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TIMING OF AUTUMN MIGRATION AND ITS RELATION TO WINTER DISTRIBUTION IN DARK-EYED JUNCOS¹

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Abstract. Migratory Dark-eyed Juncos in eastern North America migrate southward in autumn and tend to segregate in the winter range according to sex and age. North to south, the most abundant classes are young males, adult males, young females, and adult females. Because adults tend to dominate young at winter feeding sites, this distribution appears at first to conflict with the view that dominance interactions are responsible for differential avian migrations and that dominant individuals remain nearest the breeding range. However, if young juncos establish winter residency at earlier dates than adults, a prior residence effect might make them dominant. This hypothesis requires that young arrive at wintering sites earlier than adults and that residents of all classes arrive earlier than their transient counterparts.

We tested these predictions by comparing first-capture dates of juncos at Bloomington, Indiana, which is north of the latitudinal midline of the junco's winter range. During 13 autumns, individuals were classed as local residents or as transients and were sexed and aged. Contrary to predictions, residents were not caught earlier than transients. Further, adults were caught earlier, not later, than young among transients and probably also among residents. Thus, settlement of the winter range does not proceed from north to south, and dominance established through prior residence cannot account for the concentration of 1st-yr males in the northern part of the winter range.

The fact that some sex-age classes tend to winter south of others predicts that at a northern capture site the classes that migrate farthest should be commoner among transients than among residents. This expectation was fulfilled. In addition, the median capture dates of the sex-age classes were arranged approximately according to the north-to-south order of their distribution, indicating that classes with the farthest to travel passed through (transients) or settled (residents) earliest in autumn. We conclude that comparison of autumn migration schedules of transient and resident passerine birds at a single location can yield considerable information about the dynamics of settlement of the entire winter range, including possible information about differences in destination of subsets of transients.

Key words: aggressive behavior; differential migration; dominance and distribution; emberizid; Junco hyemalis; migration schedule; prior residence; winter distribution.

INTRODUCTION

In at least three classes of vertebrates, individuals of the same species but different sex and/or age differ in average distance covered by their seasonal migrations and therefore in their nonbreeding distributions. Such differential migrants include species of fish (Calhoun 1952), bats, ungulates, cetaceans (all reviewed in Baker 1978), and especially migratory birds (for reviews see Ketterson and Nolan 1976 and Gauthreaux 1978, 1982; see also Ketterson and Nolan 1983, Baker 1978). In this paper we focus on a widespread North American passerine bird, the Dark-eyed Junco (*Junco hyemalis*: Emberizidae), and consider the relationships among the timing of arrival or passage of individuals in autumn, the dynamics of settlement of the winter range, and the distribution that results from this settlement. To learn whether juncos arriving in the northern part

of the winter range early in migration might thereby achieve a competitive advantage, causing later migrants to continue southward, we classified individuals as winter Residents or Transients still migrating, then analyzed first-capture dates of the sex-age classes among Residents and Transients. We know of no other effort to investigate the dynamics of autumn settlement of a migratory bird species by studying individuals at a single location and then extrapolating to conclusions about the entire range. The method appears to apply to other migratory passerines and be especially useful for studying those that perform differential migrations.

Dominance and winter distribution

Male birds often make shorter movements into the winter range than females and, when the age classes differ, young usually migrate farther than adults (Gauthreaux 1978, 1982, 1985). Because males dominate females, on average, and adults tend to dominate young, social dominance is often cited as the cause of

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this differential migratory behavior (Gauthreaux 1978, 1982). Short movements are believed to be less costly than long ones, and dominant individuals are seen as moving no farther from the breeding range than is necessary. On the other hand, subordinates by traveling farther are thought to reduce the frequency of interactions with dominants over food, in which they are at a competitive disadvantage, and thus to improve their survivorship.

The Dark-eyed Junco in eastern North America breeds primarily in Canada and winters in southern Ontario and in the United States almost to the Gulf of Mexico (Bent 1968). (An essentially sedentary population [Nolan et al. 1986] that inhabits the southern Appalachian Mountains is not relevant to this paper.) The breeding and nonbreeding ranges overlap very little, and probably all or almost all individuals migrate. This species conforms to the typical sex-age pattern in its winter dominance relations. Males are usually dominant over females (Baker and Fox 1978, Balph 1978, Ketterson 1979), and within sexes adults tend to dominate individuals produced during the preceding breeding season (herein, young) (Ketterson 1979, Rogers et al. 1989, Cristol et al., *in press*; but Holberton et al. [*in press*] did not find dominance by adults). The sex ratio strongly favors males in the northern part of the winter range but shifts gradually until it strongly favors females in the south (Ketterson and Nolan 1976, 1979), which is consistent with dominance relations. Within each sex, however, young on average winter closer to the breeding grounds than adults (Ketterson and Nolan 1983, 1985), which is inconsistent. Our sampling of populations at five latitudes (Michigan 42° N, Indiana 39° N, Tennessee 36° N, South Carolina 35° N, Alabama 33° N) during four winters, combined with analyses of Christmas Bird Count data on abundance, indicated that young males reached peak numbers and were the most abundant class at ≈40° N. The distribution of adult males was bimodal, peaking at ≈40° N and 35° N (at 35° they outnumbered young males). Young females peaked and outnumbered every other class at ≈35° N, and adult females were the most abundant class at 33° N (Ketterson and Nolan 1983, 1985).

Because this age distribution does not fit the predictions of the dominance hypothesis, we have been skeptical that dominance alone is responsible for the differential migration of juncos (Ketterson and Nolan 1982, 1983, 1985, Rogers et al. 1989). In addition to the distribution, other reasons for skepticism are that we have observed no variation among the sex-age classes either in winter fat reserves (Nolan and Ketterson 1983) or in overwinter survivorship, even in very severe winters (Ketterson and Nolan 1982). These facts suggest that subordinates were not at a competitive disadvantage in the populations studied. However, in investigations of other species, support for the dominance hypothesis continues to accumulate (Kikkawa 1980, Lundberg et al. 1981, Sayler and Afton 1981, Arcese

and Smith 1985, Lundberg 1985, 1988). Further, Ter-rill (1987) has recently suggested that subordinate juncos are more likely than dominants to exhibit nocturnal restlessness (Zugunruhe) when food is restricted in midwinter, which might imply that dominance has a role in the individual's decision to extend or not to extend migration. In view of this evidence, we have continued to entertain the possibility that dominance may be responsible for the junco's differential migration.

Possible relation of migration schedules to dominance

Here, we examine the autumn migration schedules of the sex-age classes to learn whether differences in time of arrival in the winter range might reconcile the observed age distribution with the dominance hypothesis (as suggested in Ketterson and Nolan 1985). Specifically, if young tend to occupy the range earlier than adults, prior residence in the north might elevate the status of young, permit them to dominate some adults of their sex, and cause the latter to migrate farther southward. A prior residence effect on dominance has been reported for various bird species as well as for other taxa (e.g., invertebrates: Dingle 1969, Davies 1978; fish: Brown and Green 1976, Figler and Einhorn 1983; amphibians: Haubrich 1961, Boice and Witter 1969; mammals: Lerwill and Makings 1971, Blanchard et al. 1977) and has been observed in both free-living juncos (Sabine 1959, Balph 1979, Ketterson 1979) and caged juncos (Yasukawa and Bick 1983, Cristol et al., *in press*). Consistent with the possibility of prior residence by young are several findings. First, caged young juncos initiated autumn migratory restlessness before adults (Ketterson and Nolan 1985). Second, when site-faithful individuals were caught as young in one winter and again as adults in the next, initial capture dates were earlier in the 1st yr; in contrast, among individuals that were adults in both the first and second winter of capture, there was no difference in date between years (Ketterson and Nolan 1985). Finally, young juncos produced in early broods would be expected to be able to migrate earlier than adults, whose early nests often fail and are replaced. Also, adults sometimes raise second broods, and they undergo postnuptial molt before migrating (E. D. Ketterson and V. Nolan, *personal observation*).

The hypothesis that some adult juncos are induced to continue migration as the result of encounters with earlier arriving young is not inconsistent with observations (e.g., Ketterson 1979) that adults tend to dominate young in established winter populations. All reports of adult dominance are based on observations made at one or another single location in winter, and under the dominance hypothesis the adults that settle at any single location are those that were not dominated there and hence were not motivated to continue migrating. Those same adults, however, may have been

dominated at a more northerly location by young that had taken up prior residence at that location, causing the adults to migrate farther. The question, then, is whether the adults that migrate beyond a site do so because they arrive later and hypothetically are subordinate to young already present.

Our data, obtained during a 13-yr study, compare the arrival schedules of juncos at two banding locations near Bloomington, Indiana (39° N). Bloomington is located slightly north of the latitudinal midline of the winter range (Ketterson and Nolan 1983, 1985). Many juncos that arrive in autumn settle there, while even more continue southward, providing us with large numbers both of Bloomington winter residents and of transients.

We made four predictions based on the hypotheses that (1) dominance is the proximate driver of the junco's migration and (2) prior residence is a major determinant of dominance rank among free-living juncos. We shall conclude that neither of these hypotheses is supported by the data.

According to the dominance-prior residence hypothesis we would expect residents to arrive (and be caught) earlier than transients, on average, either when all sex-age classes are combined for analysis (prediction 1) or, alternatively, when we analyze the sex-age classes separately (prediction 2). Approaching the question from a slightly different angle, we would predict from the winter distribution that young of each sex, with residents and transients pooled, would tend to arrive (and be caught) at a northern latitude before adults of that same sex, again with residents and transients pooled (prediction 3). Further, average arrival dates of young residents should precede average arrival dates of adult transients of the same sex (prediction 4).

Order of passage and winter distribution

Testing the predictions arising out of the dominance inquiry led us to consider two additional points. The first and broader is this: In what order is the winter range settled? The logic of the dominance hypothesis implies that settlement is from north to south. If, on the other hand, the sex-age class that winters farthest south (adult females) arrives earliest, we would infer that settlement is either from south to north or is more or less simultaneous at all latitudes. The second question is whether the sex-age composition differs between the resident and transient populations in ways that are consistent with the winter distribution. An example of such consistency would be that, at a location in the northern part of the winter range, adult females should be more numerous among transients than among residents.

METHODS

Capture sites and capture efforts

From 1966 through 1978 we banded at one or both of two stations, designated the Yard and the Field,

≈ 1.5 km apart. We began work in the suburban Yard 5 yr before beginning in the Field, but our Field efforts were much more extensive, and we rely primarily on them. We therefore describe the Field operation first.

The Field site consisted of ≈ 5 ha of brush-covered land adjoined on three sides by ≈ 45 additional ha of old fields, open woods, fence rows, and grassy areas. Banding began in 1971–1972 and continued through 1978–1979 (8 yr). Each year from early October, when migrants usually begin to arrive at Bloomington, until late April we operated from 15 to 20 mist nets, some baited and others placed where juncos were likely to pass. Baited Potter traps were used when netting conditions were poor. In three of the years, capture efforts were made nearly daily, and in all they were made at least three times a week. First-capture dates were 23 October 1971, 16 October 1972, 17 October 1973, 12 October 1974, 27 October 1975, 24 October 1976, 9 October 1977, and 15 October 1978.

The effort in the Yard lasted 9 yr (1966–1967 through 1974–1975). The site consisted of 0.8 ha, about half of it covered by mature deciduous woods; the rest was a lawn bordered by shrubs. Adjacent were similar yards and, during the early years, outlying brushy areas. Capture was largely by Potter traps baited with corn and/or millet; occasionally we used mist nets. Although juncos began to arrive in the vicinity in October, these birds rarely entered the Yard until November. Trapping, therefore, was postponed until juncos appeared in the Yard and then was maintained nearly daily throughout winter. First-capture dates were 30 October 1966, 6 November 1967, 29 October 1968, 10 November 1969, 5 November 1970, 7 November 1971, 4 November 1972, 21 October 1973, and 9 November 1974. The samples from the Yard are smaller than those from the Field, but for the most part the data agree with results from the Field. We present them because they suggest that conclusions based on the Field data apply to the Bloomington region or beyond.

Determination of sex and age

All individuals were aged by examination of the state of ossification of the skull. Sex was determined by wing length and other plumage characters previously described (Ketterson and Nolan 1976, 1982). Occasionally adult females and young males are difficult to distinguish until the skulls are examined, but the combination of sexing and aging assures probably complete accuracy in placing an individual in its correct class (Ketterson and Nolan 1976, 1982).

Criteria for assigning transient and resident status

The autumn migration of juncos ends ≈ 1 December (Ketterson and Nolan 1976), although Terrill (1987) reports laboratory evidence indicating that under severe conditions individuals may make additional, facultative midwinter movements. Such movements ap-

parently are observable in the extreme southern part of the range (J. V. Remsen, *personal communication*). We confine our attention to the autumn migration and the settlement pattern that it produces on ≈ 1 December.

Transients we defined as individuals caught only once on a date no later than 30 November. Residents were juncos also caught no later than 30 November and caught again at least once during winter, after 5 December. Excluded from both categories were juncos caught more than once but never later than 30 November, because their residency status is ambiguous. Analysis of the data (not shown) for this group leads us to believe that many were moving around locally before selecting home ranges in the vicinity of Bloomington. Even as defined, the Transient category includes an unknown number of individuals that did not in fact migrate beyond Bloomington, but simply settled outside our study areas. For example, in the 4 yr in which we operated the Field and Yard sites simultaneously, we caught eight individuals (among 1545 cases) only once at each site, with the first capture no later than 30 November and the second later than 5 December. If we had been banding at only the site of first capture, we would have misclassified these birds as Transients when in fact they were Residents. Because this kind of error can occur in only one direction (there is no possibility of misclassifying a junco that was present in winter as being a Transient), its effect is to make any differences in arrival of Transients and Residents harder to detect.

For all Transients we treated the date of capture as the date of arrival. To define arrival date of Residents we used a small, strictly limited subset of individuals, which we term Arrival-date Residents (as distinguished from All Residents). Our reasoning follows: Capture dates can be used for comparing approximate arrival dates of two groups only if the members of the two groups being compared were equally likely to be captured within an identical interval after arrival. To apply this to the present problem, Transients can be caught only during a brief interval, their stopover period. A Resident on the other hand might be first caught long after its arrival, since it can remain in the vicinity of the trapping site for many weeks. This source of bias could lead us to overestimate the median arrival date and make it appear later than it really was. To eliminate or reduce this bias, the Arrival-date Residents consist only of juncos first caught no later than 30 November, caught again within 5 d, and caught yet again at least once after 5 December. We believe that for these individuals our capture efforts were efficient, i.e., that we probably caught them as soon after arrival as we caught most Transients. We required recapture within 5 d because this seems likely to approximate the mean stopover period of transients. Stack and Harned (1944) report a mean stopover of autumn-migrant juncos in Michigan of 13.6 d, but this is probably an overesti-

mate, at least for Bloomington (E. D. Ketterson and V. Nolan, *personal observation*; compare Borror 1948, King 1961, Cherry 1982, Morton and Pereyra 1987). Our definition of Arrival-date Residents would not eliminate juncos that first settled outside the bounds of our sites just after arriving and then later moved to our sites and were caught twice during a 5-d period beginning no later than 30 November. Even if there were such cases, they may be counterbalanced by instances in which Transients were caught late during unusually long stopover periods. The effect of distinguishing Arrival-date Residents was to reduce the All-Residents category in the Field from 556 cases (Table 4) to 153 cases (Table 1); in the Yard, 200 All Residents (Table 4) were reduced to 78 Arrival-date Residents (Table 2).

Excluded from the Arrival-date Residents were all data from the second and subsequent years in which we captured site-faithful individuals. This eliminates the possibility that the earliest capture of site-faithfuls in later years was delayed because their previous experience made them harder to catch. Additionally, if individuals tend to be consistently early or late migrants throughout life (compare Nolan 1978:28–29), exclusion of repeated data for the same juncos assures independence of cases.

All of the foregoing concerns methods for comparing arrival schedules. We also compared population structure of Transients and Residents, and for this we used All Residents. Site-faithful individuals were included in every year they were present and captured. To exclude them would be to mis(under)represent the proportion of adults in the overwintering population.

Treatment of data across years

Capture schedules of each sex–age class were compiled according to year and then, for each site, pooled across years. We first analyzed results by date at each site, beginning with the earliest capture date among all years worked at the site and ending 30 November. Because weather differed from year to year, we also analyzed by normalized date, taking the date of first capture in any particular year as day 1, the following day as day 2, etc., and pooling identically numbered days for all years. Analyses of calendar and normalized dates were very similar in result, suggesting that the scale of the annual variation attributable to weather was on the order of a few days and was unimportant for present purposes. We therefore present only results according to calendar.

RESULTS

The data

Table 1 summarizes the pooled Field data, showing the numbers of Transients and Arrival-date Residents according to sex–age class, the percentage that each class contributed to the total, and the median first-

TABLE 1. Transients* and Arrival-Date Residents† at Field banding station; relative frequency of sex-age classes and median dates of first capture. Data for all years are pooled.

	Males		Females	
	Adults	Young	Adults	Young
Transients				
<i>n</i>	353	671	196	576
%	19.7	37.4	10.9	32.1
Median date	11 November	16 November	10.5 November	13 November
Arrival date residents				
<i>n</i>	13	69	12	59
%	8.5	45.1	7.8	38.6
Median date	13 November	20 November	8 November	19 November

* Caught only once, before 1 December.

† Caught first before 1 December, caught again within 5 d of first capture, caught again at least once after 5 December. For individuals that were present in more than one winter, data are included only for the year in which they were banded.

capture date of each class. Fig. 1 graphs the frequency of first captures in the Field for each class of Transients and of Arrival-date Residents, according to date. Table 2 and Fig. 1 also provide similar data from the Yard. We point out that among Arrival-date Residents were

fewer adults and more young (Tables 1 and 2) than we have previously described for Bloomington winter populations (Ketterson and Nolan 1983). The explanation for the disparity arises from the exclusion of site-faithful birds from Arrival-date Residents (*Meth-*

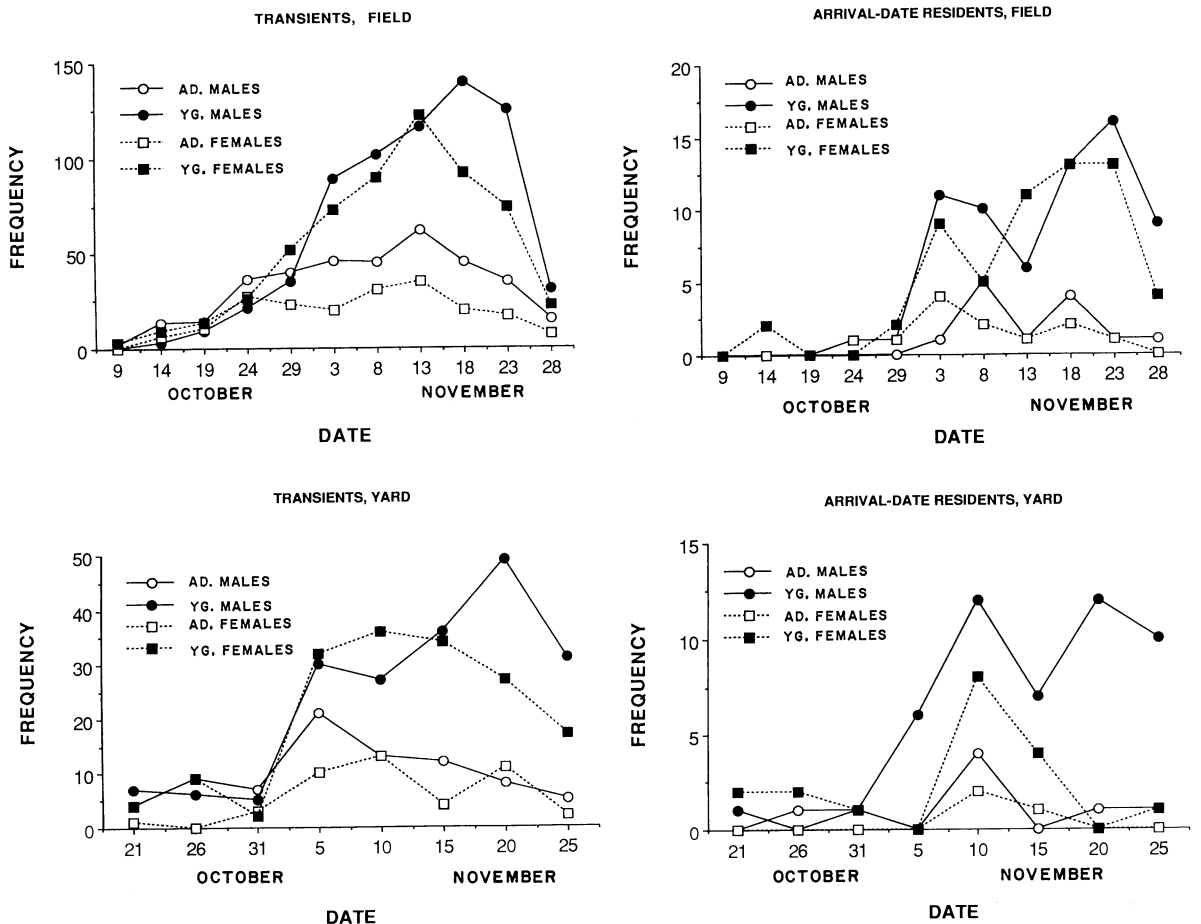


FIG. 1. Frequency of first captures of sex-age classes of Transients and Arrival-date Residents at the Field and the Yard banding stations, according to 5-d intervals (except that the final period lasted 3 and 6 d in the Field and Yard, respectively). For definitions of migration classes, see footnotes to Table 1.

TABLE 2. Transients* and arrival-date residents† at Yard banding station; relative frequency of sex-age classes and median dates of first capture. Data for all years are pooled.

	Males		Females	
	Adults	Young	Adults	Young
Transients				
<i>n</i>	79	191	44	161
%	16.6	40.2	9.3	33.9
Median date	9 November	18 November	13 November	14 November
Arrival-date residents				
<i>n</i>	8	49	3	18
%	10.3	62.8	3.9	23.1
Median date	12.5 November	18 November	13 November	11 November

* Caught only once, before 1 December.

† Caught first before 1 December, caught again within 5 d of first capture, caught again at least once after 5 December. For individuals that were present in more than one winter, data are included only for the year in which they were banded.

ods: Criteria for assigning transient and resident status; compare Tables 1 and 2 with Fig. 3). All site-faithful individuals were, of course, adult by definition.

Did Residents arrive before Transients?

With all classes pooled, the median first-capture date of Field Transients was 13 November, as opposed to 19 November for Field Arrival-date Residents (median test, $\chi^2 = 7.633$, $df = 1$, $P = .006$). In the Yard, where catching began later (see *Methods: Capture sites and capture efforts*), the median date for both Transients and Arrival-date Residents was 20 November (median test, NS). Thus prediction 1, that Residents would be caught before Transients, is not supported when sex-age classes within each category are pooled.

When the comparisons of Transients and Arrival-date Residents are made separately for the sex-age classes, Transients tended to be caught before Arrival-date Residents in the Field (Table 1) and no later than Arrival-date Residents in the Yard (Table 2). Fig. 2 depicts first-capture frequencies of Transients and Arrival-date Residents in the Field for the four sex-age classes, cumulatively according to date. In three of the comparisons of classes from the Field, the Transient median was earlier than the Arrival-date Resident median, in two classes significantly earlier (Mann-Whitney U : young males $Z = -2.5428$, two-tailed $P = .011$; young females $Z = -2.9898$, $P = .003$), and in the third class marginally so (adult males $Z = -1.930$, $P = .054$). (Note the very small sample sizes for both adult sex classes.) In the Yard, there were no significant differences in any class, but for each class except young females the median date was slightly earlier among Transients (Table 2). Prediction 2, that in each class Arrival-date Residents would be caught before Transients, is not supported.

Did young arrive earlier than adults when Residents and Transients are pooled?

In median tests comparing first-capture dates of young with first-capture dates of adults of the same sex, after pooling of Transients and Arrival-date Residents, young

were not caught earlier than adults of either sex at either site, and in three of the four comparisons they were caught significantly later (median tests, Table 3). Prediction 3, that young males would be caught before adult males and that young females would be caught before adult females, is not supported. If prior residence could be based simply on earlier arrival by individuals of one age class, then based on these data adults rather than young would be expected to have the prior residence advantage.

Did young Residents arrive earlier than adult Transients?

Under the dominance-prior residence hypothesis, Residents are expected to precede and dominate Tran-

TABLE 3. Median tests comparing first-capture dates of adults and young,* Field and Yard banding stations. Data for all years are pooled.

	Field banding station			
	Males (median 14 November)		Females (median 13 November)	
	Adults	Young	Adults	Young
Caught before and on median	237	339	133	324
Caught after median	129	401	75	311
	$\chi^2 = 34.456$ $df = 1$ $P = .000$		$\chi^2 = 10.021$ $df = 1$ $P = .002$	
	Yard banding station			
	Males (median 15 November)		Females (median 14 November)	
	Adults	Young	Adults	Young
Caught before and on median	63	107	27	88
Caught after median	24	133	20	91
	$\chi^2 = 18.715$ $df = 1$ $P = .000$		$\chi^2 = 0.718$ $df = 1$ NS	

* Transients and Arrival-date Residents (defined in footnotes of Table 1) combined.

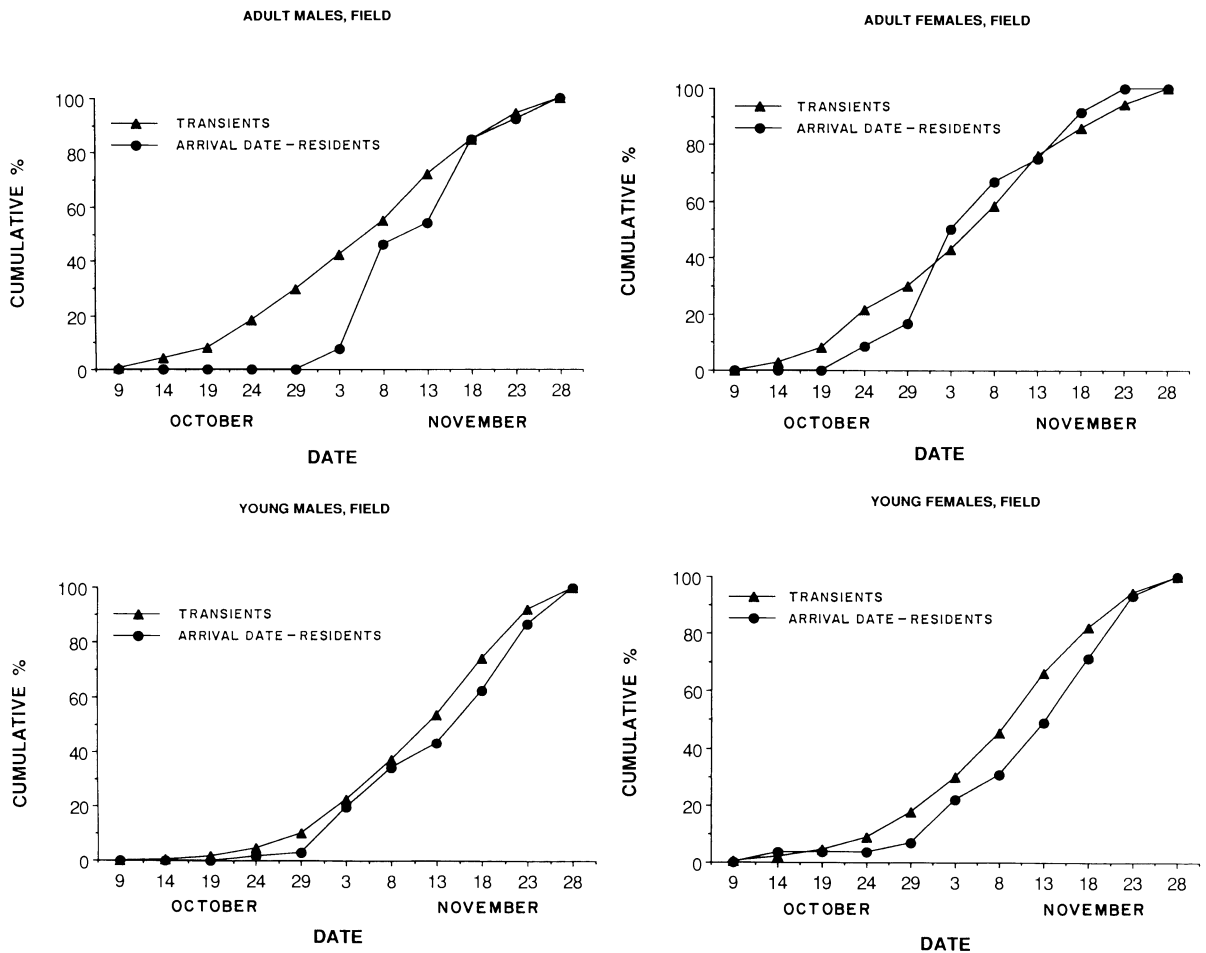


FIG. 2. Comparison of first-capture dates of Transients and Arrival-date Residents at the Field banding station, according to sex-age class, presented as cumulative percentages. For definitions of migration classes, see footnotes to Table 1.

sients and therefore to be responsible for the transient status of the latter. Contrary to prediction, in the Field young Arrival-date Residents were caught significantly later than adult Transients, both among males and among females (Table 1; Mann-Whitney *U*: young male Arrival-date Residents vs. adult male Transients, $Z = -5.4304$, two-tailed $P < .000$; young female Arrival-date Residents vs. adult female Transients, $Z = -4.6946$, two-tailed $P < .000$). In the Yard the same was true of males but not of females (Table 2; Mann-Whitney *U*: young male Arrival-date Residents vs. adult male Transients, $Z = -4.1403$, two-tailed $P < .000$; young female Arrival-date Residents vs. adult female Transients, $Z = -1.0563$, two-tailed $P = .291$). Even the most subordinate class, young females, was caught later in the Field among Arrival-date Residents than was the most dominant class, adult males, among Transients (Table 1; Mann-Whitney *U*: $Z = -4.2176$, two-tailed $P = .000$); this difference was not significant in the Yard. (For dominance status of the sex-age classes, see citations in the *Introduction*.) Prediction 4,

that young Arrival-date Residents would be caught earlier than adult Transients, is not supported.

Among Transients, how did arrival times of the sex-age classes compare?

In the Field, the Transient sex-age classes differed significantly in order of capture (Kruskal-Wallis, $H = 79.364$, $df = 3$, $P = .000$, Fig. 1A). The chronological order of passage was adult females, adult males, young females, and young males (Table 1). That is, the class with the farthest average distance still to be traveled beyond Bloomington, adult females, was caught on the earliest median date, and the classes with intermediate distances to travel were intermediate in their median arrival dates. Young males, the class with the shortest average distance remaining to be traveled in order to settle near its center of abundance, arrived last, and its median date was significantly later than those of the other three classes, which did not differ statistically from one another (Dunn's a posteriori multiple comparisons, value of P set at .049; this test is "a very

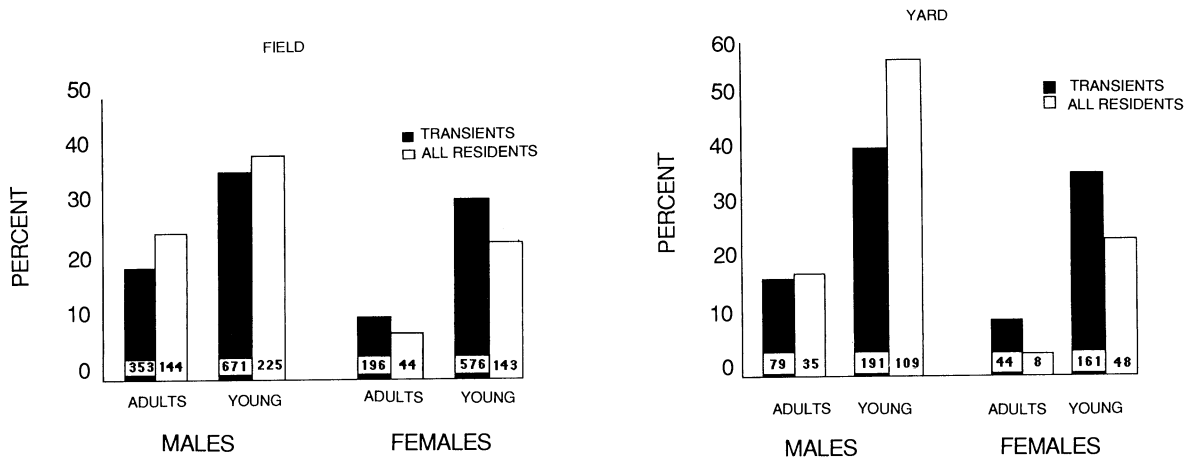


FIG. 3. Comparison of population structure of Transients and All Residents in the Field and the Yard, according to sex-age class. Transients and All Residents are defined in *Methods: Criteria for assigning transient and resident status*.

conservative approach to multiple comparisons," Holander and Wolfe 1973).

Most of the differences among Field Transients also held in the Yard. The order of median capture dates differed only slightly; adult male Transients were first, followed in order by adult females, young females, and young males (Table 2; Kruskal-Wallis, $H = 28.608$, $df = 3$, $P = .000$). In Dunn's a posteriori comparisons, young males were significantly later than adults of both sex classes but did not differ from young females. Young females were significantly later than adult males. No other differences were significant. As in the Field, the class with the shortest distance to travel passed through last.

Among Residents how did arrival dates of the sex-age classes compare?

Among Arrival-date Residents, first-capture dates differed according to sex-age class in the Field (Kruskal-Wallis, $P = .036$) but not in the Yard ($P = .149$). Furthermore, the chronological order of median dates among sex-age classes of Arrival-date Residents in the Field was identical to the chronological order of median dates among Transients in the Field: adult females, adult males, young females, young males (Table 1). The only significant interclass difference in pairwise comparisons of Field Arrival-date Residents was between the extremes, adult females and young males (Dunn's a posteriori test).

What was the relative representation of the sex-age classes among Transients and Residents?

The sex composition differed between Transient and All Resident (see *Methods: Criteria for assigning transient and resident status*) populations (Fig. 3) both in the Field and the Yard. In three-way G tests (Sokal and Rohlf 1981) with Transient-All Resident status, age, and sex as the variables, there was no three-way

interaction at either location. Age of Transients and All Residents, given the level of sex, also did not differ significantly. However, at both study sites sex differed between Transients and All Residents, given the level of age (Field: $G_{adj} = 16.249$, $df = 2$, $P < .001$; Yard: $G_{adj} = 15.136$, $df = 2$, $P < .001$).

DISCUSSION

Can dominance be the sole regulator of the junco's differential migration?

We attempted without success to reconcile the junco's age distribution in winter with the predictions of the dominance hypothesis by seeking evidence that might imply the existence of a prior residence mechanism favoring young. If dominance regulates differential migration of the junco, prior residence could account for the presence at northern latitudes of individuals belonging to classes that normally are subordinate, even young females. But at the population level, the differential latitudinal distribution of the sex-age classes could be explained by dominance-prior residence only if average capture dates of the classes met certain conditions. We stated these as predictions regarding the timing of arrival of juncos that remained at the capture site compared to those that continued migrating after a stopover, and none was fulfilled. Instead of being captured later, as predicted, Transients tended to be captured before Arrival-date Residents, in some of the comparisons significantly earlier. We tried to eliminate bias associated with potential differences in promptness of first capture of Residents and Transients. Even if we were not fully successful, i.e., if first capture of Arrival-date Residents was not as soon after arrival as was first capture of Transients, our results are at the least strong evidence that Arrival-date Residents did not arrive earlier than Transients. Further, young clearly did not arrive earlier than adults, as the dominance-prior residence hypothesis would

TABLE 4. Dates of early autumn observations of juncos in northern and southern pairs of winter range.

Location	Date	Reference
North		
Michigan, lower peninsula	mid-to-late September	Wood 1951
New York, Niagara frontier	26 September	Beardslee and Mitchell 1965
South		
South Carolina	3 October	Sprunt and Chamberlain 1970
	7 October	S. A. Gauthreaux, Jr., <i>personal communication</i>
Georgia	1 October	Haney 1986
	1 October	Tramer 1968
Florida	1 October	H. M. Stevenson, <i>personal communication</i>
Alabama	27–30 September (5 records)*	T. A. Imhof, <i>personal communication</i>
Mississippi	15 October	J. A. Jackson, <i>personal communication</i>
Louisiana	5 October	Lowery 1974

* One or more of these birds may have belonged to the nearly sedentary mountain-breeding race that occurs in small numbers in the Alabama piedmont.

predict. Not even those young that remained to join the winter population had earlier first-capture dates than the adults that moved on, and Arrival-date Resident young in the Field were captured later than adults (Table 1). It is not unusual for adult passerines to migrate earlier than young in autumn. Gauthreaux (1982), reviewing the literature on autumn migration schedules of passerine age classes, cites examples of species in which adults precede young, as well as examples of the opposite.

If we conclude on this evidence that dominance is not the sole mechanism that regulates the junco's winter age distribution, what other variables may be involved? Elsewhere (Ketterson and Nolan 1983, 1985) we proposed that a junco's sex and age are factors in determining the suitability of various wintering latitudes for its survival and future reproduction and that members of each sex-age class tend to settle where relevant selective pressures balance out for that class. We suggested that these pressures include, in addition to probable social rank, the following: (1) the favorable effect that early return to the breeding ground may have on reproductive success, probably more important for males than females and perhaps more important for young males (which must find territories for the first time) than adult males; (2) reduction of migration mortality, which almost surely increases with distance migrated and probably increases at a greater rate for young birds than adults, because young are making their first migration and are inexperienced generally; and (3) avoidance of densely populated latitudes. By migrating farther southward, some individuals reduce density effects that would arise out of association with more northern residents. Adults probably are more able than young to trade off mortality associated with longer autumn migration for the improved overwinter survivorship gained by wintering in milder southern climates (point 2 above, and Ketterson and Nolan 1983).

Finally, if the junco is unusual among migratory birds

(see citations in the *Introduction*) in that dominance alone cannot account for its winter distribution, this may well be associated with the similarly unusual fact (Gauthreaux 1978, 1982, 1985) that young juncos tend to remain north of adults.

Range-filling dynamics

The capture of Transients before Arrival-date Residents, combined with the chronological order of capture of Transient sex-age classes, suggests to us the probable process by which the winter range as a whole is occupied. First, it is not settled progressively from north to south: first capture of Transients tended to be earlier, not later, than Arrival-date Residents. Second, when we focus on median arrival dates of Transients through the Field, where arrival data were more reliable (see *Methods: Capture sites and capture efforts*), the sex-age class that concentrates farthest southward was caught earliest, the class that concentrates farthest north latest; and the classes commonest in midrange were caught at intermediate dates. (However, in multiple comparisons adult males, adult females, and young females did not differ significantly from one another.)

We next consider this order of passage in light of the dates at which the earliest juncos have been recorded at the northern and the southern extremes of the winter range (Table 4). (In this paragraph we assume that individuals seen in the south in early autumn settled there, i.e., did not quickly turn around and return northward.) Table 4 reveals that juncos first appear in the south not long after they first appear in the north. In combination, our capture data and the dates in Table 4 imply that most juncos entering the winter range early in the migration season keep moving southward. Although some may and doubtless do drop out and settle in the north, settlement of the south seems to begin early in autumn and may proceed at a faster rate than in the north.

The arrival schedules of the sex-age classes of juncos that settled the Bloomington region probably also approximately paralleled the latitudinal order of distribution. Considering again the data from the Field, the order of median dates of capture of the sex-age classes of Arrival-date Residents and of Transients was the same: adult females, adult males, young females, and young males. (In multiple comparisons only adult females and young males differed from each other.) Chandler and Mulvihill (1990) have also recently concluded, on the basis of the timing of passage of juncos through Pennsylvania, that the sex-age classes that settle farthest south pass through earliest. Further, they found significant interclass variation in wing shape associated with this differential timing of migration.

How might differences in arrival schedules of the sex-age classes be explained? Three causes, singly or in combination, are possible: classes may differ (1) in departure time from the breeding range, (2) in place of origin in the breeding range, and (3) in speed of migration. All of these, especially departure time, could be affected by date of nest-leaving among young and date of final reproductive effort (and its success or failure) among adults. Of the three possibilities, the most likely, we believe, is that the classes leave the breeding range at different dates, on average, and that the difference is correlated with the different distances to be migrated. It is also tempting to speculate that young juncos, particularly males, postpone departure for an additional reason, the importance of becoming familiar with potential breeding sites to be used the following year. As for the second possibility, King et al. (1965) have shown theoretically that differences in capture date of the sexes of migrant White-crowned Sparrows (*Zonotrichia leucophrys*) could be explained solely by differences in the geographic origin of the populations. Thirdly, Baker (1978) expects young to migrate more slowly than adults because he argues that inexperienced individuals explore a corridor on both sides of the main axis of migration, thereby enlarging the lifetime familiar area that they will traverse more rapidly in future migrations.

Relative proportions of the sex-age classes

The finding, when Transients and All Residents were compared, that females were overrepresented among Transients whereas males were overrepresented among All Residents is independent evidence of the junco's differential migration according to sex, as earlier determined by sampling of winter population structure at different latitudes (Ketterson and Nolan 1976, 1979, 1983, 1985). If fewer males migrate into the southern half of the winter range, their frequency among Transients at 39° N should be lower than among All Residents, and it was. If most females winter in the south, at 39° N the proportion of female Transients should exceed that of females among All Residents, and it did.

Given the differential distribution of the age classes within each sex (Ketterson and Nolan 1983, 1985), we might also have expected the Transient and All Resident samples to differ in age composition, but a *G* test did not produce that result.

General utility of our methods

Our conclusions specific to the Dark-eyed Junco probably need no summary, but we offer the following more general conclusions about the utility of distinguishing between transients and residents in analyses of migration schedules:

- 1) In migratory bird species whose members settle on winter home ranges, intensive mark and recapture operations at a single site in the middle of the winter range permit local residents to be distinguished from most transients. Comparison of first-capture dates of residents and transients then yields inferences about the north-south order in which the range is occupied.
- 2) In species in which the sexes and the age classes are distinguishable (passerine young of the year are usually distinguishable in autumn), these inferences will be more detailed and can be extended to suggest temporal settlement patterns of classes within the population.
- 3) If the sex-age composition varies between the transient and resident groups, that fact can corroborate, or tend to refute, views about geographical segregation of the classes in winter. Alternatively, it can suggest the presence of segregation where none was previously suspected.
- 4) Finally, the method can test whether the prior residence effect is an important basis for the winter distribution of the species.

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