

CHAPTER 12

THE EVOLUTION OF DIFFERENTIAL BIRD MIGRATION

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1. INTRODUCTION

The evolution of bird migration and the role of migration in life history have long been matters of general interest, and the volume of recent literature on these subjects (Baker, 1978; Dingle, 1980; Gauthreaux, 1978, 1979, 1982; Fretwell, 1980; Greenberg, 1980; Greenwood, 1980; Myers, 1981a; Kettersen and Nolan, 1982) reflects their continuing importance to students of avian ecology and evolutionary biology.

In the effort to understand why some birds make long migrations while others do not migrate or travel only short distances, analysis of intraspecific variation in migratory behavior seems likely to be especially fruitful (Morton, 1980). Focus on differences among individuals from a common gene pool minimizes confounding variables and offers a system more amenable to a quantitative approach. In this paper, we review hypotheses to account for differential migration, i.e., the situation in which all individuals of a population migrate but distance traveled varies according to sex and/or age. The same hypotheses can be applied to partial migration, in which some classes of a population migrate while others do not. In testing hypotheses against data from a single short-distance migrant, the Dark-eyed Junco (*Junco h. hyemalis*),

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which spends its life in the north temperate zone, we acknowledge the risk that our view may be narrower than would be ideal.

In 1976, we reported latitudinal clinal variation in the winter sex ratio of Dark-eyed Juncos in the eastern United States (Ketterson and Nolan, 1976). Male juncos were found to predominate in the northern parts of the winter range, females in the southern (see Fig. 1). We considered what factors might have led to the evolution of the differential migration that produces this distribution and suggested that among the selective pressures that might have been responsible were (1) intrasexual competition for breeding resources, which might have caused members of the sex that defends territories to winter nearer the breeding ground; (2) winter climate, which might have caused members of the smaller-bodied sex to migrate farther toward the south; (3) intersexual competition for resources during the non-breeding season, which might have forced members of the subordinate sex to segregate themselves and; (4) risk of mortality in transit, which might have varied according to sex and led one sex to abbreviate its migrations. Two or more of these factors could have operated simultaneously, as we later proposed (Ketterson and Nolan, 1979), but assessment of their relative importance is complicated by the fact that in the junco the predicted effects of the first three are the same. Regions of more severe climate are closer to the breeding ground, and males, the territorial sex, are larger than females. Thus, both factors 1 and 2 predict shorter migrations by males. Factor 3 also predicts shorter male migrations: males are socially dominant to females in winter.

Because the same conditions hold true for many, if not most, temperate-zone migrant bird species, the validity of any general hypothesis designed to account for the evolution of differential bird migration on the basis of only one of these factors becomes extremely difficult to evaluate (Myers 1981a). Strong arguments have been made, nevertheless, that one or another of these four factors has been the factor of primary importance (Gauthreaux, 1978, 1982; Myers, 1981a). In marked contrast is a multifactor model proposed by Baker (1978).

In this paper, we first report unpublished findings on the winter distribution of the age classes of migratory juncos, according to sex. We then discuss and evaluate the single-factor hypotheses for differential migration and the winter distribution that results, drawing both on general considerations and on various data from juncos. Finally, having concluded that none of these hypotheses is sufficient to explain the junco's distribution, we turn to Baker's model and find that it comes closest to dealing adequately with the complexities of differential migration, but that it lacks predictive power.

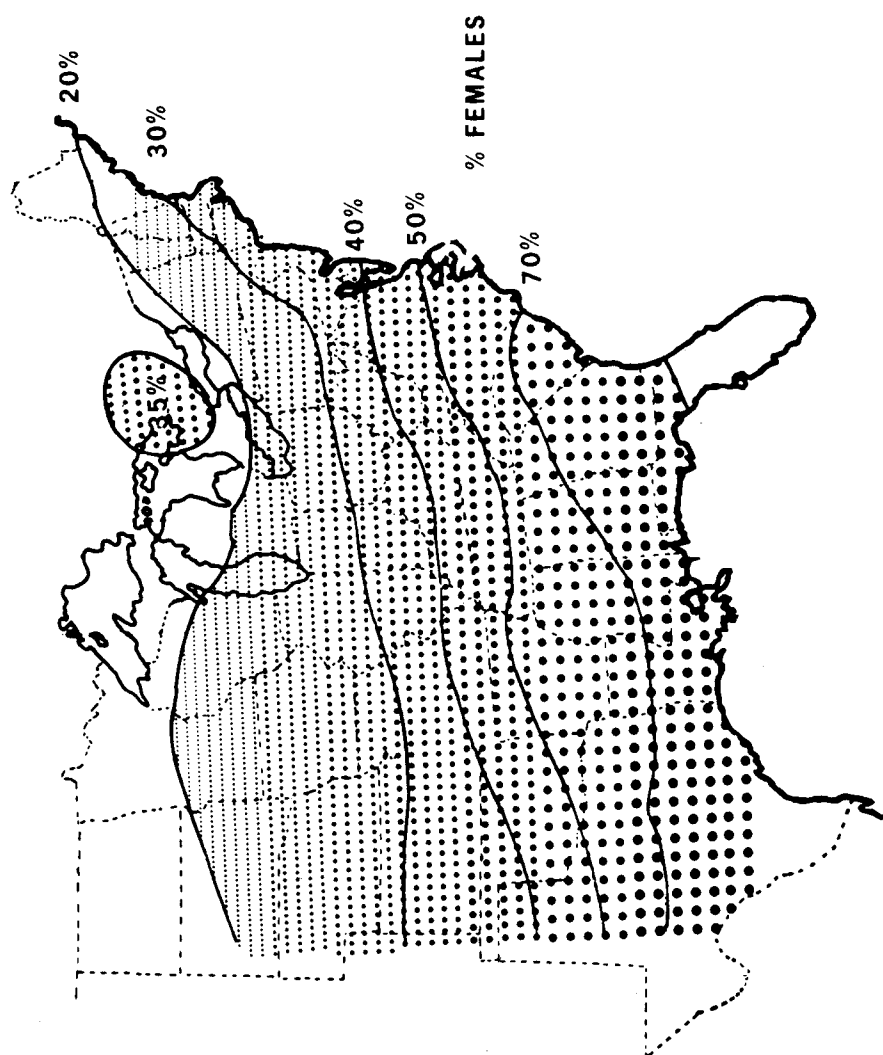


FIGURE 1. Clinal variation in the winter sex ratio of the Dark-eyed Junco (from Ketterson and Nolan, 1976, reprinted by permission from *Ecology*; copyright 1976, The Ecological Society of America).

2. WINTER DISTRIBUTION OF EASTERN MIGRATORY JUNCOS

Figure 2 shows in the upper curve the relative abundance of juncos at the various latitudes of the winter range at the end of December (see Appendix II for methods and other details about the figure). At this date, post-migratory winter populations have recently been established, and most of the severe weather of winter is still ahead. The series of lower curves indicates the relative abundance of each sex-age class at the various latitudes, again in late December. In Fig. 2 and hereafter, young juncos are those produced in the preceding breeding season and adults are all others.

We draw the following conclusions from Fig. 2: (1) The pattern of abundance at middle latitudes is trimodal. This pattern was apparent in four of six years analyzed (1974–1979), and we suspect it is real. Despite the three small peaks, however, the overall abundance from north to south is strikingly invariant. (2) Except for adult males, the distribution of each sex-age class exhibits a pronounced peak, with that for adult females farthest south, for young females at mid-range, and for young males farthest north. Adult males seem to be distributed bimodally, with a northern peak at the latitude of greatest abundance of young males and a second peak south of this. Because these patterns showed considerable stability in the years analyzed and the unimodal peaks approximately correspond to the upper trimodal pattern of overall abundance, we believe that the winter distribution of junco sex-age classes is fairly estimated by the figure. (3) Adults of each sex winter somewhat south of the young of that sex, although the difference is not as clear in males as in females. Using a Keuffel and Esser compensating polar planimeter to measure areas under the respective sex-age curves, we calculated for each class the proportion found south of 38.5°N latitude, approximately the mid-point on the north-south axis of the winter range. These percentages for adult males, young males, adult females, and young females were 49%, 44%, 80%, and 68%, respectively.

Two other points should be made about Fig. 2. First, the sex-age curves yield estimates of relative abundance of the four classes after autumn migration and before the major toll of overwinter mortality. A planimeter reveals that the areas under the four curves bear the following relations to one another: adult males to young males 1:1.20; adult females to young females 1:1.17; adult males to adult females 1:0.72; young males to young females, 1:0.71. These calculations imply that in early winter of the years investigated young birds constituted about 54% of the population and that in both age classes males constituted

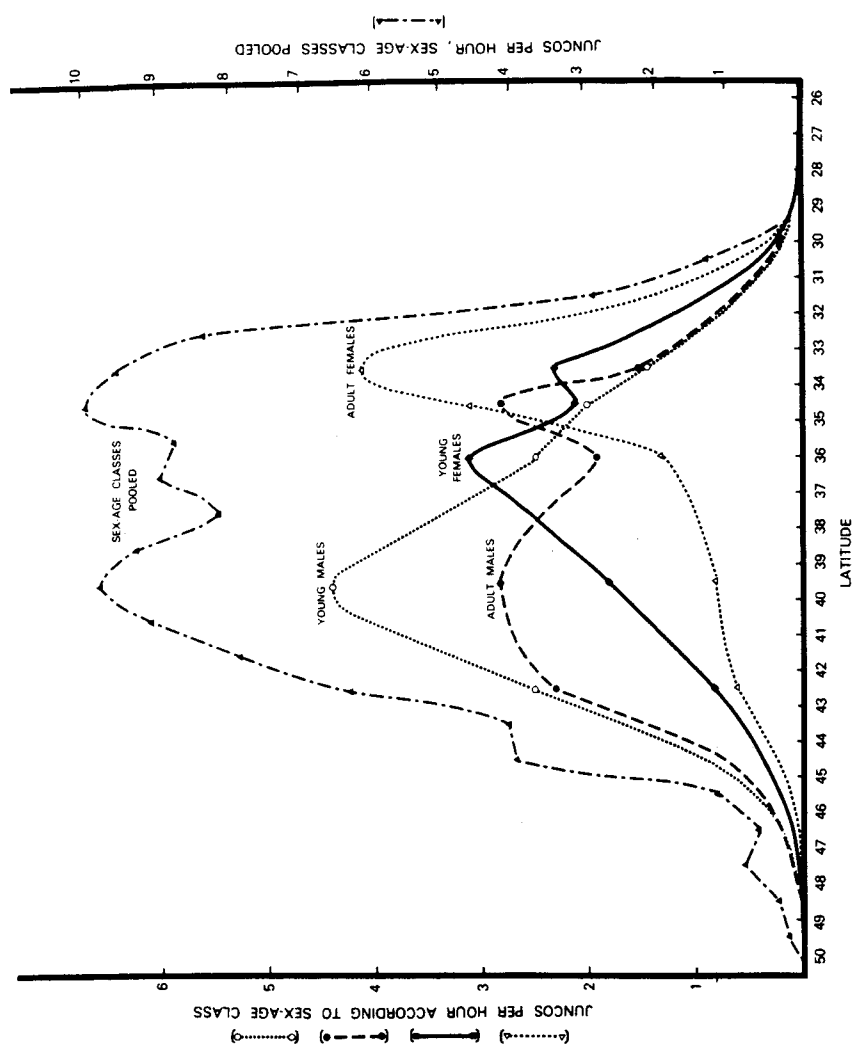


FIGURE 2. Estimated relative abundance of juncos in the winter range (top curve) and estimated relative abundance of the sex and age classes (lower series of curves), all according to degree of latitude (see Appendix II for methods).

some 59%. Second, the distributions as drawn could be maintained from year to year only if the age classes differ either in annual survivorship from December to December, or in year-to-year fidelity to the winter site, or in both. This is most easily demonstrated by the female distributions. If young and adult females at latitudes 36°N and 33.5°N had the same survival rate and survivors tended equally to return to the sites in which they had spent the previous winter, the age structure at the more northerly latitude would shift toward a higher proportion of adult females, and the age ratios at the two latitudes would soon become the same. To account for the maintenance of the age distributions in Fig. 2, we have argued elsewhere (Ketterson and Nolan, 1982) (1) that December-to-December survival of northern populations and southern populations is probably equal and that it is the same for adults and young, (2) that northern juncos show less fidelity to the winter site occupied when young than do southern juncos, and (3) that juncos that do not show winter site fidelity tend to shift southward when they are adult. Discussion of the data supporting these conclusions appears in Ketterson and Nolan (1982) and is summarized in Sections 3.2.2, 4.1.3.a, b, and c.

3. SINGLE-FACTOR HYPOTHESES FOR THE EVOLUTION OF DIFFERENTIAL MIGRATION

3.1. The Body-Size Hypothesis

3.1.1. The Body-Size Hypothesis Stated

If smaller-bodied individuals were less likely than larger-bodied conspecifics to survive winter at higher latitudes, then sex-age classes (or races) having smaller bodies might be expected to evolve toward longer migrations that would take them into milder climates (Ketterson and Nolan, 1976).

The mechanism proposed (Ketterson and Nolan, 1976) to account for this putative size-related variation in probability of overwinter survival is differential fasting endurance (Calder, 1974). On the assumption that energy stores are proportional to body mass (i.e., 1:1), bigger individuals should have greater reserves relative to their basal metabolic rate, because of the less than proportional relationship between body size and metabolism (Calder, 1974). As a result, during severe winter storms when food is temporarily unavailable, they should be able to survive for longer periods of time, drawing on their fat stores to support

their energy needs. The ultimate selective factor under this hypothesis would not operate until after migration is over; therefore, the proximate mechanism causing variation in migratory distance would be either some form of endogenous control or a differential response to one or more environmental variables encountered before final choice of the wintering site.

3.1.2. The Body-Size Hypothesis Evaluated Generally

Field evidence for the hypothesis was sought by Dolbeer (1982) in a comparative study of certain icterids and of the Starling (*Sturnus vulgaris*). Dolbeer predicted that if body size has been important in the evolution of differential migration of the sexes, then species with a higher degree of sexual size dimorphism would show a greater intersexual difference in distance migrated. A comparison of the distance separating banding and recovery locations of individuals banded during the summer months and recovered during the winter months showed that the winter distributions of both the dimorphic Common Grackle (*Quiscalus quiscula*) and Red-winged Blackbird (*Agelaius phoeniceus*) fulfill Dolbeer's prediction. That the sexes of the monomorphic Starling do not separate in winter also supports his prediction. However, female Brown-headed Cowbirds (*Molothrus ater*), although considerably smaller than males, migrate no farther than males.

The hypothesis would receive experimental support if northern-wintering, larger individuals were found to have greater fasting endurance than their southern-wintering conspecifics when both were held under identical conditions. Ketterson and King (1977) reported that among White-crowned Sparrows (*Zonotrichia leucophrys gambelii*), a species in which males are larger and females migrate farther, males can fast for longer periods than females. In contrast, among juncos and Tree Sparrows (*Spizella arborea*) no significant sexual difference in fasting endurance was found (Stuebe and Ketterson, 1982), although in both species the trend favored males. In none of these experiments were the fat stores of the subjects at the time food was withdrawn from them known, and the assumption that stores were proportional to body size may be questioned. In fact, we know of no demonstration among conspecific birds either that winter fat stores are proportional to lean body mass or that size-related differences in metabolic rate are other than negligible. Clearly both these points are testable; but in species whose fat stores vary in response to recent environmental conditions, an adequate test of the proportionality point will require a large sample of individuals collected at the same time.

3.1.3. The Body-Size Hypothesis Applied to the Junco

Among juncos, males exceed females in wing length and in lean—i.e., metabolizing—mass (Helms *et al.*, 1967). Adults of each sex are slightly heavier (wet weight) and have longer wings than young (Fig. 3; Nolan and Ketterson 1983); whether lean mass varies with age class is unknown, but it seems safe to assume that lean mass of adults is at least as great as that of young. Turning to size variation within each of the four sex and age classes, wet weight and wing length are significantly correlated (Nolan and Ketterson, 1983); but here too the relationship between wing length and lean mass is not known.

On the basis of the foregoing facts, the Body-Size Hypothesis predicts that males should winter farther north than females. It does not, however, predict a distribution in which young settle north of adults of their sex (Fig. 2). Nor, if we are willing to assume that within a sex—

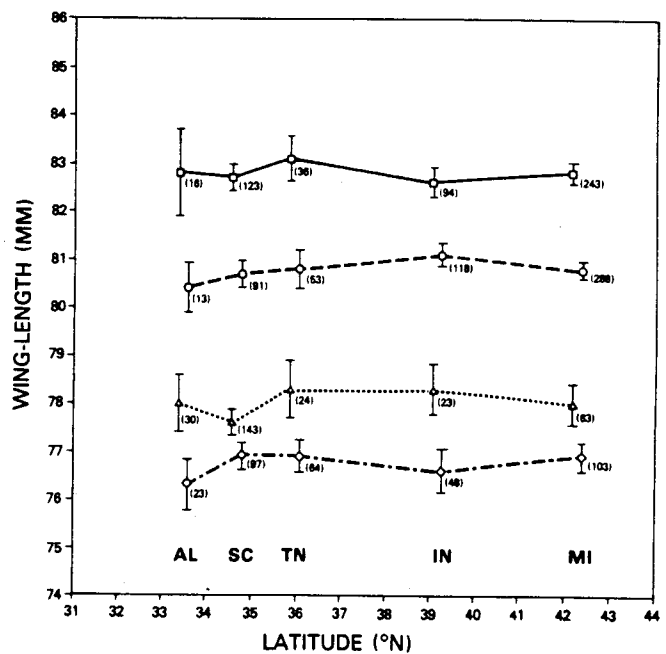


FIGURE 3. Mean wing-length of the sex and age classes of juncos at five latitudes in the winter range. Curves (top to bottom) apply to old males, young males, old females, and young females. In no class did winglength vary with latitude. (From Nolan and Ketterson, 1983, reprinted by permission from *The Wilson Bulletin*; copyright 1983, The Wilson Ornithological Society.)

age class wing length and lean mass co-vary (James, 1970), does it predict the absence of within-class latitudinal variation shown in Fig. 3.

3.2. The Dominance Hypothesis

3.2.1. The Dominance Hypothesis Stated

According to Gauthreaux (1978, 1982), a single underlying force drives all forms of intraspecific segregation in winter. These forms of segregation are habitat apportionment among sedentary populations, differential dispersal, partial migration, differential migration, and intraspecific variation in irruptive movements; and the single driving force is dominance. In the model, when competition for food or some other nonbreeding resource is intense, socially dominant individuals will be more likely to obtain an adequate supply, subordinates will then depart, and dominance-based winter segregation will result. If all individuals can survive winter within the breeding range, there will be no migration in the usual sense; subordinates will simply be found in the poorer habitats. If the breeding range can support only a portion of the population, subordinates will be those that are forced to leave. If the entire population is required to emigrate, dominants will migrate only so far as necessary to reach a suitable habitat. Subordinates will either migrate farther or, if they do not go farther, will occupy habitat of lesser quality.

In a more recent statement Gauthreaux (1982) reiterates and develops his views. He notes that a corollary of wintering on the breeding ground, or nearer to it, or (if no nearer than subordinates) in habitat that is of higher quality, is that dominants can begin to breed at an earlier date. This is true either because they do not have to migrate or, if they do, because their spring migrations are shorter or initiated sooner than those of subordinates. Gauthreaux's emphasis is not on mechanisms, but he states that dominance probably exerts its influence on migratory behavior proximately.

3.2.2. The Dominance Hypothesis Evaluated Generally

Gauthreaux's contribution has without question advanced the general understanding of the importance of social behavior in the evolution of migration. We nevertheless have three specific reservations about this hypothesis, and it is on these that we necessarily focus.

First, the Dominance Hypothesis relies to a considerable extent on

the numerous species of birds in which young and/or females tend to be both subordinate and more likely to disperse, or to migrate under circumstances in which dominants remain sedentary, or to travel farther when all migrate. Recent papers have reported similar data and interpreted them as supporting Gauthreaux (Lundberg *et al.*, 1981). Nevertheless, as pointed out in the Introduction, in most of these examples males are also larger than females and the first to initiate breeding activities, and adults are larger than young. Consequently, the examples could be cited equally well in support of the Body-Size Hypothesis or the Arrival-Time Hypothesis (see below). Further, as Gauthreaux (1982) recognizes, there are exceptions. White-crowned Sparrows (King *et al.*, 1965, M. L. Morton, personal communication) and American Goldfinches (*Carduelis tristis*; A. L. A. Middleton, personal communication) apparently migrate farther when adult, and Starlings in at least some parts of their range evidently do the same (Spaans, 1977). The behavior of female Sharp-shinned Hawks (*Accipiter striatus*) is inconsistent with the hypothesis. They are much larger than males and almost certainly dominant over them (Smith, 1982) but tend to migrate farther (Evans and Rosenfield, in press). (For other exceptions, see Section 3.3.2.)

How might we test Gauthreaux's model? Herein lies our second reservation. The hypothesis supposes that the gradients of proximity to the breeding grounds and of habitat quality either always covary and produce an orderly geographic separation of dominance classes or, if they do not, that dominants and subordinates in the same geographic area segregate according to habitat quality. Distance is a readily measurable variable, but it is not clear that variation in habitat quality can be identified independently of the very distribution for which the model seeks to account.

Our final objection refers not to the empirical support for the hypothesis or to its falsifiability, but rather arises from its assumptions of how dominants and subordinates behave and survive when resources are limiting in winter. The Dominance Hypothesis assumes that food is the resource most likely to be limiting in winter, an assumption that is often granted for the north temperate zone (Lack, 1954; Smith *et al.*, 1980; Jansson *et al.*, 1981; Pulliam and Millikan, 1982) and one we do not dispute. The hypothesis then assumes that during food shortages subordinates invariably suffer more and accordingly are the first to disperse, and it is these last assumptions that we believe should be examined. There is certainly evidence to support them. An early instance is Fretwell's (1969) much-cited report, based on a small sample of banded juncos, that subordinates were less likely than dominants to be recaptured at winter's end. Kikkawa's (1980) more convincing over-

winter-survival estimates of dominant and subordinate Silvereyes (*Zosterops lateralis*) agree with Fretwell's results. Similarly, Smith et al. (1980) found that subordinate Song Sparrows were more likely to be alive at winter's end if food supplies were supplemented. Finally, in an aviary experiment, Baker and Fox (1978) gradually restricted the food of captive juncos and noted the social status of individuals whose body mass fell below 17 g, which they took as a stage of emaciation equivalent to death. More subordinates fell below the critical value than dominants. [In evaluating this result it should be noted that female juncos tend to be both subordinate to males and to have a smaller lean body mass (Helms et al., 1967). Therefore, reduction of mass below 17 g is less likely to indicate imminent starvation in females than in males, and it may be questioned whether Baker and Fox's results are entirely convincing in view of the confounding effects of the sexual difference in body size.]

Opposed to the view that subordinates always suffer disproportionately and are the first to emigrate are our own data on juncos (Ketterson and Nolan, 1982). Male juncos are dominant over females and, within the sex classes, adults are dominant over young (Balph, 1977;

TABLE I
Recapture in Late Winter of Juncos Marked in Early Winter According to Sex, Age, and Location^{a,b,c,d}

	Male		Female		Classes combined
	Adult	Young	Adult	Young	
Indiana	10/68 (15%)	8/78 (10%)	1/13 (8%)	3/29 (12%)	24/198 (12%)
South Carolina	15/46 (33%)	10/22 (41%)	23/43 (53%)	13/25 (52%)	60/136 (44%)

^aAfter Ketterson and Nolan, 1982.

^bData are from the two winters 1977-1978 and 1978-1979 and are pooled. Denominators of fractions show the numbers of juncos marked and released in good condition in early winter, and numerators show numbers of marked juncos recaptured at the same sites in late winter. A few marked individuals were of unknown sex or age, causing the size of the "classes combined" fraction to exceed the totals of the pooled fractions for the sex and age classes.

^cIn Indiana, the sex and age classes were equally likely to be recaptured [$\chi^2 = 0.94$, $df = 2$, n.s. (female age classes combined because samples are small)]. The same was true of South Carolina ($\chi^2 = 4.72$, $df = 3$, n.s.).

^dLate-winter recapture frequencies for each sex and age class were compared for the two locations. Each 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. $\chi^2 = 9.26$, $df = 1$, $p < 0.01$).

Ketterson, 1979a). Table I shows that among juncos captured and banded in Indiana in early winter and recaptured in late winter, frequencies of recapture of the sex and age classes were statistically indistinguishable. The same was true in South Carolina, although it is notable that the South Carolina overwinter recapture rate of all classes pooled was 3.7 times higher than that rate in Indiana. In an independent and rather large Indiana sample (Table II) obtained in two winters, the sex and age structure of the junco population at winter's end was the same as it had been in early winter, i.e., before unusually severe weather had periodically restricted food. Essentially, the same was true in South Carolina with its milder climate (Table II), although this sample was

TABLE II
Early- and Late-Winter Comparisons of Sex and Age Ratios of Winter Junco Populations at Three Latitudes^{a,b}

	n	Male		Female	
		Adult	Young	Adult	Young
Indiana ^c					
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 ^d					
December 1979	37	27%	27%	14%	32%
February 1980	84	18%	30%	17%	36%
South Carolina ^e					
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%

^aAfter Ketterson and Nolan, 1982.

^bThe Indiana site was at 39°N, the Tennessee at 36°N, and the South Carolina at 34.5°N.

^cIndiana seasonal comparisons of sex and age ratios, December vs. February, 1978–1979 ($\chi^2 = 1.90$, $df = 3$, n.s.); December vs. February, 1979–1980 ($\chi^2 = 5.10$, $df = 3$, n.s.).

^dTennessee seasonal comparison of sex and age ratio, December vs. February, 1979–1980 ($\chi^2 = 1.35$, $df = 3$, n.s.).

^eSouth Carolina seasonal comparisons of sex and 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.).

not fully independent of the South Carolina recapture data in Table I. Finally, early- and late-winter sampling of a population near Nashville, Tennessee, in a single winter produced this same result. During the course of the winter the proportions of dominant and subordinate Tennessee juncos remained unchanged (Table II). Accordingly, sex, age, and dominance status appear to be unrelated to the probability of death and dispersal during winter in this species.

Can the apparent conflict between our work and that of other investigators be reconciled? The situations studied by Baker and Fox (caged flocks) and by Kikkawa and Smith *et al.* (nonmigratory populations on very small islands; see Tompa, 1964, for details on the population and the characteristics of the island on which Smith *et al.* worked) had in common the fact that dispersal or emigration was prevented or severely limited by physical barriers, whereas the juncos we studied were migratory and free to disperse both in advance of winter and during that season. We propose that in this latter situation it cannot always be assumed that subordinates will be the only class to emigrate or that they will die in greater numbers. In fact, it seems likely that there are circumstances in which middle- to high-ranking birds should benefit more from dispersal than subordinates, as the next paragraph describes.

The critical question to the individual that confronts the possibility of scarce resources is what alternatives are available to it. It is a truism, but it seems worth emphasizing, that dominance rank can be expressed only in a social context and is likely to vary with context. Individuals of equally high expected rank, i.e., rank resulting from the inherent traits of size, sex, and age, will match their expectation in varying degrees, depending upon the characteristics of their associates. The realized rank of an average male junco would almost surely be higher in a flock composed largely of females than in a group in which males predominated. Conversely, in a location in which females predominate, an individual female's realized position may greatly exceed her expectation. Further, Rohwer and Ewald (1981) have suggested that birds at the top of a dominance hierarchy may prefer association with subordinates and may attempt to drive away their social equals or near equals by directing more aggressive behavior toward them (see the similar conclusion of Ketterson, 1979b). In such a situation the more-often attacked individuals of intermediate status might suffer more than subordinates and thus be the group more likely to disperse. If both the rank an individual achieves and the impact of that rank on its access to resources vary as a function of the relative frequency of individuals

with high or low expected rank among its flockmates, then the relationships of dominance status, aggressive behavior, order of dispersal, and survival are likely to be more complex than is usually recognized.

3.2.3. The Dominance Hypothesis Applied to the Junco

The relevant data have been given in the preceding subsection.

The prediction of the hypothesis is that dominant classes will settle closer than subordinates to the breeding grounds or, if no closer, in higher-quality habitat. In juncos, dominant and subordinate sex and age classes intermingle throughout the winter range, although in proportions that vary with distance from the breeding ground. Nothing suggests that subordinates are being selected against when they overwinter with dominants. On average, male juncos select winter sites nearer the breeding grounds than do females, and this could be taken as evidence that supports the hypothesis; but the distribution of age classes, with adults of each sex farther south than young, indicates that dominance rank cannot predict the winter distribution of the junco (Fig. 2).

3.3. The Arrival-Time Hypothesis

3.3.1. The Arrival-Time Hypothesis Stated

Myers (1981a) reasons that if members of one sex (or of some other class) experience more intense competition for breeding resources than do members of the other, then individuals of the more competitive sex should benefit by returning earlier to the breeding ground. The social system sets the relative levels of intrasexual competition. Thus, where one sex establishes territory, its members should arrive first in order to gain priority of access to territories. Although early return could result either from migrating a shorter distance, and therefore wintering nearer the breeding ground, or from earlier departure in spring from a common wintering ground, Myers speculates that intense intrasexual competition may often lead members of the more competitive sex to do both. Based on his review of seven species for which the necessary information was available, including a number of shorebirds with reverse size dimorphism and unusual mating systems, Myers concluded "that to predict latitudinal segregation of the sexes, information about arrival schedules is both necessary and sufficient." A comparable statement could not be made about either the Body-Size or the Dominance

Hypothesis. Other time-related selective pressures can modify the effects expected from interclass variation in intensity of intraclass competition, as Myers recognizes when he notes that breeding at high latitudes may abbreviate the breeding season so greatly that differences in competition would have no detectable influence on arrival schedules.

3.3.2. The Arrival-Time Hypothesis Evaluated Generally

Myers has made an important contribution to our understanding of the evolution of differential migration by calling attention to the importance of social systems as a selective factor. However, as before, we concentrate on what we believe to be the limitations of the hypothesis.

First, it seems unlikely that priority of arrival should always be linked to shorter migrations. Southern-wintering White-Crowned Sparrows, for example, may arrive on their breeding grounds no later than northern-wintering conspecifics; at least, they are known to initiate pre-migratory fattening at an earlier date (King and Mewaldt, 1981). It remains to be seen whether knowledge of arrival schedules will prove a sufficient general predictor of winter distributions.

Second, Myers does not consider the impact that the winter distribution of one class may have on the distribution of the others. He proposes that for each class some ideal location or range of locations exists, presumably determined by the greater probability of survival there between breeding seasons. For the more competitive class the effect of intraclass competition for breeding resources is superimposed upon this survivorship-based ideal and may shift the class' distribution toward the breeding range. That the distribution—or the redistribution—of one class may affect the distribution of the others through density-dependent feedback is not considered, and we suggest that a comprehensive hypothesis should speak to this complication.

Third, we think it worth questioning whether males are more competitive than females, which is the reason proposed to account for their greater proximity to and earlier arrival on the breeding ground. Do the sexes differ in intensity of competition, as many (e.g., Greenwood, 1980) have concluded, or is the critical difference between them one of the seasonal timing of their competition? It is probably true that in most migratory bird species males return first, compete for territories, and court females when they appear. [In an interesting exception that supports Myers' views, female Spotted Sandpipers (*Tringa macularia*) arrive earlier than males (Oring and Lank, 1982), set up territories, and are the active sex in courtship.] Other evidence of the importance, and perhaps greater intensity, of male-male competition comes from nu-

merous removal experiments (Krebs, 1971; Samson, 1976; Thompson, 1977) in which the elimination of territorial males has increased the breeding opportunities of others of that sex. However, the literature also reports examples of female-female competition. The presence of unpaired females during the breeding season (von Haartman, 1971; Saether and Fonstad, 1981) and of females paired to other females (Hunt et al., 1980), as well as the occurrence of delayed breeding by juvenile females as the result of aggressive behavior by adult females (Hannon et al., 1982) have all been reported. Thus whether males usually are more competitive than females seems to us a question that may still be open. What does seem clear is that in territorial species, the sex that establishes territory engages in its intrasexual competition at an earlier date than does the sex whose role is to choose territory owners as mates. Apparently, for a full understanding of differential migration we must have a better understanding of what it is that selects for territoriality.

Finally, we note that the cause-effect relationship between arrival time and success in competition for breeding resources is likely to have exceptions. Late arrivals do not necessarily lose out in competition for territories. In both Song Sparrows (*Melospiza melodia*; Nice, 1943, p. 154) and Prairie Warblers (*Dendroica discolor*; Nolan, 1978, p. 40), returning males that find their previous year's territories preempted by earlier arrivals very rarely have difficulty in ejecting the usurpers; and this result may be widespread (but see the contrary results of Catchpole, 1972, and the interesting experimental findings of Krebs, 1982). In many species the percentage of breeding sites reoccupied by former owners is so high that the reoccupancy rate is probably also the survival rate. We doubt that all survivors arrive earlier than all individuals seeking sites for the first time in their lives, and we therefore suggest that priority of arrival is not sufficient to establish an indefeasible claim when the claim is contested by a former owner. One could respond that intraclass competition would then be greatest among inexperienced breeders, and we would agree. Our point is only that the most competitive class, even if it arrives first, does not always have its choice of resources. We regard this not as inconsistent with Myers' view but as a refinement of it.

3.3.3. The Arrival-Time Hypothesis Applied to the Junco

The hypothesis would predict that classes of juncos that arrive first in spring also migrate the shortest distances in autumn and/or depart earliest in spring, and that they do so because for them competition at the start of the breeding season is most intense.

We have no observations about the order of arrival and can find nothing in the literature. Thus we cannot test directly Myers' thesis

that knowledge of arrival sequence is necessary and sufficient to predict winter distribution. We do have extensive data on the spring migration through Indiana, and these indicate that the peak of male passage precedes that of females by several days (Nolan and Ketterson, unpublished data). We therefore expect that males arrive first, a result that does not require, however, that they depart earlier. If all juncos from all wintering sites began to move northward at about the same time and rate, the earlier peak of male passage through Indiana and the assumed earlier male arrival on the breeding ground could result entirely from the differential sexual distribution in winter. Is there evidence of such simultaneous initiation of spring migration? We have considered this possibility for a single Indiana population by comparing (Table III) final capture dates of banded juncos skull-aged (in December or earlier) and known to have wintered at the study site. The median dates of last capture of adult males, young males, adult females, and young females were March 22, March 25, March 26, and March 29, respectively. Differences were nonsignificant, although young juncos did show greater variability than adults. If departure also does not differ among latitudes, then winter distribution alone would determine arrival time, and the predicted order of arrival would be young males, adult males, young

TABLE III
Latest Spring Capture Dates of Migratory Juncos Known to Have Wintered
Near Bloomington, Indiana: An Approximation of Their Departure Time^{a,b}

	Males		Females	
	Adult	Young	Adult	Young
<i>n</i>	32	93	12	34
Median date	March 22	March 25	March 26	March 29
Extremes	March 6– April 8	March 2– April 13	March 12– April 8	March 1– April 14

^aJuncos in the sample met the following criteria: first captured on or before January 2 and aged by skull ossification; captured at least two times during December, January, or February; last captured on or after March 1. Capture efforts were made on a near-daily basis from October 1–May 1 near Bloomington, Indiana during the winters of 1973–1974, 1974–1975, 1975–1976, 1976–1977, 1977–1978, and 1978–1979 and the data were pooled across years.

^bThe classes did not differ significantly in date of last capture (Kruskal–Wallis one-way analysis of variance, $H = 2.70$, $df = 3$, n.s.). The median date regardless of class was March 25. Females were no more likely than males to be among those captured after March 25 (28 females, 56.5 males, $\chi^2 = 3.14$, $df = 1$, 2-tailed $p < 0.10$), nor were young more likely than adults (66 young, 20.5 adults, $\chi^2 = 0.19$, $df = 1$, n.s.).

females, adult females. If this prediction were borne out, Myers would be supported.

We also have no information on the relative intensity of intrasexual competition among juncos, but competition probably occurs earlier among males than females, given the territoriality of males. Further, it seems likely that at the beginning of the breeding season young males are more competitive among themselves than are males that have bred previously. We base this statement on the degree of male site fidelity we have observed to breeding locations, applying the argument made above (Section 3.3.2) about the inference to be drawn when all survivors reoccupy their former breeding territories. In field studies at Wawa, Ontario, Canada, 50% of males banded in the preceding year reoccupied their former territories, and in the only exception the former territory had been flooded. This 50% reoccupancy rate is the same as three independent estimates that put the annual survival rate of juncos at about 50% (Ketterson and Nolan, 1982; Sections 4.1.3.a and 4.1.3.b), indicating that surviving males regularly are able to take over their territories of the year before. Accordingly, competition among them should be less intense than among young males, which must contest for the habitat left unoccupied by the death of former owners. In this competition we could expect priority of occupation to confer a considerable and perhaps decisive advantage (see Balph, 1979; Yasukawa and Bick, 1983), putting young males under strong pressure to arrive early.

In contrast to males, few banded females have returned to nest on our breeding-study areas, although females are fully capable of showing site fidelity: they home to their former winter sites in the same proportions as males (Section 4.1.3.a). Because we have no reason to suspect a sexual difference in survivorship, we attribute the lower fidelity of females to the breeding site either to weaker motivation to reoccupy former sites or to lesser ability to retake former sites from competitors that arrive earlier. The first alternative would be expected if competition were slight and if reoccupation of the former site conferred little reproductive advantage derived from experience there. The second alternative might be true if there were strong intrasexual competition for sites but if prior residents had no psychological or other advantage in such contests. Whatever the level of competition among females may be, the age classes appear to be on an equal footing.

We conclude that the fact that young males winter somewhat closer to the breeding site than older males fulfills the prediction and rationale of the Arrival-Time Hypothesis. But if our argument based on the low site fidelity of females is sound, that is, if female age classes are equally competitive, then the tendency of these classes to separate in winter

does not conform to expectation. Therefore, while we suspect that advantages associated with arrival time on the breeding range are important to the junco's differential winter distribution, we think that arrival time is only one of several important pressures and that a multifactor model is necessary to explain the data.

4. A MULTIFACTOR HYPOTHESIS FOR THE EVOLUTION OF DIFFERENTIAL MIGRATION

4.1. The Migration-Threshold Hypothesis

4.1.1. The Migration-Threshold Hypothesis Stated

Baker's (1978) model appears to remain unfamiliar to most, perhaps because few choose to devote the necessary time to its complex presentation. (The present paper arose out of an invitation to apply Baker's model to birds.) Two reviews of current knowledge of the evolution of migration have paid it scant attention and/or have ignored what we view as its essential points (Keast and Morton, 1980; Gauthreaux, 1982). Therefore, in Appendix I, we summarize those elements of the model, its symbols and its terminology, that we believe most interesting to avian biologists and here assume that the reader will consult this appendix, if interested. Baker uses the word "migration" to include any non-accidental change of location by any metazoan, but we confine our statement here to migration as it is usually defined for birds, i.e., to cyclic to-and-fro movements between the breeding and the non-breeding ranges. (For general reviews of Baker's book see, e.g., Krebs, 1979, and Dingle, 1979.)

According to Baker, birds migrate when their migration thresholds have been exceeded. Each individual has an inherited threshold that has been shaped by natural selection in such a way that it will be exceeded, and the individual will initiate migration, at the point at which the advantages of remaining at a site are just outweighed by the advantages of leaving it. This point is described by relating the suitability of the currently occupied habitat, h_1 , to the suitability of habitats attainable by migration (\bar{h} , e.g., h_2 , h_3 , etc.), corrected for the cost of making a round trip to one of those latter habitats and back again. Habitat suitability is measured in terms of potential reproductive success (p.r.s.), and the suitability of any particular habitat is the ratio of the individual's p.r.s. at the time it departs from that habitat to what its p.r.s. was at the time it arrived. Because p.r.s. declines throughout

life, h is always equal to or less than 1.0. The relative suitability of two alternative habitats is Baker's habitat quotient, h_q .

The migration factor, M_R , which is also measured in terms of potential reproductive success, expresses p.r.s. at the termination of a migration as a proportion of what it would have been at that same time had the animal not undertaken the migration. Because it is typically more costly to be moving than to remain in a familiar location, M_R is also usually a number less than 1.0.

These ideas are expressed in two equations used repeatedly by Baker. First, it becomes advantageous for an animal to migrate at the point

$$h_1 < h_2 M_R,$$

where h_1 is the suitability of the breeding or natal site, h_2 is the suitability of the wintering site, and M_R is the migration factor for the round trip. Once the migration threshold has been exceeded, selection should favor behavior that acts to maximize the quantity

$$h_2/h_1 M_R = h_q M_R.$$

In one of his several contradictions, Baker suggests that in order to maximize $h_q M_R$ birds will sometimes initiate segments of the migration under conditions where $h_q M_R$ is less than 1.0 for that segment, because by doing so they are able ultimately to reach and spend the winter in regions of very high suitability.

If classes of individuals differ in the incidence of migration, the necessary implication is that they also differ in the average value per class of h_1 , h_2 , M_R , or some combination of these. Further, in those classes that migrate, if distance migrated differs, the classes must vary with respect to the location of habitats where $h_q M_R$ approaches a maximum. We now consider briefly how $h_q M_R$ might differ according to sex and age, beginning with the habitat quotient.

Suitability of the winter habitat is a composite variable, the value of which for a given individual is a function of (1) the physical attributes of the habitat (h_p), (2) the individual's prior experience (if any) in the habitat, and (3) the distance of the winter habitat from the breeding site. Also important are (4) the density of the population in the habitat (h_d) and (5) the individual's resource holding power relative to the power of the other occupants of the habitat (h_{rhp}). When suitability is determined by several factors, e.g., h_p , h_d , h_{rhp} , the overall habitat suitability is the product of the separate suitabilities and thus remains a

number less than 1.0. Suitability for sex and age classes will differ only if the value of the component(s) is sex- or age-dependent.

For example, h_p , the habitat's physical and biological suitability (excluding competition), is determined by its climate, absolute abundance of predators and of food, availability of roosting sites, and many similar factors. Because climate generally improves for birds that move away from the earth's poles in autumn, habitat suitability and thus the habitat quotient should improve accordingly. However, unless climatic conditions are more important to the fitness of members of one class than of another (as in the Body-Size Hypothesis), climate can play no role in explaining interclass variation in the incidence of migration. Prior experience at a non-breeding location can also influence the suitability of that location, and several authors have suggested that in a species for which the attributes of a non-breeding habitat are stable from year to year, experience gained there in earlier years should be sufficiently beneficial to select for high site fidelity. Fretwell (1980) has gone so far as to suggest that prior residency provides so great an advantage in winter (because it confers dominance at the site) that selection has caused some species or populations to become sedentary simply because to do so preserves the advantage of familiarity with the winter site. In any case, since young of migratory species can have had no prior experience in the winter range, that aspect of the non-breeding habitat quotient will necessarily vary with age. Finally, if occupation of more distant habitats delays return to breed in the spring in a way that diminishes fitness, then the habitat quotient will also be reduced. If that delay is more important to one class than to another, suitability will be correspondingly reduced for that class. (Baker is inconsistent in his treatment of distance. On p. 678, distance is treated as a component of habitat suitability, but in his definition of the migration factor he includes loss of copulations as a cost that may be associated with migration. Because in the former treatment he refers specifically to the evolution of seasonal return migration in birds, we infer that to be his view and take distance to be a component of h_q .)

The components of habitat suitability considered in the preceding paragraph are density-independent in their effects. Variation in population density also has important effects on mean habitat suitability, which will be depressed if density is high in relation to resource levels. If individuals do not differ in resource holding power (and they differ only when they have unequal access to a necessary resource that is in short supply), then each will have an equally depressing effect on the mean habitat suitability of its associates. In the case where alternate habitats of greater suitability are available, some will respond to high

density by emigrating to one of these habitats. The effect of this on those that remain (and do not incur the cost of migration) will be to reduce density and improve habitat suitability, and the cost and benefits to those that emigrate and those that remain will be balanced. This situation is said to be free (*sensu* Fretwell, 1972), and the fitness of migrants and of non-migrants is equal. On the other hand, when individuals differ in resource holding power and those with lower power suffer from reduced access to resources, a *despotic* situation prevails. In this case, for individuals or sex and age classes of low power the habitat is less suitable than for conspecific individuals or classes of higher power. These latter will be expected not to migrate (or, assuming that the entire population has migrated and has reached the most suitable site in the winter range, they will be expected not to migrate any farther); they will settle and restrict access to resources by those with less power, which by definition will have lower reproductive success. Whether these less favored birds nevertheless remain in the habitat or migrate (or continue to migrate) depends upon whether, for them, the suitability of the currently occupied habitat, despite the presence there of individuals of greater resource holding power, is greater or less than the suitability of other available habitats, corrected for the cost of getting there. Only if it is less will they initiate migration. [Although Gauthreaux (1982) equates dominance with resource holding power, we suggest that the concept of h_{rhp} will be most useful if it is defined not strictly in terms of rank but in terms of rank-associated gain or loss of potential reproductive success. For example, if subordinates are not at a disadvantage relative to high-ranking birds so long as they co-occur in low relative frequencies, their resource holding power may be equal to that of birds of higher rank. We stress again our view (Section 3.2.2) that predicting the behavior or relative fitness of individuals of subordinate rank is no simple matter.]

We turn now to possible sex- and age-related variation in the migration factor, M_R , a variable whose value rises as the risk of mortality during migration falls. That value probably varies with age in two opposing ways. First, all other things being equal, a given migration cost (m ; see Appendix I) is more likely to be assumed by young individuals than by old. The reason is that potential reproductive success decays throughout life, and therefore the p.r.s. remaining to younger individuals at any particular time is higher than that of older individuals. Thus the impact of any given value of m will be proportionately smaller in young birds than in adults. On the other hand, young animals are inexperienced, and any variation in migration cost associated with experience will clearly favor older individuals. In small birds that do not

travel in organized social groups, we regard the higher probability of death confronted by first-time migrants as greatly outweighing any advantage associated with their higher potential reproductive success (see Ralph, 1971; Nolan, 1978, pp. 448–451, 472–473; Greenberg, 1980). Turning from age to sex, sex-associated differences in migratory cost per unit distance migrated have rarely been described. In small-bodied, essentially size-monomorphic birds that do not store energy for reproduction in advance of migration, no sex differences are anticipated; but waterfowl, shorebirds, hawks, and gallinaceous birds may provide interesting exceptions.

In summary, individuals tend to initiate migration when the cost is low relative to the gain in habitat suitability. To the extent that members of sex–age classes differ in assessing these variables because over evolutionary time the variables have exerted different selective pressures according to sex or age, classes will differ in the frequency with which they initiate migration and thus in the distance they travel.

4.1.2. The Migration-Threshold Hypothesis Evaluated Generally

An indication of the all-encompassing scope of Baker's model is the fact that all of the premises and predictions of the single-factor hypotheses can be comfortably accommodated within it. Thus the model's treatment of the despotic situation makes it broad enough to incorporate the Dominance Hypothesis: when sex-age classes differ in dominance rank, they may (but they need not) also differ in resource holding power. Migration distances will then be greater in those with lower power if (but only if) the alternative habitats available to them are sufficiently suitable to offset the cost of reaching those habitats. Note also, however, that if dominants do not have greater resource holding power, Baker's model would not predict dominance rank-associated differences in migratory behavior. The concept of the habitat quotient can also incorporate the Arrival-Time Hypothesis. If early arrival on the breeding ground is advantageous and is correlated with wintering nearby, the relative suitability of the more distant habitats is reduced by a measure that reflects the loss of potential reproductive success resulting from delayed return. Finally, as already noted (Section 4.1.1) the model includes a counterpart of the Body-Size Hypothesis.

While the comprehensiveness of the model makes it admirable in the abstract, in practice it may render predictions untestable. Thus, in order to apply the migration equation to differential migration by sex and age classes, numerous, detailed, species-specific data are required. Assuming these are obtainable for a particular species, predictions based

on them would probably no longer be necessary for that species and would be unlikely to be generalizable to others.

At a different level of criticism, the physiological reality of the proposed critical mechanism, the migration threshold, seems debatable and largely beyond reach of investigation. When it is noted that the seasonal migration threshold is only one of a supposed large family ("hierarchy") of inherited thresholds on the basis of which Baker would account for every change of location ("migration")—a threshold for leaving the nest to forage, for leaving the foraging site to roost, for flying from roost to song post, etc.—it seems that we are dealing more with a convention for describing bird behavior than with real mechanisms.

This is not to suggest that Baker's model has no value, but to us its utility lies in providing an organizing and heuristic scheme for a *posteriori* analysis of data and in emphasizing how numerous and varied the relevant data are likely to be.

4.1.3. The Migration-Threshold Hypothesis Applied to the Junco

As will become obvious when we attempt to use Baker's ideas in relation to the winter distribution of the junco, we are not testing the model in the scientific sense. Rather, we are accepting it more or less at face value for the purpose of argument and asking whether its predictions are consistent with what we already believe to be true about the junco. These beliefs are based to a large extent on information on population dynamics, and we emphasize that the data are imperfect. Nevertheless, in spite of insufficiencies, a considerable number of independent data sets (from free-living populations at several latitudes in the winter range, from two locations in the breeding range, and from United States Fish and Wildlife Service recovery records) all converge to provide an interpretation that is at least internally consistent. One especially important gap (Myers, 1981b), however, probably cannot be filled. We do not know the breeding-range origins of the populations that we follow in winter, nor do we know the wintering sites of the individuals composing our breeding populations.

Baker's model predicts that the sex-age classes should concentrate in those regions in which, for them, $h_q M_R$ reaches its maximum. If $h_q M_R$ is at a maximum for young males at high latitudes, whereas for adult females the maximum lies at lower latitudes, these facts would support the model (see Fig. 2). Rough approximations of the relative mean values of certain components of h_q and M_R can be obtained if we initially grant that overwinter survival approximates h_2 and that the product of autumn and spring migration mortality is inversely proportional to M_R .

If we further make the simplifying assumption that on the breeding ground (h_1) habitat suitability in winter falls to some unknown but geographically invariant value, then h_q will vary as a function of h_2 . We now examine data on population dynamics and interpret them in terms of h_q and M_R .

4.1.3.a. *Estimates of Junco Population Parameters, Adults.* Over-winter survival appears to be lower among male and female adults of northern-wintering junco populations than among male and female adults of southern-wintering populations (see Section 3:2.2, Ketterson and Nolan, 1982). Despite this latitudinal difference in survivorship during winter, we believe that when the full year is considered members of northern-wintering populations survive as well as southern. This conclusion is based on two observations: (1) Annual recapture rates of marked adults in the north and south in the year subsequent to capture were equal (Table IV, statistical comparison restricted to males). (2) After the first return to the north by marked individuals, returns by these same birds in subsequent years produced an estimated survival rate of 53%, a conclusion based on an independent and much larger sample (Ketterson and Nolan, 1982). That percentage is not lower than the expected annual survivorship of many temperate-wintering species

TABLE IV
Recapture in December of Juncos Caught in a Previous December According to Sex, Age, and Location^{a,b,c,d}

	Male		Female		Classes combined
	Adult	Young	Adult	Young	
North	25/220 (11%)	9/260 (3%)	1/59 (2%)	3/100 (3%)	38/639 (6%)
South	6/71 (8%)	8/46 (17%)	8/100 (8%)	8/58 (14%)	30/275 (11%)

^aAfter Ketterson and Nolan, 1982.

^bSites treated as "North" were in Michigan and Indiana, those regarded as "South" were in South Carolina and Alabama. Denominators of fractions are the numbers of juncos marked and released in good condition in December, and numerators are the numbers of those marked juncos recaptured at the same sites in a subsequent December. Recapture efforts were made in three Decembers in Michigan, Indiana, and South Carolina and in two Decembers in Alabama.

^cComparisons of return of three sex and age classes to northern and southern locations follow: adult males: adj. $\chi^2 = 0.23$, $df = 1$, n.s.; young males: adj. $\chi^2 = 11.28$, $df = 1$, $p < 0.001$; young females: adj. $\chi^2 = 4.85$, $df = 1$, $p < 0.05$. For all classes pooled, rate of return to the South was significantly higher (adj. $\chi^2 = 7.07$, $df = 1$, $p < 0.01$). Returns of adult females were too few to be compared.

^dFrequency of return of the sex and age classes to northern sites differed ($\chi^2 = 17.87$, $df = 3$, $p < 0.001$). Returns to southern sites did not differ ($\chi^2 = 3.80$, $df = 3$, n.s.).

(Greenberg, 1980), nor is it lower than the return rate of male juncos to Canadian breeding sites (50%; Section 3.3.3). These facts make it unlikely that southern-wintering juncos have a higher annual survival rate than the 53% found for northern-wintering juncos. If, then, annual survival is equal among winter populations, juncos from the southern part of the winter range must suffer more heavily than do northern juncos in seasons other than winter; and for several reasons (Ketterson and Nolan, 1982), it is more likely that this compensating heavier mortality occurs during the longer migrations of southern winterers.

Expressing the foregoing in Baker's terms, h_q of adult juncos increases with distance traveled in migration, but because M_R decreases, the product, $h_q M_R$, does not vary with latitude of the wintering site.

4.1.3.b. Estimates of Junco Population Parameters, Young. Whether annual survivorship is independent of latitude of the wintering site in young juncos as well as in adults depends on the date selected as the start of the annual period. If survivorship is measured forward for a 12-month period beginning at the onset of winter, say from December 1, young at a site probably survive at the same rate as those adults that winter at that same site, for the reasons that follow. Based on the argument in the preceding paragraph, it appears that young survive the 12 months equally well whether they winter in the north or the south. For two reasons we believe in this geographic equality despite the capture-recapture evidence (Table IV) that young exhibit a lower rate of return to the north than do adults (and also than do southern-wintering young to the south): (1) Recapture rates in late winter of young first caught and banded in early winter at northern and southern stations do not differ from recapture rates of adults at those same locations (Section 3.2.2.). Any youth-related disadvantage in survivorship during the period December 1–December 1 would be expected to be most pronounced early in that period, when the individuals are youngest and the weather most severe. (2) United States Fish and Wildlife Service data indicate that juncos banded in northern localities are more likely than those banded in southern localities to be recovered in subsequent winters away from the banding site (Ketterson and Nolan, 1982). That is, northern juncos are less site-faithful than southern, and most individuals that change wintering sites move southward in the second or subsequent winter (Fig. 4). The sex and age of the group that moves is unknown. But because the rates of return of adults to northern and southern sites are equal, in contrast to the rates of young (see above), the non-site-faithful element among northern winterers probably consists largely of young. When these move to more southerly locations in the second winter of life, their migrations as adults are longer. The



FIGURE 4. Initial capture location and recovery location of juncos shown by United States Fish and Wildlife Service records to have been captured and recovered in different winters and at places separated by at least 30 min of latitude. Each line represents an individual. The arrow point is at the recovery location (from Ketterson and Nolan, 1982, reprinted by permission from *The Auk*; copyright 1982, the American Ornithologists' Union).

population structure in Fig. 2, showing adults to be more common at lower than at higher latitudes, is an entirely independent finding that is consistent with this conclusion.

If we tentatively accept our crude estimate of the ratio of young to adults—54:46 (Section 2)—on December 1 and look not forward from that date but backward, it seems probable that the mortality of young

juncos exceeds that of adults in the months between the end of the breeding season and December 1. Clutch size in juncos is often five, and six-egg clutches are reported (Godfrey, 1979). Further, second broods are common, at least in some years in parts of the range (personal observations). If we take as a possible indicator of the junco's productivity the productivity of other temperate-zone passerines like the Red-winged Blackbird (4.2 fledglings per female) and the Song Sparrow (6.4 fledglings per female; see Greenberg, 1980; Table II), it seems that in the junco the ratio of young to adults in August could be as high as 75:25. Thus it is likely that young suffer a greater loss than adults during autumn migration, their first migration, even though they tend to travel shorter distances. If the migrations made by young were prolonged, this age differential could presumably be even greater.

If we express these points in Baker's terms, we conclude that h_q increases with distance migrated and the increase is the same as that described for adults. M_R declines with distance as it did in adults but, because the autumn death rate is higher among young, $h_q M_R$ is lower in young than in adults.

4.1.3.c. *Estimates of Junco Population Parameters, Males and Females.* Because females as a whole are concentrated toward the southern part of the winter range, their overwinter survival will exceed that of males as a whole. However, female survivorship during autumn and spring will be lower than male survivorship, because females make longer migrations. In early winter the population sex ratio favors males (59%; Section 2); by the following breeding season, it should approach 50:50. In terms of $h_q M_R$, this product does not vary within any age class according to sex, but h_q tends to be greater for females and M_R greater for males.

4.1.3.d. *Predicting Sex and Age Distribution in Terms of $h_q M_R$.* According to Baker's model, the latitude of its maximal $h_q M_R$ represents the ideal wintering location for each class, and the upper and lower latitudes of the region within which $h_q M_R$ is greater than 1.0 define the limits of its winter range. When our data on seasonal survival and inferences from those data are used to estimate h_q and M_R , the model predicts that young juncos should winter north of adult juncos: M_R is lower for young than for adults, whereas h_q as estimated by overwinter survival is independent of age. On the other hand, we have no data that would predict a sex bias in $h_q M_R$, and in the absence of such information the model does not predict the fact that male juncos winter north of females. In an effort to obtain such information we would, if we could, examine the relationships within each sex (1) between lat-

itude of the wintering site and time of arrival at the breeding site and (2) between this arrival time and reproductive success. But data bearing on the first point would require that we track individual juncos between nonbreeding and breeding sites, an impossible feat in the current state of technology; thus testing of this aspect of the model cannot be completed.

Despite the conclusion just reached, it seems useful to continue in our original objective of applying Baker's hypothesis to a bird species, making reasonable assumptions where data are lacking. Figure 5A-E does this, graphing what we consider to be the critical elements of $h_q M_R$ separately; Figure 5F then combines these elements to show for each sex-age class a north-south range of values of $h_q M_R$ that would produce a distribution like that presented in Fig. 2.

To explain Fig. 5: Our data indicate that overwinter survival for all sex and age classes improves with distance migrated, and we suspect this is attributable to the north-south winter climatic gradient. For each class then, h_p should increase toward the south, probably reaching an asymptote (Fig. 5A). We expect this asymptote because (1) variation in snow cover is probably the prime determinant of h_p , and snowfall becomes infrequent well to the north of the southern limits of the winter range; and (2) prolongation of southward migration could contribute to delayed return to the breeding ground and loss of time for breeding, even in the absence of competition for breeding resources. Assuming that to some extent delayed return lowers the reproductive success of males more than of females, h_{at} (habitat suitability as a function of arrival time), and thus h , at any latitude should be lower for males (Fig. 5B, C; for the sake of simplicity, sexes not subdivided into age classes). The southward increase of h_q should therefore differ according to sex; and for males h_q might ultimately begin to decrease (Fig. 5D), if in that sex competition for breeding resources is more intense (or earlier) and the outcome of the competition more dependent on time of arrival on the breeding ground. As distance migrated southward increases M_R should decrease, with good reason to believe that the decrease is greater for young birds because of their higher probability of death during their first migration (Fig. 5E). Combining these considerations, Fig. 5F locates hypothetical maxima of $h_q M_R$ of the four sex-age classes on the north-south axis of the winter range. As was intended, their relative positions correspond to those derived from field data and shown in Fig. 2. Thus, if the necessary information could be obtained, Baker's model is capable of predicting the distribution reported herein. But its very flexibility in allowing new and alternate terms to be inserted at will as components of h and therefore h_q (as we inserted h_{at} above) may render its predictions uninteresting.

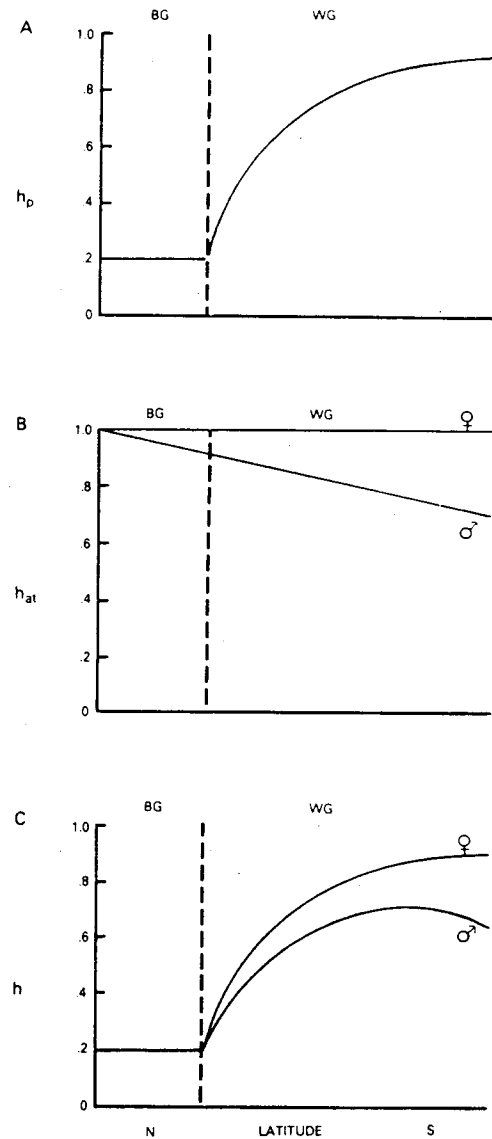
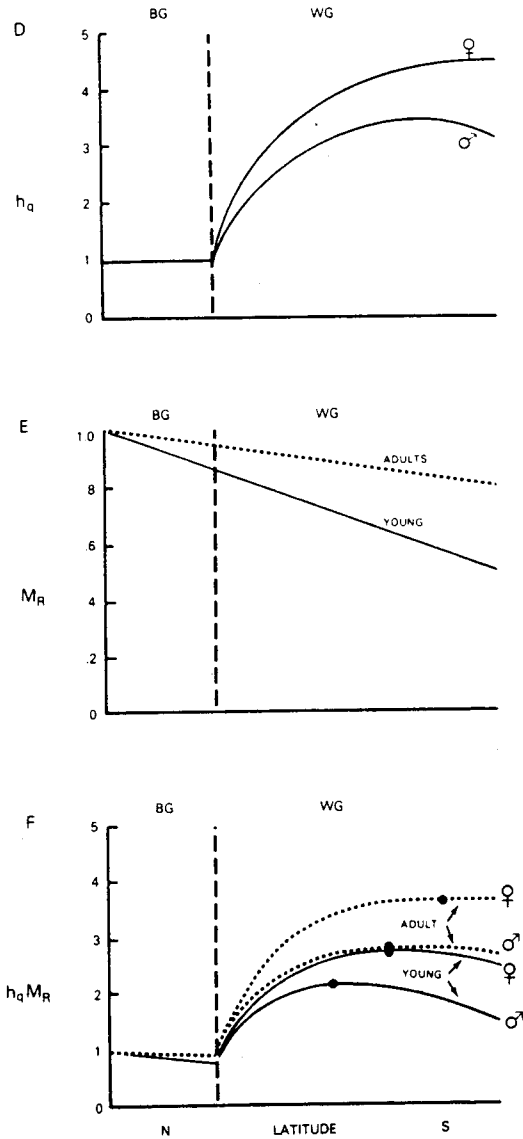


FIGURE 5. Habitat suitability and/or the migration factor in relation to latitude. BG signifies breeding ground and WG signifies wintering ground. (A) Physical habitat suitability (h_p) in relation to latitude: h_p improves north to south. The rate of improvement with latitude is presumed greater at high than at low latitudes because of snow and non-class-specific impact of added distance on time available for breeding. (B) (Spring) arrival-time component of habitat suitability (h_{at}) which estimates the impact of delayed arrival on intraclass competition for breeding resources. Because male juncos are believed to arrive sooner than females and to benefit more from early arrival, added distance has greater impact on h_{at} for males. (C) Sex-specific habitat suitability, the product of 5A and



5B. (D) Habitat quotient (h_q), the ratio of winter habitat suitability to breeding (or natal) habitat suitability, in relation to latitude. We assumed that the suitability of the breeding ground in winter is (1) invariant with latitude and sex, and (2) is some non-zero number, arbitrarily 0.2. (E) Migration factor (M_R) in relation to latitude. We assumed that risk of mortality in transit is distance-dependent and greater per unit distance in young during their first migration than in adults. (F) Product of habitat quotient and migration factor ($h_q M_R$) in relation to latitude: migration is advantageous only if $h_q M_R > 1.0$ and most advantageous where $h_q M_R$ is a maximum. The points in the curves indicate the respective latitudes where $h_q M_R$ achieves its maximum for each sex-age class.

5. CONCLUSIONS

In closing, we ask whether this review brings us closer to understanding how or why differential migration has evolved in the junco or in any other bird species? Based on the data now available, no single-factor hypothesis predicts the winter distribution we have described here. As we see it, each sex-age class of the junco tends to settle where for it an optimal balance of several selective pressures—migration mortality, overwinter survival, and reproductive success as a function of time of return to the breeding ground—may be achieved. Males presumably set a higher premium on early return than do females. The behavior of young birds is probably shaped more strongly by advantages of minimizing risk of death en route and perhaps of early arrival to breed than is the behavior of adults. Adults may also tend to avoid regions where young are most abundant, because for adults the risks inherent in prolonged migration are balanced by the increased probability of overwinter survival. These views are summarized in Fig. 6.

Attempting now to generalize to other species, we tend to agree with Myers' (1981a) views as stated in Section 3.3 and to reach the following much-qualified restatement of his conclusion: Where priority in time of arrival on the breeding range permits control of limiting resources there and a consequent gain in productivity, and where members of one class have more to gain by early arrival than do members of another, then the class with more to gain would be expected to evolve a migration schedule and/or a nonbreeding distribution that promotes priority of arrival, provided the gain is great enough to counteract any costs associated with that schedule or distribution.

Whether there are interclass differences in potential gain in productivity as the result of early arrival, and also the magnitude of such gain, will be strongly affected (1) by the species' mating system, (2) by the degree of spatial and temporal variability or stability of breeding-season resources, insofar as these are independent of mating system, and (3) by the duration of the period available for breeding. Polygynous males and polyandrous females that defend territories should have more to gain than their prospective mates (Myers, 1981a), as should the sex (usually male) that acquires and defends the nest site when sites are limiting, as in cavity nesting species (von Haartman, 1968; Lundberg, 1979). In the many monogamous species in which males are territorial but nest sites are not limiting, males with previous experience in breeding should gain less by arriving early than should first breeders, provided the breeding habitat remains suitable from year to year. Given temporal stability, experienced breeders typically show site fidelity

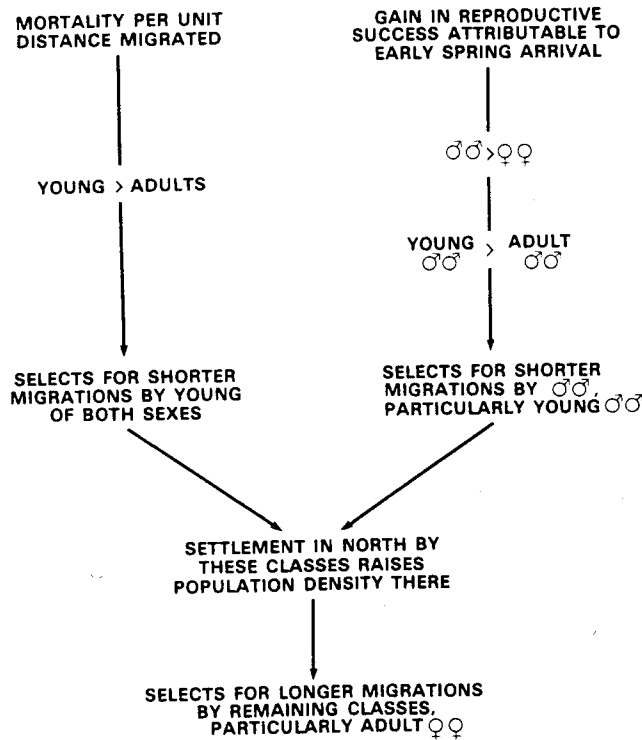


FIGURE 6. Selective factors proposed to account for the differential winter distribution of juncos.

(Greenwood, 1980) and apparently are often able to reclaim their former territories even if they are not the first to arrive on them (Section 3.3.2). If under these circumstances, breeding habitat is also homogeneous over large areas, experienced breeders would profit little from moving to new locations. They would also lose whatever benefits are associated with familiarity with the territory, its boundaries, and its neighbors of the previous season that have survived and returned (see Nolan, 1978; p. 41–42); site fidelity should then be even stronger and the gain from arriving early even less. Finally, when time for breeding is short, any interclass differences in potential gain from early arrival may be swamped by the uniformly shared necessity to arrive as early as conditions permit or risk losing any opportunity to reproduce. Time may be short in an absolute sense, as at high latitudes (Myers 1981a; Greenberg, 1980), or it may in effect be constraining because high rates of nest predation

put a premium on the ability to make repeated renesting attempts (Nolan, 1978; pp. 92-93).

Longer migrations by younger birds, rather than the reverse, have been most often reported in the literature (Gauthreaux, 1978, 1982). We suggest that in fully migratory species shorter migrations by young may be more common than is realized and that information to date may be biased by emphasis on species that are partial migrants or species whose young delay maturation. Partial migration may be one attribute of species in which breeding resources are in such short supply that they must be defended on a year-round basis, thus causing experienced breeders to remain on or near the resources that they possess (again, cavity nesters come to mind as an example). In these cases, young birds, not yet the possessors of breeding resources, may have more to gain by migrating and thereby raising their probability of survival. In extreme cases the expected reproductive success of young may be so low that postponement of breeding has been selected for and migratory behavior so modified that younger individuals do not return to the breeding range until they attain reproductive age.

Assuming that the migratory behavior of members of one class has been shaped by the greater significance that arrival time on the breeding range holds for their productivity, how might the winter distribution of that class interact with the distribution of the other classes? The answer depends in part on whether the gain in productivity associated with early arrival causes the class with more to gain to winter where survivorship is less than maximal. If it does, the areas where winter survivorship is highest will be open to settlement by members of the other classes, which would be expected to occupy them. A sex or age bias in distribution would result. If, however, the gain in productivity by members of the class most influenced by priority of arrival is not sufficient to cause its members to sacrifice overwinter survivorship (if they as well as members of the other classes attempt to settle where survival is maximal) and if habitat suitability at those most favorable locations is density-dependent, then the distributions of the other classes may or may not be affected. That is, if more distant habitat is available and is of sufficient suitability to offset the associated cost of migrating there, differential migration should result and the class with least to gain by early arrival should migrate farther with no resulting loss of fitness. If equally suitable habitat is not available, then the magnitude of the inequality of habitats and the relative resource holding power of the classes will determine whether there are differences in migratory behavior and what any differences will be.

In the junco we envision a free distribution (Fretwell, 1972), re-

sulting from the availability of extensive suitable winter habitat that can be reached at bearable cost; but the junco's solution is obviously only one possibility. In some species, migration cost will be too high or the geographic extent of the winter range too narrow to permit one or more classes to prolong migration and settle where their potential reproductive success is equal to that of the other classes. We conclude that predicting the factors accounting for a species' differential migration and estimating the relative values of these factors for the population classes involved will never be easy and may prove impossible. But even *a posteriori* explanations may serve a useful purpose in attempts to understand the evolution of migration.

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APPENDIX I

Abstract of Baker's View of Avian Migration

Baker (1978) defines migration to include any non-accidental movement by a metazoan from one spatial unit to another. He assumes that migrations have evolved because they are, or historically have been, adaptive at the level of individual selection. (As he puts it, chickens cross the road because they find conditions sufficiently better on the other side to have made worthwhile the risk involved in getting there.) Although we do not agree with all of his ideas, we summarize them

here because we think they will stimulate considerable discussion and are not readily accessible in their original form.

The individual begins life with a certain maximum *potential reproductive success*, S_{\max} , that is measured in terms of number of offspring that individual and its descendents are capable of producing before some arbitrarily set date, assuming all of them, ancestor and progeny, live in a perfect environment. Because the environment is not perfect, potential reproductive success (S) declines throughout life, even before the individual in question reaches reproductive age, but at any particular time has a specific value, S_p . Spending time in any spatial unit, a *habitat* (H), will consequently result in some "measurable" loss of potential reproductive success. S_p will be lower at departure than arrival, and this loss is a measure of the habitat's suitability and is some number less than 1.0. Focusing on the reproductive potential that remains and that is capable of being affected by the individual itself, i.e., its *action-dependent potential reproductive success*, S_d , rather than its *action-independent reproductive success* (which will be realized through the success of any offspring that are already independent), it is possible to determine relative *habitat suitabilities* (h) of two habitats. This requires comparison of the relative diminution in S_d that would be expected as the result of residence in one habitat or the other.

Presented with two habitats, H_1 and H_2 , with respective expected habitat suitabilities of h_1 and h_2 , under what conditions would a bird gain a selective advantage by migrating from H_1 to H_2 ? The answer depends on how superior H_2 is to H_1 , as measured by the *habitat quotient* (h_2/h_1), and on the cost of getting from H_1 to H_2 . Obviously, in order for the migration to prove advantageous, h_2 must be greater than h_1 , but how much greater? From the time an animal departs from H_1 and arrives in H_2 , or, if it does not depart, from the time it would have departed and would have arrived, its S_d will undergo the usual process of diminution. Typically, this diminution will be greater during time spent in migration than it would be if the animal spends that same time period in H_1 . This *migration cost* (m) of moving is written as $(S_1 - S_2)$, where S_2 is the potential reproductive success remaining at the moment of arrival at H_2 , and S_1 is the potential reproductive success it would have had at that same moment if it had not migrated from H_1 . The *migration factor*, M , refers not to the absolute difference between S_2 and S_1 , but to S_2/S_1 , the individual's (action-dependent) potential reproductive success, again at the time it arrives in H_2 , relative to what it would have been at that time in H_1 if it had not migrated. [An equivalent expression for M is $1 - (m/S_1)$]. Note that M varies from 0–1 and

large values of M are associated with small values of m . After arriving (or not arriving because it remained in H_1), the animal's potential reproductive success will continue to decay at one rate or the other until some specified time, the difference in rate of decay depending upon the habitat quotient, i.e., the relative suitabilities of H_1 and H_2 .

The migration equation states that if h_1 is less than h_2M , an animal should initiate migration. In Baker's words, "migration is an advantage when the realization of potential reproductive success on the way to and in a spatial unit to which an animal migrates is greater than the realization of potential reproductive success that would have been achieved during the same period if the animal had remained in the spatial unit vacated" (Baker, 1978, p. 37).

Migrations are *calculated* or *non-calculated*, depending upon whether the migrant has information about its destination (H_j) and the habitat suitability there (h_j). Information is acquired by prior experience, current sensory contact, or social communication. For such a migration the equation can be written $h_1:h_jM_j$. Calculated migrations are more likely than non-calculated migrations to prove advantageous, and therefore they are selected for. The migrant making a non-calculated migration can expect only to settle in a destination with average habitat suitability (\bar{h}) after a migration of average cost (\bar{m}). Thus, its mean expectation of migration (\bar{E}) is $\bar{h}\bar{M}$, and the migration equation for non-calculated migration compares the ratio $h_1:\bar{E}$. When birds show fidelity to a seasonal home range occupied in a previous year, their migrations obviously are calculated and presumably have been selected for by the advantages of familiarity with the site to which the migration is made, i.e., its food sources, refuges, in many cases its conspecific occupants, and sometimes by the advantages of having made structures there in previous years. Depletion or exhaustion of non-renewable resources at a previously occupied site would, of course, select against return to it.

The most important mechanism by which selection is expected to minimize the ratio of non-calculated to calculated migrations is *exploratory migration*. All birds have a *familiar area* within which they are able to move from any point to any other point. An exploratory migrant is one that leaves its familiar area but retains the ability to return there, i.e., to the starting point. Thus, the act of exploring enlarges the familiar area and presents the explorer with a series of new habitats in which to settle. If one of these proves superior to H_1 and the explorer does settle, the exploratory migration is considered to have become a calculated migration.

In birds making seasonal return migrations in which individuals depart and return to a breeding (or wintering) area, the return trip, at least, is often calculated. The migration equation for a return migration must take into account the migration factor for both the to and from components of the journey. If M has the same value on both legs of the journey, then the animal should initiate the first leg of a return migration when $h_1 < h_2 M^2$ (or more generally $h_2 M_R$). This concept is elusive, and we present an example. A migrant departing from its breeding grounds in Canada and arriving in the northern United States has the choice of settling (in H_1) or continuing southward (to H_2). Climate will improve if it continues, but because the bird must return to Canada to breed it must compare not only the suitability of its present location (h_1) with that of the one farther south (h_2); it must also account for the relative loss of potential reproductive success in transit both during movement from H_1 to H_2 and from H_2 back to H_1 in the spring. It must compare that loss in both autumn and spring migrations to the loss that would be experienced during the same time periods had it remained in H_1 .

To relate seasonal return migrations to the familiar area concept, Baker believes that the individuals of many, probably most, bird species migrate over a familiar area that was thoroughly explored during the first migration of life. Each stopping place along the way is also a familiar area.

How are h_1 and h_2 and M evaluated? In every "decision" to migrate or not, at least two of three different classes of environmental variables are monitored in H_1 . *Habitat variables* are those whose fluctuating values are correlated directly with the probability of surviving and of reproducing in H_1 . Food availability and nest-site abundance are examples. *Indirect variables* are those that change predictably on some cyclical basis but whose changes have no immediate and direct impact on chances of survival and reproducing. Photoperiodic change is a common indirect variable. Birds whose habitat suitability varies unpredictably (is not correlated with fluctuations in indirect variables) must of necessity actively monitor habitat variables and initiate migration when the value of these falls below the threshold described by the migration equation. Such birds are *facultative* migrants (roughly, what others have called weather or irruptive migrants). But such monitoring requires energy and takes time, and the very fact that habitat suitability is deteriorating means that attainment of the physiological state necessary for migration may be difficult at the time h_1 falls below $h_2 M$. Accordingly, when the variation in habitat suitability is predictably correlated with an indirect variable, selection favors incorporation of a response to that variable. Migrants that respond to indirect variables

are obligatory. A field observer noting the departure of obligatory migrants (roughly, what others have called instinct migrants) when an indirect variable reaches a certain level would probably not consider that there had been any deterioration in habitat suitability.

A third category of environmental variables must be evaluated by both obligatory and facultative migrants. This group consists of *migration-cost variables*, those factors that impinge on the bird while migrating and affect the probability that it will reach its destination at the optimal time and in optimal condition. Wind direction and wind speed are examples.

A key concept is the *migration threshold*, which is proposed to be the physiological mechanism that suppresses or leads to the initiation of natural selection, the ability, albeit imperfect, to assess h_1 and h_1M_f (or $\bar{h}\bar{M}$) through (1) perception of habitat variables, migration cost variables, or indirect variables, and (2) comparison of the perceived levels of those variables with its own internal state. This state can be expected to vary, particularly according to age and season. The migration threshold is then that inherited value, v_t , of habitat, migration cost, or indirect variable (or composite of all three) that is perceived by an animal having a particular internal state and above which the animal initiates migration (Baker, 1978, p. 346). Translating, birds may initiate migration as the result of wholly endogenous events, as the result of endogenous cycles entrained by predictive external variables such as daylength, or wholly as the result of events in their immediate environment, such as diminishing food supply, a severe winter storm, favorable winds, or changing photoperiod.

Baker then refines the model to account for the differences in migratory behavior found among individuals of the same sex and age and also among classes of individuals that differ in sex and age. Two factors are said to account for within-sex-age-class variation: individual differences in (1) experience, or (2) migration threshold. As an example of the first, consider two adult females having identical inherited thresholds and with the same migration "decision" to resolve. Suppose the first female were still in molt because molt had been arrested while she had been successful in raising a second brood. She might initiate migration later than the other female, which had produced no fledglings and had molted early. On the date the unsuccessful female departed, the molting female's migration cost would still be high, M low; for her, $h_1 > h_2M$.

Intraclass variation in the inherited migration threshold will exist to the extent that, all other things (including resource holding power; see below) being equal, h_1 is a function of population density. In a free

distribution (Fretwell, 1972) of the sort described, selection should favor the evolution of a within-class frequency distribution of migration thresholds wherein, for any particular population density, some individuals perceive h_1 to be less than h_2M , while others do not. Departure of members of the former group reduces population density, thus increasing h_1 for those that remain. The migrants, in turn, benefit from having responded to an \bar{E} that is relatively high because of the presence of suitable but underoccupied habitats, and both non-migrants and migrants have equal potential reproductive success. Each time h_1 deteriorates, a new exodus occurs by the fraction of the population whose migration threshold is exceeded. Selection should stabilize at the frequency distribution of thresholds at which potential reproductive success is the same for all members of the population, whatever the setting of their individual thresholds. When these conditions hold, the migratory fraction of the population, f_m , is determined by the current size of the population, N_m , and that population size, N_e , which corresponds to $h_1 = \bar{E}$, i.e., the habitat suitability for those that remain is equal to the mean expectation of migration for those that depart; $f_m = 1 - (N_e/N_m)$. The greater the excess of N_m over N_e , the higher the proportion of individuals that migrate.

Predicting the incidence of migration becomes more complicated if some individuals are better able to defend resources than others and if in the entire range of the population resources are limiting. In that case, the *despotic* situation, potential reproductive success of individuals with high resource holding power will be greater than that of low-power individuals. Higher power individuals will settle (or remain) in areas of greatest habitat suitability (H_1). Individuals of lower power will then either find $h_1 < h_f M_f$ (or \bar{E}) or $h_1 > h_f M_f$. In the former case they will migrate because their potential reproductive success will be greater than if they stay behind, although it will not be as high as that of the high-power non-migrants in H_1 . On the other hand, if $h_1 > h_f M_f$ (or \bar{E}), they will not migrate despite the greater resource holding power of their co-occupants in H_1 and their own resultant lower potential reproductive success. Thus, in order to predict whether an individual will initiate migration one must know, in addition to everything else, whether the situation is free or despotic, and if it is despotic, what that individual's relative resource holding power is.

Turning now to sexual and ontogenetic variation in the incidence of migration (and to the subject of this paper), Baker defines for each sex and/or age class an *initiation factor*. Recall from the basic migration equation that an animal should migrate when h_1 falls below $h_f M_f$ if the migration is calculated, or below \bar{hM} if it is non-calculated. Extrapo-

lating to a group of potential migrants of a particular class occupying a habitat, H_1 , the proportion that experiences the condition $h_1 < h_f M_f$ (or $\bar{h}\bar{M}$) depends on the average perception within the group of the suitability of the habitat, \bar{h}_1 , in relation to both the suitability of other available habitats and also to the migration factor, i.e., in relation to $\bar{h}_f \bar{M}_f$ (or $\bar{h}\bar{M}$). The initiation factor, i' , is defined as $\bar{h}_f \bar{M}_f / \bar{h}_1$; and the incidence of migration, I , which may be measured as the percentage of migrants (or the proportion initiating migration at a particular time), should be some positive function of i' . Baker rationalizes as follows: As long as members of a group remain in H_1 , we may presume that for them $\bar{h}_1 > \bar{h}_f \bar{M}_f$ (or $\bar{h}\bar{M}$). As suitability of H_1 deteriorates (or migration risk decreases, or alternate habitats become more suitable) \bar{h}_1 will approach $\bar{h}_f \bar{M}_f$ (or $\bar{h}\bar{M}$) in value, and i' will approach unity (from below unity). As i' increases, so does I , and the biologist observes an increase in the incidence of migration. For reasons we shall not explore, Baker chooses to rewrite his expression as follows:

$$i = \bar{h}_q (1 - \bar{m}/\bar{S}_d),$$

or, in the case of seasonal return migration, as $i = h_q M_R$. From these formulations it follows that the incidence of migration should be higher in groups that (1) experience a greater habitat quotient, (2) a lower cost of migration, or (3) will have remaining to them at the conclusion of migration a higher portion of their potential reproductive success.

Obviously, the value of \bar{m} that results in $\bar{h}_1 < \bar{h}_f \bar{M}_f$ (or $\bar{h}\bar{M}$) depends on the simultaneous values of \bar{S}_d and \bar{h}_q , and this is true for each of the other variables. Just as obviously, the values of \bar{m} , \bar{h}_q , and \bar{S}_d may be expected to vary with sex and age, e.g., \bar{S}_d will typically be higher in young animals. Consequently, the values of the habitat variables, migration-cost variables, or indirect variables that combine to set the value of v_i are expected to vary in a corresponding manner, and the incidence of migration of the sex-age classes will vary under any particular set of environmental conditions.

Once the migration threshold is exceeded, Baker contends that selection should act to maximize for each individual the quantity $h_q M_R$ (Baker, 1978, p. 678). That is, individuals should seek the maximum gain in habitat suitability compared with the minimal cost of a round trip migration, and members of sex-age classes should concentrate in regions in which for them $h_q M_R$ is greatest. Baker grants that maximization of $h_q M_R$ may entail the initiation of segments of a migratory journey at values of $h_1 > h_2 M$ if rapid travel serves to increase the ultimate value of $h_q M_R$.

APPENDIX II

Methods Relative to Data Presented in Fig. 2 and Table V

As described in detail elsewhere (Ketterson and Nolan, 1982; Nolan and Ketterson, 1983) we conducted early-winter (December 1–January 10) capture and banding operations during 2–4 years at five sites (Table V). The efforts, each several days long, were at Kalamazoo, Michigan (42°N), Bloomington, Indiana (39°N), Nashville, Tennessee (36°N), Clemson, South Carolina (34.5°N), and Birmingham, Alabama (33.5°N). Similar operations were also conducted in late winter (February 18–March 3) at Bloomington and Clemson in 2 years and at Nashville and Birmingham in 1 year. Birds were sexed and aged as described previously (Ketterson and Nolan 1976, 1982).

To obtain a single percentage for each of the four sex–age classes in the winter population at the five sites mentioned, we first calculated annual percentages of each class (Table V). For Tennessee, this process involved averaging the two sets of numbers from early and late winter, 1979–1980. We then obtained the mean of the annual percentages in order to produce Fig. 2. Significant annual variation existed only in Michigan and Indiana and age ratios were considerably more variable than sex ratios.

In the other process that gave rise to Fig. 2, we analyzed Christmas Bird Counts published by the National Audubon Society for counts made between 70°W and 100°W in six consecutive winters beginning 1974–1975. So-called censuses at about 750 sites per winter yielded the number of juncos seen at each site in the period we regard as early winter. We divided each count by the total party hours devoted to that count (juncos/party hour), adjusting the number of party hours to take account of the fact that in most counts some stated percentage of time was spent in habitats not occupied by juncos, e.g., pelagic habitats. We then grouped counts according to degree of latitude and determined the mean adjusted number of juncos per party hour for each latitudinal group of counts, considering the mean per degree to be a measure of relative junco abundance at that latitude in early winter of the year analyzed. We next calculated for each latitude the mean of annual means for the years for which we had data on sex–age structure, i.e., 1976–1977, 1977–1978, 1978–1979, 1979–1980 and plotted these (Fig. 2). Finally, we multiplied the relevant latitudinal mean of means by the percentages of the four sex–age classes represented in the samples captured in Michigan, Indiana, Tennessee, South Carolina, and Alabama (Table V). The products gave the points on the lower curves seen in Fig. 2, (curves drawn by hand).

TABLE V
Sex-Age Ratios According To Year and Location^a

	n	Male		Female	
		Adult	Young	Adult	Young
Michigan (42°N)					
1976-1977	119	42%	34%	15%	8%
1977-1978	105	44%	39%	7%	10%
1978-1979	240	29%	46%	6%	19%
1979-1980	114	<u>31%</u>	<u>41%</u>	<u>11%</u>	<u>17%</u>
		37%	40%	10%	14%
Indiana (39°N)					
1976-1977	33	33%	39%	9%	18%
1977-1978	80	35%	46%	5%	14%
1978-1979	395	28%	42%	10%	21%
1979-1980	346	<u>17%</u>	<u>52%</u>	<u>10%</u>	<u>21%</u>
		28%	45%	8%	18%
Tennessee (36°N)					
1978-1979	62	21%	29%	15%	35%
1979-1980	121	<u>22%</u>	<u>28%</u>	<u>15%</u>	<u>34%</u>
		22%	29%	15%	34%
South Carolina (34.5°N)					
1976-1977	123	25%	19%	37%	19%
1977-1978	87	37%	17%	27%	18%
1978-1979	132	27%	17%	33%	24%
1979-1980	113	<u>22%</u>	<u>28%</u>	<u>26%</u>	<u>23%</u>
		28%	20%	31%	21%
Alabama (33.5°N)					
1976-1977	59	22%	14%	36%	29%
1977-1978	23	13%	22%	39%	26%
1979-1980	37	<u>11%</u>	<u>19%</u>	<u>54%</u>	<u>16%</u>
		15%	18%	43%	24%

^aLocations were sampled in early winter except that the Tennessee sample from 1979-1980 was sampled in December and February and the data combined, and the Alabama 1979-1980 sample was taken in February 1980. Except for Michigan and Indiana, there were no significant annual differences in sex and age structure at a locality (Michigan: $\chi^2 = 25.85$, $df = 9$, $p < 0.01$; Indiana: $\chi^2 = 22.04$, $df = 9$, $p < 0.01$; Tennessee: $\chi^2 = 0.07$, $df = 3$, n.s.; South Carolina: $\chi^2 = 13.21$, $df = 9$, n.s.; Alabama: $\chi^2 = 8.29$, $df = 6$, n.s.). There was no significant annual variation in sex ratio at any location.

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