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Indiana University Foundation

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P. O. Box 1847, Bloomington, Indiana 47402

TITLE OF PROPOSED PROJECT

Proximate Factors Accounting for Stable Sex and Age Differences in the Winter Distribution of Dark-eyed Juncos (Junco h. hyemalis)

REQUESTED AMOUNT	PROPOSED DURATION	DESIRED STARTING DATE
$199,676	3 years	1 September 1981

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Department of Biology	Indiana University	812 337-8837 / 812 337-7443

PI/PD NAME	SOCIAL SECURITY NO.	DATE OF HIGHEST DEGREE ACHIEVED	MALE	FEMALE
Ellen D. Ketterson		1974		*
Val Nolan Jr.		1949	*	
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PRINCIPAL INVESTIGATOR/ PROJECT DIRECTOR	AUTHORIZED ORGANIZATIONAL REP.	OTHER ENDORSEMENT (optional)
Ellen D. Ketterson Val Nolan Jr.	NAME John W. Ryan	NAME
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TITLE Associate Scientist Professor of Biology	TITLE Chairman, Indiana University Foundation	TITLE
DATE 31 January, 1981	DATE 2 February, 1981	DATE

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P. O. Box 1847, Bloomington, Indiana 47402

3. PRINCIPAL INVESTIGATOR AND FIELD OF SCIENCE/SPECIALTY

Ellen D. Ketterson	Population Biology of Birds
Val Nolan Jr.	Population Biology of Birds

4. TITLE OF PROJECT

Proximate Factors Accounting for Stable Sex and Age Differences in the Winter Distribution of Dark-eyed Juncos (Junco h. hyemalis)

5. SUMMARY OF PROPOSED WORK (LIMIT TO 22 PICA OR 18 ELITE TYPEWRITTEN LINES)

Relatively little is known about the role of migration in life histories or the proximate factors controlling distances the individual migrates.

Sex-age classes of Dark-eyed Juncos differ in winter·distribution, therefore in distance migrated. Capture-recapture rates from various latitudes, abundance data from the winter range, and records of movements by banded juncos all suggest that the distributional differences are attributable to (1) high northern overwinter mortality, (2) low northern site fidelity and (3) a southward shift of some juncos with increasing age. Annual mortality appears equal, north to south, indicating that seasonal differences in mortality balance out.

To test point (1) above, we propose to compare overwinter dispersal rates in northern and southern populations. To test points (2) and (3) above, we plan to equalize risks of mortality of a northern and southern sample during all seasons but breeding, then to compare recapture rates as indices of site fidelity.

To determine the relative importance of endogenous factors and environment or experience in the regulation of distance migrated into the winter range, we propose to compare the seasonal duration of Zugunruhe (an expression of the migratory state) of all sex-age classes under a common environmental regime.

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I. INTRODUCTION

Despite the common occurrence of migration and the interest that the subject has long aroused, relatively little is known of the role of migration in life histories. Several workers have recently called attention to the need for empirical data if we are to proceed beyond rather general and qualitative speculation about migration's function (Baker 1978, Gauthreaux 1979, Dingle 1980). Further, advances in understanding of much studied related subjects, e.g., sensory systems associated with migratory orientation, may depend on more precise knowledge of migration in the species involved, for example on differences in migratory tendency associated with sex, age, social status, or breeding origin.

Our work on the winter distribution and population dynamics of the migratory Dark-eyed Junco, an abundant sparrow (Fringillidae or Emberizidae), has disclosed regular patterns of intraspecific variation. We focus on winter distribution because it is the aggregate product of the movements of all individuals that succeed in completing migration, and the dynamics of the various winter populations are the consequences of individual choices of wintering sites. We have studied winter junco populations in six states, from Michigan to Mississippi, and we know of no other efforts to investigate conspecific populations across a wide geographic range (winter population studies of migratory non-game birds are few). We attempt to show herein the important contribution this and similar work can make to knowledge of vertebrate migration and life histories.

We chose to study the junco in the eastern United States for several reasons. Most important were the size and varied environments of the winter range. The eastern migratory race breeds primarily in the boreal forest of Canada and winters from nearly the northern to nearly the southern border of the United States (Bent 1968). The enormous winter range offers the individual junco a diversity of climates in which to spend a critical season, but the price of settling in a moderate or a benign climate is an increasingly long migration. Juncos are easily captured, which promised us a large data base from our own efforts and supplemental information from the banding records of the U.S. Fish and Wildlife Service. They are also easy to maintain in captivity. Finally, since modern investigation of migratory physiology began, the junco has been a primary subject of study (Rowan 1925, Wolfson 1942, 1945, Eyster 1954, Johnston 1962), paralleled probably only by the closely related white-crowned and white-throated sparrows, Zonotrichia leucophrys and Z. albicollis. This fact offered an unusually good opportunity for interpretation and correlation of field data with physiological information.

We here summarize our early results. Before our currently funded work began, we had found clinal variation in the winter sex ratio, with males ranging from 30% in the northernmost to 25% in the southernmost populations (Ketterson and Nolan 1976). These ratios do not vary significantly from year to year or from early to late winter within years (Ketterson and Nolan 1979). Seeking an explanation for the evolution of differential migratory behavior according to sex, one of us studied dominance relations in free-ranging flocks. Males dominate females and, within a sex, adults dominate young (Ketterson 1979a, 1979b; see also Sabine 1959, Balph 1977, 1979, Baker and Fox 1978). When compared for rate of overnight weight loss, the sexes do not differ (Ketterson and Nolan 1978), but sexual differences in

fasting endurance may nevertheless play a role in the maintenance of differential sexual migration (Ketterson and King 1977).

Our current objectives derive from our more recent findings, which are described in the next section. Briefly, the questions we want to ask are these:

1. Does the rate of short-distance, mid-winter dispersal differ in northern and southern winter junco populations?

2. Are young juncos less faithful than adults to the site occupied in the previous winter, particularly if that site was in the north?

3. Do the sex and age classes in juncos differ in the extent to which the duration of their migratory behavior is endogenously regulated?

II. PROGRESS REPORT

We begin this section by presenting conclusions drawn from our work to date; then we report the methods and results that led to them. In the next section, we shall introduce our future plans.

A. FINDINGS

Our work leads us to the following view of the winter distribution of juncos and the dynamics that maintain it:

1. Age as well as sex influences distance migrated in autumn. In winter, young juncos tend to be concentrated north of adults and males north of females.

2. Northern wintering populations exhibit higher overwinter mortality than southern; but at northern (and also southern) sites, sex and age do not influence probability of mortality during winter.

3. Members of northern populations return to the same sites in successive winters less often than do those from southern. The difference is attributed not to differential mortality but instead to the fact that among young juncos, fidelity to the winter site is greater in southern populations than in northern.

4. The northern young that are not site faithful tend to move southward in subsequent winters, and this accounts for the maintenance year after year of the winter age-class distributions referred to in 1, above.

5. Annual mortality is similar in northern and southern populations, but its seasonal occurrence differs. A greater proportion of northern winterers tend to die overwinter; but this difference is offset among southern winterers, probably by greater mortality during migration.

B. METHODS

The sources of our data are three: (1) results of repeated live sampling of winter populations, (2) Christmas Bird Count data, and (3) recovery records obtained from the Banding Laboratory of the United States Fish and Wildlife Service (USFWS).

Winter Population Structure and Recapture Rates

We conducted early-winter (1 December-10 January) capture and banding during 2-4 winters at 5 sites (Figure 1). The efforts, each several days long and involving similar methods, were carried out at Kalamazoo, Michigan (42°N), Bloomington, Indiana (39°N), Nashville, Tennessee (36°N), Clemson, South Carolina (34°N), and Birmingham, Alabama (33°N). The purpose was to characterize early-winter population structure and to mark individuals or recapture those previously marked. Similar efforts at Bloomington and Clemson in late winter (February) of 2 years were intended (1) to determine the proportion of birds banded in early winter still present in late winter, and (2) to compare early- and late-winter population structure. Other late-winter efforts were carried out in Nashville, Birmingham, and Starkville, Mississippi; but because of their timing, we used them only as further estimates of geographic variation in population structure.

Captured birds were sexed by plumage traits and wing length and by laparotomy when that was necessary (Ketterson and Nolan 1976). Early winter aging was by examination of skull for degree of ossification and permitted assignment of individuals to one of two age classes: young birds hatched the preceding breeding season and adults. Because most skulls are completely ossified by February, we determined age at that time by plumage, eye color, and wing measurements (Yunick 1978, Ketterson 1979a). We had earlier ascertained the reliability of this method by aging the same individuals in November-December and again in February, i.e., with and without skull examination as an aid. Our accuracy in late winter is about 95%, with no greater tendency to call adult individuals young than vice versa.

Recapture rates were calculated for the sets of juncos released in good condition in early winter at their place of capture and resampled late in the same winter (hereafter, overwinter recapture rates) or in the subsequent winter (hereafter, annual return rates or recapture rates in winter II). Birds marked in one winter, missed in the second, but captured in the third, were treated as if they had been present in the intervening winter for the purposes of calculating the return rate between winters I and II but were not included in the calculation from winters II and III.

Abundance Analysis

We analyzed Christmas Bird Counts published by the National Audubon Society for counts made between 70°W and 100°W in the five early winters be-ginning 1974-75 (data from 1979-80 published recently, analysis in progress). So-called censuses at about 750 sites per winter yielded the number of juncos seen at each. We divided each count by the total party hours devoted to that count (juncos/party-hour) and adjusted this result to take account of the fact that in most counts some stated percentage of time was spent in habitat not occupied by juncos (adjusted juncos/party-hour). We then grouped counts

according to degree of latitude and determined the mean adjusted number of juncos per party hour for each group of counts. We considered the mean per degree of latitude to be a measure of relative junco abundance in early winter of the year analyzed. We next calculated the mean of these means at each latitude for the years of the study, 1976-78. Finally, for our various capture-recapture sites, we multiplied the relevant latitudinal mean of means by the percentages of the four sex-age classes represented in our captured samples. These results were used to estimate the abundance of each sex-age class, relative to the other three classes, from north to south in the winter range as a whole.

Recovery Records

We analyzed USFWS records (1925-1975) of all juncos caught (70°W to 105°W) during December-February and recovered in that period either during the same winter or in a different winter, inquiring whether recovery site differed from initial capture site and whether the answer to this question varied with latitude. To avoid possible bias arising from the fact that bird banders are more numerous in the northern United States, all cases of juncos recovered by banders were eliminated. The Banding Laboratory did not have useful information on the sex or age of the recovered juncos.

C. RESULTS AND INTERPRETATION

Sex-age Ratios

Geographic Variation in Population Structure

Table 1 presents our data on geographic variation, by year, in early-winter population structure. From these data, we conclude that there is very little annual variation in the percentages of the sex-age classes at the sample sites (Michigan is the only exception; the annual variation there remains unexplained, but may be attributable to the recent harsh winters). Because sample size differed from year to year and we desired a single representative value for each site, we took the means of the observed percentages and used them to characterize each site (Figure 2). Site-to-site comparisons indicate that the highest percentage of adult males was found in Michigan, of young males in Indiana, of young females in Tennessee, and of adult females in Alabama.

Relative Abundance by Latitude

Figure 3 presents the data of Figure 2 corrected for relative early-winter abundance (by Christmas Bird Count data). We draw the following conclusions from Figure 3:

(1) There is a trimodal pattern of overall abundance. Because this trimodality was apparent in four of the five years analyzed (1974-78), we take the pattern to be real.

(2) Except for adult males, each individual sex-age class is distributed with a single pronounced peak: adult females farthest south, young females at mid-range, and young males farthest north. Adult males

apparently distribute themselves bimodally. Because these patterns repeated themselves in each of the three years for which we have both abundance data and sex-age ratios, we take them to be real. (However, see proposed research regarding the pattern in adult males, p. 8.)

(3) The three upper peaks of overall junco abundance correspond so closely with the peaks of the three unimodally distributed sex-age classes that it seems likely that the peaks of the upper curve represent the latitudes of peak abundance of adult females, young females, and young males. We emphasize that the concordance is not an inevitable consequence of the methods used: whatever the shape of the upper curve, the sex-age ratios were free to vary, e.g., such that the sex-age curves would have no peaks at all.

Figure 3 also implies information about the relative abundance of the sex-age classes in the eastern winter range. Using a Keuffel and Esser compensating polar planimeter before the figure was reduced for reproduction, we measured the areas under each sex-age curve. These areas bear the following relations to one another: adult males to young males, 0.89:1.00; adult females to young females, 0.87:1.00; adult males to adult females, 1.55:1.00; young males to young females, 1.51:1.00. That is, in both sex classes, our methods indicate that in early winter (i.e., after the fall migration is complete but before the major toll of overwinter mortality), young birds constituted about 53% of the population and that in both age classes males constituted 60-61%.

Interpretation

These results raise an interesting question: because there is little annual variation in the ratios observed, how are the distributions of the sex-age classes maintained? Each breeding season produces a new generation of young, and last year's young have become adults. Thus, the distribution of adults in any winter is composed of the survivors of the adult and young age classes from the preceding winter. If we assume that adults survive at an annual rate of 50% (as we know that site-faithful juncos do in Indiana) and return to the general region in which they spent the preceding winter, then the age distributions of adult females and adult males shown in Figure 3 would be stable from year to year only if (1) northern young die at a greater rate than southern (the survivors presumbly experiencing some compensatory reproductive advantage), or (2) northern young tend to move southward for their second winter (when they are adults) and thereby (in terms of Figure 2) add to the heights of the adult peaks in the south. Because the first alternative supposes greater mortality in northern than southern young and the second alternative supposes lower site fidelity, the two alternatives might be summarized as "unequal survivorship-equal site fidelity" and "equal survivorship-unequal site fidelity." We emphasize that equal survivorship and equal site fidelity could not produce Figure 2 as a stable distribution, because after the passage of a single year, adults would increase in relative abundance in the north and decrease in the south; these and other population changes would continue until a distribution quite unlike Figure 2 would result. The rest of our results, which follow, bear on the question of whether unequal survivorship-equal site fidelity or equal survivorship-unequal site fidelity is actually at work.

Survival and Site Fidelity Estimates

Seasonal Trends in Sex-age Ratios

Table 2 indicates that in neither Indiana nor Tennessee did sex-age structure of winter populations change from beginning to end of winter. In South Carolina, there was no significant change in 1978-79; in 1977-78, the percentage of adults declined. Thus, there is little suggestion that the sex-age classes survive differentially at a location.

Overwinter Recapture Rates

Rate of recapture in late winter was considerably greater (3.8x for the two years pooled) in South Carolina than in Indiana during each year of the study (Table 3). Each sex-age class was more likely to be recaptured in the south, but the classes did not differ significantly from one another at either site. The latter finding confirms the conclusion drawn from Table 2. That is, equal recapture rates and little overwinter change in population structure both support the view that, having once selected a winter home, the sex-age classes survive winter equally well.

Assuming no great north-south difference in mid-winter dispersal (which we deal with below), the difference in overwinter recapture rates implies higher winter mortality in the north by all classes. Notably, field observations have revealed that in periods of prolonged cold and snow cover juncos become emaciated and die (Johnston 1962, Roseberry 1962, Graber and Graber 1978).

Annual Return Rates

Frequency of recapture of individuals banded in previous winters differed significantly in the north and south (Table 4, Michigan-Indiana compared to South Carolina-Alabama, Tennessee omitted as being in mid-range). The geographic difference is attributable to the lower rate of recapture in Winter II in the north of birds that wintered there as young; adults did not differ north to south. These data suggest either (a) higher death rates of northern young, or (b) lower site-fidelity.

Recovery Records

Table 5 and Figure 4 show that juncos banded in the north during the past 50 years were more likely than southern-banded juncos to be recovered in a subsequent winter at a location other than place of original capture and that changes of location were southward in the second winter. Spaans (1977) has reported comparable changes of location in successive winters by Starlings (Sturnus vulgaris). Birds that wintered in the Netherlands in one year have been caught in England and Ireland in a later year, which Spaans interprets as a shift toward a milder climate. In contrast to the evidence of latitudinal variation in across-winter site fidelity by the junco, the within-winter data reveal no geographical difference in tendency to disperse. We point out, however, that the USFWS notes location of capture only according to 10-minute blocks of latitude and longitude (≈ 120 km^2); geographic differences in short-distance dispersal are not detectable from their records.

Interpretation

Together, the early-late winter comparisons of population structure, the overwinter recapture rates and annual return rates, and the recovery data imply that northern populations are reduced by winter mortality to a greater degree than are southern but not differentially with respect to sex or age (unequal north-south overwinter recapture, Table 3; equal north-south midwinter dispersal, Table 5; equal overwinter recapture rates of sex-age classes, Table 3; no change in population structure overwinter, Table 2). They also indicate to us that members of northern and southern populations survive equally well on an annual basis but that some northern young move southward in their second winter (equal north-south <u>adult</u> return rate, Table 4; unequal north-south site fidelity, Table 5; southward movement by between-season movers, Figure 4). These findings favor the "equal survivorship-unequal site fidelity" explanation for the maintenance of the sex-age class distributions.

They have a second implication that is relevant to the role of migration in life histories. If seasonal survivorship is unequal between northern and southern populations but annual survivorship is equal, when does the compensating mortality occur? We submit that it occurs during migration and that the price of overwintering in a mild climate is a greater risk of death in transit to and from the wintering grounds. The calculation of an approximately 1.5:1.0 early-winter sex ratio (page 5) in a species whose breeding sex ratio would be expected to be at unity may reflect the fact that in early winter, females have paid the price of their longer migration whereas the season of heavy mortality for most males still lies ahead. (See Appendix A for further justification of the view that annual mortality and productivity of northern and southern winter populations do not differ.)

We have deliberately not mentioned the evolution of the different migration patterns of the sex-age classes. Contributory factors that have been proposed by us and others (Ketterson and Nolan 1976, Myers in press) include the advantages of avoidance of intersexual competition, optimal timing of return to the breeding grounds, minimizing various risks of mortality associated with migration (see Baker 1978, Nolan 1978) and selection of a mild winter climate. These advantages may differ according to an individual's sex and age and thus balance out at different latitudes for different sex-age classes. For example, early return to the breeding range may be of greatest significance to young males because they require a territory and do not have the advantage of having possessed one in an earlier year. Adult males, on the other hand, as members of the socially dominant sex-age class, may benefit most from avoidance of members of their own class during winter, which would produce hyperdispersion. Later return to the breeding grounds would probably not prevent them from reassuming ownership of their previous year's territory (see Nolan 1978, for a description of this phenomenon in Prairie Warblers).

We agree with Myers (in press) that the question of the evolution of differential migration will best yield to a comparative analysis across species, although at present, we do not think it as likely as he does that a single factor will be found to account for the evolution of differential avian migration. Consequently, our research on juncos in the immediate future will concentrate not on ultimate factors but on (1) testing aspects of the interpretation presented on page 2, and (2) attempting to determine what, at a proximate level, regulates distance migrated by the sex-age classes.

III. RESEARCH PLAN


A. SHORT-DISTANCE OVERWINTER DISPERSAL

Introduction

    We have tentatively concluded that the comparatively high southern overwinter recapture rate is attributable to lesser overwinter mortality in the south and not to a lesser tendency to disperse. We propose to test this point by measuring relative overwinter dispersal in a northern and a southern population. As indicated, the USFWS data are evidence of equality in dispersal, but we believe that a direct, systematic attack on the dispersal question is desirable both for its own sake and because of the problem referred to earlier, in relying on USFWS data. Our capture-recapture stations occupied considerably less area than 10-minute blocks of latitude and longitude which constitute the only record that the USFWS keeps of locations. Thus, any greater tendency of northern juncos to move short distances could have reduced our northern overwinter recapture rate but not have been detectable in the analysis of dispersal as shown by official banding records. Therefore, it is important to investigate relative dispersal, north and south, as a factor that affects overwinter recapture rates. In the course of this study, two added useful results will be obtained: (1) a second comparison of overwinter recapture rates, with the southern site at the same latitude as South Carolina but in line longitudinally with the other study sites, and (2) a second estimate of the abundance of adult males at 34°N latitude to determine whether the bimodial distribution of adult males is real.

    The relatively few studies of dispersal in vertebrates have concentrated on movement from the natal site to the first and subsequent breeding sites (e.g., Caughley 1977, Barrowclough 1978). General models tend to assume random, time-dependent movement by individuals away from a central site (e.g., Pielou 1969). We know of no studies or models to help us compare dispersal of conspecific non-breeding populations, some members of which show strong site attachment, in different parts of the geographic range.

Methods, Rationale, and Feasibility

    During early winter of 1981-82, we shall establish at a northern (Indiana) and a southern location (probably Alabama) two intersecting linear transects along which juncos will be captured at stations 0.7km apart. Each transect will be 4.2km long. These values are based on home range size of juncos near Bloomington, on knowledge of the normal "drawing power" of a baited banding station (radius 0.35km), and on the outcome a 2-year pilot study (see Appendix B) which indicated no detectable dispersal beyond 2km. The following diagram depicts the transects:
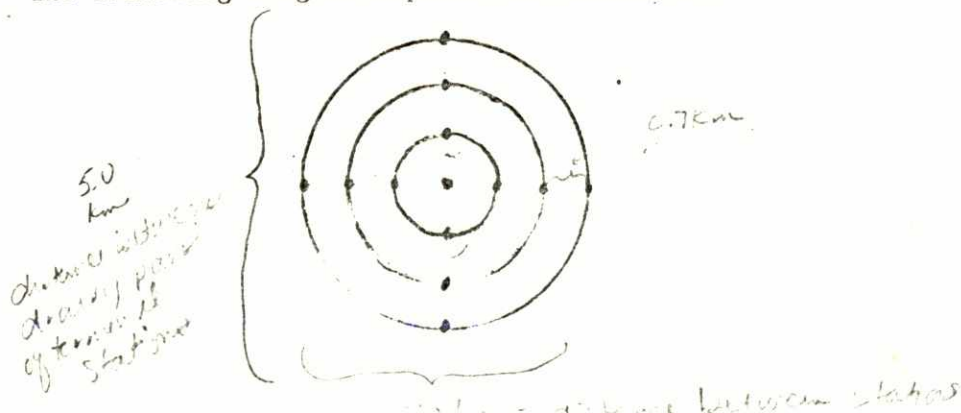
Ideally, one would mark 1,000 juncos at the center of the intersecting transects, each transect passing through homogeneous surroundings, and then record the appearance of marked birds at the outlying stations. With the resulting data, one could construct a three-dimensional frequency distribution, which would resemble a bivariate normal but would probably be strongly leptokurtotic. By calculating the area beneath the curve, it would be possible (1) to determine the number of juncos that survived between capture and recapture and (2) to determine the relative positions of these. Then one could determine if the values were different in the north and south. This method cannot be used in fact because juncos do not occur at the required densities, and their rate of dispersal is too low to yield useful measures based on small samples trapped at a single central site.

What we can do is mark approximately 50 juncos at each site along the transects, note the percentages of birds recaptured at sites other than the initial capture sites, and measure the distances separating the capture and recapture sites. We shall then know (1) whether dispersal is equally likely in all directions (habitat effects on this point are discussed below), (2) the percentage of birds moving linear distances of one, two, or as many as six stations, and (3) the percentages moving not along a single transect but moving between stations on different transects. Observations will be corrected for the "opportunity to detect" dispersers. For example, a bird originally marked at the right-hand end of the horizontal transect can be detected only if it moves due west or deviates no more than 45° from west, while a bird marked in the center station can be detected only if it moves up, down, right, or left. After correcting for opportunity to detect, pooling observations across stations, and ascertaining whether there is directional bias in dispersal, we shall be able to construct the three-dimensional frequency distribution referred to in the preceding paragraph. Details of the method are tedious and we direct the interested reader to Appendix B, which presents results, analysis, and conclusions about methods drawn from a pilot study.

The rest of this section deals with feasibility. (1) In early winter of 1978-79 and 1979-80 we captured 741 juncos near Bloomington along a single linear transect of eight sites, each separated from the other by 1.5-2.0km. Thus, we are confident we can capture sufficient numbers of juncos. (2) Six dispersers were detected, none beyond 2.0km from its capture site. Thus we know (a) that some dispersal occurs and can be detected, (b) that in order to increase the number detected, capture stations must be closer together, and (c) that it is possible to narrow consideration of dispersal to distances of less than 5km without losing too much information. (3) The most important feasibility point to address involves the "habitat(s)" lying within and surrounding the study areas depicted as circular on page 8. Since identical, homogeneous northern and southern circular areas cannot be hoped for, we here state what we think is critical. We then say why we expect to be able to satisfy the requirements. (a) Given a north-south difference in overwinter recapture rate, a test of the role played by dispersal must be carried out at the sites at which the overwinter recapture data are obtained. The fact that the nature of the "habitats" may differ between north and south is not relevant. (b) The essential point is that the freedom of the juncos to disperse or "diffuse" in all directions through and out of the northern and southern circular areas be the same. This calls for either (i) a homogeneous habitat suitable for juncos or (ii) a heterogeneous set of habitats ideally of

small, fine-textured patches all about equally attractive to juncos (i.e., no barriers, nc differential diffusion). (c) For results to be generalizable to the geographic scale that interests us, study areas should be representative of junco habitat in the northern and southern United States.

Point (a) above presents no problem: we shall make a simultaneous overwinter recapture and a dispersal study at two sites. As for point (b), we have found juncos to be common in mixed coniferous-deciduous forests that homogeneously cover vast areas in southern states and also in extensive cedar barrens in Tennessee. A suitably homogeneous southern study area should be easy to identify. Around Bloomington, Indiana, heterogeneity is the rule, but it is a heterogeneity of small patches of land all of which appear about equally attractive to juncos—old fields, wood lots, small cultivated field and fence rows of part-time farmers who work in town, farm buildings and associated swine and cattle feed. We see little problem in selecting study areas near Bloomington within which juncos might be expected to move freely and more or less equally in all directions. Point (c) calls for judgement as to whether southern mixed-forest stands and patchy northern farm-woods-old fields are typical enough to make comparisons between them interesting. We think they are typical enough and must rely on the reader to agree.

B. SITE-FIDELITY

Introduction

This aspect of the research has the following purpose: to test experimentally our hypothesis that lower site fidelity, not lower survivorship, produces the comparatively low recapture rate in Winter II at northern sites of juncos that wintered there as young. To distinguish between the site fidelity vs. survivorship alternatives we plan to treat a northern and a southern sample composed of both young and adult females as nearly identically as possible by (1) eliminating all mortality in Winter I and (2) equalizing the total migration distance each sample would have to travel in order to demonstrate fidelity in Winter II to its Winter I site. The effect will be to produce two samples alike in surviving Winter I and also alike in probability of surviving risks of migration associated with distance traveled.

One possible result is that the two age classes of northern experimentals will be captured at the northern site in Winter II in the same age ratio that we have previously determined for untreated birds (more adults than young) and also that the age ratio of returns among the southern experimentals (equal adults and young) will not change. If that happens, we can conclude that differential site fidelity and not differential survivorship accounts for the geographic difference in distribution of age classes. The alternative result is that the treatment will elevate the rate of return in Winter II of northern young more than it does the rate for northern adults and produce an age-class ratio among the returning northern birds comparable to the ratio for the southern sample. We would then conclude that, contrary to our prediction, heavier northern overwinter mortality of young juncos is what maintains the curves seen in Figure 3.

Methods and Rationale

First to describe the methods in general terms, early in Winter I we shall capture large samples of old and young females at Nashville, Tennessee and Birmingham, Alabama, the northern and southern sites, respectively, and hold these in outdoor aviaries at Bloomington. (The reason for treating Nashville as northern for this experiment is given in the next paragraph.) In March we shall have samples of known size and in good condition, each to be released at the capture site of the other. The effect of releasing the Tennessee sample in Alabama and the Alabama sample in Tennessee is that the Alabama birds will have to travel a shorter-than natural distance to reach the breeding range, while the Tennessee birds will have an abnormally long spring migration. In order for each sample to return next autumn to its Winter I capture site, the Alabama sample must, as normal, travel farther southward than the Tennessee birds. Adding the artificially modified spring migration distance to that of a natural fall migration, returning birds from the two groups would have traversed about the same distance from the northern limit of the winter range (see diagram on next page).

Details and the rationale for the elements of this design follow. (1) Capture and recapture will be early in Winters I (1982-83) and II (1983-84), because our annual return rates of free-living juncos are based on early-winter sampling. (2) The sites were selected because (a) recapture rates of the two age classes vary significantly between them, (b) females are abundant at both, and (c) both are sufficiently distant from Indiana to justify the assumption that neither sample will be biased in favor of return because it spent the winter in an aviary near its natural home. (3) The belief that risks of annual mortality for the two samples will be equalized is based on the assumption that Alabama-wintering and Tennessee-wintering juncos have equal survivorship during the breeding season. (4) Only females will be used because (a) the assumption of equal mortality during breeding is easier to grant if the sex role of all individuals is the same, and (b) the bimodal distribution of old males would complicate predictions and interpretation of an experiment using male age classes. (5) Elimination of overwinter mortality should elevate the annual survival, and therefore the recapture rate in Winter II of both samples, but the effect on the Tennessee sample should be greater than on the Alabama sample because Tennessee has a more severe winter climate. However, raising survivorship should not alter the ratio of the adult return rate to the young-bird return rate to either location if differential site fidelity accounts for the normally lower rate of return of young to Tennessee.

We summarize the argument for this experiment in the following diagram:

DESIGN
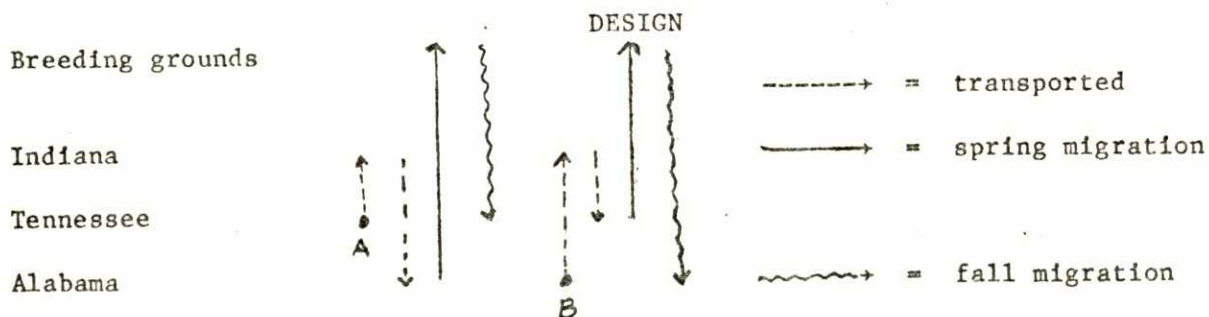
POSSIBLE RECAPTURE RATES IN WINTER II

	Control rates ✗ from free-living birds		Predicted Experimental Rates			
			Equal survivorship-unequal site fidelity		Unequal survivor-ship-equal site fidelity	
	Adults	Young	Adults	Young	Adults	Young
Tenneseee	17%	9%	17% + X	9% + X	17% + X	9% + Z
Alabama	20%	18%	20% + Y	18% + Y	20% + Y	18% + Y

where X = the effect of eliminating normal overwinter mortality in Tennessee; effect on adults and young equal

Y = the effect of eliminating normal overwinter mortality in Alabama; effect on adults and young equal

Z = the effect of eliminating normal overwinter mortality in Tennessee, effect on young greater than on adults

and   Z > X > Y

Feasibility

The proposed work requires (1) that juncos return in a subsequent winter to their original capture location, even if released at a considerable distance from it, (2) that such an expression of site-fidelity not be adversely affected by several months in captivity, and (3) that attachment to the winter site form before we displace experimental birds to Bloomington.

Points (1) and (3) have been the subject of limited research in passerines, with information best developed for two crowned sparrows, Zonotrichia leucophrys and Zonotrichia atricapilla, regarded by some as probably congeneric with juncos. Considering first long-distance transport, some crowned sparrows returned after having been displaced from California to Maryland and Louisiana, but after transport to Korea there were no returns (Mewaldt 1963, 1964). More is known regarding the effects of short-distance transport (Ralph and Mewaldt 1975, 1976). Both young and adult Zonotrichia displaced 20-160 km returned the next winter to the capture location, adults at a rate of 17%, young at 8%. Some young (3%), however, fixed on the site to which they were transported, whereas no adults did so. The tendency to return to the original site was greater when experiments were carried out in late winter, but some individuals of each age class fixed on their chosen site as early as November (see Benvenuti and Ioalè 1980, who report early-winter fixation in European Robins). In a control population in which no individuals were transported, site fixation occurred in December. In all these experiments, birds were held no longer than necessary to transport them to the release points.

The little that is known about juncos is the result of our preliminary studies. During the winter of 1978-79 we held in our aviary 65 banded juncos that had been captured at several sites near Bloomington between 1 and 7 December. The birds were released at the aviary in March, and netting there

✗ *Data from Table 4. Alabama results are combined with South* ...

conditions of caging, members of all or some classes do not differ in measures Zugunruhe, we may conclude that the winter distribution of these classes does not result from sex and/or age differences in internal rhythms but, instead, from some past or present factor(s) encountered in the free-living state.

To our knowledge, this is the first time that sexual differences in Zugunruhe will be measured and also the first effort to relate the duration of Zugunruhe to distributional differences of sex and age classes. Finally, we believe that this is the first attempt to measure social influences on this particular biological rhythm (Regal and Connolly 1980).

Feasibility and Preliminary Results

In the interest of brevity, we direct the reader to Appendix C for (1) a review of Zugunruhe literature as it relates to this proposal and (2) for a description of the methods employed and results deriving from a pilot study carried out in 1979 and 1980. Our most encouraging 1979 finding appears below:

ZUGUNRUHE*

SEX-AGE CLASS	MEDIAN START** DATE	MEDIAN STOP** DATE	MEDIAN DURATION (DAYS)	EXTREMES (DAYS)	N (BIRDS)
ADULT MALES	10 OCT.	28 NOV.	50	--	1
ADULT FEMALES	16 OCT.	2 DEC.	48	32, 64	2
YOUNG MALES	30 SEPT.	30 NOV.	62	38, 77	4
YOUNG FEMALES	16 SEPT.	22 DEC.	99	94, 107	4

*Duration of autumnal Zugunruhe in a sample of 11 juncos captured on their Canadian breeding ground in July, 1979, and monitored under the outdoor sky from September-December, 1979, in Bloomington, Indiana.

**where start equals first date with at least 5 minutes' activity in the first third of the night and stop equals last day of activity in the last~~first~~ third of the night. The night was divided 2100-2330, 2331-0200, 0201-0430.

A sexual difference in date of onset and duration is evident in young, and the higher measures of Zugunruhe in females is consistent with the longer migration of that sex. The meager data on adults do not justify comment, beyond noting their briefer Zugunruhe and the absence of a sexual difference.

In July, 1980, 54 new subjects were captured in Wawa, Ontario, and these were monitored at Bloomington from September to December. Because summarizing a single night's results requires 15 hours and we have greater than 120 nights to summarize, we do not yet know the outcome. However, 1980 does tell us the following about feasibility: (1) We can capture large numbers of juncos,

transport them successfully from Canada to Bloomington, and maintain them there in excellent condition. (2) By capturing on the breeding grounds, we know each individual's breeding origin, sex, age (in approximate number of days, if young), and often who its parents and siblings are. Interpretation of many Zugunruhe studies has been hampered by unexplained variation. We believe that consideration of all the factors listed above will allow us to account for most of the variability we observe. (3) Zugunruhe studies have also found that activity often persists beyond the normal dates of migration. In both 1979 and 1980, all our juncos ceased all nightime activity by dates that compared favorably with free-living birds (i.e., many before 1 December, all before January).

One interesting and unexpected outcome is known from the 1980 data. None of five juncos that (1) wintered in Bloomington prior to 1979-80, (2) returned there in 1979-80 , and (3) were captured then and held in captivity until autumn, 1980, showed any Zugunruhe in 1980. That is, juncos that had once demonstrated site-fidelity to Bloomington did not enter the migratory state when held on their chosen wintering grounds. Contrarily, two holdover Canadian subjects from 1979 did show Zugunruhe despite treatment similar to that received by the site-faithfuls. This spring, we shall again monitor the five and compare their behavior to Canadian adults. If the site-faithfuls show Zugunruhe like that of other captives, then the autumn results do not reflect loss of the behavior but its suppression, possibly associated with the fact that at the beginning of the season of autumn migration the birds were already at the winter home. We feel confident that these juncos would have been headed for Bloomington, since the return rate of juncos that have once been site faithful is 50%, a rate almost certainly equal to their annual survivorship.

Planned Research

In this section, we confront a dilemma. Until we know the rest of our 1980 results, it is difficult to indicate which of several possible lines of research we shall pursue. However, based on 1979 results, the 1980 data are likely to indicate one of two patterns, each leading to a somewhat different interpretation but each calling for certain follow-up experiments. The alternatives are:

Probable Outcome of 1980, Alternative I: Zugunruhe of adult females lasts longer than that of young females, which lasts longer than that of young males; adult males have greater variance than other classes. Interpretation: Endogenous factors are primary in determining winter distribution of the sex-age classes.

Probable Outcome of 1980, Alternative II: Zugunruhe of young females lasts longer than that of young males, which lasts longer than that of adults; no sexual difference in adults. Interpretation: Endogenous factors are primary in determining winter distribution of young, but experience or environmental factors (including social ones) must control migration distance in adults.

In either alternative, we feel the following experiments ought to be performed.

(1) Experiment for autumn, 1981: Monitor 1980 subjects again and compare results for the two years, predicting (a) in Alternative I, that young males (now adult) will show greater variance and that young females (also now adult)

will increase the average duration on Zugunruhe or (b) in Alternative II, that Zugunruhe will fall to adult levels and be the same for both sexes.

(2) Experiment for autumn, 1982: Monitor Zugunruhe of a newly caught sample from a location as far north of Wawa as possible. The purpose is to determine the generality of our results and, perhaps as a corrollary, to learn something of the relative location of breeding and wintering sites in northern and southern breeders (by comparing durations of their Zugunruhe).

(3) Experiment for autumn, 1983: Test the hypothesis (Gauthreaux 1978) that social status is the proximate factor controlling distance traveled from the breeding range (i.e., that individuals migrate until a sufficiently favorable social environment is reached) by placing newly captured Canadian subjects into aviary flocks in which they are either dominant (e.g., adult females with small young females) or subordinate (same class housed with large adult males). After a hierarchy is formed and the status of an individual is known, monitor its Zugunruhe, reintroducing it into the flock periodically (and correcting for possible changes in status). The hypothesis predicts that subordinates will show more Zugunruhe. In Alternative I, treatment should have little effect of the endogenous patterns of Zugunruhe; in Alternative II, longer Zugunruhe should be induced in adult females.

At least 3 other experiments would be interesting and some or all will be carried out if time, money, and prior results so indicate. Each is slightly extraneous to the question of regulation of winter distribution of the sex-age classes, but all derive naturally from the Zugunruhe studies.

(4) Tentative experiment for spring, 1983: Monitor Zugunruhe of young juncos to determine the role of endogenous factors in the first spring migration.

(5) Tentative experiment for spring, 1984: Monitor effects of social factors in spring—this time sexual—by comparing Zugunruhe of adults spending their daylight hours interacting with the other sex compared to the Zugunruhe of juncos also housed in large aviaries during the day, but alone (Helms 1963).

(6) Tentative experiment for autumn, 1981, spring, 1982, autumn, 1983: If site-faithfuls do show Zugunruhe in the spring of 1981, repeat this study in autumn, 1981, with winter site-faithful juncos that we have begun to stockpile in our aviary. Monitor Zugunruhe in spring as well, to confirm or reject any spring, 1981, result with a larger sample. If preliminary observations are borne out, capture juncos site faithful to Tennessee in 1982, and monitor these in autumn, 1983; compare juncos that presumably would have headed for a site south of Bloomington with juncos whose migratory goal would have been Bloomington.

For those interested in specifics concerning measurement of Zugunruhe, see Appendix C, page C4.

Table 1. Sex-age ratios according to year and location.[a]

	n	Male		Female	
		Adult	Young	Adult	Young
Michigan (42°N)					
1976–77	119	42%	34%	15%	8%
1977–78	105	44%	39%	7%	10%
1978–79	240	29%	46%	6%	19%
1979–80	114	31%	41%	11%	17%
Indiana (39°N)					
1976–77	33	33%	39%	9%	18%
1977–78	80	35%	46%	5%	14%
1978–79	116	38%	38%	8%	16%
1979–80	51	26%	31%	14%	21%
Tennessee (36°N)					
1978–79	62	21%	29%	14%	36%
1979–80†	121	21%	29%	16%	35%
1980–81	79	19%	29%	15%	37%
South Carolina (34.5°N)					
1976–77	123	25%	19%	37%	19%
1977–78	87	37%	17%	27%	18%
1978–79	132	27%	17%	33%	24%
1979–80	104	22%	28%	26%	23%
Alabama (33.5°N)					
1976–77	59	22%	14%	36%	29%
1977–78	23	13%	22%	39%	26%
1979–80*	51	11%	19%	54%	16%
Mississippi (33.5°N)					
1979–80*	51	26%	18%	39%	18%

[a]Locations were sampled in early winter except that those noted with star were sampled in February, and the Tennessee sample from 1979–80 was sampled in December and February and the data combined. Except for Michigan, there were no significant annual differences in sex-age structure at a locality: Michigan $X^2 = 22.78$, d.f. = 9, p<.01; Indiana $X^2 = 6.63$, d.f. = 9, n.s.; Tennessee $X^2 = 1.16$, d.f. = 6, n.s.; South Carolina, $X^2 = 13.22$, d.f. = 9, n.s.; Alabama $X^2 = 4.69$, d.f. = 6, n.s.

Table 2. Early-late winter comparisons of sex-age ratios of winter junco populations according to location.

		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%
Tennessee[c]					
December, 1979	37	27%	27%	14%	32%
February, 1980	84	18%	30%	17%	36%
South Carolina[d]					
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]The sample sizes at Indiana differ from those reported in Table 1 because a larger number of sites was sampled (see section on dispersal under Proposed Research for a description of of methods).

[b]Indiana seasonal comparisons of sex-age ratios, December vs. February, 1978-79: $X^2 = 1.90$, d.f. = 3, n.s.; December vs. February, 1979-80: $X^2 = 5.102$, d.f. = 3, n.s.

[c]Tennessee seasonal comparison of sex-age ratio, December vs. February, 1979-80, $X^2 = 1.38$, d.f. = 3, n.s.

[d]South Carolina seasonal comparisons of sex-age ratios, December vs. February, 1977-78, $X^2 = 7.96$, f.g. = 3, $p < .05$; December vs. February, 1978-79, $X^2 = 5.95$, d.f. = 3, n.s.

Table 3. Rate of recapture in late winter of juncos marked
in early winter according to sex, age, year, and location.[a,b,c]

	Male		Female		
	Adult	Young	Adult	Young	Combined
Indiana					
1977-1978	22% (27)	6% (36)	0% (4)	0% (10)	10% (80)
1978-1979	10% (41)	14% (42)	11% (9)	16% (19)	14% (118)
years combined	15% (68)	8% _10%_ (78)	8% (13)	10% (29)	12% (198)
South Carolina					
1977-1978	26% (31)	40% (15)	50% (22)	38% (13)	37% (81)
1978-1979	47% (15)	43% (7)	57% (21)	67% (12)	54% (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
greather 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. $X^2 = 0.94$, d.f. = 2,
n.s. (female age classes combined because samples small). The same was true
of South Carolina, $X^2 = 4.59$, d.f. = 3, n.s.

[c]Late winter recapture rates of a sex-change class at the different
locations were compared after combining data for the 2 years. Each sex-age
class was significantly more likely to be recaptured in South Carolina than in
Indiana (adult males: $X^2 = 4.4$, d.f. = 1, p < .05; young males: $X^2 = 12.12$, 9.36
d.f. = 1, p < .001; adult females: $X^2 = 8.47$, d.f. = 1, p < .01; young
females: $X^2 = 9.26$, d.f. = 1, p < .01). 6.77

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

| | Male | | Female | | |
	Adult	Young	Adult	Young	Combined
North					
(Michigan–Indiana)	11% (220)	3% (260)	2% (59)	3% (100)	6% (639)
Middle					
(Tennessee)	16% (25)	8% (26)	17% (12)	3% (30)	10% (93)
South					
(South Carolina–Alabama)	8% (73)	18% (44)	9% (103)	15% (55)	11% (275)

[a] Sample sizes are in parentheses and represent the number of individuals
that were released in good physical condition after their initial capture and
at a location that was sampled in the subsequent December. Juncos captured
one December, not captured the subsequent December, but caught again in a
later December were considered present in the intervening winters.

[b] To compare rate of return of the sex-age classes to a location, Michigan
and Indiana were considered northern and the data from these sites were
combined; South Carolina and Alabama were considered southern, and the data
from those sites were combined. The sex-age classes did not return with equal
frequency to northern sites, $X^2 = 17.67$; d.f. = 3, p < 0.001, but they did to
southern sites, $X^2 = 3.59$, d.f. = 3, n.s.

[c] To compare the rate of return of the various sex-age classes to
different locations, we again combined data at the northern and the southern
locations: adult males, north vs. south, $X^2 = 0.34$, d.f. = 1, n.s.; young
males, north vs. south, $X^2 = 11.39$, d.f. = 1, p < .01; adult females, north
vs. south, $X^2 = 2.11$, d.f. = 1, n.s.; young females, north vs. south, $X^2 =
4.06$, d.f. = 1, p < .05. Without regard to sex or age, rate of return to the
south was significantly higher ($X^2 = 7.21$, d.f. = 1, p < .05).

[d] Because our arguments repeatedly cite equal return of adult females to
the north and south and the reader might conclude that this result derives
purely from small sample sizes, we state here that many years of sampling of
juncos at Bloomington reveals that adult females do return thre and the rate
of return is similar to that observed in South Carolina.

Table 5. Percentages of dark-eyed juncos recorded (United States
Fish and Wildlife Service, 1925-1975) as recovered at and away from
place of capture, according to latitude of place of capture.

Place of capture	n	Recovered subsequent winter at place of capture[b]	n	Recovered same winter at place of capture[b]
42-40°N	67	51%	143	94%
39-37°N	46	74%	63	89%
36-34°N	10	90%	13	85%
33-31°N	3	100%	10	100%

[a]Data were taken from files of the Banding Laboratory of United States
Fish and Wildlife Service for juncos banded and recovered between longitude
70°W and 105°W. The laboratory records locations only as within ten-minute
blocks of latitude and longitude; thus recovery at place of capture means
within the same block. To avoid any bias associated with the northward
concentration of United States bird banding stations, the sample is confined
to juncos recovered other than by a bird bander. Note that most initial
captures were in the northeastern United States (Figure 4).

[b]Chi-square analyses of latitudinal variation in tendency to be recovered
at place of capture follow: subsequent winter, $X^2 = 11.61$, d.f. $= 3$, $p <
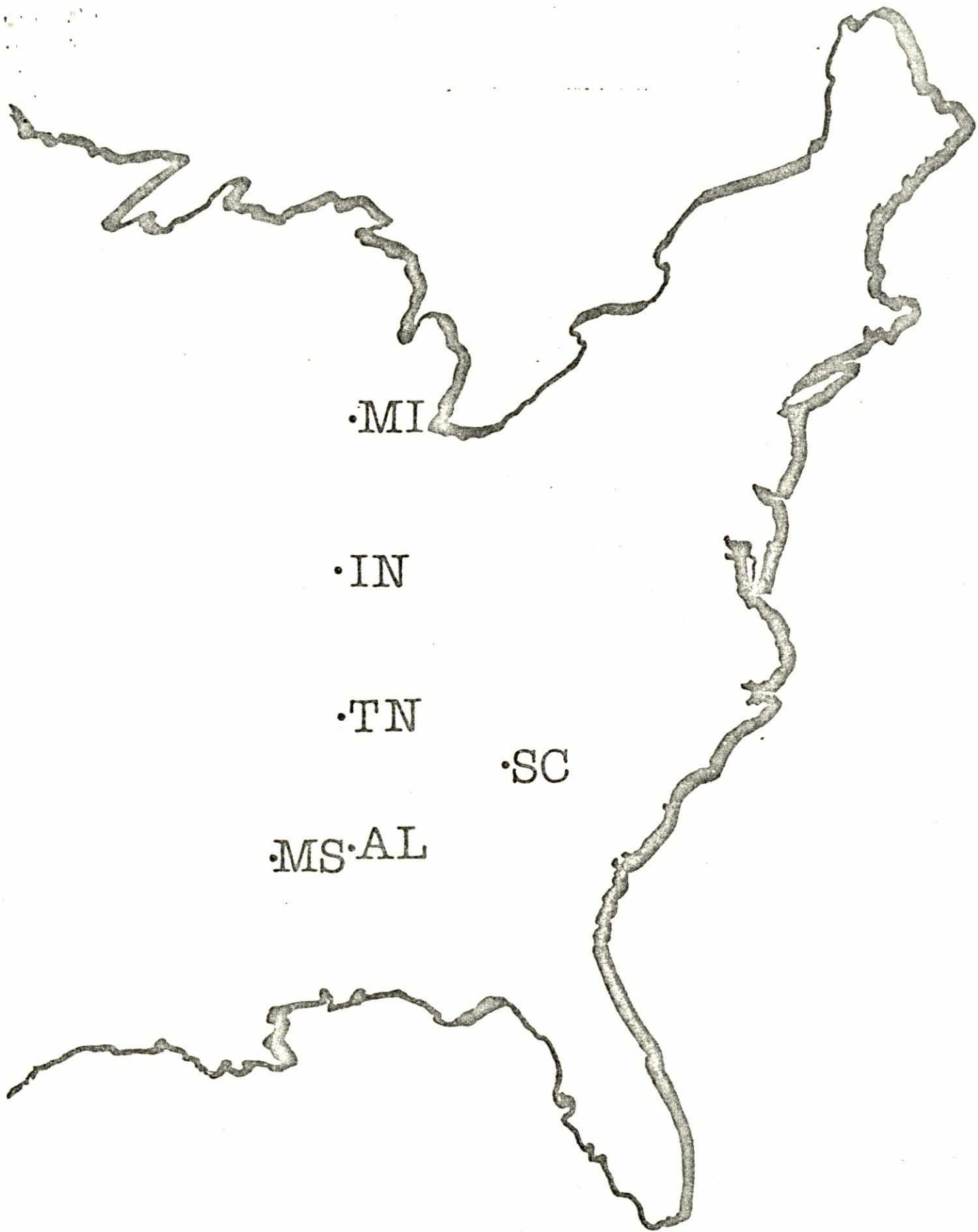0.05$; same winter, $X^2 = 3.27$, d.f. $= 3$, n.s.

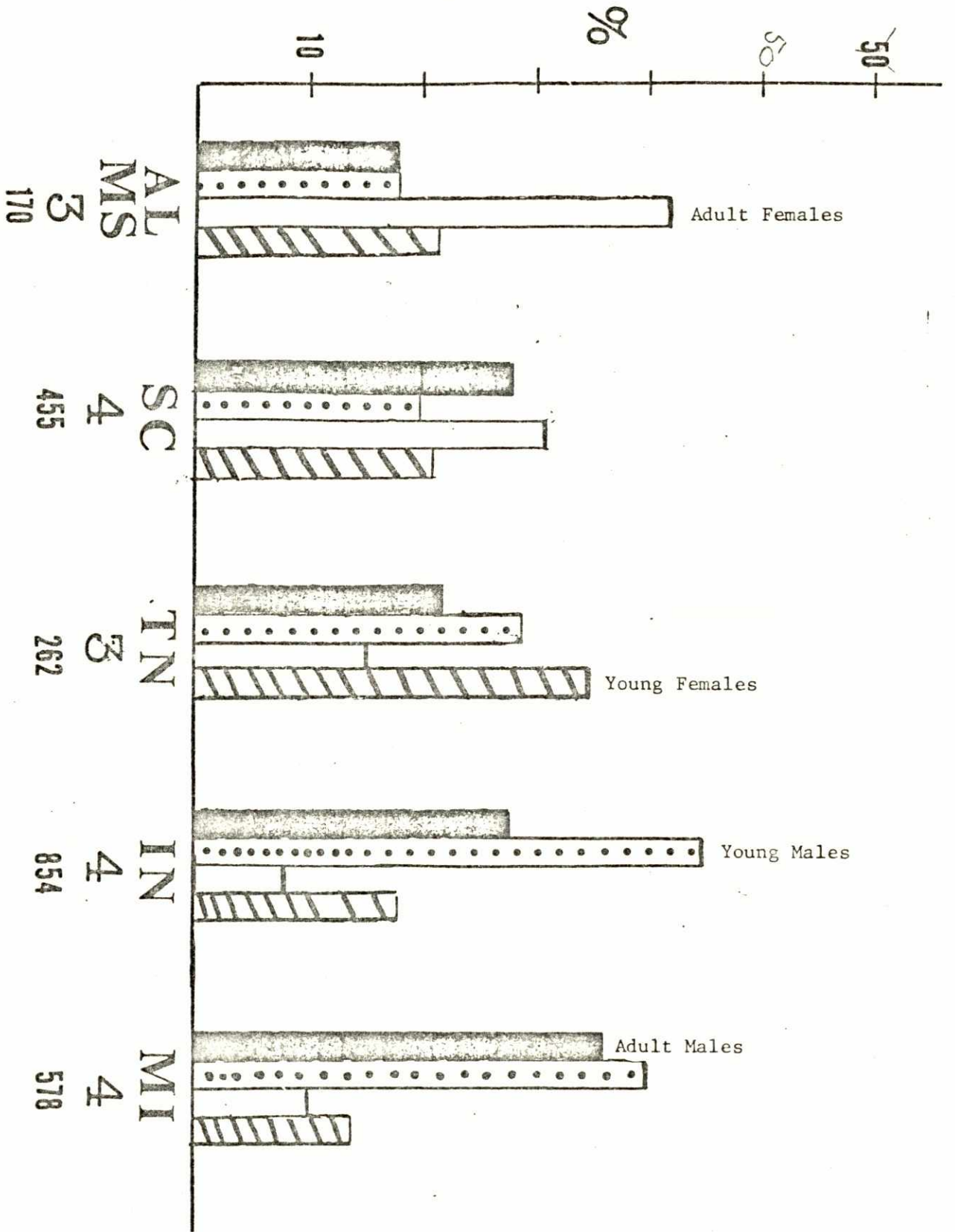Figure 1. Locations of capture sites.

Figure 2. Sex-age ratios according to location; data from Table 1. Indicated are average percentage of each sex-age class, number of early winters sampled, and number of birds on which percentages are based.
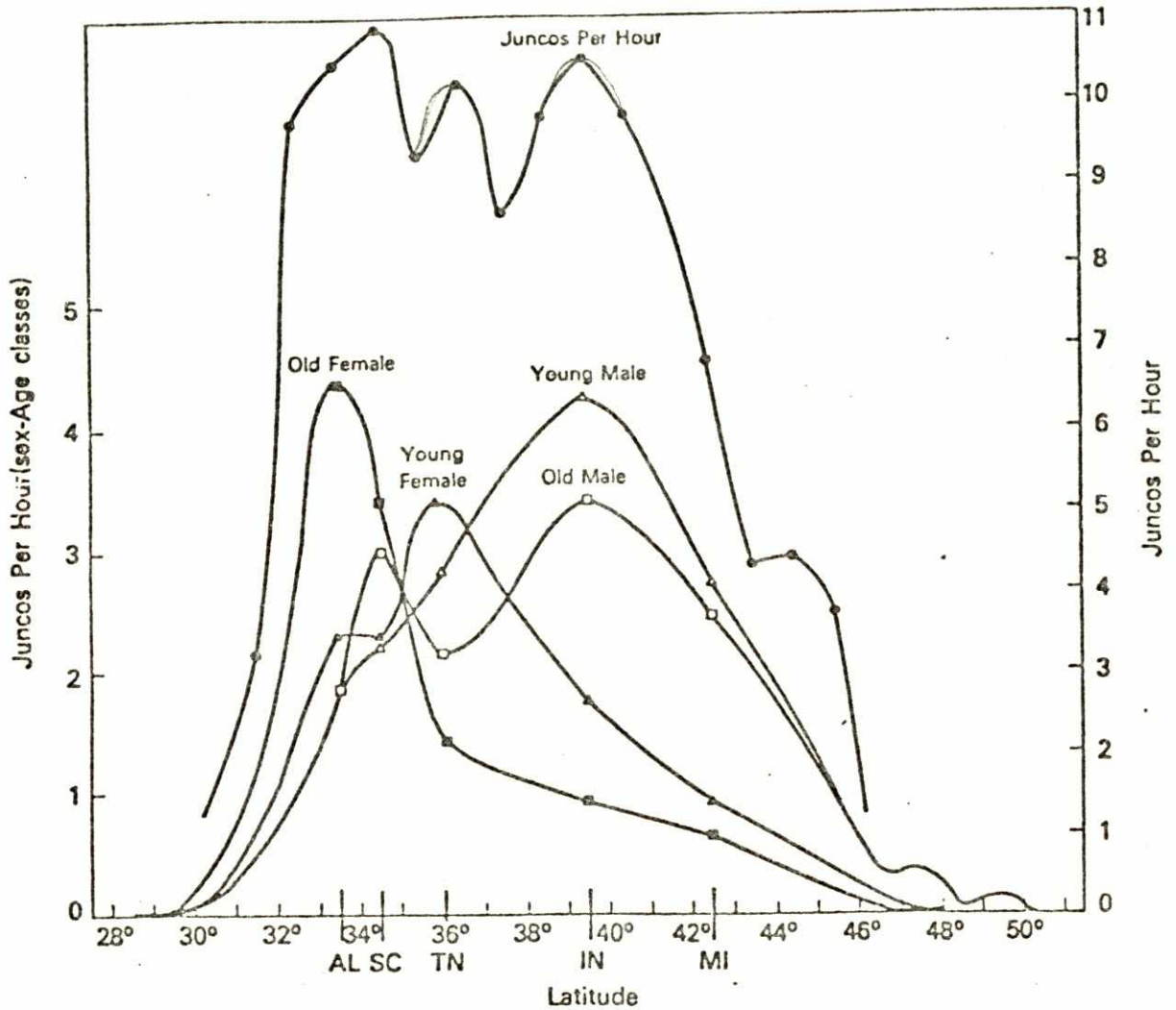
Figure 3. Upper curve and right-hand Y axis: relative abundance
of juncos throughout winter range (70°W to 100°W) in December 1976,
1977, 1978 (years averaged), based on Christmas Bird Counts adjusted
for habitat; see text. Overlapping lower curves and left-hand Y
axis: relative abundance of sex-age classes in 3-4 winters (Table 1,
Figure 2). Curves drawn by inspection to connect points obtained
by multiplying sex-age ratios from Alabama-Mississippi, South
Carolina, Tennessee, Indiana, and Michigan samples by abundance
data in upper curve.

Figure 4. 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 (see text for other details). Each line represents
an individual junco. The dot is at the original capture location and the
arrow point at the recovery location.

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