THE ROLE OF MIGRATION AND WINTER MORTALITY IN THE LIFE HISTORY OF A TEMPERATE-ZONE MIGRANT, THE DARK-EYED JUNCO, AS DETERMINED FROM DEMOGRAPHIC ANALYSES OF WINTER POPULATIONS

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Abstract.—This study of migratory Dark-eyed Juncos (*Junco h. hyemalis*) investigates differences in winter population structure and dynamics associated with north-south variation in wintering site and considers the relationships between these winter differences and population dynamics at other seasons. Banded juncos were captured and recaptured in several winters at four latitudes (42°–33.5°), and results were integrated with long-term United States Fish and Wildlife Service records of recoveries throughout the winter range.

The data suggest: (1) Populations wintering in the north experience higher winter mortality than populations wintering in the south. (2) Sex and age do not affect the probability of overwinter survival; therefore, dominance may not affect that probability. (3) Some individuals do and others do not return to the same wintering site year after year. Individuals that do not return tend to be those that have spent the first winter of life in the north, and these shift southward. (4) Annual mortality of northern and southern winter populations probably is the same. This conclusion is based in part on a comparison of north-south annual return rates and on logic arising out of the geographical distribution of the sexes during winter. In juncos, because males tend to winter north of females, greater annual mortality of northern winter populations would be expected to skew the primary and secondary sex ratios in favor of males. No evidence of such skews has been detected. (5) If annual mortality is the same, it is likely that southern populations suffer heavier mortality during their longer migrations and that these migration losses offset the advantage described in (1), above.

In north temperate-zone breeding species that migrate southward into an extensive winter range, distance traveled probably is correlated closely and positively with both mortality rate during migration and survival rate during winter. If these rates offset each other, annual survivorship among winter migratory populations (and among sedentary and migratory populations of partially migrant species) can be equal. Therefore, it is unnecessary to postulate for different winter populations either unequal reproductive success (von Haartman's hypothesis) or unequal year-to-year survival rates that balance out over the long term (Lack's hypothesis).

Migration can cause breeding populations to be redistributed in various ways in winter; e.g. they may mix randomly, or northern breeders may leapfrog southern breeders. Each variation in migration pattern would produce winter populations with predictable characteristics. We consider the extent to which winter junco populations have these characteristics. *Received 26 January 1981, accepted 30 September 1981.*

The Dark-eyed Junco (*Junco h. hyemalis*), an abundant ground-feeding emberizid, migrates between a breeding range lying largely in the boreal forests of Canada and, in eastern North America, a winter range reaching from southern Ontario and the northern boundary of the United States almost to the Gulf of Mexico (Bent 1968). Because the winter range is so extensive, northern-wintering juncos spend that critical season (Lack 1954, Fretwell 1972) in cold and often snow-covered regions, whereas others, by migrating farther, move into progressively more moderate and even mild climates. Male juncos tend to winter north of females (Ketterson and Nolan 1976, 1979). Assuming an equal sex ratio on the breeding grounds—and both field study and theoretical considerations of sex ratio and mating systems support this assumption (see below)—the winter sexual separation necessarily implies that members of southern-wintering populations have migrated a greater average distance than members of northern populations. Further, in both sexes individuals produced in the preceding breeding season and adults exhibit differences, on the average, in winter distribution. The pattern of age distribution is stable from year to year and is complex (Ketterson and Nolan in prep.), but its most interesting feature is that the young of each sex tend to concentrate north of their adult counterparts. As with the sexual separation, this pattern implies differential migratory behavior associated with age, with adults traveling farther. When age classes of bird species separate in the winter range, it is usual for adults to make the shorter migration (Gauthreaux 1978), although the pattern we find in the junco has been observed in the American Goldfinch (*Carduelis tristis*) (A. Middleton pers. comm.) and the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) (King et al. 1965).

Predicting that juncos that winter in the north would experience greater overwinter mortality than those that migrate into the south, we also expected that annual survivorship of southern winter populations would be higher. A corollary of this latter prediction is that members of such southern populations should have lower reproductive success, assuming that fitness of juncos does not vary according to the latitude of the wintering site. As we here report, the expectation about unequal overwinter mortality appears to be correct, but the evidence does not support the prediction that wintering in the south confers greater annual survivorship. This implies that southern winterers have higher mortality than northern winterers at some other stage of the annual cycle, and the most probable occasion for such compensatory mortality is during their longer migrations.

Recent evolutionary speculations have stressed how little is known of the impact of migration on survival and reproduction and have urged that more attention be devoted to acquiring data that will further understanding of these subjects (Baker 1978, Gauthreaux 1979, Krebs 1979, Dingle 1980). For such inquiries the Dark-eyed Junco provides an exceptionally good system. Its extensive winter distribution and sex-age differences in distance migrated permit comparison of seasonal and annual survivorship among conspecific populations that differ greatly in the way they balance the risks of migration against the rigors of winter.

In this paper we present data on minimum overwinter survivorship and minimum annual survivorship in northern- and southern-wintering populations that we sampled by capture-recapture techniques at the beginning and end of single winters and also in successive early winters. Interpretation of such data requires that death and dispersal be separated out as factors affecting the recapture data. We therefore analyze United States Fish and Wildlife Service (USFWS) Bird Banding Laboratory records bearing on the question of north-south variation in the winter dispersal tendency of juncos in the eastern United States. We also examine these USFWS records for time elapsed between banding and recovery, which we take as an estimate of survivorship, and compare them with a long-term estimate of survival of an Indiana sample.

Our results, like the USFWS data that we consider, are limited to eastern winter populations. The breeding sites of these birds were unknown, and all references to northern and southern juncos are to winter populations, except where it is explicitly stated otherwise.

METHODS

Capture-recapture data.—Juncos end their autumnal migration about 1 December and begin spring migration about 1 March (evidence for this is reviewed in Ketterson and Nolan 1976), with indications that few move very far in the interim (see below). Therefore, individuals found from December through February we consider to be winter residents. We captured juncos at a series of sites in early winter (December, except that an occasional effort extended into the first few days of January), then made recapture efforts in late winter (February, except that one effort extended into early March) and/or in the subsequent December; all unmarked juncos, whenever caught, were given USFWS bands. Early-winter sampling was at Kalamazoo, Michigan (42°N); Bloomington, Indiana (39°N); Clemson, South Carolina (34.5°N); and Birmingham, Alabama (33.5°N) in the winters of 1976–1977, 1977–1978, 1978–1979, and, except for Alabama, 1979–1980 (Fig. 1). Late-winter sampling was restricted to the Indiana and South Carolina sites in 1977–1978 and 1978—1979.

Long-term mean temperatures for the period December–February and annual snowfall at the four capture-recapture sites follow: Michigan, −4.0°C, 139.9 cm; Indiana, −0.6°C, 59.9 cm; South Carolina, 6.5°C, 8.4 cm; Alabama, 7.8°C, 4.6 cm (U.S. Weather Bureau 1932).

Each capture effort was limited to a 3- to 6-day

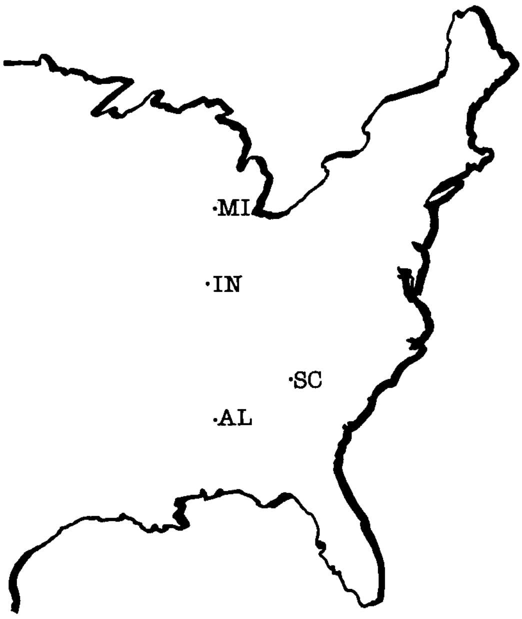

Fig. 1. Sites at which juncos were captured.

period of intensive field work that had been preceded by several days of baiting at the spots (hereafter called subsites) at which nets and traps were set up. One to four subsites were sampled at each site. At the end of all capture efforts, baiting stopped, except in Michigan, at one subsite in South Carolina, and at one subsite in Alabama. We made every attempt to standardize capture methods from site to site, with the exception that weather differences affected the ease of capture and therefore caused the length of capture efforts to vary. For example, snow usually covered the ground in Michigan and did so in late winter in Indiana and once even in South Carolina; this led juncos to concentrate at our bait and let us abbreviate our operations. At all sites on the last day of an effort, the proportion of recaptured individuals that had been caught and banded during that effort was approximately the same.

We sexed juncos by examination of plumage traits and wing length (Ketterson and Nolan 1976), performing laparotomies when in doubt. The degree of skull ossification in early winter revealed which individuals had hatched in the preceding breeding season (herein called young) or in some earlier breeding season (herein adult). In late winter, juncos caught for the first time were aged on the basis of plumage, wing length, and eye color (Ketterson 1979b). This method has proved 93% accurate in cases in which we tested late-winter age determinations of previously banded individuals against our original age determinations based on skull examination. Only birds released in good condition were considered in calculating recapture rates. A few were marked in one effort, not caught in the next, then recaptured in still the next. These we treated as having been present during the intervening effort, even though we had not caught them, but, having counted them as present on that one occasion, we eliminated them from subsequent recapture calculations.

Samples collected under the time constraints described are smaller than ideal for statistical purposes, and for some comparisons we have been compelled to pool across years. We have also combined the data from Michigan and Indiana, which we regard as northern wintering locations, and from South Carolina and Alabama, which we regard as southern. We tested for statistical homogeneity before such combining; despite nonhomogeneity in one case, we combined, because to do so produced a conservative result that did not affect the argument.

Other Indiana data.—We draw also on the results of two independent studies carried out near Bloomington at locations other than those referred to above and involving other juncos. (1) In December 1978 and 1979, as the first part of an investigation (in prep.) of dispersal within single winters, we caught, banded, and released juncos at eight stations, each 1.5–2 km apart, along a transect. In February 1979 and 1980, we again trapped and netted at these stations. Sexing and aging were as described above. We present these data here in order to show the sex-age structure of the Bloomington population at the beginning and end of two winters and to draw conclusions about the relative overwinter mortality of the different sex-age classes there. It is important to note that the structure at all eight stations was about the same; we detected no sex or age segregation in early or late winter. Recapture rates are not shown, although they were very much like the Indiana rates presented in Table 1, because our methods were different from those described above. (2) For a more accurate measure of the annual survivorship of juncos that winter in Indiana, we selected 128 site-faithful individuals caught between 1961 and 1977 at two sites at which trapping and netting were carried out nearly daily from October into May (the approximate limits of the junco's occurrence in Indiana). Male and female numbers in this sample were representative of the proportions in the Bloomington winter population; the sexes did not differ significantly in returns and accordingly were pooled. All 128 were present in at least two winters and three were present in six; not every bird was caught in an uninterrupted series of winters. Ignoring calendar years, we formed a composite in which each individual's banding year was the base line and subsequent years were +1, +2, etc. As is typical in avian survivorship studies (Nolan 1978: 466 and citations therein), the proportion of any year's birds that were present the following year did not change as the birds aged. We applied Caughley's (1977: 151) method to estimate

TABLE 1. Rate of recapture in late winter of juncos marked in early winter according to sex, age, year, and location.[a,b,c]

	Male		Female		Classes combined
	Adult	Young	Adult	Young	
Indiana					
1977–1978	6/27	2/36	0/4	0/10	8/80
1978–1979	4/41	6/42	1/9	3/19	16/118
Years combined	15% (68)	10% (78)	8% (13)	10% (29)	12% (198)
South Carolina					
1977–1978	8/31	6/15	11/22	5/13	30/81
1978–1979	7/15	3/7	12/21	8/12	30/55
Years combined	33% (46)	41% (22)	53% (43)	52% (25)	44% (136)

[a] Sample sizes are in parentheses and represent the number of juncos marked in early winter and released in good physical condition at a location that was sampled in late winter. The size of the combined sample is sometimes greater than the sum of samples of the respective sex-age classes, because a few individuals marked were of unknown sex or age.

[b] Late-winter recapture rates of the sex-age classes at a location were compared after combining data for the two different years. In Indiana, the sex-age classes were equally likely to be recaptured [$\chi^2 = 0.94$, df = 2, n.s. (female age classes combined because samples small)]. The same was true of South Carolina ($\chi^2 = 4.72$, df = 3, n.s.).

[c] Late-winter recapture rates of a sex-age class at the different locations were compared after combining data for the 2 yr. Each sex-age class was significantly more likely to be recaptured in South Carolina than in Indiana (adult males: adj. $\chi^2 = 4.15$, df = 1, $P < 0.05$; young males: adj. $\chi^2 = 9.36$, df = 1, $P < 0.01$; adult females: adj. $\chi^2 = 6.77$, df = 1, $P < 0.01$; young females: adj. $\chi^2 = 9.26$, df = 1, $P < 0.01$).

the annual mortality rate of the group. Use of site-faithful birds was necessary, of course; we recognize the possibility that nonfaithful individuals may have a different mortality rate.

USFWS data.—The Bird Banding Laboratory stores information on the date and location of initial banding and recovery as well as on the method of recovery, but it records locations only according to their 10-min blocks of latitude and longitude (roughly speaking 100 km^2 in the eastern United States). Recoveries made by bird banders are identified as such. The fact that banders are concentrated in more populous areas, especially in the northeastern United States, would bias the estimates made herein if recoveries by banders were included in our analysis, and we therefore considered only juncos recovered dead by the general public (i.e. we omitted cases with the Laboratory's recovery code numbers 10, 16, 29, 51–53, 87, 89, 99). From the resulting records for the years 1921 through August 1976, we selected the 368 cases of individuals that were both banded and recovered in winter (December–February) east of 106°W longitude. Each case we categorized according to (1) latitude of initial capture location, (2) whether recovery was during the winter of banding or during a subsequent winter, and (3) whether recovery was at or away from the initial capture location. We then examined the results for latitudinal trends in tendency to disperse from the banding location, either in the winter of initial capture or a later winter. When banding and recovery were in different winters and at different locations, we noted the directional relationship between the locations. If the locations were the same, we noted the interval in years between the two events.

Because juncos cannot be sexed reliably without considerable experience and the method of aging by skull ossification is both relatively recent and not used by all banders, we could not analyze USFWS data for possible variation associated with sex and age. We recognize that the USFWS data set is small, with few cases from the south. Further, the areas encompassed by 10-min blocks of latitude and longitude are much larger than the areas of our capture sites. This presents a difficulty, described in detail below, in combining USFWS recovery data with our recapture data. Of course, the size of the 10-min blocks has no effect on the validity of comparisons of northern and southern juncos when these comparisons are restricted to the USFWS data.

RESULTS

Recapture in winter of banding.—Minimum overwinter survivorship, as estimated by the percentage of juncos that were recaptured at the end of winter, differed geographically. A much larger proportion of South Carolina birds than of Indiana birds (44% vs. 12%) was recaptured in late winter (Table 1). A February snow storm, an unusual event in South Carolina, may have been partly responsible for the high recapture rate there. Even in the winter in which February weather in South Carolina was normal (1977–1978), however, the recap-

TABLE 2. Sex-age[a] structure (percentages of individuals) of early- and late-winter samples of juncos in Indiana and South Carolina.

		Male		Female	
	n	Adult	Young	Adult	Young
Indiana[a,b]					
December 1978	395	28	42	10	21
February 1979	400	24	45	9	22
December 1979	346	17	52	10	21
February 1980	320	22	44	13	22
South Carolina[a,c]					
December 1977	87	37	17	28	18
February 1978	170	23	15	34	28
December 1978	132	26	17	33	24
February 1979	104	34	10	41	15

[a] Indiana samples were caught in a study of dispersal at eight sites; individuals in them differ from those in all other tables. South Carolina juncos were caught in the overwinter survival study. See text.

[b] Indiana seasonal comparisons of sex-age ratios, December vs. February 1978–1979: $\chi^2 = 1.90$, df = 3, n.s.; December–February 1979–1980: $\chi^2 = 5.10$, df = 3, n.s.

[c] South Carolina comparisons of sex-age ratios, December vs. February 1977–1978: $\chi^2 = 7.96$, df = 3, $P < 0.05$; December vs. February 1978–1979, $\chi^2 = 5.95$, df = 3, n.s.

ture rate was significantly higher than the Indiana rate, and all Indiana late-winter recapture efforts were conducted after heavier snow storms than the one in South Carolina.

Comparing sex-age classes within each site, the late-winter recapture rates in Indiana were statistically indistinguishable for all sex-age classes, and the same was true in South Carolina (Table 1). In accordance with this evidence that at neither latitude did age or sex affect the probability of overwinter survival, data from our study of winter dispersal in Indiana (Table 2) reveal no statistical change in sex-age ratios between early and late winter and certainly suggest no disadvantage associated with being immature or female. When the structure of December and February samples caught in South Carolina is compared (Table 2), we see that in one winter it remained the same and in one it changed. In the latter, adult males were less frequent in late February–early March, and all females were more frequent. If this was not sampling error, it might mean that old males had begun to migrate (in which case our already high overwinter recapture rate might not be high enough); but it is most unlikely that it means old males survive winter in South Carolina less well than do females.

TABLE 3. Percentages of juncos recorded by United States Fish and Wildlife Service (1921–1975) as recovered in winter at the place of original capture, according to latitude of place of capture: an estimate of the relationship between dispersal and latitude.[a,b]

	Recovered in subsequent winter		Recovered in same winter	
Latitude of place of capture	Total cases	Percentage at place of capture	Total cases	Percentage at place of capture
45–44	2	100	3	100
43–42	25	52	73	95
41–40	45	53	75	91
39–38	42	74	60	90
37–36	6	83	6	83
35–34	8	88	9	77
33–32	3	100	11	100
	131		237	

[a] Data were taken from files of the Banding Laboratory of the United States Fish and Wildlife Service and restricted to juncos banded in the months December–February and recovered in those months in the same or in any later winter. Banding and recovery sites were located between longitude 70°W and 105°W. The Laboratory records locations only as within 10-min blocks of latitude and longitude; thus, recovery at the place of capture means within the same block. To avoid possible bias associated with the northward concentration of bird banding stations in the United States, the sample is confined to juncos recovered other than by a bird bander. Note that most initial captures were in the northeastern United States (Fig. 2).

[b] In correlating the percentage of recovery at the place of original capture (i.e. fidelity to a 10-min block as defined in footnote a) and latitude of place of original capture, intervals of latitude represented by fewer than five recoveries are ignored. For recoveries in a winter subsequent to that of original capture, r_s (Spearman's rank) between latitude and fidelity = 1.0, $n = 5$, $P < 0.05$. For recoveries in same winter as that of original capture, $r_s = 0.14$, $n = 6$, n.s.

USFWS data: recovery in winter of banding.—When analysis is limited to USFWS recoveries during the winter of initial banding, no geographic variation in overwinter dispersal is evident. Only 18 juncos among 237 that were thus recovered had moved to a different 10-min block, and such dispersal was as frequent among southern as among northern birds (Table 3). We interpret this below as support for the view that the difference in overwinter recapture rates in Indiana and South Carolina reflects, at least in part, differential winter mortality. However, if juncos that disperse from northern banding sites tend to move very short distances whereas those from southern sites move long distances, the USFWS method of recording only 10-min blocks would underestimate the relative numbers of northern dispersers and make the

TABLE 4. Rate of return from one December to the next according to sex, age, and location.[a,b,c]

	Males		Females		Classes pooled
	Adult	Young	Adult	Young	
North					
Michigan	19/141	4/165	1/43	2/64	26/413
Indiana	6/79	5/95	0/16	1/36	12/226
Combined	11%	3%	2%	3%	6%
	(220)	(260)	(59)	(100)	(639)
South					
South Carolina	5/62	7/40	4/78	5/44	21/224
Alabama	1/9	1/6	4/22	3/14	9/51
Combined	8%	17%	8%	14%	11%
	(71)	(46)	(100)	(58)	(275)

[a] The numbers of birds recaptured from among those released in good condition at the capture site in the preceding winter are presented for each location. A few juncos were recaptured only after an intervening winter, and these were considered to have been present in the first postbanding winter. Juncos were marked in four winters, and recapture efforts were made in three at Michigan, Indiana, and South Carolina. Only two recapture efforts were made at Alabama. The percentages were computed on the combined northern and combined southern locations.

[b] Comparisons of return of each sex-age class to northern (Michigan, Indiana) and southern (South Carolina, Alabama) locations follow: adult males, north vs. south, adj. $\chi^2 = 0.23$, df = 1, n.s.; young males, north vs. south, adj. $\chi^2 = 11.28$, df = 1, $P < 0.001$; young females, north vs. south, adj. $\chi^2 = 4.85$, df = 1, $P < 0.05$. For all classes pooled, rate of return to the south was significantly higher (adj. $\chi^2 = 7.07$, df = 1, $P < 0.01$).

[c] Frequency of return of the sex-age classes differed at northern sites ($\chi^2 = 17.87$, df = 3, $P < 0.001$) but not at southern sites ($\chi^2 = 3.80$, df = 3, n.s.).

data useless for our purposes. At the present time, we can say only that we have no reason to expect such a geographical difference.

Recapture subsequent to winter of banding.—The percentage of birds recaptured in a winter subsequent to that of banding, i.e. the return-recapture or minimum annual survival rate, showed both geographical variation and variation according to sex-age class. When data pooled from Michigan and Indiana without respect to sex or age and combined across all years are compared to similarly pooled and combined data from South Carolina and Alabama, return-recapture at the northern sites (6%) was significantly lower than at the southern sites (11%) (Table 4).

When the data are broken down by sex and age, the frequency of returns at the combined northern sites differed for the four classes ($P < 0.001$), but this was attributable to variation between the two most numerous classes: adult males returned and were caught more frequently than young males (11% vs. 3%, $P < 0.001$) (Table 4). This difference, in conjunction with the preponderance of males in the north, also causes the northern adult rate to exceed the rate for northern young (9% vs. 3%) significantly. Sample sizes do not permit statistical comparison of northern female age classes (2% vs. 3%), because so few adult females winter in the north. Similarly, adult females cannot be compared statistically with adult males, although the percentage of adult male returns was higher (11% vs. 2%).

In contrast to the variation between northern age classes and also between northern sex classes, all sex-age classes in the south were recaptured with statistically equal frequency.

Turning to sex-age comparisons between north and south, young northern juncos of each sex returned and were recaptured at the banding site less often than young southern juncos of the same sex (males: 3% vs. 17%, females: 3% vs. 14%). Adult male returns were the same, north and south; again the small northern sample of adult females prevents statistical comparison (males: 11% vs. 8%, females: 2% vs. 8%).

Because we believe the low return rate of northern adult females to be largely a product of sampling error—recall that the Indiana sample of site-faithful individuals showed no sexual bias—we summarize and interpret Table 4 as follows. The difference in the pooled return-recapture rates between northern and southern locations is apparently largely or entirely due

Fig. 2. Initial capture location and recovery location of juncos shown by USFWS records to have been captured and recovered in different winters and at different places. For clarity, movements of less than 30 min are not plotted. See text for other details. Each line represents an individual junco. The dot is at the original capture location and the arrow point is at the recovery location.

either to lower survivorship or lesser site fidelity among young northern juncos of both sexes. These alternative possibilities are discussed below.

USFWS data: recovery subsequent to winter of banding.—We consider the extent to which the juncos in the USFWS sample tended to select a new location in the later winter. Of 131 individuals banded in one winter and recovered in another, 46 had moved away from the 10-min block in which they had first been caught (Table 3). This considerable shift was largely confined to birds first captured at higher latitudes (Table 3). The concentration of data from more northerly locations makes statistical comparison somewhat arbitrary. Table 3 employs a Spearman's rank coefficient, but here we compare the subsets from latitudes 42–45° (15 returns in 27 cases), 40–41° (24 returns in 45 cases), 38–39° (31 returns in 42 cases), and 32–37° (15 returns in 17 cases): $\chi^2 = 9.16$, df = 3, $P \leq 0.05$. Both approaches indicate that site fidelity was greater to more southerly locations. In addition, a directional component is apparent in cases in which individuals chose new sites. Most tended to move southward, sometimes great distances, in later years (Fig. 2); among 28 cases of latitudinal shifts equal to or greater than 30 min, i.e. shorter movements and east-west movements excluded, 24 were southward.

This interesting result caused us to reanalyze the initial capture (banding) dates of the juncos that shifted to new sites. Our question was whether these individuals really had been winter residents where first caught: if the capture dates had fallen in early December, this might support the view that these birds were still migrating southward when caught, i.e. had not necessarily resided in different places in the two winters. No such support was found, however. Only two banding dates were prior to 18 December (on 11 December of different years), and seven and nine, respectively, were in January and February.

USFWS data: life expectancy.—We examined the number of whole years elapsed between banding and recovery of the 85 USFWS juncos that were taken in two different winters in the same 10-min block and that had therefore been exposed to the same climates, if not weather, in both those winters (and probably in any intervening winters as well). Treating years elapsed as an estimate of life expectancy at the time of banding, we looked for variation according to latitude. No variation is detectable (Table 5). Approximately half the juncos that survived to be recovered in a winter subsequent to that of banding had lived at least 2 yr after first capture, regardless of the latitude of the banding site.

Translating the data in Table 5 into a survival rate and making the usual assumption of constant annual mortality with advancing age, the survival rate is 54%.

Survival of site-faithful Indiana juncos.—Caughley's method estimates the annual survival rate of the juncos site-faithful to Bloomington to be 53%, as follows:

$$\bar{q} = 1 - \frac{m_1 + m_2 + m_3 + m_4 + m_5}{m_0 + m_1 + m_2 + m_3 + m_4}$$

$$\bar{q} = 1 - \frac{99}{187}$$

$$\bar{q} = 0.47$$

where $\bar{q}$ = finite rate of annual mortality and m_n = number of marked juncos caught at time n.

DISCUSSION

OVERWINTER SURVIVORSHIP AND DOMINANCE STATUS

Indiana samples, which were large as well as diverse in method and location of collection (Tables 1 and 2), were alike in indicating that sex and age did not influence the probability that an individual would survive the winter. As discussed above, we interpret the less numerous data from South Carolina as indicating that the same was true there (Tables 1 and 2).

TABLE 5. Years elapsed between banding and recovery of juncos recovered in some subsequent winter at the banding location, according to latitude: an estimate of the relationship between wintering latitude and life expectancy (USFWS data).

Latitude[a]	Total cases[a]	Recovered more than 1 yr (winter) after banding[b]	
		n	Percentage
45°–42°	15	8	53
41°–39°	44	26	59
38°–36°	16	7	44
35°–32°	10	5	50
	85	46	

[a] Sample consists of juncos recovered in same 10-min block at least 1 yr (one winter) after winter of banding. Extreme northern and extreme southern bands of latitude are 4° wide; middle intervals are 3° wide in order to make sample sizes comparable.

[b] Comparing latitudes for number of juncos recovered more than 1 yr (winter) after banding and number recovered only 1 yr after banding, $\chi^2 = 1.20$, df = 3, $P > 0.5$; time elapsed (survived) between banding and recovery is independent of latitude.

These results have interesting implications for theories about the importance of dominance, which until quite recently (Ketterson 1979b, Baker et al. 1981, Rohwer and Ewald 1981) has been generally accepted as affecting survival.

The sex-age classes of juncos differ in dominance rank when winter flocks assemble at food (Balph 1977; Ketterson 1979a, b), and in juncos dominance rank has been related to survival in nature (Fretwell 1969) and in the laboratory (Baker and Fox 1978). These facts would lead to the prediction that overwinter survivorship varies according to the rank associated with each sex-age class, that is, in descending order from adult males to young males, adult females, and young females. Survivorship differences of this kind might have been expected to be especially conspicuous in the severe winters of Indiana. Our observations to the contrary suggest either (a) that dominance played no role in the evolution of geographic variation in winter sex-age ratios (see Myers 1981), because it does not influence overwinter survivorship, or (b) that dominance did play a role and has produced a pattern of varying ratios in which subordinate classes suffer differentially only when population structures or densities shift from those that obtained during this study. Aviary experiments in which sex-age ratios are varied, food restricted, and behavior and survivorship noted are underway in an effort to pursue this problem.

DIFFERENTIAL OVERWINTER MORTALITY IN NORTH AND SOUTH

The lower overwinter recapture rate in Indiana as compared to South Carolina, when considered with the USFWS data suggesting no geographic difference in overwinter dispersal, points to greater winter mortality among northern juncos. That juncos do die during severe weather is a fact. Their emaciated carcasses are found after periods of prolonged snow cover and low temperature (Roseberry 1962, Johnston 1962, Graber and Graber 1979, pers. obs.), which are frequent in the north and rare or absent in the south. Furthermore, our 2-yr study of dispersal in Indiana and over 20 yr of intensive winter banding there at several sites about 0.1–0.3 km apart have revealed little dispersal and none on a scale that could produce the substantial difference in Indiana and South Carolina overwinter recapture rates.

We conclude that very probably northern juncos of all sex-age classes die more frequently in the average winter than do southern juncos. Because our data were obtained during only two winters, we do not propose that they are necessarily representative of the long-term difference between Indiana and South Carolina.

FACTORS OFFSETTING DIFFERENTIAL OVERWINTER MORTALITY IN NORTH AND SOUTH

Theoretical considerations.—If the conclusion just reached is correct and if, as we take for granted, choice of winter site is governed by natural selection, the mortality difference associated with wintering in the north must be offset by advantages that tend to equalize the fitness of members of northern and southern winter populations. (We assume that fitness does not vary according to location of wintering site, i.e. that directional selection is not in the process of shifting the junco's winter distribution either southward or northward.) The compensatory advantage(s) of wintering in the north must take the form of (1) higher survivorship than that of southern juncos during some other season(s), thus bringing annual survivorship toward equality, or (2) greater reproductive success, or (3) a combination of these.

Investigation of the nature of the putative advantage accruing to northern winterers encounters, at the threshold, the fact that data on comparative reproductive success are nonexistent and probably unobtainable. Getting them would require that members of winter populations be traced to their summer locations in a vast breeding range. Good estimates of long-term annual survival rates of northern and southern winter populations can be developed, however, and comparison of these will give an idea whether, and to what extent, differential reproductive success is operating to equalize fitness. If long-term annual survivorship is found not to vary with the latitude of the wintering site, the assumption of stability in the existing winter distribution would exclude the possibility of unequal long-term reproductive success. There would remain only the alternative that seasonal survivorship is unequal, not simply in winter but during other segments of the year as well.

The data to be discussed below suggest to us that the average annual survival rates of northern and southern winter populations are the same. We argue that southern winterers probably suffer heavier mortality during, and because of, their longer migrations and that this equalizes their survivorship with that of northern winterers.

Evidence for equal annual mortality.—(1) The life expectancy of juncos banded in one winter and recovered in the same 10-min block in a later winter, as recorded by the USFWS, was invariant with latitude. The sample is not large, but it gains strength from having been compiled over many years. Probably the result is not much distorted by random annual variation.

(2) Our estimated annual survival rate of 53% among site-faithful Indiana juncos agrees very closely with the independent estimate, 54%, from the USFWS data. It is important to note that 53% is well within the range of annual survival rates reported for temperate-zone passerines (Farner 1955, Greenberg 1980, Searcy and Yasukawa 1981). If our estimate is representative of juncos that winter in Indiana, there is no a priori reason to expect South Carolina juncos to have higher survivorship, nor is it necessary to suppose that Indiana popu-

lations require some unusual reproductive advantage to maintain equal fitness with southern juncos.

(3) The return-recapture rates in Table 4 show equal minimum annual survival of adults in northern and southern winter populations. The 53% Indiana survival rate obtained by continuous efforts throughout the junco's residence there shows that in Indiana sampling lasting only a few days fails to recapture many banded individuals that are in fact present. That this is also true at our other sites is indicated by the fact that at all of them we sometimes caught banded juncos that had escaped capture in the preceding effort. We assume that the probability of failing to recapture an individual even though it was present was equal at all sites. If this conservative assumption is correct, annual survivorship of adults in those samples did not vary with latitude.

In contrast to the adult rates, the return-recapture rate of northern young fell below the rate for northern adults, for southern young, and for southern adults, all of which were statistically indistinguishable. Despite this difference, for two reasons we believe that northern young survived the year between sampling and resampling as well as did the other classes. (1) The survival of northern adults from December to December would not be expected to be higher than that of northern young if it were no higher in the first 3 months of that 12-month period. Any survival disadvantage associated with inferior age and experience should show up early, particularly because the early part of the year used in our calculations was winter. But Tables 1 and 2 reveal no disadvantage; northern young were as likely as adults to be recaptured in late winter, and in each of two winters rather large Indiana samples revealed no change in age ratios between December and February. Evidently, young juncos have passed beyond the "initial juvenile period of higher mortality" (Farner 1955: 403) by December. In this they are like many other north temperate-zone passerines, for which, as a rule of thumb, 1 January is often taken as the date at which life expectancy stabilizes at the adult rate (see discussion and citations in Farner 1955). (2) The low return-recapture rate of northern young can be explained plausibly by supposing that some survivors of that age class choose new sites in their second winter and thus are responsible for the lower fidelity to northern latitudes revealed in the USFWS data. We emphasize that the junco's age distribution in winter would have led us to predict a lower return-recapture rate of northern young even before that lower rate was found. That is, a distribution in which young tend to winter north of adults could be maintained year after year only by lower survivorship of young than of adults between December sampling operations (a possibility just considered and dismissed) or by choice of a different and more southerly second winter site by some individuals that have spent their first winter farther north. Notably, Spaans (1977) has reported similar between-winter shifts toward milder climate in the Starling (*Sturnus vulgaris*).

In sum, the return-recapture rates, the USFWS records, and our winter demographic data converge from independent directions and point to equal annual mortality of northern and southern wintering populations.

Consequences of unequal annual mortality.—Without regard to the affirmative evidence for equal annual mortality, unequal mortality of winter populations would have demographic consequences that can be predicted from, or tested against, theory. All the expected consequences would be observable in the field, and none has been observed.

Any hypothesis that northern winter populations have lower annual survivorship must also take account of, and be reconciled with, five points that we regard as facts or fair assumptions about the junco. (1) More males winter in the north, more females in the south. (2) Overwinter survival of the sexes in the north is equal. (3) Southern juncos are more likely to survive winter than are northern; therefore, because of points 1 and 2, fewer females than males die during winter. (4) Mortality of adults, i.e., experienced migrants, is probably no higher during autumn migration than during spring migration, because weather is less certain at the time of spring migration, and the preceding year's seed crop is depleted after having supported consumers throughout the winter. (5) The hazards of migration per unit of distance traveled are probably the same for females as for males; if the two sexes depart from the same spot for the same destination, females should be at least as likely as males to survive and arrive. This assumption seems reasonable in view of the absence of any sex role associated with the behavior involved in

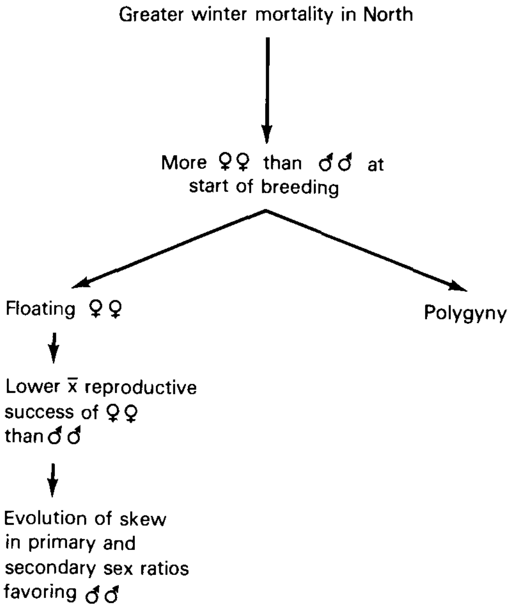

FIG. 3. Possible evolutionary consequences of a situation in which winter mortality, and as a result annual mortality, of males exceeds that of females, producing an excess of females among potential breeders. See text.

migrating. If a bias does exist, it is likely to be against males, because males migrate earlier (spring only, pers. obs.), when weather conditions are both less predictable and less moderate.

In addition to the five points just enumerated we make another assumption, which, though it is conservative, must be justified. In the next section we present our reasons for assuming (6) that survivorship of the sexes is approximately equal during the breeding season, but for the present we simply proceed on the assumption.

Now suppose a breeding population, its sex ratio at unity and its members about to migrate varying distances into the winter range. Under the hypothesis that annual mortality rates of winter populations are unequal because of higher survivorship of southern winterers, more females than males from this breeding population will be alive at the start of and during the next breeding season. The imaginable consequences of a breeding-season surplus of females are either (1) that some females will not get mates or (2) that some females will mate polygynously (Fig. 3). The first of these possibilities results in greater reproductive success for males, the minority sex, than for females (*sensu* Fisher 1930). Such a situation, in which a floating population of females exists, will not be stable: instead, the sex ratio at conception (hereafter, primary sex ratio) would be expected to evolve toward a skew in favor of males and this skew would persist in the sex ratio at the end of parental care (hereafter, secondary sex ratio). The second alternative, polygyny, supposes that this mating system would evolve as a response to an unbalanced tertiary (breeding) sex ratio. Such an evolutionary sequence was at one time accepted as a satisfactory mechanism to account for avian polygyny, but it is now generally rejected, because it probably confuses cause and effect (Selander 1965, Orians 1969, Emlen and Oring 1977; but see Wiley 1974).

Field data bearing on the alternative possibilities just presented are as follows. *Mating system:* Juncos are reported to be, like the great majority of birds (Lack 1968a, Verner and Willson 1969), monogamous. During 8 weeks (spread over 4 yr) of intensive study of juncos in July and early August, when most females have dependent young, we have found 30–35 broods, all of them closely attended by an adult male and an adult female. Sexual dimorphism of juncos is slight, which supports the view that monogamy is their normal mating system (Emlen and Oring 1977).

Secondary sex ratio: At Wawa, Ontario, we netted randomly for 3 days in early September 1979 and for 10 days at the end of July 1980 and caught 43 newly independent young that were still in complete juvenal plumage. Of these, 22 were male and 21 female. (The birds were held in captivity and sex determined in the usual way after postjuvenal molt was completed.)

Breeding sex ratio: We have seen no evidence of a floating nonbreeding female population. Instead, all females that we have netted randomly, even early in the breeding season (June), have had incubation patches. Twice we have observed males, known to be unmated, advertise for at least 2 weeks in June.

In sum, the hypothesis that southern-wintering juncos have greater annual survivorship implies a sexual difference in mortality because of the clinal variation of the winter sex ratio. None of the consequences of a sexual difference in annual mortality has been observed, and what field evidence there is tends to falsify the hypothesis.

Mortality at other seasons.—If further evidence should establish that annual mortality is invariant for northern and southern populations sampled in December, during what season(s) is it likely that southern winterers compensate by experiencing higher mortality than northern?

We turn first to the breeding season. It is most unlikely that higher mortality during breeding would be *caused* by wintering in the south, but there are two possible reasons for a *correlation.* (1) If breeding location determined winter location in the sense that members of breeding populations wintered together, e.g. if northern breeders were northern winterers, latitudinal variation in some factor causing summer mortality might offset latitudinal variation in winter mortality. Although we can conceive of clinally varying summer mortality (e.g. as the result of distribution of predators), we reject this first alternative, because breeding populations do not remain intact in winter: the partial sexual separation and, probably, the partial age separation at that season eliminate this possibility. (2) Higher survivorship by southern winterers would tend to be offset by higher summer mortality if breeding females had a greater mortality rate than breeding males. We know of no evidence bearing on a sexual difference in breeding mortality, except that we have not seen dependent young being tended by only one parent (see above). If, however, excessive male mortality in winter were balanced by excessive female mortality in summer, a nonbreeding surplus of females would arrive—and for a time survive—on the breeding range, unless the primary and secondary sex ratios shifted to adjust for the greater reproductive success of males or unless some mating bonds were polygynous. These points have been examined above, where it was concluded that existing evidence does not point to a surplus of females, or a skewed secondary ratio, or a polygynous mating system. We therefore propose that southern winter populations compensate for their greater overwinter survivorship by greater mortality during, and because of the increased risks involved in, their longer migrations.

If annual mortality of southern winterers is equalized during their migrations, in an average year approximately the same number of males and females will arrive on and leave the breeding grounds. Males will predominate in the winter range at the beginning of winter, be in the minority just before spring migration begins, and be in parity again after migration mortality has reduced southern winterers, with their disproportionate female numbers.

It may be objected that a substantial increase in mortality during migration into the south is unlikely when the difference in distance traveled to southern sites is probably at most about 1,000 km, approximately the distance separating our Michigan and Alabama sites. It is true that some juncos have been found (Johnston 1962, Helms et al. 1967) to carry migratory fat reserves sufficient to permit them to cover 1,000 km in only two flights, with a stopover to fatten up, although we see few fat juncos in spring and autumn in Indiana. Theoretical arguments and limited evidence (reviewed by Baker 1978: 679) suggest, however, that overland migrants do not make long flights, whatever their fat reserves. Instead, they are believed to migrate in numerous short moves separated by stopovers, a conclusion that Johnston (1962) drew for juncos after field and experimental physiological study of North Carolina populations. At each stop the migrant may confront dangers arising out of unfamiliarity with locations of food, shelter, and refuge from predators. We imagine such dangers to be considerable and to increase in stepwise fashion with the number of stops. So far as we know, the extent to which hyperphagia leads birds to run greater risks of predation has not been investigated, but the increase may be important. Certainly, hungry, free-living juncos will tolerate the close approach of humans before interrupting their foraging (e.g. when snow covers the ground), and we have seen many apparent migrants with such low energy reserves that they can be assumed to have been hungry. For example, juncos caught in midafternoon in Indiana during the migration seasons sometimes starve before morning if held at room temperature without food. In contrast, Indiana juncos caught in winter normally can fast for 40–45 h at 4°C and still recover (Ketterson and Nolan 1976, 1978; Stuebe and Ketterson 1982).

The magnitude of the disparity in migration mortality that would be necessary to equalize

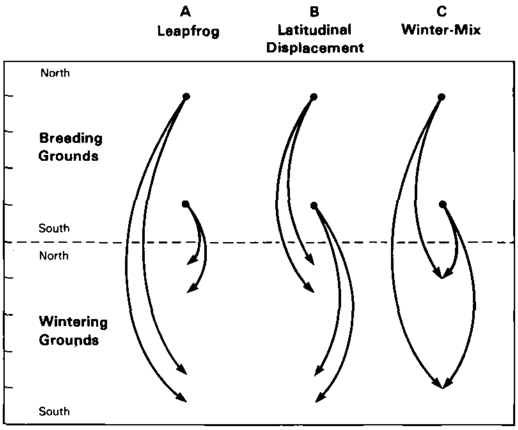

Fig. 4. Three possible migration patterns in the Dark-eyed Junco: leapfrog, latitudinal displacement, and winter-mix. Two breeding populations, each consisting of males and females making long- and short-distance migrations to their wintering sites, are shown for each pattern. Hatching on lefthand vertical axis indicates arbitrary units of distance. The predicted consequences of the patterns are summarized in Table 6.

annual survival is easy to overestimate if one thinks only in terms of the overall annual rate. As an example, consider two adult populations of equal size leaving the same breeding ground, one heading for a northern winter site and the other for a southern. In order to reduce each by 50% at the start of the next fall migration and to impose on the northern population a winter mortality rate twice as great as that of the southern population, seasonal mortality rates during the year could be as follows: northern population—fall migration, 13%; winter, 30%; spring migration, 13%; breeding season, 5%; southern population—fall migration, 21%; winter, 15%; spring migration, 21%; breeding season, 5%.

Consequences of patterns of migration.—To this point, consideration has been virtually confined to winter junco populations and to why and how we believe these probably arrive at equal survivorship, on average, from December to December. Breeding populations have been referred to only when necessary to project the effects that various mortality patterns might have on sex ratio or the mating system. These expected effects would be independent of the latitude of the breeding site. But breeding latitude will have important consequences if we are correct in proposing that migration mortality is positively correlated with distance migrated, and we now deal with that aspect of the subject. The question is whether the model for winter populations—equal annual mortality rates and therefore no need to suppose unequal reproduction—suffices for breeding populations or must be modified to permit variation in reproduction among these. The answer, we think, depends on what migration pattern (defined below) has evolved in the junco.

Figure 4 depicts three basic ways (hereafter patterns) in which breeding populations can arrange themselves on the wintering grounds. (Intermediate patterns can be imagined, but consideration of them would add nothing to this analysis.) In the leapfrog pattern (Greenberg 1980) (A), the southernmost breeders make the shortest migration and therefore winter farthest north, etc., and populations from different latitudes do not intermingle in the winter range. In the latitudinal displacement pattern (B), all breeding populations travel the same distance; the northernmost breeders are the northernmost winterers, and here again breeding populations remain intact in the winter range. In the winter-mix pattern (C), no relationship exists between latitudes of breeding and of wintering sites, and breeding populations mingle randomly in winter.

Before predicting the different consequences these patterns would have for the dynamics and other characteristics of junco populations, we state those respects in which we assume all patterns will be alike: (1) members of breeding and winter populations have equal average fitness; (2) females from each breeding population tend to winter south of males from the same population; (3) because migration mortality and winter survivorship correlate positively with distance migrated and can offset each other, southern winterers from each breeding population are equal in fitness with northern winterers from that population; (4) breeding-season mortality does not vary clinally with latitude. (This last assumption can be discarded with predictable consequences, but we see no reason to complicate matters by doing so here.)

Table 6 presents consequences we expect each pattern to produce. In A, the southern breeding population migrates the shortest distance and trades its higher migration survivorship for higher winter mortality; equal fit-

TABLE 6. Predicted consequences of possible migration patterns in juncos, based on the conclusion that migration mortality increases with distance traveled, while winter mortality decreases.

	Migratory pattern of breeding populations		
	A Leapfrog	B Latitudinal displacement	C Winter-mix
Northern vs. southern breeding populations[a]			
Annual mortality	=	≠, N > S	≠, N > S
Migration mortality	≠, N > S	=	≠, N > S
Winter mortality	≠, S > N	≠, N > S	=
Reproductive success	=	≠, N > S	≠, N > S
Northern vs. southern winter populations[a]			
Annual mortality	=	≠, N > S	=
Migration mortality	≠, S > N	=	≠, S > N
Winter mortality	≠, N > S	≠, N > S	≠, N > S
Reproductive success	=	≠, N > S	=
Variance in genetically based characters greater in winter than in breeding populations?	No	No	Yes
Preserves during winter any clinal variation occurring on breeding grounds?	Yes (but cline reversed)	Yes (and cline in same direction)	No

[a] N = northern; S = southern.

ness across populations (both winter and summer) can be achieved without inequality of reproduction. In B, migration mortality is equal for all populations, but winter mortality of northern breeders is higher; these must have higher reproduction if they are to be as fit as southern breeders. Because C mixes northern and southern breeders on the wintering ground, winter mortality is invariant with breeding latitude, but northern breeders make longer migrations, die at a higher rate for that reason, and must have greater productivity if their fitness is to equal that of southern breeders.

Each pattern predicts its own set of characteristics of winter populations, and these can be compared with what is known to date about wintering juncos. Annual survival rates measured from December to December (i.e. at start of winter) could be equal under A but not under B. They could also be equal under C, but the situation would be somewhat complex: equality across winter populations would exist despite inequality across breeding populations. Restated in terms of fitness, the equal average fitness of members of winter populations would be attained because each population would consist of two elements: (1) southern breeders with lower migration mortality and lower reproduction, and (2) northern breeders with higher migration mortality and higher reproduction. As for winter sex ratios, in our view only a migration that incorporated some degree of pattern C would produce clinal variation. Finally, to the extent that breeding populations vary morphologically (Miller 1941: 317 describes some geographical variation in *Junco h. hyemalis*), A and B would preserve such variation in the winter range, whereas C would tend to abolish it. Variance in relevant morphological characters of winter populations (or in other genetically based traits) would in that case be greater than that of breeding populations under C but not under the other two patterns.

It will be apparent that if the junco satisfies the assumptions set forth above, its partial sexual segregation in winter suggests that its migration pattern approaches C more closely than A or B. The evidence favoring equal annual mortality from December to December is consistent with C but also with A. Our body-size data for winter and summer populations are still being analyzed, but we can state now that if there are latitudinal body-size clines in summer they are not preserved in winter.

In conclusion, it is obvious that adequate breeding studies in northern and southern Canada, although they would be difficult to carry out, would reveal whether reproductive success varies with latitude and would thus contribute to an understanding of the junco's migration pattern.

THE ROLE OF MIGRATION IN LIFE HISTORY

How do our evidence and interpretations relate to current theory concerning the significance of migration for individual fitness? Most consideration of variation in distance migrated by conspecifics has approached the problem from the point of view of breeding populations. In particular, the question has been the identification of the advantages and disadvantages of remaining on the breeding ground throughout the year among so-called partially migratory species. The logic of theories about systems in which fewer than all individuals are migratory, however, appears applicable also to fully migratory species in which elements of the population travel varying distances and therefore settle in different winter sites.

Baker (1978: 635) summarizes the literature on partial migrants and derives two models to account for the fact that selection has not eliminated either the migrant or the nonmigrant element. The models are alike in assuming (1) a stable system (i.e. equal fitness for migrants and nonmigrants), in which (2) the nonmigrant element in some or all years suffers higher winter mortality than the migrant (3) as the result of failure to leave the breeding range. One model proposes that a higher reproductive rate compensates for the greater winter mortality of nonmigrants and attributes this reproductive gain to priority of access to limiting breeding resources (von Haartman 1968) or to a longer period in which to reproduce. [Compare Nolan (1978) on the advantages in terms of breeding time gained by male Prairie Warblers that return early to the breeding ground, and see Greenberg (1980), who argues that temperate-zone breeding species wintering in the tropics pay for enjoying a benign winter climate by losing time for reproduction.] This view, as we read it, does not concern itself with mortality associated with migration, assumes that the benefits of migrating are self-evident, and considers the theoretical problem to be accounting for the continued existence of the nonmigrants. The other model is that of Lack (1954, 1968b), who starts from the proposition that migration is costly. In some years migration mortality is higher than the winter mortality of sedentary individuals, in other years lower. Over time, the annual rates for migrants and nonmigrants balance out, and both elements continue to exist. Productivity apparently is taken as unvarying with migratory status.

Lack's view, because it weighs migration losses against winter losses, resembles the model proposed herein for winter junco populations. It differs, however, in that its concern is with unequal year-to-year mortality rates that fluctuate around equal long-term means. We do not disagree with Lack, in that we do not suppose that the annual mortality rates of northern- and southern-wintering juncos are identical from year to year, although in theory annual rates could be invariant despite large and important differences in their seasonal components. Nevertheless, it seems clearly desirable to analyze population dynamics over the shortest possible, biologically meaningful time intervals, even though other temporal perspectives may be equally important. With special reference to the subject of this paper, study of geographic differences in winter mortality of conspecific populations may permit estimates of the scale of mortality during migration if annual and breeding-season survivorships of the populations are known.

ACKNOWLEDGMENTS

We thank the many people who have helped make our capture efforts possible, particularly the following: Ray Adams, Pat Adams, Sidney Gauthreaux, Jr., Paul Hamel, Carl Helms, James V. Peavy, Jr., Anna Ross, Ruth Schatz, and Paul Schatz. Members of our own group who accompanied us and whose field work was indispensable were Sue Braatz, L. Jane Clay, Mary Latham-Weeks, Dorothy Mammon, Catherine Meyer, J. P. Myers, Cindy B. Patterson, Toy S. Poole, Richard Rowlands, Michael Shelton, Robert Steel, and Ken Yasukawa. Sidney Gauthreaux, Jr., John M. Emlen, and James Blank made valuable suggestions about an earlier version of this paper. Bowling Green State University, Indiana University, Clemson University, the Kalamazoo Nature Center, and the Banding Laboratory of the U.S. Fish and Wildlife Service supported us in important ways. This research was funded in part by NSF DEB-78-11982 and DEB-81-10457.

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The AOU Student Awards Committee issues the following reminders to all students interested in competing for the AOU Student Paper Award and the two Nellie Johnson Baroody Student Paper Awards at the 1982 AOU meetings: (1) To qualify for the competition, each student must submit an expanded abstract of the paper directly to the chairperson of the AOU Student Awards Committee (**Douglas Mock, Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069**) by the "Call for Papers" deadline in the meeting announcement. (2) Appropriate applications with expanded abstracts must be submitted separately for the student paper awards and for the Marcia Brady Tucker travel awards. (3) A student is ineligible for student paper awards if she/he shares authorship of a paper, i.e. the student must be the exclusive author.

The American Ornithologists' Union will hold its annual meeting in Chicago, Illinois from **10–14 October 1982.** A formal call for papers is enclosed with this issue of *The Auk*, with a deadline for submission of abstracts for papers and poster sessions of **20 May 1982.** For further information on the scientific program, contact **James R. Karr, Program Chairman, Department of Ecology, Ethology, and Evolution, University of Illinois, 606 E. Healey, Champaign, Illinois 61820 USA.**