dominance status had been determined. On average, we observed each dyad during 2.6 days (range 1-4 days).

Experiment 2

This experiment addressed the question of whether dominance determines the winter site in juncos of different age.

Capture dates; sex and age determination

This experiment was conducted in the winter of 1985–1986. Capture dates of old and young males were 1–11 January 1986 in Indiana, and 6–10 January 1986 in Michigan. Sexing and ageing proceeded as in experiment 1.

Dyad establishment

Prior to dominance testing, MI and IN birds were housed separately as described for experiment 1. Because dyad members differed in age class in experiment 2, we did not control for age-associated factors affecting dominance status, i.e. wing length and, correlated with wing length, body size (both are significantly greater in old than young males, Nolan & Ketterson 1983). Experimental dyads were housed outdoors as described above for the 1986 dyads employed in experiment 1.

Dyad observation

We again used displacements and avoidances to determine relative dominance status of the dyad members. As in experiment 1, members were introduced simultaneously to experimental cages. Groups of old male–young male dyads were established on 26 January 1986 (12 dyads) and 7 February 1986 (13 dyads). Observation began 3–5 days after establishment (23/25 dyads were first observed after 3 days had passed, and the mean was 3.2 days) and continued until dominance status had been determined. On average, we observed each dyad during 1.7 days (extremes 1–4 days).

Sampling of 1986 winter junco populations

Sampling of natural junco populations at Bloomington, IN took place from 4 to 31 December 1985, and 485 juncos were caught, aged and sexed. A comparable effort at Kalamazoo, MI from 6 to 10 January 1986 yielded 255 juncos.

RESULTS**Experiment 1**

Latitude of winter residence was not significantly associated with dominance status (Table I). Of the 16 contests involving young males, eight were won by IN juncos. In the interactions of 21 young female dyads, Indiana females were dominant in eight. In the adult male group, all four contests were won by IN juncos. After pooling, 20 of the 41 contests were won by IN and 21 by MI juncos; this distribution did not differ significantly from a 50:50 win:lose ratio ($\chi^2=0.024$, $df=1$,

$P>0.90$). When outcomes based on fewer than 15 displacements (Table I: four dyads of young males and six of young females) were eliminated from analysis, the statistical result was unchanged ($\chi^2=0.290$, $df=1$, $P>0.5$).

Because we matched dyad members for potential determinants of dominance, it is not surprising that winners and losers did not differ in wing length, body mass, or fat class (*t*-tests of wing length and body mass, Mann–Whitney *U*-test of fat class, Table I). Thus the only known difference remaining between them, chosen wintering site, did not influence dominance status.

Experiment 2

In marked contrast to the first experiment, in experiment 2 the latitude of winter residence was significantly associated with dominance status, but in a direction opposite to that predicted by the dominance hypothesis (Table II). Of the 25 contests involving old IN males versus young MI males, 19 were won by the old IN males (Table II; $\chi^2=6.760$, $df=1$, $P<0.01$). Again, when dyads with fewer than 15 displacements were eliminated, the result was unchanged ($\chi^2=4.260$, $df=1$, $P<0.05$). Interestingly, ties occurred in several of these mixed-age dyads when a flying bird attempted to displace a perched bird but failed. These were rare, however, and even if they had been treated as reversals would not have contradicted assigned dominance status.

Sampling of the natural MI and IN winter populations showed that, as in previous years (Ketterson & Nolan 1983), in the winter of experiment 2 old males formed a significantly higher proportion of the total junco population in Indiana than in Michigan (see Fig. 1). That is, there was nothing unusual about the winter demography when experiment 2 was conducted, and there was no reason to suppose that its subjects were drawn from populations with atypical structures.

DISCUSSION**Implications for Dominance-influenced Differential Migration**

Proponents of the dominance hypothesis have advanced it to account both for segregation or partial segregation of the sexes and for differences in the distribution of age classes. Since migrant

juncos exhibit both forms of winter segregation, our discussion is separated according to age and sex.

Age

The results of experiment 2 indicate that old males from IN dominated young males from MI. The novel element of this experiment is that the birds were taken from two latitudes; those from the more southerly latitude were dominant, which contradicts the prediction of the dominance hypothesis. Furthermore, the contemporaneous sampling of the two natural populations from which the experimental subjects were drawn shows that young birds, as usual (Ketterson & Nolan 1983), tended to settle north of old birds. Can the experimental result be explained as an artefact of our methods? We can think of three possibilities.

First, contests in experiment 2 were held in a neutral and unnatural setting, which may have deprived the young juncos of an advantage that they would have had in nature. Contests in cages are likely to be dependent on larger body size, greater experience (age), and darker plumage; old males should dominate under these circumstances (Ketterson 1979b). If young males arrive in the northern part of the winter range before old males, prior residence (Balph 1979; Ketterson 1979a; Yasukawa & Bick 1983; Ketterson & Nolan 1985) might provide them with an advantage that would outweigh the advantages inherent in greater age and permit young juncos to dominate in natural contests during migration. The evidence as to whether young males arrive before old is mixed. In an autumn Zugunruhe experiment, young of the year showed readiness to migrate at an earlier date than did adults (Ketterson & Nolan 1985). Also, when young juncos are banded in Indiana and return there the following year, the date of capture tends to be later in the second winter than in the first winter (Ketterson & Nolan 1985). In contrast, there is a high proportion of old males among the earliest autumn migrant juncos in Indiana (October, early November), higher than the proportion found a few weeks later after the winter population has settled (Nolan & Ketterson, unpublished data). Thus, at least some old males migrate very early. In sum, we cannot exclude the possibility that young Michigan juncos would have dominated old Indiana juncos under more natural circumstances, but at least on neutral ground they do not.

A second factor that might have led us to a false conclusion is that two study populations had inadvertently been selected from habitats of different quality. In addition to its prediction of geographical segregation, the dominance hypothesis predicts that when microgeographical variation in habitat quality exists at a single location and superior habitat is in short supply, subordinates will be forced into habitats of lower quality (Gauthreaux 1978). If this prediction is correct and if young MI males were obtained from low-quality habitat into which they had been forced by other, more dominant young MI males, we could have dealt with an unrepresentative sample of MI birds. However, in both Michigan and Indiana juncos were caught in habitats that appeared to be comparable and of high quality. In both locations, after 1 December natural food was supplemented and in both locations the presence of coniferous trees provided numerous, protected potential roosts. Hence, we have no reason to believe our subjects were atypical members of their respective classes.

Finally, it may be argued that our results can be reconciled with the dominance hypothesis on the ground that our Michigan and Indiana sites were too close to each other and that therefore no correlation between latitude and dominance relations could be expected. This too seems to us to be an unlikely explanation. Juncos are abundant in winter in the eastern United States only between 33° and 42°N (Ketterson & Nolan 1983, 1985). Our sites were separated by three degrees of latitude, thus 25% of the region of abundance. Furthermore, it is within this 25% that over half the young male population winters. The argument that the dominance hypothesis is not designed to predict distributions on this scale is difficult to accept.

Sex

Neither experiment bears directly on the adequacy of the dominance hypothesis to account for the junco's sexual distribution in winter, and we think it possible that an ultimate cause of the longer migrations of females may be the advantage of reduced competition with males during winter (Ketterson & Nolan 1983). Social interactions during autumn migration may also play a proximate role in determining where females settle. Nevertheless, the evidence that dominance explains neither within-class nor across-male-age-class dis-

tributions suggests one must be cautious before accepting the dominance hypothesis with respect to sex.

Juncos in general

While the distribution of eastern migratory juncos violates the dominance model's straightforward prediction that dominant birds (males and adults) should winter north of subordinate birds (females and young), factors underlying the migratory junco's distribution may not be typical (compare Rabenold & Rabenold 1985; Wiedenmann & Rabenold 1987 for inter-racial comparisons). The foundation of the dominance model is the assumption that in competition for scarce resources subordinates must either emigrate or face the probability of reduced survivorship. There is evidence for this assumption in some species. Thus, artificially increased food supplies raised winter survivorship in subordinate song sparrows (*Melospiza melodia*; Smith et al. 1980), and dominant silvereyes, *Zosterops lateralis*, survived better in winter than subordinates (Kikkawa 1980). In contrast, demographic data on juncos that winter in Indiana and South Carolina suggest that neither overwinter survival nor winter dispersal varies according to dominance status of age-sex classes. When large numbers of juncos were aged, sexed, banded and released at the beginning of winter and the banding sites sampled again at winter's end (with no artificial food supplied in the interim), two findings emerged. (1) The proportion of banded individuals recaptured at the end of winter was invariant across age-sex classes, and (2) the sex-age structure of the early-winter and late-winter samples (i.e. counting all juncos, banded and unbanded, in late winter) remained unchanged (Ketterson & Nolan 1983, 1985, additional unpublished data). It is possible that the junco's winter distribution may be ideal-free as opposed to despotic. That is, fitness may be independent of potential dominance status or wintering site.

A recent study by Terrill (1987) provides an interesting contrast. In his experiments, after dominance had been established between members of dyads, food was severely restricted and the amount of nocturnal restlessness of dyad members was then measured. (Nocturnal restlessness accompanied by fattening during the seasons of migration is generally accepted as evidence that caged migratory birds, including juncos, are in the migratory physiological state; Berthold 1975; Ketterson & Nolan

1987a, b.) Subordinate juncos became more restless than dominant juncos, and in one experiment their movements were oriented southward. None of the birds fattened. Terrill concluded that subordinate juncos should migrate out of an area before dominant juncos 'in situations where dominants are able to maintain relatively high probabilities of survival, but directly decrease the probability of survival by subordinates'. Our results would suggest that a similar situation does not occur in the course of a typical junco fall migration.

The results of these experiments suggest that for the junco, the dominance hypothesis must be modified to admit the possibility that additional selective pressures underlie the differential migration and winter distribution. Ketterson & Nolan (1983) have proposed other pressures, which may bear unequally on the age-sex classes; optimal balancing of these factors by members of each class might then result in the observed winter distribution. Among the suggestions are: (1) the relationships among proximity to the breeding range, early return to the breeding range, and reproductive success (perhaps more important for males than females); (2) mortality rate per unit distance travelled during migration (possibly higher in young birds with no previous experience of migrating); (3) achievement of a compensatory trade-off between greater mortality associated with longer migration but lower overwinter mortality associated with wintering in a more southerly climate (possibly more attainable by older birds that are more experienced at avoiding the risks inherent to migration). Finally, to the extent that these pressures make one class more resistant than others to prolonging its southward migration, those other classes might then move farther southward to avoid the consequences of high population density. This could account for the longer migration of adults than of young birds of the same sex.

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