

AN ENDOGENOUS BASIS FOR DIFFERENTIAL MIGRATION IN THE DARK-EYED JUNCO¹

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Abstract. Male and female Dark-eyed Juncos, *Junco hyemalis hyemalis*, partially segregate along a latitudinal gradient in North America during winter. The sex ratio favors males in the north and females in the south. The sexes differ, not only in their midwinter distribution, but also in the timing of fall migration, with females passing through stopover sites earlier than males. To investigate the basis for these differences in migration patterns, several measures of migratory behavior, including the date of onset and the duration of migratory activity (*Zugunruhe*), were compared in captive adult male and female juncos. When held under the same photoperiod and given free access to food, females initiated fall *Zugunruhe* twelve days earlier than males and continued to be active after the males stopped. This resulted in females showing, on average, 21 more days of migratory activity. There was no difference between the sexes in the proportion of nights during the migration period spent exhibiting migratory activity or in the average amount of activity per bird for the season. Females briefly showed higher migratory activity in early September. Both sexes exhibited a significant increase in body fat at the onset of migratory activity but there was no significant difference between the two groups at any time during the sampling period. Although differences in social status, physiological constraints, and/or importance of early arrival have been proposed as both past and current factors influencing differential migration in many species, these data illustrate sufficient endogenous sex-related differences that can result in differential migration in Dark-eyed Juncos.

Key words: *Junco*; *Junco hyemalis*; migration; endogenous control; differential migration; sex-related differences.

INTRODUCTION

Differential migrants are species or populations whose age or sex classes segregate along an altitudinal or latitudinal gradient (Terrill and Able 1988). Segregation along a latitudinal gradient has been reported for many species including the Dark-eyed Junco, *J. h. hyemalis* (Ketterson and Nolan 1976, 1979), White-crowned Sparrow, *Zonotrichia leucophrys gambelii* (Morton 1984), House Finch, *Carpodacus mexicanus* (Belthoff and Gauthreaux 1991), Blackcap, *Sylvia atricapilla* (Terrill and Berthold 1989 and references therein), Snowy Owl, *Nyctea scandiaca* (Kerlinger and Lein 1986), Eurasian Wigeon, *Anas penelope* (Campredon 1983), and several species of shorebirds (Myers 1981).

Terrill and Berthold (1989) suggested two levels of regulation for the expression of differential migration: (1) environmental influences; and (2) endogenous control. Whereas several studies have

emphasized environmental factors such as competition for food and/or nest sites (Campredon 1983, Lundberg 1985, Kerlinger and Lein 1986, Byrkjedal and Langhelle 1986, Smith and Nilsson 1987), fewer studies have investigated the internal control of these behaviors (Schwabl et al. 1984, Ketterson and Nolan 1985, Terrill and Berthold 1989).

The Dark-eyed Junco is a short-distance temperate zone migrant, and much is known about its winter distribution. Ketterson and Nolan (1976, 1983a) reported the latitudinal segregation of age and sex classes of juncos in early to mid-winter. In general, they found males farther north than females and, within each sex class, first-winter birds north of adults. The sex-related pattern was stronger than that reported for the age classes. Not only do juncos segregate spatially, but males and females also differ in the timing of fall movements. Chandler and Mulvihill (1990a) reported the differential passage of the sex and age classes of juncos during fall migration in Pennsylvania, with adult females moving through first followed by hatching-year females, adult males and hatching-year males,

¹ Received 5 October 1992. Accepted 29 March 1993.

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respectively. These classes also showed a similar pattern of passage times for migrants and arrival times for winter residents in Indiana, except that the appearance of hatching-year females and adult males was reversed (Nolan and Ketterson 1990a).

Because fall migration in juncos begins while insects and seeds are relatively abundant, competition for food is probably not a proximate factor in its initiation. Even if food became limiting, several studies have shown that premigratory fattening (often influenced by the amount of available food) is not always necessary for the onset of the fall migration (for review see Berthold 1975). While laboratory studies of migratory activity in juncos have shown that food availability (directly or through social interactions) can influence the expression of *Zugunruhe* (Terrill 1987, Holberton 1991), males and females respond similarly to these factors. Thus it may be necessary to seek elsewhere for the basis of differential migration.

I investigated sex-related differences in the migratory behavior of adult male and female juncos in captivity and attempted to control as many environmental variables as possible. If females winter farther south than males and pass through stopover sites earlier, I predicted that (1) females may initiate *Zugunruhe* earlier than males, (2) females might show greater amounts of *Zugunruhe* and (3) females may show migratory behavior for a longer period of time. In addition to monitoring nightly *Zugunruhe*, I also compared the changes in the scores of subcutaneous body fat (often a measure of migratory condition in birds) between males and females throughout the migratory period.

METHODS

Juncos were captured with mist nets at baited sites in Albany County, New York (42°N), in October and November, 1987. All birds that had completely ossified skulls at the time of capture were considered to have hatched in a previous year and classified as "after hatching year." Those birds whose skulls showed some area of incomplete ossification were classified as "hatching-year" and were considered to have hatched during 1987. All of the birds were considered adults at the beginning of the next migration season and were treated equally. I pooled these two age classes because the only known age-related segregation in juncos is between hatching-year and after-hatching year birds (Ketterson and Nolan 1976,

1983a) and, therefore, any endogenous differences in migratory behavior would probably be undetectable between the two "adult" classes. The sex of each bird was determined on the basis of plumage characteristics and wing chord. Laparotomies performed in the following spring confirmed that the birds had been sexed correctly at the time of capture.

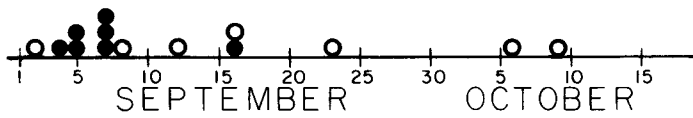
All birds were held under natural photoperiod, as experienced in New York State, in a large indoor aviary from fall, 1987 until August, 1988. Throughout the captive period the birds were offered, *ad libitum*, water and a mixture of turkey starter and white millet.

Beginning in August, 1988, I isolated 10 males and 10 females, selected at random, in individual wood and plexiglass activity cages, measuring 30 × 30 × 60 cm. Each cage contained one stationary perch and one perch that rested upon a microswitch wired to a counter so that I could measure individual *Zugunruhe*. All counters were controlled by a central power source that was connected to a clock-timer. Counters were turned on one-half hour after lights-out and switched off one-half hour before lights-on. A small, dim nightlight (approximately 3–5 lux) allowed the birds to exhibit perch hopping activity. All birds were housed in the same room but were visually isolated from each other. Appropriate seasonal changes in photoperiod were made each week.

I weighed and assigned furcular fat scores used by Manomet Bird Observatory (described in Cherry 1982) to each bird four times throughout the migratory period (26 Aug, 28 Nov, 12 Dec, 4 Jan). The birds were not handled between 26 Aug and 12 Nov because handling often suppresses *Zugunruhe* in this species (Holberton, unpublished data), and I wished to maximize the probability of each bird expressing true onset of *Zugunruhe*.

Based on experience with juncos in this laboratory, I defined, *a priori*, a rule for identifying the onset and termination of the migratory period. *Zugunruhe* was recorded as total hops per bird each night. A bird was considered to have initiated fall migration when it showed at least ten consecutive nights with at least ten hops/night. Each bird's migratory period was considered to have begun on the first night of the ten-day period meeting this criterion. Similarly, to have ceased showing migratory activity, a bird had to exhibit ten nights in a row with fewer than ten hops per night. The end of the migratory

ONSET



TERMINATION

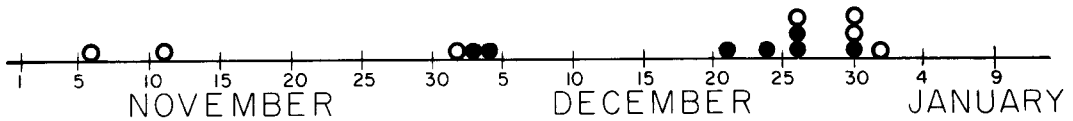


FIGURE 1. Dates of onset and termination of fall migration in seven male (open circles) and seven female (solid circles) juncos. See Table 1 for statistical comparisons.

period was defined as the first night of that ten-day period. Juncos show no nocturnal perch hopping activity when not in migratory condition.

Because females migrate longer distances than males (Ketterson and Nolan 1976, 1983a) and females pass through stopover sites earlier than males (Chandler and Mulvihill 1990a), I proposed directional alternate hypotheses and applied one-tailed statistical tests to examine sex-related differences in date of onset and termination of *Zugunruhe*, mean amount of activity for the season, and length of individual migration period. I used paired-sample *t*-tests for within-group comparisons and *t*-tests with transformations of the proportions for comparing the percent of nights with activity between males and females. Otherwise, I used non-parametric analyses because of the small sample sizes and lack of independence between mean and variance.

RESULTS

The study ended 4 January 1989, a date chosen, *a priori*, to encompass the migratory period of juncos in the Northeast (Chandler and Mulvihill 1990a). All of the females met the criterion for exhibiting *Zugunruhe* while only eight of the 10 males did so. This proportion of inactive birds is not uncommon for all age and sex classes of juncos and may be the result, not of an absence

of migratory activity, but of the inability to register hopping if the bird chooses to be active elsewhere in the cage (Holberton, unpubl. data). Seven of the active females and seven of the active males ceased *Zugunruhe* before the end of the experiment (4 January 1989). Because the beginning and ending dates for each bird were necessary to determine the length of the migratory period and the proportion of active nights, I included only those 14 birds in the analyses.

ACTIVITY

Females, on average, exhibited *Zugunruhe* 12 days earlier than males ($P < 0.05$, Mann-Whitney *U*-test), but the mean dates of termination of activity were not significantly different (Mann-Whitney *U*-test, Fig. 1, Table 1). The individual migration periods of the females were, on average, 21 days longer than those of the males ($P < 0.05$, Mann-Whitney *U*-test, Table 1). The mean activity of females was significantly higher than that of males only two times in the migration season ($P < 0.05$, Mann-Whitney *U*-test, Fig. 2). The relatively high amount of activity by males during the latter half of the migration period was heavily influenced by two birds whose activity contributed over 90% of the total amount of *Zugunruhe* for the group during November and December. The two groups did not differ in

TABLE 1. Measures of migratory activity for male and female juncos during fall 1988. Values are given as $\bar{x} \pm 1$ SE.

Beginning date	Ending date	Duration ^b (days)	Activity (hops/bird/night)	% nights with activity
Females				
8 Sept \pm 1.5	20 Dec \pm 4.5	104 \pm 4.3	760 \pm 317	88 \pm 3.6
Males				
20 Sept \pm 5.3	11 Dec \pm 9.4	83 \pm 6.8	1,315 \pm 710*	91 \pm 2.1

^a Sexes differed, $P < 0.05$, Mann-Whitney U -test, one-tailed.

^b Sexes differed, $P < 0.05$, Mann-Whitney U -test, one-tailed.

* Two males contributed at least 90% of the total activity for the group during November and December.

the individual mean hops/bird/night for the entire season (Mann-Whitney U -test, Table 1). Both sexes had similar proportions of nights when the birds were considered active (two-sample t -test, with angular transformations of the proportions, Table 1).

FAT

Males and females began the migration season with similar fat scores (26 August: $\bar{x}_m = 0.26 \pm$

0.1 SE, $n = 7$, $\bar{x}_f = 0.26 \pm 0.1$ SE, $n = 6$, data from one female were not obtained on this date, Mann-Whitney U -test, two-tailed, Fig. 3). Both sexes showed a significant increase in fat after *Zugunruhe* had begun (28 November: $\bar{x}_m = 1.5 \pm 0.2$ SE, $n = 7$, $\bar{x}_f = 1.5 \pm 0.2$ SE, $n = 6$, $P < 0.05$, paired-sample t -test, two-tailed). There was no significant difference in fat scores between the sexes throughout the study (Mann-Whitney U -test, two-tailed).

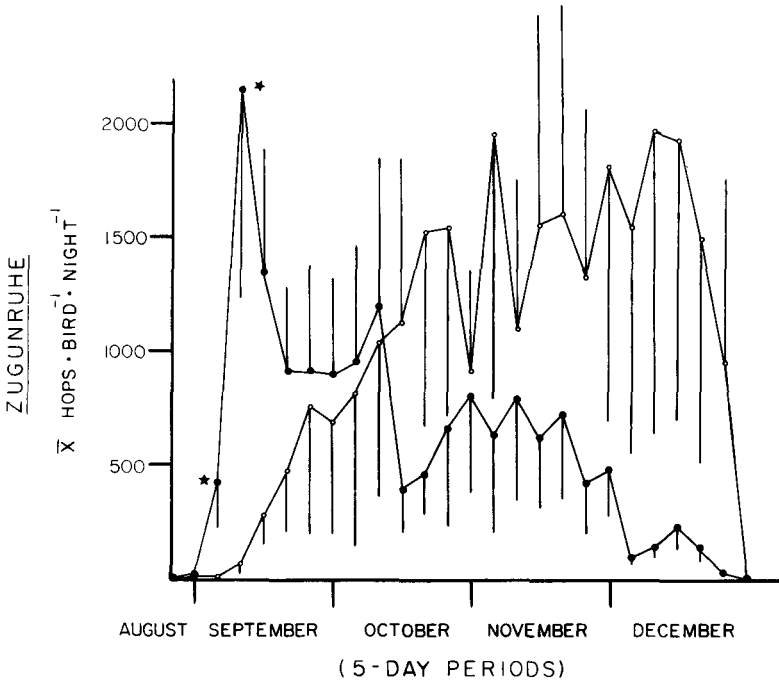


FIGURE 2. Mean (\pm SE) *Zugunruhe* (hops/bird/night) of seven male (open circles) and seven female (solid circles) captive juncos. Each point represents a group mean (of individual means) for each five-day period beginning 26 August and ending 4 January. Females showed statistically higher levels of activity only two times throughout the migratory period (stars) ($P < 0.05$, Mann-Whitney U -test, two-tailed). The unusually high activity of two males accounted for 90–95% of the group activity during November and December.

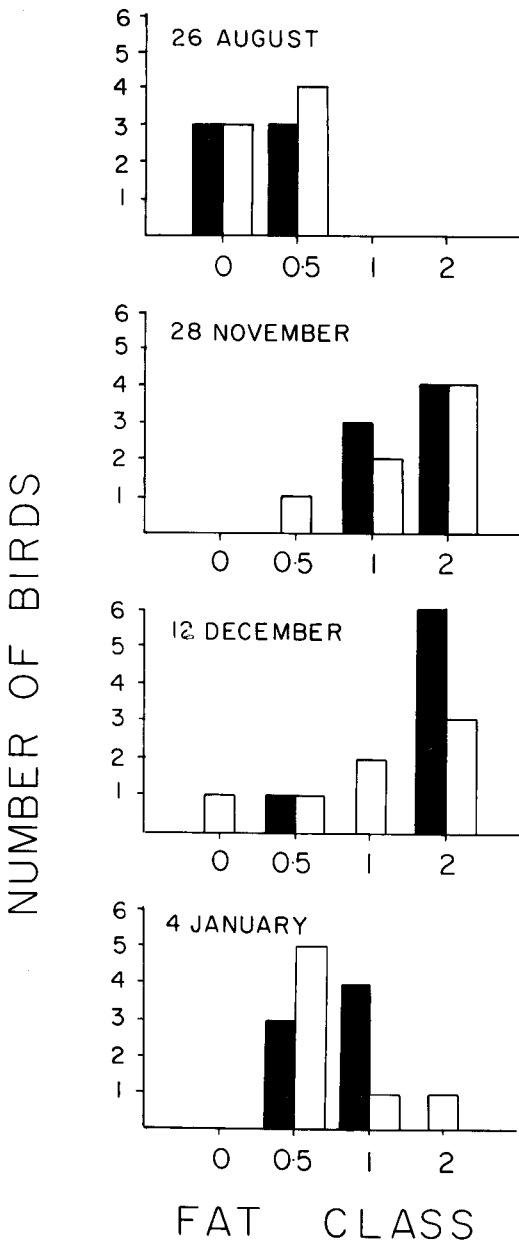


FIGURE 3. Changes in frequency distributions of fat classes for males (open bars) and females (solid bars) during fall migration. Fat data were not obtained for one female on 26 August.

DISCUSSION

Female juncos began to show migratory activity significantly earlier than males, resulting in a longer migration season for females. Although no statistically significant difference in termination

date was observed, the trend for females to shut off migratory activity later suggests that females may continue to migrate after males have ceased. The continuation of activity of three females after 4 January further support this. Females, on average, spent three weeks longer than males showing migratory activity. A longer migration period has been translated into greater distances migrated in the field (Berthold 1973). The genetic basis for differences in migration distance has been demonstrated in the Blackcap, another differential migrant (Berthold and Querner 1981, Berthold et al. 1990).

While some studies have also found endogenous differences in migratory behavior with age or sex (i.e., Blackcap, Terrill and Berthold 1989, European Robin, *Erithacus rubecula*, Biebach 1983), Ketterson and Nolan (1985) did not detect significant sex-related differences in captive adult juncos. Perhaps this disparity is related to the experimental methods employed. Ketterson and Nolan, with comparable sample sizes as this study, recorded *Zugunruhe* two nights each week during the migratory period. Individual *Zugunruhe* in juncos is highly variable from night to night (Able, pers. comm., Holberton 1991), and daily sampling may be required for the resolution needed to determine when a bird actually initiates or ceases migratory activity. In addition, I held the birds indoors and tested them inside where environmental factors such as precipitation and temperature, before or during the season, could not be confounding variables when investigating endogenous mechanisms of behavior.

Ketterson and Nolan (1983b, 1987; Nolan and Ketterson 1990b) demonstrated the effect of capture on the subsequent expression of *Zugunruhe*. In their studies, birds that were known to be held at, near or south of their normal overwintering sites showed a suppression of pre-migratory fattening and *Zugunruhe*. This was in contrast to birds that were held far from, and perhaps north of, their known winter sites that showed normal migratory activity. In my study, there was no evidence of the large-scale suppression of *Zugunruhe*. This suggests that the males and females used in this study were not local winter residents. Birds of both sexes exhibited a distinct period of migratory activity congruent with the passage of free-living juncos in the Northeast (Chandler and Mulvihill 1990a) and in juncos tested in other similar experiments in this lab (Terrill 1987,

Holberton 1991). This may not be unexpected in that Albany is nearer the northern limit of junco winter distribution than is Bloomington, Indiana where Ketterson and Nolan's study took place.

The physiological mechanism controlling the differential timing of migration of male and female juncos is not known, but Chandler and Mulvihill (1990a) have suggested that the differences may originate in premigratory events such as the timing of post-nuptial (prebasic) molt. For most migrant passerine species that breed in north temperate and arctic areas, molt has little overlap with migration (Chandler and Mulvihill 1990a and references therein). There are no reported studies on the differential timing of molt in adult male and female juncos, but Chandler and Mulvihill (1990a) refer to unpublished data that suggest that juvenile males and females differ in the extent of their first prebasic molt. They suggested that this difference in molt could result in a difference in the onset of fall migration, as suggested for American Kestrels, *Falco sparverius* (Smallwood 1988). Unfortunately molt was not recorded in detail in this study, but it is intriguing to consider the possibility that differential timing of molt (i.e., differences in temporal organization within the annual cycle) may directly influence the temporal and spatial segregation of the sexes in the fall and winter. It has been shown recently that many annual cycle events in juncos have an endogenous basis (Holberton and Able 1992). These findings do not preclude nor address any environmental influences such as food availability or weather conditions that may have an effect on the expression of junco migratory behavior, but experimental evidence has shown that these factors can modify this behavior in captivity (Terrill 1987, Holberton 1991).

Three major hypotheses have been proposed to explain the ultimate factors responsible for differential migration (body size, social dominance, and arrival time). The body size hypothesis (Ketterson and Nolan 1976, 1979; Ketterson and King 1977) assumes that differential physiological constraints on fasting and cold tolerance are a function of body size and, therefore, smaller individuals overwinter more successfully at lower latitudes. Two measures of winter hardiness as a function of body size have been investigated in juncos, the onset of hypothermia as an expression of cold tolerance (Swanson 1990) and fasting endurance (Stuebe and Ketterson 1982).

Swanson (1990) found that smaller birds expressed hypothermia at higher temperatures when exposed for a period of time to temperatures well below freezing. Stuebe and Ketterson (1982) reported that males were able to fast for an average of 6 hr longer than females, although the difference was not statistically significant. Their birds were held at 8–10°C, a temperature well above freezing. Statistically significant differences in fasting endurance may have been observed if the birds had experienced more energetically demanding temperatures.

Swanson (1990) proposed that thermogenic capabilities and/or the ability to mobilize energy reserves are size-related. Therefore, females, as a consequence of smaller body size, may incur higher thermogenic costs and are less able to meet energy demands than males when access to food becomes limited. Social dominance may magnify this effect. Male juncos are dominant to females (Balph 1975, 1977; Ketterson 1979) and social dominance has been proposed as another proximate factor influencing differential migration (Lack 1944; Balph 1975; Gauthreaux 1978, 1982; Ketterson 1979). If a physiological advantage as a function of body size is combined with males' ability to monopolize food, male juncos may have a real impact on overwinter survivorship of females at northern latitudes. By beginning their migration earlier and subsequently passing through stopover sites ahead of males (Chandler and Mulvihill 1990a), females can reduce the effects of intersexual dominance during migration. Therefore, social dominance probably has little influence on the timing of early migratory decisions of females and there is no empirical evidence for juncos that it influences the winter distribution of the sexes in a proximate way. A similar conclusion can be made regarding physiological constraints in that the majority of birds migrate and reach their wintering sites before environmental conditions deteriorate.

Finally, if the arrival time hypothesis (Ketterson and Nolan 1976, Myers 1981) is applied to juncos, males would be expected to arrive on the breeding grounds earlier than females to compete for breeding territories and/or mates. Both field and laboratory evidence support this hypothesis for juncos. Ketterson and Nolan (1985) found that males held in captivity began to show spring migratory activity 14 days earlier than females, and free-living males pass through stopover sites

in Indiana earlier than females (Ketterson and Nolan 1983a). Yunick (1988) observed in early spring that juncos in eastern New York show a distinct male bias in sex ratios. Yunick's data were further analyzed by Chandler and Mulvihill (1990b) to show that this bias was due to males initiating migration earlier or migrating at faster rates than females and was not simply a function of the spatial distribution of the sexes. Yunick's observations and Chandler and Mulvihill's subsequent analyses compliment the results of this study particularly well because Yunick's stop-over site is within 80 km from where the birds in this study were collected. It is not unreasonable that the birds in the two studies come from the same population of migrant juncos.

Unfortunately there are no published arrival times for juncos on their breeding grounds but the results from both laboratory and field studies suggest that males arrive earlier than females. Ketterson and Nolan (1983a) suggest that, since males show greater site fidelity to breeding sites, intrasexual competition for territories, and, thus selection that favors early arrival by males, may be a force presently influencing the differential winter distribution in adult juncos. The arrival time hypothesis accounts for males overwintering as far north as possible, but does not explain, by itself, why females migrate farther.

Any of these factors (physiological constraints, social dominance and early arrival advantage), independently or in concert, could be considered ultimate mechanisms that may have acted as selection pressures resulting in endogenous differences in the migratory program of male and female juncos. Although environmental factors such as food availability and social interactions may still influence the junco's behavior, the difference in endogenous sex-related behaviors is a sufficient proximate mechanism resulting in segregation of the sexes on the wintering grounds.

ACKNOWLEDGMENTS

I am indebted to Mary Able and Mary Van Auken for their assistance in obtaining juncos and grateful to Edda Schmidt and Ken Able for their invaluable help in caring for the birds. Ken Able, Jim Belthoff, Steve Brown, Jerry Brown, C. Ray Chandler, Ellen Ketterson, John Wingfield, and an anonymous reviewer provided valuable criticisms on an earlier draft of this manuscript. This research was supported by grants from the SUNY Benevolent Association and NSF grant # BNS-8608653 to Ken Able.

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