

# INTRASPECIFIC VARIATION IN AVIAN MIGRATION: EVOLUTIONARY AND REGULATORY ASPECTS

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## ABSTRACT

When some classes of a bird population migrate and others do not, or when classes migrate varying distances, survivorship during the non-breeding season is likely to differ among the classes because they spend that season in different environments. Knowledge of relationships among seasonal mortality rates, annual mortality rates, and productivity of migratory classes contributes to understanding of the advantages and disadvantages of migration and of the maintenance of the behavioral differences in the populations studied. At the proximate level, investigation of intrageneric and intraspecific variation in migratory behavior has been and continues to be important for elucidating mechanisms that regulate migration.

We have studied migratory dark-eyed juncos (*Junco hyemalis hyemalis*), in which females migrate farther southward into the winter range than males and adults farther southward than young of the year. These differences in winter distribution result in geographic variation in winter mortality of the sex-age classes, but evidently not in differences in annual mortality. We summarize the population dynamics by which we believe the winter distribution is maintained year after year and the ultimate factors that may select for the interclass differences. We also report results of an experiment in which the autumn and spring zugunruhe (nocturnal restlessness) of members of the four classes, all from a single breeding locality, was monitored. We asked whether quantitative differences in restlessness existed among sex-age classes and, if so, whether these correlated with the observed differences in distance migrated. Classes making longer migrations did tend to be more restless, but in most comparisons not significantly so. If zugunruhe reflects a physiological disposition to migrate whose duration and intensity have an underlying genetic basis, we conclude for the junco that conditions experienced in transit probably modify this disposition and therefore play an important role in determining average distance migrated by the sex-age classes.

## INTRODUCTION

The existence of variation in migratory behavior among members of the same species provides unusual opportunities for probing both ultimate and proximate factors underlying migration (Myers, Maron and Sallaberry 1985). Among avian migrants, three types of intraspecific variation have been described.

1. In some species there are migratory and non-migratory populations; all individuals migrate from some regions of the breeding range, but all are sedentary in others.
2. In partially migratory populations, a portion of the individuals from a given population migrates, while the other portion remains sedentary.
3. Finally, in differential migrants all individuals migrate, but they differ predictably from one another in distance traveled (or, some would add, in direction and/or timing of movement; Gauthreaux 1982). All types of variation can occur within a single species. For example, high-latitude breeding populations may be entirely but differentially migratory, middle-latitude populations partially migratory, and low-latitude populations resident, as seems to be the case with *Sylvia atricapilla* (Mead 1983, p. 57).

In birds the intraspecific migratory differences that have been most often described (Gauthreaux 1982, Ketterson and Nolan 1976, 1983a) are associated with sex and/or age. When the difference is sexual, males are more likely than females to be the resident class or the class that migrates the shorter distance. When age bias occurs, the pattern is less clear. In partial migrants the tendency to migrate usually decreases with age, but in differential migrants, adults may travel either longer or shorter distances than young (in addition to citations in Gauthreaux 1982, see Spaans 1977, Ketterson and Nolan 1983a, p. 366, Morton 1984). Whether predictable variation also occurs commonly among members of a single sex-age class is not known. Across-class differences in migratory tendency can be relatively easily identified by studies at the population level, i.e., either (1) by detecting at one or more points in the winter range, deviations from the expected sex or age ratio of the population as a whole or (2) by observing variation among ratios in different parts of the range. On the other hand, determination that differential migration occurs within a single sex-age class usually (but not invariably) requires knowledge of the breeding and non-breeding locations of specific, marked individuals of that class, and information of this kind is scanty.

In this paper we first review hypotheses that have been advanced to account for the long-term maintenance of intrapopulation differences in distance migrated, i.e., to explain why selection has not eliminated the variation. We then focus on the differentially migratory population of the dark-eyed junco (*Junco h. hyemalis*), a bunting of the north-temperate zone. Our purposes are (1) to summarize the geographic variation in the junco's winter population structure, which we view as the product of a differential autumn migration; (2) to consider the population dynamics that maintain the geographic differences over the years; (3) to describe ultimate factors

that we believe underlie differences in distance migrated; and (4) to present results of an experiment investigating physiological mechanisms that may regulate the variation in the junco's migratory behavior. Data on points (1), (2) and (3) are summarized from work already published (Ketterson and Nolan 1976, 1982, 1983a); data on point (4) appear for the first time.

### EVOLUTION AND MAINTENANCE OF INTRASPECIFIC VARIATION IN MIGRATORY BEHAVIOR

#### General Hypotheses

If all members of a species are migratory because the probable benefits of seasonal movement exceed (or, historically, exceeded) the probable benefits of remaining sedentary, then it follows that when only certain individuals migrate (or migrate farther), for them the advantages of migration (or prolonged migration) should outweigh the advantages of remaining sedentary. For their non-migratory or less migratory conspecifics the reverse should be true. These generalizations are, of course, idealized. Environments change, phylogenetic constraints limit the precision of selection, and chance may play a powerful role. Further, the individual is probably rarely in a position (or physiological state) that lets it first assess the full range of options available and then adopt the optimal course of behavior. Still, we would argue that assumptions of the general efficiency of selection and of the malleability of migratory behavior may be more justified when applied to the migrations of birds than to those of animals that are less mobile. Many birds, because they can cover long distances at high speed, are exposed within a single lifetime to a wide choice of environments in which to settle. It seems likely that each generation gives rise to some individuals that lack the mechanisms responsible for departing on the population's usual schedule, or for departing at all, others that settle between the normal breeding and wintering ranges, and still others that move entirely beyond the limits of one or both ranges. (Thus in a sample of migratory prairie warblers *Dendroica discolor* found outside the winter range of the species, all that could be aged were young individuals that were making or had just made the first migration of life (Nolan 1978, pp. 449–451; see also De Sante 1983).) If any of these deviations in migratory behavior were genetically based, and if it improved reproductive success, it would appear that in birds, unusually favorable and frequent opportunities exist for selection to increase the frequency of such variants (see Berthold and Querner 1982, Berthold, this volume).

When variation in the migratory behavior of a bird population is assumed to be stable over time, questions like the following arise: Do migrants and non-migrants, or long- and short-distance migrants, whatever their genetic distinctness, represent equally adaptive alternative strategies? If so, is that because environmental variation and unpredictability makes neither alternative consistently more advantageous than the other, or would the variation persist in the absence of environmental differences from year to year? Can alternatives be maintained even if they are not equally adaptive?

Various authors have addressed these problems and proposed models designed to answer one or more of them. We summarize these here but note in advance that data, particularly demographic and population-genetic data, are too scanty to test them in most cases (Myers et al. 1985).

Two hypotheses (Lack 1954, p. 224, 1968, von Haartman 1968)—both advanced to explain how a sedentary element and a migratory element can persist indefinitely and thus maintain a partially migratory population—assume that the elements are genetically differentiated forms. Although von Haartman (1968, p. 1) did not emphasize this, it is clear that his model requires a genotypic difference. Both authors also assumed that fitness of the migrant and non-migrant morphs must be equal over the long term or one would be eliminated. The equality must derive from some combination of compensatory trade-offs in (1) probability of surviving to adulthood, (2) annual productivity, and (3) annual survivorship while reproductive. Lack focused on survivorship alone and on the unpredictability of temperate-zone winters: more migratory individuals survive in years of unusual severity; in moderate winters mortality associated with migration exceeds the mortality of sedentary individuals. Over the years, annual survivorship balances out. Von Haartman proposed no equality of survivorship. In his view, non-migrants might always suffer greater winter (and therefore annual) mortality; but if competition for breeding resources was intense and sedentary individuals were more successful competitors, their greater productivity might compensate for their higher mortality. Thus, for cavity-nesting birds, nest sites may be limiting, and year-round residency may confer priority of access to these (Lundberg 1979).

More recently, Greenberg (1980) extended and modified von Haartman's argument, noting that among new-world passerines higher annual survivorship and lower productivity are associated with longer migrations; long-distance migrants live longer but produce fewer young per breeding season (Table 1). In Greenberg's view, however, greater productivity of sedentary species and short-distance migrants does not stem from prior access to resources. Rather, such species have more time to devote to breeding and are more productive as a consequence. Consistent both with von Haartman's and with Greenberg's views is a recent report by Schwabl (1983) that sedentary male European blackbirds *Turdus merula* are more productive than migrants, evidently because they become territorial before migrants return to breed and therefore are able to occupy better breeding territories and also to begin breeding earlier, when nest success is high. Migratory blackbirds, Schwabl suggests (citing Lack), may compensate for their loss of productivity by higher annual survivorship.

For the junco's differential migration, we proposed (1983a) a hypothesis that, like Lack's (1954, 1968), both emphasized differences in winter mortality according to location of the winter residence and also treated migration as an important cause of mortality. But whereas Lack emphasized that survivorship of migrants and non-migrants balances out only over the years, we proposed for juncos that equalization between the survivorship of long- and short-distance migrants might occur over the winter and migration seasons, i.e., within a single year. This argument is developed below.

**Table 1**  
The effects of migration distance and wintering latitude on  
passerine population dynamics (after Greenberg 1980).<sup>a</sup>

	Adult Annual Survivorship $\bar{x}$ of (n spp)	Annual Productivity <sup>b</sup> $\bar{x}$ of (n spp)
Long-distance migrants overwintering in subtropics or tropics	57% (14)	2.68 (13)
Residents, partial migrants overwintering in temperate zone	47% (14)	5.14 (5)

a = Data summarized from Tables 1 and 2, Greenberg (1980). Where Greenberg listed several estimates for the same species, we averaged these to produce a single estimate.

b = Number of young leaving nest, on season-long basis, per female adult.

Finally, Baker (1978), drawing on ideas of Fretwell (1972), reasoned that variation in the migrations of population classes may continue indefinitely despite inequality of fitness among the classes. If winter occupancy of a certain region leads to greater productivity without associated decrease in probability of survival, and if the winter resources of the region are insufficient to support the entire population, one or more classes may be more successful than the other(s) in controlling these resources. In this despotic situation (Fretwell 1972), the less successful birds will migrate if to do so raises their expected fitness above the level that is probable if they do not migrate. This model may account for cases in which adults are dominant over young and are sedentary or make short migrations while young make longer movements (see Gauthreaux 1982 and this volume). Thus Hilden (1982) found that in the partially migratory Finnish goldcrest (*Regulus regulus*), adults, which are dominant over young, tended not to migrate and young to migrate. Winter mortality of migrants and non-migrants was equal, but non-migrants were more productive because they were able to occupy the best territories, doing so before migrants returned in spring. Because migratory behavior differences were associated with age (an individual's behavior changed as it grew older), Hilden regarded genetic polymorphism as an unlikely mechanism to account for his data. The age difference in migratory behavior could be proximately caused (Pulliam and Parker 1979; Gauthreaux 1978, 1982); e.g., young might migrate only as the result of direct interactions with adults (Hilden 1982). Or, if it were almost invariably advantageous for young to migrate, selection may have produced a developmental program having that obligate result.

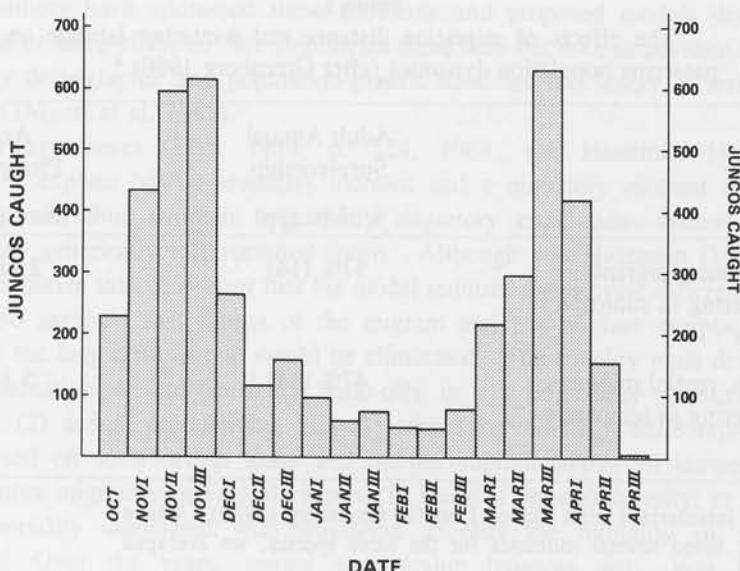


Figure 1

Dates of first capture in southern Indiana of 4550 individual juncos, according to approximately ten-day intervals, four years pooled. Capture efforts were approximately equal at all dates in all years.

Sexual differences in migratory behavior would seem to provide the special case. Because fitness of the sexes is equal by definition, any sexual differences in average survivorship (e.g., Prŷs-Jones 1977) would have to be made up in average productivity. Males, if despotic over females, might be more likely than females to survive winter, but their chances of obtaining a mate might then be decreased, and differences in migratory behavior could persist.

Because of the rarity of demographic data relevant to these hypotheses, we summarize data for the dark-eyed junco, despite their gaps, and describe our view of the evolution and maintenance of differential migration in that species.

#### DIFFERENTIAL MIGRATION IN THE DARK-EYED JUNCO

The dark-eyed junco breeds principally in Canada and winters in the United States. In the eastern United States where our field work has focused, autumn migration is first detected in September, reaches its peak at the middle latitudes of the winter range in November, and concludes by about 1 December (Fig 1). Spring migration takes place between about 1 March and early May (Fig 1).

In winter, female juncos are found, on average, farther from the breeding ground than males, and within each sex, adults (birds in the second or later winter of life) tend to be located south of young produced in the preceding breeding season (Fig 2). Males dominate females at food sources in winter, and adults dominate young of their sex (Balph 1978, Baker and Fox 1978, Ketterson 1979). Body size varies in the

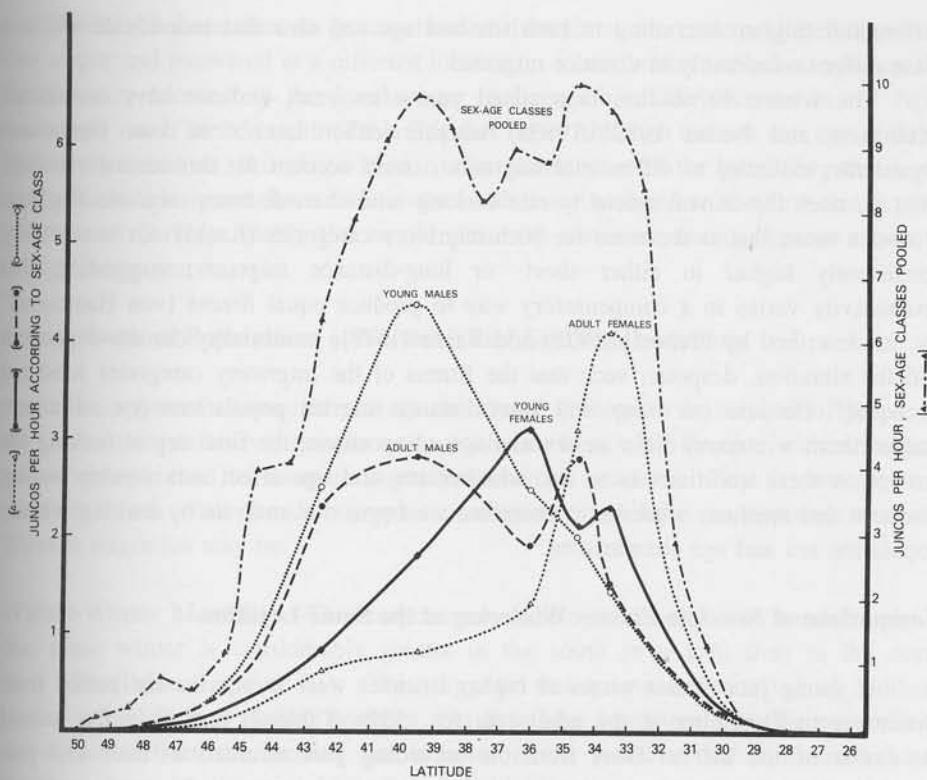


Figure 2

Estimated relative abundance of juncos in the winter range (top curve) and estimated relative abundance of the sex and age classes (lower series of curves), all according to degree of latitude (from Ketterson and Nolan 1983a; reprinted by permission from Current Ornithology, Volume 1, Copyright 1983, Plenum Publishing Company).

same order, and the differences in body size appear to cause the correlation between dominance rank and sex and age (Ketterson 1979). Juncos are monogamous, and our field observations (unpublished) indicate that individuals of both sexes regularly breed as yearlings.

The breeding origins of winter populations are unknown, but we conclude from the winter distribution that (1) females make longer migrations, on average, than males, and (2) adults make longer migrations than young. Conclusion (1) assumes either that the adult sex ratio in the breeding range is invariant with latitude or, if it is not, that the proportion of breeding adult females does not decrease toward the north. Conclusion (2) assumes either that the ratio of young to adults just preceding fall migration is invariant with latitude or, if southern breeding populations produce more young per adult, that the migration of juncos is not of the leap-frog type. Evidence to date is against the possibility that breeding populations tend to remain intact in the winter range, which would be the effect produced by leap-frog migration. Reasons for thinking instead that breeding populations intermingle in winter are detailed elsewhere (Ketterson and Nolan 1982). Figure 1 thus reveals, we believe, that the junco is a

differential migrant according to both sex and age and also that individuals within a class differ considerably in distance migrated.

The winter distribution is repeated year after year, and we have considered (Ketterson and Nolan 1982, 1983a) whether either Lack's or von Haartman's arguments, extended to differential migration, could account for this annual stability. That is, does the annual mortality rate of long- and short-distance migrants fluctuate around a mean that is the same for both migratory categories (Lack)? Or is mortality consistently higher in either short- or long-distance migrants, suggesting that productivity varies in a compensatory way to produce equal fitness (von Haartman)? Or, as described by Fretwell (1972) and Baker (1978), is mortality density-dependent and the situation, despotic, such that the fitness of the migratory categories need not be equal? Because our long- and short-distance migrant populations (i.e., southern and northern winterers) differ in sex and age composition, the first step in seeking the answer to these questions is to ask whether sex and age affect survivorship among southern and northern winterers. Therefore we begin our analysis by making within-population sex and age comparisons.

### Comparison of Sex-Age Classes Wintering at the Same Location

If young juncos that winter at higher latitudes were to survive the period from December to December at the adult rate (ca. 50%, Table 2) and if in the second December of life all survivors from the preceding year returned to their first-year wintering latitudes, the observed annual surplus of young juncos in the north could not be maintained. Instead, the proportion of adults to young would be 50:50 throughout the range. Since the proportions do vary year after year from north to south, either (1) annual survivorship is lower among northern-wintering first-year juncos than among northern-wintering adults, or (2) survivors among northern-wintering first-year juncos tend to travel farther southward in their second autumn migration when they are adults, or (3) both. The annual rate of return to (recapture in) the north by juncos banded there as young is lower than the rate of return there by those banded as adults (Table 3, point A1). This could be seen as support for either possibility (1) or (2), but for several reasons we believe that northern-wintering young probably survive the period December-to-December as well as do northern-wintering adults. First, in each of two winters at northern, midrange, and southern latitudes, the sex-age ratios of samples of junco populations ( $n$  ca. 1300) caught in early winter remained constant until winter's end (Table 3, point A2). This absence of overwinter change suggests strongly that first-year birds, regardless of sex, survive winter (a season when young birds might still be at special risk because of inexperience and probably the limiting season for juncos) as well as do adults at the same place. Second, in two winters and at two locations (northern and southern), the likelihood that a bird captured and banded in early winter ( $n = 335$ ) would be recaptured at the same site in late winter was independent of sex and age (Table 3, point A3). This too points to equal overwinter survivorship among the sex-age classes. As for possibility (2) above—that some individuals migrate farther southward when adult than when young—U.S. Fish

and Wildlife Service data on juncos banded throughout the eastern United States in one winter and recovered at a different location in a later winter, reveal a tendency for the recovery location in the later winter to lie south of the location in the first, sometimes much farther south (Table 3, point B4). Although the sex and age of these birds were unknown, this observation is also consistent with the possibility that some young birds that spend the winter in the north form no bond to the first winter site, i.e., do not develop fidelity that would cause the survivors among them to return in the following year.

### Comparisons of Populations at Northern and Southern Locations

The apparent absence of sex-age associated differences in survival of juncos at the same location (above) permits us to pool data from each location without respect to sex or age, then to compare populations across locations. That is, we are in a position to ask what the demographic consequences of long- as opposed to short-distance migration may be.

**Within-Winter Mortality**—The recapture rate in late winter of juncos banded early in that same winter is considerably greater in the south ( $n = 136$ ) than in the north ( $n = 198$ ; Table 3, point B1). This suggests that overwinter survival of southern juncos is higher than that of northern, but it is also consistent with the possibilities that dispersal from the banding site is lower in the south or that both survival and dispersal vary with latitude. U.S. Fish and Wildlife Service records indicate no lower within-winter dispersal in the south (Table 3, point B2), although these records are summarized in a way that would not reveal geographic differences in movement over very short distances. We suspect that northern-wintering juncos are, in fact, likely to have larger home ranges than those in the south, because food is more patchily distributed when snow and ice cover the ground, as is more frequently the case in the north. But this climatic difference also makes it highly probable, and there is anecdotal evidence, that winter mortality is greater in the north.

**Annual Mortality**—Despite the geographic difference in within-winter recapture rates, annual rates of return (year-to-year recapture rates) of adults to the north ( $n = 279$ ) and the south ( $n = 171$ ) are statistically invariant (Table 3, point B3). This leads us to propose that annual mortality is independent of latitude of the wintering site. A corollary hypothesis is then that mortality rates at some season(s) other than winter also vary with wintering latitude, i.e., that compensating seasonal rates account for the geographical equality among annual rates. If southern-wintering juncos suffer high non-winter losses that balance out their greater survivorship during winter, it is most probable that these losses occur during and as a result of their longer migrations. It follows that all sex-age classes, regardless of wintering location, could survive equally well in the 12 months between one December and the next. Further, it is unnecessary to hypothesize, as the basis for the winter distribution, either variation in productivity correlating with distance migrated or the existence of a despotic situation. In offering

**Table 2**  
 Independent estimates place annual survival of adult juncos  
 at approximately 50%

1.	Based on return rate of of male juncos to former breeding territories, Wawa, Ontario <sup>a</sup>	53% <i>n</i> = 49
2.	Based on return rate of juncos already known to be site-faithful to wintering area, males and females, in Bloomington, Indiana. <sup>b</sup>	53% <i>n</i> = 128
3.	Based on interval between banding and recovery among birds banded in one winter and recovered in a later winter, USFWS data. <sup>c</sup>	54% <i>n</i> = 85
4.	Based on proportion of adult birds present at beginning of winter. <sup>d</sup>	≥ 46%

<sup>a</sup> = Ketterson and Nolan 1983a, plus additional data. Included were birds known to be territorial in one year and to have returned in the following year. Data were gathered in summers of 1981, 1982, and 1983.

<sup>b</sup> = Ketterson and Nolan 1982, p. 250.

<sup>c</sup> = Ketterson and Nolan 1982, Table 5.

<sup>d</sup> = Ketterson and Nolan 1983a, planimetry of Figure 2.

We summed the areas under the sex-age curves and computed the percentage of that sum contributed by adults. In a stable population, the age structure would correspond to survivorship.

this view, we emphasize two points. First, we expect that the mortality of young between attaining independence and beginning fall migration exceeds that of adults (Perrins 1980) and that their death rate continues to be higher during migration (Greenberg 1980). But those still alive in December, at the conclusion of migration, appear to have passed beyond the period of special risks stemming from youth (compare the similar findings for the great tit *Parus major*, Perrins 1980). Second, we do not argue that populations from different wintering latitudes invariably experience equal annual mortality, i.e., that seasonal mortality rates of winter populations balance out every 12 months. We wish only to point out that equalization

**Table 3**Summary of junco population dynamics<sup>a</sup>

- A. Within population comparisons at wintering sites:
  - 1. Annual return rates differ geographically and, at a single location, according to age. In the north, adults are more likely than young to return the following year. In the south, return rates are equal.
  - 2. Sex-age ratios differ geographically, but at a single location they do not change from early to late winter.
  - 3. Frequency of recapture at end of winter of individuals marked in early winter differs geographically, but at a single location it is independent of sex and age.
- B. North-south comparisons across wintering populations:
  - 1. Late-winter recapture of birds banded early in same winter are significantly greater in south than in north.
  - 2. USFWS recovery data do not indicate geographic variation in mid-winter dispersal.
  - 3. Annual return rates to north and south are equal among adults.
  - 4. USFWS recovery data indicate that northern-wintering juncos are more likely to move between seasons; moves tend to be southward.
  - 5. Annual return rates among young are lower to north than to south.
- C. Interpretation:
  - 1. Beginning in early winter, survival at a wintering site is sex- and age-independent.
  - 2. Southern-wintering juncos survive winter at a higher rate than northern-wintering juncos.
  - 3. Southern-wintering juncos apparently experience higher migration mortality than northern-wintering juncos.
  - 4. Annual survival from one early winter to the next does not differ north to south.

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<sup>a</sup> After Ketterson and Nolan 1982, 1983a.

of mortality rates appears, among juncos, to be capable of taking place over shorter time intervals than the long periods proposed by Lack (1954, 1968).

**Interspecific Comparisons**—Is there inconsistency between this hypothesis and that of Greenberg (1980), who also emphasizes variation in overwinter survivorship but finds compensation in countervailing variation in productivity rather than mortality associated with distance migrated? Given that Greenberg was concerned with

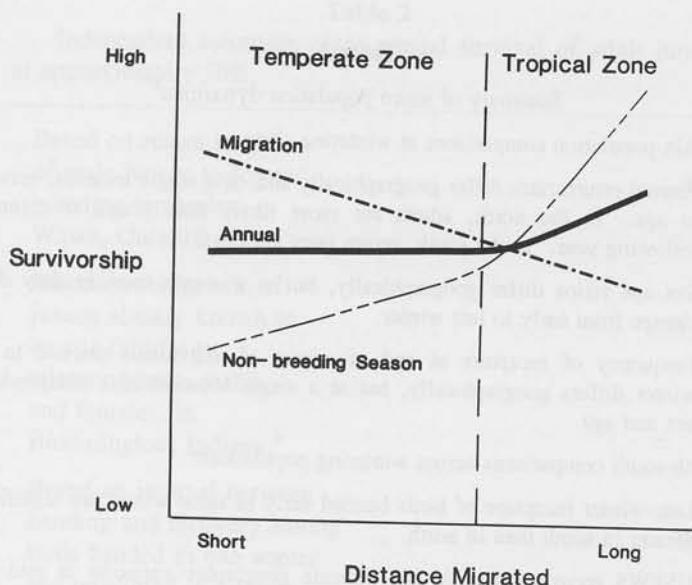


Figure 3

Schematic hypothetical representation of the manner in which temperate- and tropical-wintering passerine bird species that breed in the temperate zone might differ with respect to the interaction of winter and migration mortality resulting in variation in annual survival among species.

interspecific differences and therefore could not control for many variables that are automatically controlled for in within-species comparisons, there is no necessary tension between the two models. Nevertheless, because of the importance we attach to the relationship between migration distance and migration mortality, we ask how tropical-wintering passersines that make longer migrations than juncos can exhibit higher annual survivorship. If the slope relating migration distance to migration mortality is shallow, whereas the function relating migration distance to winter survival is steep or sharply curvilinear (as depicted hypothetically in Figure 3), tropical migrants could experience higher annual survivorship than temperate-zone migrants, even though the two groups suffered comparable mortality per unit distance traveled during migration.

#### WHY SEX-AGE DIFFERENCES IN TENDENCY TO MIGRATE OR IN DISTANCE MIGRATED?

If male and female juncos, young and adult, survive equally well from winter to winter regardless of distance separating breeding and wintering sites, what ultimate factors might be responsible for the observed sex-age differences in migratory distances? If we assume that average survivorship or productivity of the members of the various classes would decrease were they to behave other than they do (Ketterson and Nolan 1983a), then the question is not only what the ultimate factors are, but how they may differ in their impact according to class. Recent reviews addressing these

questions (Gauthreaux 1978, 1982 and this volume; Baker 1978; Greenwood 1980; Myers 1981; Ketterson and Nolan 1983a) have proposed as ultimate factors a number of social and other environmental variables, among them: (1) breeding-season social organization, including whether males defend territories (i.e., resources) or mates (Greenwood 1980), and degree of intrasexual competition for breeding resources (Myers 1981); (2) non-breeding-season social organization, including the extent to which family units remain together, thus precluding partial or differential migration (Emlen 1978), and the impact of any interclass differences in competitive status arising out of dominance (Gauthreaux 1978, 1982, this volume); (3) sex- or age-related differences in physiological tolerance of severe weather or in costs of migrating (Ketterson and Nolan 1983a); or (4) some combination of the above (Baker 1978, Ketterson and Nolan 1983a). For example, in an effort to account for a sexual difference in a species' migratory behavior, it might be supposed that something about the breeding social organization (e.g., a monogamous mating system, with males territorial) would cause the productivity of the average male to decline if he were to winter farther from the breeding ground. To females, non-breeding social organization might be of paramount importance. If females suffered dominance-related disadvantages when overwintering with males, selection might favor longer migrations by females.

Applying these notions to the junco, we have identified (Ketterson and Nolan 1983a) as the selective factors most likely to have affected the sex-age classes differentially: (1) the likelihood of death during migration, (2) the importance of early return to the breeding ground, and (3) the advantage of avoiding high densities of conspecifics (Fig 4). Factors (1) and (2) would favor shorter migrations, and factor (3), because the winter range apparently fills from north to south, would favor continuation of migration southward (Pulliam and Parker 1979). Shorter migrations by young are probably primarily attributable to factor (1) because the probability of death per unit distance migrated is doubtless higher during their first autumn than ever again in their lives (Ralph 1971, Nolan 1978, Greenberg 1980). On the other hand, factor (3) may have been predominant in the evolution of the adult pattern. That is, individuals of any class moving southward would be likely to experience the advantages stemming from escaping high population densities (Pulliam and Parker 1979); but if the costs of extending the migration were lower for adults, it is they that would be expected to keep moving. Factor (1) probably accounts for the sexual differences observed. Young males, never having occupied a territory and soon to require one if they are to breed, are likely to benefit most from early return. But males, regardless of age, must have territories before females arrive, or they will at best have abbreviated opportunities to reproduce.

What of the role of dominance? In the present state of knowledge, dominance alone cannot account for the junco's migration pattern. Adults are dominant to young, yet they tend to make longer migrations, and at none of the sites we studied did the dominant sex or age class appear more likely than the subordinate ones to survive winter. It is possible, however, that those adults that settle south of young did in fact

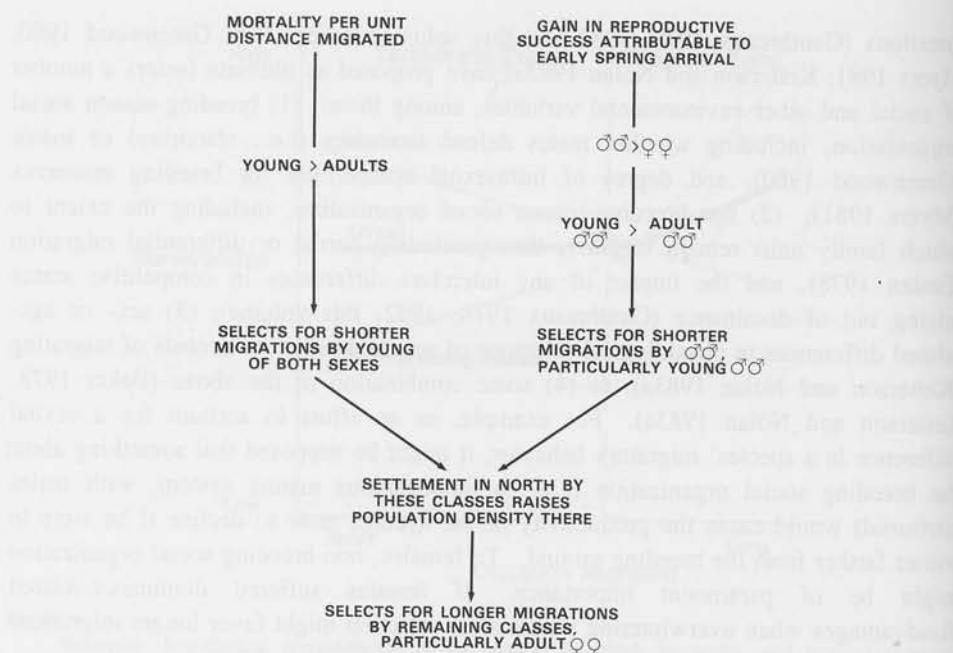


Figure 4

Selective factors proposed to account for the differential winter distribution of the dark-eyed junco in eastern North America (from Ketterson and Nolan 1983a; reprinted by permission from Current Ornithology, Volume 1, Copyright 1983, Plenum Publishing Company).

extend their migrations because they were unable to dominate those young. That is, investigations of sex- and age-related dominance rarely consider the histories of individuals making up the population sampled, and the young members of the sample may already have excluded some potential adult settlers before the investigation began. Alternatively, the distribution of adult males might be explained as the hyperdispersion of those individuals that are *a priori* most likely to be at the top of a dominance hierarchy. However, in our opinion, until more is known of the relationships between rank in a hierarchy, ability to defend resources, and tendency to disperse or migrate, further speculation would be premature.

## REGULATION OF DISTANCE MIGRATED

### Introduction

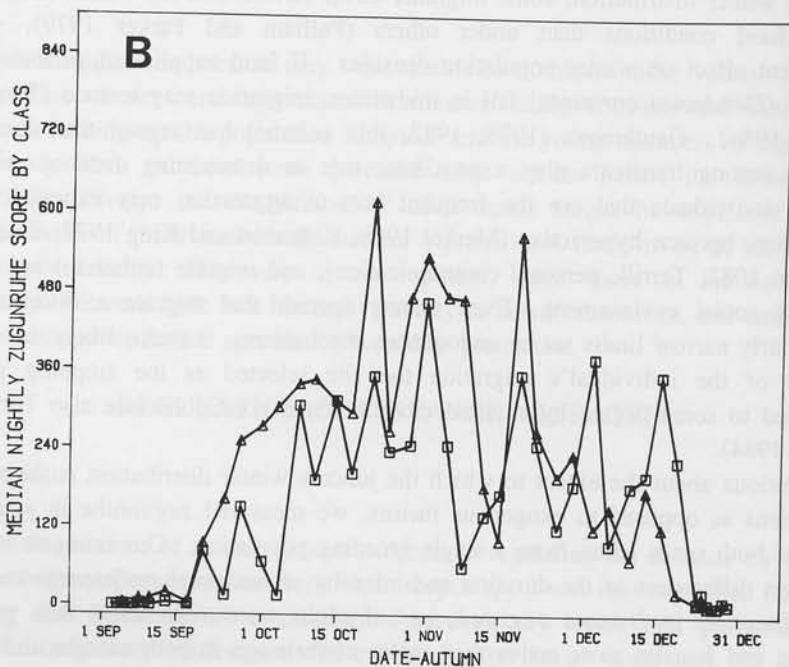
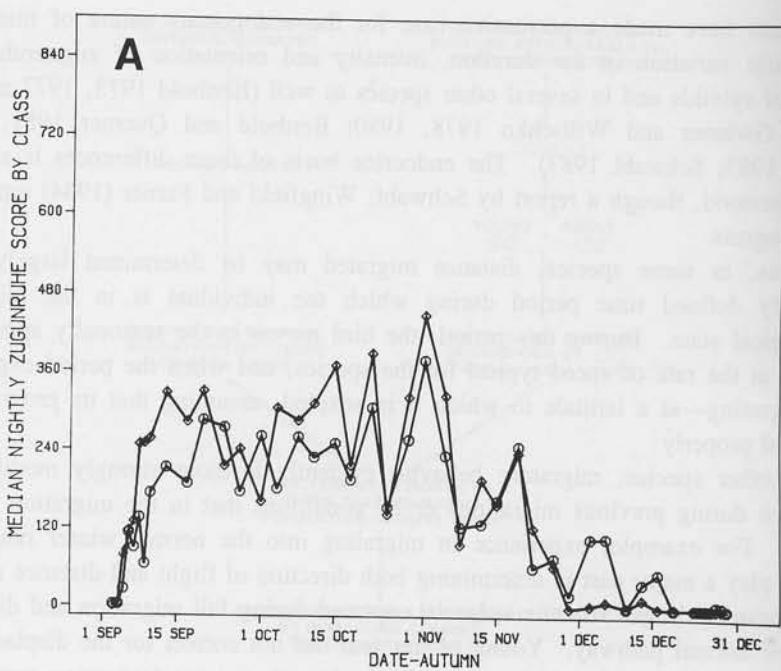
The importance of an endogenous program in regulating the distance traveled by first-time migrant European warblers (*Phylloscopus spp.*) was first suggested (Gwinner 1968) by the discovery of a correlation between (1) levels and proportions of zugunruhe (migratory restlessness) in caged, inexperienced birds and (2) distance covered toward the winter range during the same time interval by migrating conspecifics. Since that discovery, comparative studies and more recently breeding

experiments have made a persuasive case for the endogenous nature of inter- and intraspecific variation in the duration, intensity and orientation of zugunruhe in a number of sylviids and in several other species as well (Berthold 1973, 1977 and this volume; Gwinner and Wiltschko 1978, 1980; Berthold and Querner 1981, 1982; Biebach 1983; Schwabl 1983). The endocrine basis of these differences is still not well understood, though a report by Schwabl, Wingfield and Farner (1984) represents recent progress.

Thus, in some species, distance migrated may be determined largely by a genetically defined time period during which the individual is in the migratory physiological state. During this period, the bird moves in the seasonally appropriate direction at the rate of speed typical for the species, and when the period expires, it quits migrating—at a latitude to which it is adapted, assuming that its program has functioned properly.

In other species, migratory behavior evidently is more strongly modified by experience during previous migrations or by conditions met in the migration then in progress. For example, experience in migrating into the normal winter range was found to play a major part in determining both direction of flight and distance traveled by European starlings (*Sturnus vulgaris*) captured during fall migration and displaced from their normal pathway. Young of the year did not correct for the displacement, whereas many adults did correct and headed back to the winter destination appropriate for the population, where presumably they had spent the previous winter(s) (Perdeck 1958, 1967). Food abundance along the route of migrating sparrows has been shown to affect winter distribution; some migrants travel farther into the winter range under certain food conditions than under others (Pulliam and Parker 1979), with a consequent effect on winter population densities. If food supplies of yellow-rumped warblers (*Dendroica coronata*) fail in midwinter, migration may resume (Terrill and Ohmart 1984). Gauthreaux (1978, 1982, this volume) has argued that dominance relations among transients play a proximate role in determining distance migrated. That is, individuals that are the frequent butt of aggression may experience food deprivation, become hyperactive (Merkel 1966, Ketterson and King 1977, Stuebe and Ketterson 1982, Terrill, personal communication), and migrate farther toward a more favorable social environment. Even among species that migrate a distance fixed within fairly narrow limits set by endogenous mechanisms, it seems likely that toward the end of the individual's migration the site selected as the stopping point is influenced to some degree by external environmental conditions (see also Terrill and Ohmart 1984).

Curious about the extent to which the junco's winter distribution is the result of endogenous as opposed to exogenous factors, we measured zugunruhe in young and adults of both sexes taken from a single breeding population. Our rationale was that if sex-age differences in the duration and intensity of nocturnal restlessness correlated with differences in distance migrated, i.e., if adults were more active than young of their sex and females more active than males of their age in both autumn and spring, then some role for an endogenous program would be indicated. Such an observation would open the possibility of a sex-linked genetic basis for the differential migration



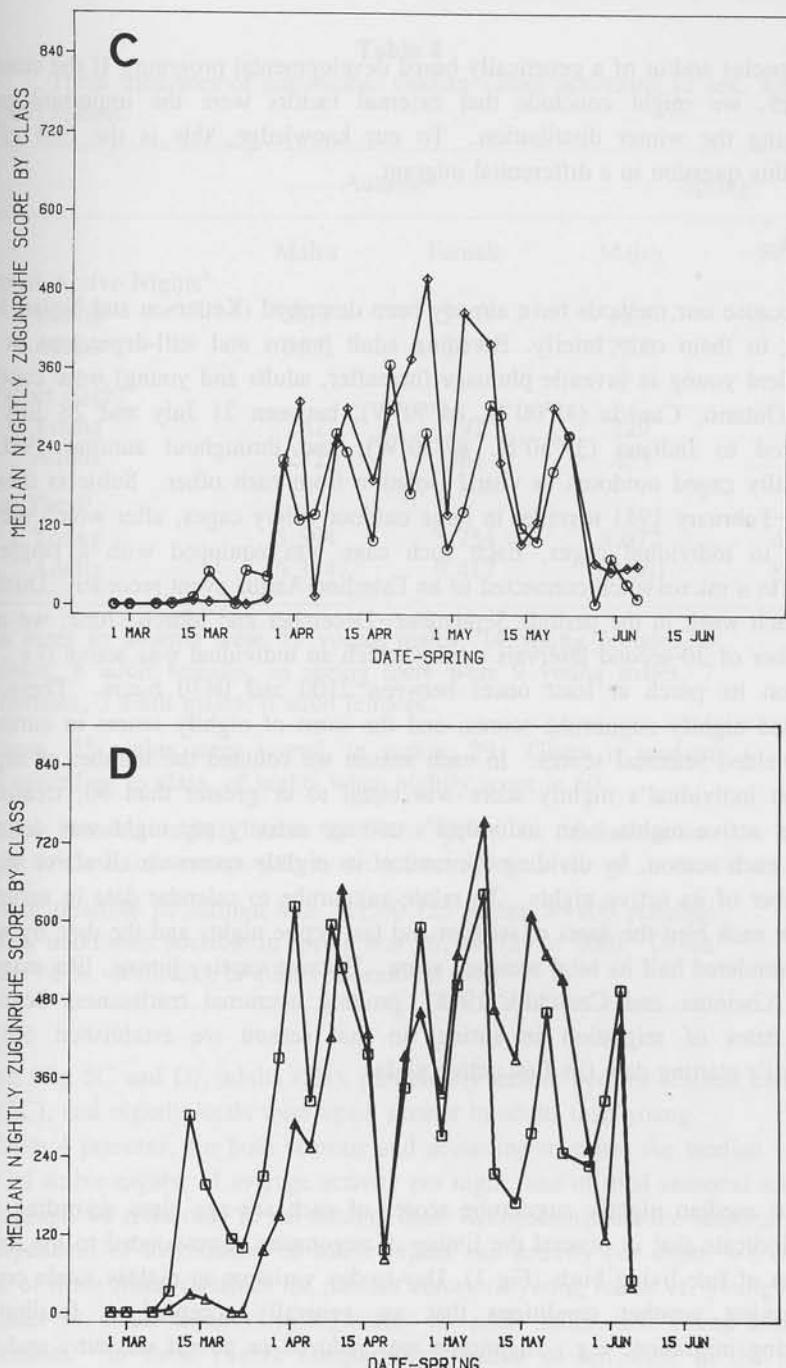


Figure 5

Median nightly zugunruhe score (number of 30-second intervals with activity between 2100 and 0430) according to date (activity determined two nights per week), season, and sex-age class. (Young males,  $n = 19$  in autumn, 9 in spring, circles; young females,  $n = 14$  in autumn, 7 in spring, diamonds; adult males,  $n = 8$  in autumn, 3 in spring, squares; adult females,  $n = 9$  in autumn, 6 in spring, triangles.) (A) upper, facing page: young in autumn; (B) lower, facing page: adults in autumn; (C) upper, above: young in spring; (D) lower, above: adults in spring.

of this species and/or of a genetically based developmental program. If the classes did not differ, we might conclude that external factors were the important ones in determining the winter distribution. To our knowledge, this is the first effort to address this question in a differential migrant.

### Methods

Because our methods have already been described (Ketterson and Nolan 1983b), we refer to them only briefly. Breeding adult juncos and still-dependent or newly independent young in juvenile plumage (hereafter, adults and young) were captured at Wawa, Ontario, Canada ( $48^{\circ}00'N$ ,  $84^{\circ}50'W$ ), between 21 July and 28 July 1980, transported to Indiana ( $39^{\circ}50'N$ ,  $87^{\circ}30'W$ ), and throughout autumn 1980 were individually caged outdoors in visual isolation from each other. Subjects then spent January–February 1981 together in large outdoor aviary cages, after which they were returned to individual cages. Each such cage was equipped with a single perch attached to a microswitch connected to an Esterline-Angus event recorder. During two nights each week in the periods September–December and March–June, we counted the number of 30-second intervals during which an individual was active (i.e., left or landed on its perch at least once) between 2100 and 0430 hours. These values constituted nightly zugunruhe scores, and the sums of nightly scores in autumn and spring yielded seasonal scores. In each season we counted the number of nights on which an individual's nightly score was equal to or greater than 60, treating such nights as active nights. An individual's average activity per night was determined, again in each season, by dividing the total of its nightly scores on all active nights by the number of its active nights. To relate zugunruhe to calendar date in autumn, we noted for each bird the dates of its first and last active nights and the date by which it had accumulated half its total seasonal score. Because captive juncos, like many other species (Gwinner and Czeschlik 1978), prolong nocturnal restlessness beyond the normal dates of migration in spring, in that season we established only each individual's starting date (its first active night).

### Results

The median nightly zugunruhe scores of each sex-age class according to date (Fig 5) indicate that in general the timing of zugunruhe corresponded to the timing of migration of free-living birds (Fig 1). Day-to-day variation in nightly totals correlated with varying weather conditions that are generally accepted as facilitating or suppressing migration, e.g., zugunruhe was reduced or absent on rainy and stormy nights. Inspection of Figure 5A and B, reveals several trends in autumn:

1. young juncos (5A) appear to have begun and ended zugunruhe at earlier dates than adults (5B),
2. nightly totals appear to have been greater in adults than in young, and
3. sexual differences were slight, with females tending to be more active than males early in the season and males more active than females later in the season.

**Table 4**

Three measures of zugunruhe; median values according to sex, age and season.

	Autumn <sup>a</sup>		Spring <sup>a</sup>	
	Males	Female	Males	Females
Number of Active Nights <sup>b</sup>				
Young	23.7	21.0	15.8	18.3
Adults	21.0	23.0	23.0	20.5
Activity per Night <sup>c</sup>				
Young	247	292	229	272
Adults	272	361	453	432
Seasonal Total <sup>d</sup>				
Young	5,594	5,754	4,072	4,522
Adults	6,314	9,417	10,861	8,842

<sup>a</sup>Sample sizes in autumn were 19 young males, 14 young females, 9 adult males, 8 adult females; in spring there were 9 young males, 7 young females, 3 adult males, 6 adult females.

<sup>b</sup>In autumn, 35 nights were scored; in spring, 29. Given is median number according to class, of nights when nightly score  $\geq 60$ .

<sup>c</sup>Maximum possible nightly score is 900. Given is median score, according to class, of average activity on active nights.

<sup>d</sup>Maximum possible in autumn was 31,500 (35 nights  $\times$  900 possible per night), maximum possible in spring was 26,100 (29  $\times$  900). Given is median value, according to class, of seasonal total.

In spring (Fig 5C and D), adults (5D), particularly males, became restless earlier than young (5C), and nightly totals were again greater in adults than young.

Table 4 presents, for both seasons and according to class, the median values of number of active nights, of average activity per night, and of total seasonal scores. In this paragraph we refer only to the autumn data. Recognizing that the seasonal score is not independent of the number of active nights and activity per night, we compared for each of these three variables the median values of young males vs. young females, adult males vs. adult females, young males vs. adult males, and young females vs. adult females. In these twelve comparisons, results of ten were in the direction predicted by the winter sex-age distribution. Despite this, few statistical tests permit rejection of the null hypothesis that the classes did not differ (Table 5). For number of active nights, classes were statistically indistinguishable. For average activity per night, adult females were more active than adult males, but other comparisons showed no differences. For seasonal scores, adult females accumulated higher totals than young females. One pattern was clear (Table 6): age determined the calendar

**Table 5**  
Results of statistical comparisons according to sex and age<sup>a,b</sup>.

		Number of Nights	Activity/Night	Seasonal Total
<b>Autumn 1980</b>				
Age	Young male/adult male	n.s.	n.s.	n.s.
	Young female/adult female	n.s.	<i>p</i> < 0.10	*
Sex	Young male/Young female	n.s.	<i>p</i> < 0.10	n.s.
	Adult male/Adult female	n.s.	*	<i>p</i> < 0.10
<b>Spring 1981</b>				
Age	Young male/Adult male	*	*	*
	Young female/adult female	<i>p</i> < 0.10	n.s.	*
Sex	Young male/young female	n.s.	n.s.	n.s.
	Adult male/Adult female	n.s.	n.s.	n.s.

<sup>a</sup>Mann-Whitney U; \* signifies one-tailed *p* < 0.05; n.s. signifies one-tailed *p* > 0.10.

<sup>b</sup>See text for definitions of variables.

schedule of restlessness, with young birds, regardless of sex, beginning and ending their autumn restlessness some two weeks ahead of adults.

Turning to spring, nine of twelve comparisons were in the predicted direction (Table 4), and despite the small samples, several comparisons were statistically significant (Table 5). Adults became active significantly earlier (Table 6) and therefore tended to accumulate more active nights than young, and among males, adults were more active per night. In both sexes, adults had higher seasonal scores. None of the sexual comparisons produced statistically significant differences.

### Interpretation

If zugunruhe reflects a state of readiness to migrate, in autumn that state lasts approximately 85 days among juncos from the Wawa, Ontario, breeding population, regardless of sex-age class (Table 6). During this period these birds would probably migrate only on nights when weather conditions are favorable (Muller 1976, Richardson 1978) and energy stores adequate. Temporal variation in the occurrence of zugunruhe suggests that first-time migrants may begin and end migrating earlier i.e., may arrive at the winter site before adults. Thus adults, which undergo a complete molt after reproducing, may delay departure from the breeding range longer than

**Table 6**  
Onset and termination of zugunruhe according to sex-age class.<sup>a</sup>

	Autumn			Spring
	First Date $\geq 60$	50% Date	Last Date $\geq 60$	First Date $\geq 60$
Young males	7 Sept	18 Oct	9 Dec	29 Mar
Adult males	20 Sept	5 Nov	16 Dec	12 Mar
Young females	7 Sept	18 Oct	30 Nov	26 Mar
Adult females	19 Sept	1 Nov	16 Dec	26 Mar

<sup>a</sup>Median date, according to class, of individuals' first and last nights when nightly score  $\geq 60$  and date by which 50% of the seasonal total score had been accumulated. Age classes differed significantly (sexes combined, Mann-Whitney U, one-tailed  $p < 0.001$  for starting date in autumn;  $p < 0.05$  for ending date and 50% date in autumn and for starting date in spring). Sample sizes as in Table 4.

young (particularly early-brood young), which do not molt the remiges or the rectrices in acquiring the first basic plumage. If adults do migrate later, young might have the opportunity to establish some measure of site-related dominance on their winter home range based on their earlier arrival, i.e., prior residence (Balph 1979, Yasukawa and Bick 1980). Later-arriving adults may possess mechanisms that enable them to assess population densities and resources which are likely to be available in the coming winter at stop-over points and to react, either by migrating farther or by settling (Pulliam and Parker 1979). Alternatively, the earlier zugunruhe of young may correspond to late-summer and early-autumn movements having no southward orientation among free-living young of the year (Baker 1978, p. 630); in that case it would not translate into earlier arrival in the winter range.

Preliminary analysis of first-capture dates of juncos in relation to date does not indicate that the bulk of early-autumn arrivals in Indiana are made up of young (data not shown). However, when we compare dates of first capture of the year among individuals caught in two different autumns (no later than December), initially as young and later as adults, we obtain the following results (Table 7). Among 41 cases, 28 juncos were caught at an earlier date when they were young than when adult (sign test,  $z = 2.19$ , two-tailed,  $p = 0.028$ ). When the same comparison is made of 16 cases of birds caught in two autumns in *both* of which they were adult, the date in the first year was earlier in eight instances and later in the other eight. Further, in both the sample of 41 and the sample of 16, the median and mean first dates for the capture of young were at least one week earlier than the median and the mean first dates for adults (Table 7). These results are consistent with our data showing earlier onset and termination of zugunruhe in young, and priority in arrival time may play an important

**Table 7**

Initial capture dates<sup>a</sup> of juncos<sup>b</sup> caught in Indiana during more than one autumn, according to age in autumn of first capture.

Age in autumn of first capture	Date of First Capture		
	Autumn of first capture	mdn	Autumn of subsequent capture <sup>c</sup>
Young ( <i>n</i> = 41)	24 Nov	25 Nov	3 Dec
Adult ( <i>n</i> = 16)	18 Dec	10 Dec	17 Dec

a = Only individuals caught for the first time no later than December in both the first and later year are included.

b = Both males and females are included.

c = In a few cases the year of subsequent capture was separated from the year of first capture by a winter in which the individual was not caught at all.

role in determining the structure of winter populations. However, the results could be explained in other ways. Adults may be harder to catch than young and may escape capture for a longer time after settling in their winter quarters. Also, the rate of fidelity of juncos to winter sites is low. Therefore, site-faithful birds are not representative of the full population, and they may differ in other aspects of their migratory behavior as well, including its timing.

Whatever the significance of the age difference in the timing of autumn zugunruhe, the role of endogenous factors in determining differences in distance migrated is apparently not great. As indicated, the duration of the migratory state did not differ among classes, but there was a tendency toward greater activity per night by classes making longer migrations, and this might translate into earlier take-offs and longer flights by members of those classes. Greater activity per night might also reflect greater motivation to migrate under any particular set of weather conditions and therefore a higher probability that the individual will fly under those conditions. Collectively or alternatively, these tendencies could foster longer migrations by both females and adults, and further study of these possible mechanisms seems warranted.

Possible interpretations of the spring data are clouded by the persistence of restlessness beyond the normal dates for termination of migration (compare Figs 1 and 5). In addition, our samples were small. For either or both reasons, the differences in spring seasonal scores may be meaningless. The two tendencies in caged adults to become restless at earlier dates and to engage in more activity per night might represent, respectively, either an earlier initiation of migration or a longer migration

by free-living adults and longer flights per night. However, field evidence from Indiana has as yet revealed no earlier start of migration by adults than by young, when comparison is made of juncos known to have been members of the winter population (Ketterson and Nolan 1983a, Table 3).

## CONCLUSION

Clearly, our results are inconclusive as to the importance of endogenous factors in regulating distance migrated by the junco's sex-age classes. We are reluctant to ignore the fact that in both autumn and spring the interclass variation in zugunruhe scores tended to be consistent with expectations derived from the winter distribution, even though few differences were significant. On the other hand the data are equivocal at best, and it is reasonable to think that selection may have favored exogenous regulation in the junco. Weather varies greatly and unpredictably from year to year throughout eastern North America, affecting seed production in summer and food availability in winter (Pulliam and Parker 1979). The capacity to respond flexibly to this variation would have its advantages. Rabenold and Rabenold (1985) have found that members of the non-migratory mountain race of the dark-eyed junco disperse to different elevations from year to year, depending upon winter conditions. We might therefore expect in the migratory junco the ability to abbreviate migration distance when conditions predict favorable winter foraging conditions, at least to the extent of curtailing movement after completing some initial leg(s) of the migration.

Even if interclass differences are in some measure the product of endogenous regulation, we now believe that this would be difficult to detect in the junco. Monitoring of zugunruhe yields only an imprecise measure of the underlying physiological state, and in differential migrants all individuals are, by definition, in that state. Unlike the qualitative differences that distinguish migratory categories in partially migratory species like the European robin *Erithacus rubecula* and probably other partial migrants (Biebach 1983), any differences among differential migrants would be quantitative. Furthermore, winter populations of juncos at all latitudes are made up of all four sex-age classes. Only the ratios differ, and this suggests considerable variance in the distance migrated by members within the same sex-age class. For these reasons, even among juncos from a single local breeding population, detection of the existence of any endogenous regulatory component and of interclass differences in that component would require larger samples than we studied.

We conclude that our data provide some support for the hypothesis that an endogenous mechanism may affect the distance juncos migrate, but it seems unlikely that it supplies migrants with sufficient information to account for the differential distribution shown in Figure 2.

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