



BREEDING DISPERSAL IN INDIGO BUNTINGS: CIRCUMSTANCES AND CONSEQUENCES FOR BREEDING SUCCESS AND POPULATION STRUCTURE

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Abstract. In southern Michigan, nearly half of the male Indigo Buntings, *Passerina cyanea*, returning from a yearling season settled on a new territory in their second breeding season, whereas 95% of the older adult males returned to the same territory in consecutive years. First-year males were significantly more likely to disperse after a failed breeding season than after a successful one; no such difference was found in females. Males were more likely to disperse after their first year than after a later year. Females were more likely to disperse than were males. Female breeding dispersal was more closely associated with a site than with the return of an individual mate, and more with the return of an individual male than with their previous breeding success. In the two populations, 49.5% of the returning females whose mate also returned ($n = 222$) re-united with their former mate on the old territory, and the other 50.5% took a new mate, usually when the female settled on a new site. The dispersal behavior of 30 buntings that were banded as nestlings and returned to their natal area in both their first and second breeding seasons was independent of the behavior of their parent of the same sex when it was the same age; we found no trend indicating heritability of differences in dispersal behavior. Site choice in females and social constraints in males appear to explain much of the difference in dispersal observed with sex, age, and breeding success.

Seasonal and adult lifetime breeding successes generally were independent of whether an individual had dispersed from first to second year. Birds that dispersed were as successful as birds that returned to their earliest breeding site. Breeding success in a later year did not differ from breeding success in the previous year, either in the dispersers or in the birds that returned to the same territory. However, the males that dispersed to a new territory in their second year had marginally higher ($P = 0.058$) mean adult lifetime success in one population. In the two study areas, about 30% of all fledged buntings were produced after breeding dispersal by the male parent, and 70% were from broods where at least one parent had changed its breeding territory. Dispersing birds generally were successful after they dispersed, at least in the sample observed, which consisted of birds that found a suitable breeding site. The estimated effective population size of buntings was increased slightly by breeding dispersal, but natal dispersal has an impact greater by orders of magnitude, both in the number of young produced and in the proportion of breeding birds that dispersed into the local population from other natal areas. The dispersal variance effective number N for bunting populations is estimated at about 1 million birds, which is an order of magnitude less than the total population size for the species.

Key words: *Dispersal; breeding success; remating; social behavior; population structure; Passerina cyanea.*

INTRODUCTION

Several neutral and adaptive hypotheses have been proposed to explain "breeding dispersal," the movement of adult birds and mammals from

one breeding site to another (Greenwood 1980, Dobson and Jones 1985, Chepko-Sade and Halpin 1987, Johnson and Gaines 1990). Neutral or null hypotheses predict no differences in the probability of dispersal, either after successful and unsuccessful breeding seasons, of males and females, or between individuals of different age.

¹ Received 29 April 1992. Accepted 9 September 1992.

They also predict no differences in the consequences of dispersal, such as in the breeding success of birds on sites where they were resident in the previous season and birds on new sites. In contrast, adaptive hypotheses propose that the choice of dispersal or site fidelity can affect their subsequent breeding success.

Four adaptive hypotheses may be compared to account for the proximate and ultimate significance of breeding dispersal. (1) Birds may disperse in order to find a better mate than they had in the previous year ("mate choice" hypothesis). (2) Birds may disperse to find a better territory or site ("site choice" hypothesis). (3) Birds may disperse as a result of social constraints, with differences between the sexes and age groups reflecting social differences between them ("social constraint" hypothesis). (4) Birds may disperse or not depending on genetic predispositions which are passed along kinship lines ("heritability" hypothesis).

These hypotheses lead to testable predictions about the circumstances of dispersal behavior. A mate choice hypothesis predicts that (1a) females are more likely to re-unite with the same male after a successful season, and with a new male after an unsuccessful season, and (1b) females are more likely to disperse than males and will disperse further, because females are the active sex in mate choice. A site choice hypothesis predicts that (2a) birds are more likely to return to their old territory after a successful breeding season, and to disperse after an unsuccessful season. A social constraint hypothesis states that differential dispersal is a consequence of social behavior. Because one sex, usually the male, may defend its site more exclusively, and the other may disperse to a new site where it would encounter little resistance to settlement, the hypothesis predicts that (3a) females are more likely to disperse than males, and will disperse further. Also, because adults defend their sites more successfully against younger birds than the reverse in consequence of their experience in asserting social dominance, the hypothesis predicts that (3b) young birds are more likely to disperse than older adults, and will disperse further. The heritability hypothesis states that dispersal is determined by heritable differences between dispersers and nondispersers. The hypothesis predicts (4a) that parents and offspring of the same sex and age have the same behavior. Additional tests of heritability of dispersal behavior would in-

volve separating common environmental factors of parents and offspring (Payne and Payne 1989).

In addition to establishing the circumstances that lead to dispersal, an adaptive view of dispersal may examine the consequences of a change of breeding site, to test whether the behavior improves the biological success of the individuals (Beletsky and Orians 1987, Pärt and Gustafsson 1989). The same hypotheses of mate choice, site choice, social context, and heritability are considered in terms of the consequences of dispersal. All four hypotheses predict that dispersing birds should breed successfully after they disperse—a necessary condition of an adaptive hypothesis. Nevertheless, certain hypotheses lead to more restricted predictions of their consequences. If breeding dispersal is primarily directed at finding a different mate, then we predict a high proportion of new partners in the second year in birds that disperse (1c), and a high proportion of remating between previous partners in birds that return to the same site (1d). If dispersal is an adaptive response that increases success due to a change in breeding site, then birds that disperse should be more successful than their counterparts that do not disperse (2b).

On the other hand, if dispersal depends on breeding success in the first year, with the experience gained in reusing a previous breeding site enhancing their breeding there in the following year, then birds that return to their old site should be more successful there than they were in their first year (2c). Also, if dispersal increases success due to a change in breeding site, individual birds that disperse should be more successful than they were on their former site (2d). The social constraints hypothesis makes no direct prediction of breeding success, but it predicts that (3c) male neighborhoods are more stable in composition from year to year than are female neighborhoods. If neighborhood stability is advantageous, then returning to an old site might have adaptive benefits for the males (3d). The heritability hypothesis indicates that dispersal is not failure, but is a viable behavior. Like the other hypotheses, it predicts (4b) that both dispersing birds and returning birds are successful in their second year and later. We list it separately from the more general prediction of all four dispersal models to emphasize that both dispersers and birds that return to their old site are predicted to be successful, and that neither strategy leads to failure.

TABLE 1. Predictions of four adaptive hypotheses of breeding dispersal.

Hypothesis	Circumstances of dispersal	Consequences of dispersal
1. Mate choice	<p>1a. Females choose a new male after an unsuccessful season, and re-unite with old male after a successful season.</p> <p>1b. Females disperse more frequently and further than males, due to mate choice.</p>	<p>1-4. Birds are successful breeders after dispersal.</p> <p>1c. Birds that disperse to a new site get a new mate.</p> <p>1d. Birds that return to an old site re-unite with the old mate.</p>
2. Site choice	<p>2a. Both males and females disperse after an unsuccessful breeding season, and return after a successful one.</p>	<p>2b. Birds that disperse are more successful than birds that do not.</p> <p>2c. Birds that return to the old site increase their breeding success.</p> <p>2d. Birds that disperse to a new site increase their breeding success.</p>
3. Social constraint	<p>3a. Females disperse more frequently and further than males, due to within-sex aggression and attraction.</p> <p>3b. Young birds disperse more frequently and further than older birds.</p>	<p>3c. Male neighborhoods are more stable than female neighborhoods.</p> <p>3d. Adult males in familiar social neighborhoods are more successful than other males.</p>
4. Heritability	<p>4a. Offspring's behavior is like parent's behavior.</p>	<p>4b. Both dispersers and birds that return are successful breeders.</p>

A few predictions were not mutually exclusive with predictions from other hypotheses (Table 1). All four hypotheses of adaptive dispersal predict that dispersing birds will be successful in the next year, that is, that dispersal is an adaptive behavior. Also, "mate choice" and "site choice" hypotheses of breeding dispersal in birds both predict that birds are more likely to settle on a new territory after an unsuccessful breeding season than after a successful one, and both assume that dispersal is a consequence of proximate experiences of the breeders. In some cases, hypotheses with nonexclusive predictions can be distinguished by comparing individuals with different histories of age, breeding success, and availability of the mates from the previous season, not all summarized in the Table. We note that different factors may be important in different species. Comparative observations of individuals with different histories of mate, site, and social competition (Rowley 1983; Beletsky and Orians 1987, 1991; Drilling and Thompson 1988, 1991; Jackson et al. 1989) are needed to differentiate among the adaptive bases of breeding dispersal within each species.

In addition to its effects on the success of individual breeding birds, dispersal has emergent effects on populations. Dispersal increases the number of possible mating partners within the range of an individual (Wright 1931, 1943, 1969; Crow 1954; Barrowclough 1980; Chepko-Sade et al. 1987; Rockwell and Barrowclough 1987). In this way breeding dispersal can affect the size and scale of demographic and genetically effective populations. The size and scale of natural populations are of considerable interest in population biology. Conservation biologists are interested in determining effective population size, as size can affect the long-term survival of populations, due to stochastic extinction of small populations and to depletion of genetic variability (Goodman 1987, Lande and Barrowclough 1987, Koenig 1988, Lande 1988, Stacey and Taper 1992). Evolutionary biologists are concerned with the assumptions of a "biological species" concept with geographically separated populations being connected into a larger, continuous metapopulation within which gene flow accompanies dispersal (Mayr 1963, Wright 1969, Templeton 1989). Both natal dispersal and breeding dispersal are important aspects of population structure, yet little information is available on dispersal in bird populations.

The objectives of the study were (1) to determine the circumstances of change in breeding site and mate between seasons, (2) to compare patterns of breeding dispersal of males and females, (3) to compare the breeding success of birds with different histories of breeding dispersal or fidelity to a territory, in their first year, second year, and lifetime, and (4) to estimate the population effects of breeding dispersal and natal dispersal, including their impact on the genetically effective population size.

METHODS

STUDY AREAS

Observations of dispersal and breeding success were part of a population study of individually marked Indigo Buntings, *Passerina cyanea*, common small songbirds in eastern North America (Payne 1989, 1991, 1992). Buntings are long-distance migrants and winter in the tropics. Indigo Buntings were observed in southern Michigan from 1978 through 1992 in two local breeding populations. One study area was located at the E. S. George Reserve and neighboring Pinckney State Recreation Area (42°27'N, 84°00'W), in woodland, in old fields that had been cultivated before the 1930s, and in shrubby swamps. The other area was near Niles (41°55'N, 86°14'W), along shrubby roadsides and a railway right-of-way, in secondary woodland, in old fields, and in cultivated fields of maize and beans (Payne 1982, 1983a, 1983b, 1989, 1991, 1992; Payne and Westneat 1988; Payne et al. 1988; Payne and Payne 1989, 1990).

Sizes of the areas were set by our effort and success in locating the birds and their nests. Six observers were active through most of the breeding season in most years and they completed a total of more than 20,000 person-hours in the field. The areas were enlarged during the first years and maintained in later years to locate any dispersing birds. The area at the George Reserve was enlarged from 6 to 10 km², when 1,080 ha were under close observation and the longest dimension of the study area was 4,500 m. The area at Niles was enlarged from 1.4 to 4 km², when 406 ha were checked for nesting, 700 ha were checked for banded birds, and the longest dimension was 3,750 m. Maps of territories were made by using a 100-m² grid with aerial photographs.

FIELD METHODS

Within each study area the buntings were individually marked with color bands and a numbered Fish and Wildlife Service band, nearly all nests were found, and the nestlings were banded. Each year from 1979 through 1985, more than 80 marked resident, territorial males were observed. Similar numbers were present in the two study areas, with from 80 to 120 breeding pairs in each year at the George Reserve from 1978 through 1982 when buntings became less numerous, and at Niles through 1984, the last year they were abundant there. Birds banded by 1985 were observed through 1992; a few new males were banded during the last seven years. On the main study area at the George Reserve, 278 males were banded either as yearlings through 1984 or as new adults from 1980 through 1985. Of these, 118 returned for two or more consecutive years. At Niles, 227 males were banded through the same period, and 141 returned in one or more later years. At the George Reserve, 68 banded females returned in two or more years, and at Niles, 132 banded females returned in two or more years. We also banded more than 2,600 nestlings that survived to fledge, and we observed 138 of these birds when they returned to the natal area and bred as yearlings or older adults in a later year (Payne and Payne 1989, Payne 1991, and subsequent observ.). We compared the breeding dispersal of these returning birds when they were seen for two or more years with the dispersal histories of their parents of the same sex, where both offspring and parent returned for a second year ($n = 30$), to test whether they behaved in the same way; that is, whether the observed variation among birds in breeding dispersal was heritable.

Males were captured by playback of a recorded song and attraction to a dummy adult male near a mist net. All were defending their singing site and were territorial. Females were netted after they had a nest. To avoid desertion (Westneat et al. 1986), we delayed capture until the female had incubated for a week and often until she had nestlings. The plumages of first-year and older adult birds were determined by comparison with birds of known age that were banded as nestlings. Males in their first spring have brown greater primary coverts, and older adults have all blue greater primary coverts (Payne 1992). Males that first appeared as adults in the parts of the study

area where all residents were banded in previous years were considered to be adult immigrants. No age-related plumage traits were found in females (Payne and Payne 1989). We estimate that we found more than 90% of all bunting nests in both areas and nearly all the nests that produced fledged young, and we banded more than 90% of the breeding males and about half of the breeding females (Payne et al. 1988, Payne 1989).

Most males were identified repeatedly during censuses in every week of the breeding season. Each sighting and nest was located on a map. Territory maps were made from the weekly maps. We restricted analysis of dispersal to males that were "residents." We considered a male to be a "resident" if he remained on the study area for at least 28 days, the minimum period to mate, nest, and rear a brood to fledging. The breeding season was long (laying extends from 20 May through 20 August; Payne 1989, 1992), and boundary changes and territory replacements occurred within a season. Some first-year males sang in more than one territory; most residents were active on only one territory through the season.

"Breeding dispersal" was defined as a bird that was present as a breeder in one year returning to a different territory in the next year. We observed the incidence and distance of movements between territories and nesting sites within a breeding season and between years for all banded males and females. Because each study area was large (several km²) in relation to territory size (mean 1 ha; Payne 1989, 1992), any returning buntings were unlikely to be missed, at least if they moved no further than a few territories. Each year that a bunting returned was a separate "case," so a bird present on a different territory in each of three consecutive years would give two cases of between-year breeding dispersal, while a bird present on the same territory would give two cases of site fidelity or return. We scored a male as returning to the "same" territory if any portion of the area where he sang overlapped between the consecutive years. Female dispersal was determined in relation to the territory of the males. We recognized "breeding dispersal" when a female nested outside the territory where her mate had sung in the previous year, and "site fidelity" when she nested within the territory where her mate had sung in the previous year. We measured the dispersal distances of birds that moved between years from the maps. Breeding dispersal

from the first to second year was compared between offspring and parents of the same sex in cases where both the offspring and the parent appeared for two years or more.

Breeding status was determined by observations of the male that sang on the territory where a nest was located and of the female that attended the eggs and young. Because both observations of extra-pair copulations (Payne 1983a, Westneat 1987a) and molecular and morphometric results indicate that not all young buntings in a nest are fathered by the resident male (Westneat 1987b, 1990; Payne and Payne 1989), there is an uncertainty in assigning to a male the offspring reared in nests on his territory. However insofar as males might observe the young in their nests to assess their own success, and as males do not direct their parental care differently to young that they sired and that were sired by a neighbor (Westneat 1988), we expect the subsequent behavior of dispersing or returning to the old territory to be independent of an effect of extra-pair copulations. All males and females included in the comparisons are considered to be "breeders" whether or not they were successful. Females were breeders because all were netted at their nests. Males were "breeders" because all were resident 28 days or longer, sufficient time to have a female nest on their territory, and for those that did not have a nesting female, sufficient opportunity for an extra-pair fertilization of a neighboring female. Our minimal criterion of 28-day territory residence excluded transients that were likely ineffective in breeding, because only the territorial male buntings were found to be effective in extra-pair fertilizations as determined by DNA fingerprinting (Westneat 1990).

STATISTICAL ANALYSES

Statistical analyses were made using MIDAS, a set of programs developed by the Statistical Research Laboratory, the University of Michigan (Fox and Guire 1982). Associations between dispersal, breeding success, mate choice, and age were compared with chi-square tests and log-likelihood *G*-tests of independence. Associations of behavior of parent and offspring were tested with Fisher exact tests. Breeding success of birds with different dispersal histories was compared with one-way analysis of variance (ANOVA) and success of birds before and after dispersal was compared with paired Student *t*-tests. Dispersal distances were standardized to mean of 0 and

SD of 1 and compared with ANOVAS. Statistical inferences were made with the significance level $\alpha = 0.05$.

RESULTS

BREEDING DISPERSAL OF MALES

The proportion of males that returned to the same territory in consecutive years was compared with their age, whether they occurred on the study area as first-year males, and their past breeding success. We compared all banded males from 1979 through 1985.

Age. A social constraints hypothesis predicts that older adults are better defenders of territories than are young males. Males were more likely to settle on a new territory after returning from their first year than from an adult year (prediction 3b; Table 2). Males in their second year returned to their first-year territory more often than not; about a third of them settled on a new territory. Older adults returned to their previous territory; in fewer than 5% of the cases when a male returned after an adult year, he settled on a new territory.

In addition to the males captured as yearlings, some males were captured as older adults. These males first appeared within the intensely-studied area where we had banded all territorial males in the previous year, so they were not local residents in the previous year. Also, most of these males had song types that were new for the study area, indicating that they learned a song outside our study area in the previous year; 80% of the resident birds in their first year copy the song type of a neighbor (Payne et al. 1981, 1988), and songs of these new adults matched neither an earlier resident nor a former first-year male on our study area. It is likely that nearly all were in their second breeding season. The annual survival rate of male buntings is about 0.56 (Payne 1989, 1992; Payne and Payne 1990), so a population has nearly as many two-year-olds as all older ages combined, and nearly half of the new adult males would be expected to be in their second year from demographic considerations. The assignment of an age of two years for these immigrant males is based on two supporting observations. (1) For banded males of known age, nearly all short-distance dispersals within a year and between years involved birds that were yearlings, not older birds, in the prior year (Table 2); these marked birds were in their second year when they returned and settled on a new terri-

TABLE 2. Breeding dispersal of male buntings in relation to age.

Area	Age ^a	Territory		χ^2	P
		Old	New		
George Reserve	first-year	70	32	34.4	<0.001
	adult	147	7		
Niles	first-year	95	37	37.1	<0.001
	adult	169	6		

^a "First-year" includes all males that were banded as first-year males and remained for at least 28 days, and all males banded as first-year males regardless of their period of residence if they returned to the study area in a later year. "Adult" refers to males in later years and includes males that were originally captured as new adults.

tory. (2) Seven adult males not resident on the study area in the previous year were of known age when they first arrived there as adults, because they had been banded as nestlings, and all seven were born two years previously (Payne 1991).

These "new" adults are considered to be the immigrant counterparts of the first-year males in our study area that we infer to have survived and settled outside the area in their second year. We observed several color-banded males that had moved across the margin of the study area, both within a year and between years, and nearly all of these were yearlings (Payne et al. 1988). If we include the "new" adult immigrants (George Reserve, $n = 52$; Niles, $n = 21$) with the males of known age in Table 2, then we can estimate the proportion of all surviving males that resettled on a new territory. Including these new adults as settling on a new territory in their second breeding season, 70 males returned to their old territory at the George Reserve (Table 2) and 84 (32 from Table 2 and 52 new adults), or 54.5% of all males returning for a second breeding season, settled on a new territory. At Niles, 95 returning two-year-old males returned to the same territory, and 58, or 38%, settled on a new territory. In both areas, nearly half of the yearling males that survived to a second breeding season settled on a new territory.

Few adult males moved from one territory to another between years. For a few of the 13 cases of dispersing adult males, the switch in territory involved a deterioration of habitat. Habitat disturbance by off-road vehicles led to two consecutive changes in two years in one male. One male moved 200 m after three unsuccessful adult years on his old territory. Circumstances in most other cases were not obviously due either to repeated breeding failure or to habitat change. The results suggest that male breeding dispersal is strongly affected by age, with the younger birds being more

likely to move, as predicted by the social constraints hypothesis (3b).

Breeding success. A site choice hypothesis predicts (2a) that dispersal is more likely following an unsuccessful season. For males that returned, we compared the proportion that re-occupied the same territory and that settled on a new territory. More than half of the males in their second breeding season returned to their first-year territory regardless of their breeding success (Table 3). Returning males were more likely to settle on a new territory if they had not fledged young in their first year. The tendency was marginally significant in both areas. When results were combined for the two areas (which differed in a lower breeding success and a higher proportion of males that switch sites at the George Reserve; Payne et al. 1988, Payne 1989), males were significantly more likely to switch territories when they had been unsuccessful ($\chi^2 = 7.25$, $P = 0.007$). The results were predicted by a site choice hypothesis, that unsuccessful breeders are more likely to disperse (2a).

BREEDING DISPERSAL OF FEMALES

Because females are thought to exercise greater mate choice than males, we limited the predictions of the mate choice hypothesis to a com-

TABLE 3. Breeding dispersal of males returning in the next year, in relation to breeding success in their first year.^a

Area	First-year breeding success ^b	Territory		χ^2	P
		Old	New		
George Reserve	yes	35	9	3.96	0.047
	no	20	14		
Niles	yes	58	11	2.97	0.076
	no	31	13		

^a Includes all males banded as first-year birds in 1979 through 1984, resident in the first year for at least 28 days, and returning the next year.
^b Breeding success indicates whether young buntings fledged.

TABLE 4. Breeding dispersal in females in relation to age.

Area	Minimum age (years)	Breeding site		χ^2	P
		Old	New		
George Reserve	one	34	37	2.61	NS
	≥ two	22	12		
Niles	one	73	59	1.46	NS
	≥ two	51	29		

parison of females, for which we also tested the other hypotheses. We restricted the analyses to cases where we identified the female in consecutive years, and did not include cases where she missed a year. We compared all females banded from 1979 through 1987. The proportion of females that returned to the same site was compared in relation to their past breeding success and to whether the mate of the previous year also returned. To distinguish between mate choice and site choice as determinants of dispersal, we then tested whether the returning females were associated more closely with the mate or with the breeding site.

Age. Age at capture was unknown except when females had been banded as nestlings. Most were probably yearlings, both because about half of the females observed on the study area in the previous year had been banded and females have low annual survival, and because 47 of 56 females that were banded as nestlings and returned to the study area in a later breeding season were captured in the year after they were born (Payne 1989, 1991; Payne et al. 1988; Payne and Payne 1989).

Although on average the females were more likely to disperse to a new site in their second year than in later years (George Reserve, 52% vs. 35%; Niles, 45% vs. 36%), the difference was not significant in either area (Table 4). We found no significant age-related differences in dispersal in the females. Since females are not territorial in their occupation of a site, but males are territorial, prediction (3b) is appropriate for males but not for females.

Breeding success. The site choice hypothesis predicts that females are more likely to disperse after an unsuccessful breeding season than after a successful season (2a). At the George Reserve, 10 of 21 (48%) unsuccessful females moved to a different site, whereas 39 of 84 (46%) successful

females moved between years ($G = 0.01$, $df = 1$, NS). At Niles, 22 of 48 (46%) returning females moved to a new site after an unsuccessful season, and 64 of 160 (40%) successful females moved between years ($G = 0.51$, NS). Although in the direction predicted with unsuccessful females more likely to disperse, the association was not statistically significant.

When age and breeding success both were taken into account, the unsuccessful females of lower minimum age were no more likely than older females to disperse (George Reserve, 9 of 16 dispersed after their first year, 1 of 5 after a later year, $G = 2.13$, $df = 1$, NS; Niles, 16 of 33 dispersed after the first year, 6 of 15 after a later year, $G = 0.30$, $df = 1$, NS). Successful females were not significantly less likely to disperse in a later year than in their first year (George Reserve, 28 of 55 [51%] dispersed after the first year, 11 of 29 [38%] after a later year, $G = 1.30$, $df = 1$, NS; Niles, 43 of 99 [43%] dispersed after the first year, 21 of 61 [34%] after a later year, $G = 1.29$, $df = 1$, NS). We conclude that breeding success in one year does not determine whether a female returns to the same breeding site in the following year.

Return to a territory and to a mate. Breeding dispersal and mate choice in females was associated with dispersal of the returning male (Table 5). In 311 cases, we determined both the breeding success of a female in the prior year and the territory where the old male returned (George Reserve, $n = 103$; Niles, $n = 208$). At the George Reserve, 29 of the 45 successful females that returned to their old site had the same mate, and all but 1 of the 39 females on a new site had a new mate; the other was with her old mate ($G = 45.6$, $df = 1$, $P < 0.001$). Five of the 11 unsuccessful females on their old site had the same mate, and all 10 on a new site had a new mate ($G = 9.97$, $df = 1$, $P < 0.01$). At Niles, 64 of the 96 successful females that were on the same site mated with the same mate, and 1 of 64 that were on her old site mated with a new male ($G = 83.6$, $df = 1$, $P < 0.001$). Nine of 26 unsuccessful females that returned to the old site were with their old mate, and all 22 that were on a new site had a new mate ($G = 12.8$, $df = 1$, $P < 0.001$). The results are consistent with a prediction of the mate choice hypothesis, that return is associated with remating with the old mate, and dispersal is associated with a change of mates (1a). However, as noted, the successful females were

not significantly more likely to return to their old site than were unsuccessful females. Females on a new site were significantly less likely to remate with their old returning mate than were females that returned to their old site, regardless of their breeding success in the previous year. The results are consistent with predictions from the mate choice hypothesis (1c, 1d), that females dispersing to a new site are likely to obtain a new mate as a consequence of dispersal, and females returning to an old site often mate with their old mate.

Returning females whose mate did not return to the study area were somewhat more likely to settle on a new site if they were unsuccessful in the previous year. The results were not significant, though the trend observed was in the direction predicted (2a) (George Reserve, 6 of 8 [75%] of the unsuccessful females dispersed, 12 of 24 [50%] successful females dispersed, $G = 1.59$, $df = 1$, NS; Niles, 7 of 13 [54%] unsuccessful females dispersed, 24 of 45 [53%] of the successful females dispersed, $G = 0.001$, $df = 1$, NS).

To distinguish between the site choice and mate choice hypotheses, we compared the breeding dispersal of females when the old mate returned to the study area and when he did not. When he returned to the old territory, females usually remated with their old male (Table 5). When her old mate dispersed to a new territory, females more often returned to the old site than to the old mate. In two cases a female re-united with her old mate on a new territory. One female paired with her old mate on a new territory that was two territories (200 m) from the old one. The other female paired with her old mate two territories (500 m) from their previous breeding site. Both pairs had successfully fledged young in the previous year.

Few females returned to the study area when the old male settled on a new territory, so to compare female behavior when the male dispersed and when he did not return, we combined areas. For the 22 females whose male dispersed to a new territory, 9 (41%) settled on the old site. In comparison, 41 of 90 (46%) returning females whose mate did not return to the study area nevertheless settled on their old site ($G = 0.16$, $df = 1$, NS). That is, female behavior did not differ when the old male dispersed to a new territory and when he did not return to the area. The results are more consistent with the site choice

TABLE 5. Breeding dispersal and mate fidelity in female buntings, when the old mate returned to the study area.

Area	Breeding site	Female remated with her old male		χ^2	P
		Yes	No		
George Reserve	old	35	6	46.6	<0.0001
	new	1	29		
Niles	old	73	22	79.4	<0.0001
	new	1	55		

hypothesis (2a) than with the mate choice hypothesis (1a).

To test whether her prior breeding success or the return of her old mate explained her behavior, we compared the proportion of females that returned to the previous year's site, in all females with breeding success known in the previous year and with the male returning to the study area (the data are given in the first paragraph of this section). At Niles, females tended to return to the old site if the male returned; at the George Reserve, the association was not significant (George Reserve, $n = 103$, $G = 1.74$, $df = 1$, $P = 0.19$, NS; Niles, $n = 208$, $G = 4.81$, $df = 1$, $P = 0.028$). By comparison, females were not more likely to return if they had bred there successfully in the previous year (George Reserve, $G = 0.01$, $df = 1$, $P = 0.92$, NS; Niles, $G = 0.51$, $df = 1$, $P = 0.47$, NS). The results are more consistent with prediction (2a) than with (1a). In this test, the return of her mate was a better predictor of whether a female would return to the old site or settle on a new one than was her past breeding success.

Re-pairing: observed and expected frequencies. At the George Reserve, both members of a pair returned in 71 cases, for 71 possible re-pairings. Of these, 36 females remated with the same male (50.7%). At Niles, 74 of 151 females remated with the same male (49.0%). The other females mated with a different male. The proportion of females remating when both members of the pair returned was the same in the two areas ($\chi^2 = 0.06$, $df = 1$, NS), or 49.5%. If female survival P_{sf} is low, a male would not be expected to defer mating until the appearance of his mate of the previous year; and since male survival P_{sm} is uncertain, a female may not wait until she finds her previous mate, especially if he has dispersed.

At the George Reserve, the probability of survival $P_{s/m} = 0.52$ and $P_{s/f} = 0.34$; at Niles $P_{s/m} = 0.59$ and $P_{s/f} = 0.47$ (Payne and Payne 1990, Payne 1992). The proportion observed to re-unite with the old mate (49.5%) is much higher than the proportion expected by chance, based on the number of returning females and males where remating was possible ($n = 71 + 151 = 222$), and the males available at any one time in a study area ($n = 80$). The proportion expected is $222/80$, or 2.775%, and the number expected to re-mate with the old mate is 0.02775×222 , or 5.55 pairs. A chi-square goodness-of-fit test indicates that the proportion of returning females that re-unite with their former mate is much higher than expected with random mating ($\chi^2 = 2,016$, $df = 1$, $P < 0.001$).

The expected values of random remating may be biased if a male is already mated and not available to a female. The effect of this bias would be to inflate the number expected, though the mating status of neighboring males might also be affected. We suggested that the expected values as given above are reasonable, because female buntings in fact do mate with males that are already mated. About 15% of all males that were mated gained 1–3 additional females in a season. The frequency distribution of the number of females mated with a male appeared to be random, as it was not significantly different (F -test, $P > 0.05$) from that expected with a negative binomial distribution (Payne 1983a:65, Payne et al. 1988).

The rematings observed probably were due largely to mutual attraction of male and female to a common site. Nevertheless, remating may be due in part to active mate choice. In two cases we first observed a returning bird after its old mate had already paired. At Niles, a female returned late to her previous year's territory and mate, harassed a new female that had already nested and laid, and repeatedly chased the nesting female from her nest, which was then abandoned; the female then nested on her territory with her old mate. At the George Reserve, a returning female mated with a male that was a neighbor in the previous year when he expanded his territory to include her former area. After she had a nest and eggs, her old mate returned and fought actively with the new male, who withdrew to his former territory. The female fledged her young, then moved to mate with her old neighbor.

Summary: circumstances of dispersal in females. In females the breeding site depended less on their breeding success in the previous season than on whether their old mate returned, and they were more likely to return to the old site when the old mate was there. Also, females were more likely to return to the same site than to the same mate regardless of their breeding success. Many females re-united with their old mate, and this may be a consequence of male and female each returning to the same familiar site. Females often returned to the old breeding site even when their old mate did not return to the study area, but only two females remated with their old mate when he dispersed to a new territory, so females appear to be more strongly attracted to a familiar site than to an old mate, independently of their breeding success.

COMPARISON OF BREEDING DISPERSAL IN MALES AND FEMALES

The mate choice and social constraints hypotheses both predict that females are more likely to disperse than males. In both areas, females were significantly more likely to disperse between years (Table 6). The returning females were nearly half again as likely to settle on a new territory as were the first-year males (George Reserve, 80% vs. 47%; Niles, 50% vs. 42%) and were several times more likely to move than were the older males. The results support predictions of the mate choice hypothesis and the social constraint hypothesis (1b, 3a).

The two hypotheses also predict longer dispersal distances in females than in males (1b, 3a), and longer distances in young birds than in older adults (1b, 3b). The between-year dispersal distances overlapped considerably between the study areas, sexes, and ages (Table 7). Mean distances varied significantly among all groups compared together ($F_{7,218} = 3.00$, $P = 0.005$). The mean distances differed between areas ($F_{1,224} = 4.93$, $P = 0.027$) and were larger at the George Reserve than at Niles. None of the four comparisons of birds of the same sex and age showed significantly different mean distances between the two areas (Scheffé tests, $F \geq 3.27$, $P > 0.07$). The sampling area at the George Reserve was larger, where territories were larger and groups of territories were further apart, and the different dispersal distances may reflect the quality of the habitat as well as size of the area. The differences in mean distances were marginally significant

TABLE 6. Incidence of breeding dispersal by resident males and females between consecutive years.

Area	Sex	Territory		χ^2	<i>P</i>
		Old	New		
George Reserve	male	39	217	39.9	<0.001
	female	49	56		
Niles	male	43	264	38.6	<0.001
	female	90	123		

among sex and age groups within each area (George Reserve, $F_{3,133} = 2.44$, $P = 0.07$; Niles, $F_{3,133} = 2.53$, $P = 0.06$). At the George Reserve the mean dispersal distance of first-year males and adult males was significantly greater than of adult females (Scheffé tests, $F \geq 4.29$, $P < 0.05$). At Niles the mean distance of first-year males was significantly greater than that of first-year females and adult females (Scheffé tests, $F \geq 5.4$, $P < 0.05$), consistent with prediction (3b) of mean dispersal distance varying with age in the males (though not in the females). Females did not disperse further than males, and the distance results involving comparison of females with females, or females and males, give no strong support for these predictions (1b, 3a, 3b).

HERITABILITY OF DISPERSAL BEHAVIOR

If genetic differences among individuals account for the differences in whether they disperse, then we should find that parents and offspring have associated behavior, as an evidence for heritability of behavior differences (4a). From 1979 to 1989, we captured 138 buntings during the breeding season that we had banded as nestlings in an earlier year (Payne and Payne 1989, Payne 1991, subsequent observ.). For 30 of these birds both the returning nestling and its parent of the same sex survived to return for at least two sea-

sons. We determined the breeding dispersal from first year to second year for the offspring and for its parent to test whether the behavior was associated with kinship (4a). We observed all combinations of breeding dispersal and nondispersal of offspring and parent from the first to second breeding season. There was no significant association of breeding dispersal in the offspring and parent of the same sex (males, $n = 14$, Fisher exact test, $P = 0.14$, NS; females, $n = 16$, Fisher exact test, $P = 0.32$, NS).

Because paternity in buntings is uncertain (Payne 1983a; Westneat 1987b, 1990; Payne and Payne 1989), the lack of association in males might be due to incorrect allocation of paternity on the basis of the location of a nest on a male's territory. However, the data show no strong trend for association, whereas we would expect a 30% error in misallocation of paternity (Westneat 1987b, 1990; Payne and Payne 1989) to be dominated by a 70% correct allocation, which should still show a trend for any significant factor of heritability in explaining the variation in behavior among young males. Also, maternity is certain in buntings (Westneat 1987b, 1990) and even in females we found no strong trends as predicted (4a). As mentioned earlier, prior occupancy of a breeding site by another female does not determine that a second female would fail to settle

TABLE 7. Dispersal distances between breeding territories in consecutive years, in buntings that switched territories.

Area	Sex	Age	Distance (m) between territories				
			<i>n</i>	Min	Max	Mean	SD
George Reserve	male	first-year	32	100	3,040	679	736
		adult	7	510	1,300	790	244
	female	first-year	37	20	3,300	487	619
		adult	12	25	450	213	130
Niles	male	first-year	37	40	2,800	548	676
		adult	6	100	400	273	103
	female	first-year	59	20	1,600	333	325
		adult	29	20	1,640	300	340

TABLE 8. Incidence of breeding success in males in their second year (first adult year) in relation to dispersal.^a

Area	Dispersal	Breeding success in second year		χ^2	P
		No	Yes		
George Reserve	no	23	41	1.13	NS (0.57)
	yes, within study area	13	16		
	yes, new adult	12	25		
Niles	no	32	58	0.36	NS (0.84)
	yes, within study area	9	21		
	yes, new adult	6	13		

^a Males first arriving and banded as yearlings from 1979 through 1984, and males first arriving and banded as adults from 1980 through 1985. Data include only males that were resident for 28 days or more in their second year on the area.

there as well. For males, because most returning males settle on the old site (Table 2) it is unlikely that many others are deterred from doing so by the earlier arrival of another male. We conclude that the variation in breeding dispersal of buntings of the same age and sex is explained by circumstance, and is not determined in a simple manner by heritability.

BREEDING SUCCESS AFTER DISPERSAL OR NONDISPERSAL

The breeding success of birds that disperse and those that return to their old breeding site provides a test of whether breeding dispersal affects reproductive performance. Breeding success was compared for the second breeding season and also over their life time on the study area.

Males. We compared the breeding success of males in their second year (the first adult year) that returned to the previous site, males that dispersed to a new site within the study area, and males that immigrated as adults. The probability of fledging one or more young buntings in their second year did not differ between known second-year males that returned to their old site, known second-year males that settled on a new

site, or the males that first appeared as adults (Table 8). Also, the number of fledglings they produced in their first adult year did not differ among males with different dispersal histories (Table 9). These comparisons of incidence and mean breeding success in males of different dispersal histories showed no difference in their breeding success in their second year, and failed to support either prediction of a fitness consequence of dispersal (2b, 2c).

Breeding success might improve with a change of territory in the individual males that were unsuccessful in their first year (2d). It might also improve with experience in males that were successful in their first year and returned to the same territory (2c). Breeding success was compared between their first two years for males that were resident for at least 28 days on the study area as yearlings and returned in the following year. The mean number of fledglings produced in their first and second years (\bar{y}_1 and \bar{y}_2) did not differ with dispersal history, in a series of paired *t*-tests (George Reserve, males returned to the same site, $n = 57$, $\bar{y}_1 = 1.77$, $\bar{y}_2 = 1.79$, $SD = 2.79$, $t = 0.47$, NS; males dispersed, $n = 23$, $\bar{y}_1 = 1.39$, $\bar{y}_2 = 1.47$, $SD = 0.15$, $t = 0.15$, NS; Niles, males

TABLE 9. Breeding success (number of young buntings fledged) in males in their first adult year, in relation to their dispersal history.^a

Area	Dispersal	n males	n fledglings			P
			Mean	SD	F	
George Reserve	no	64	2.20	2.21	0.23	NS
	yes, within study area	29	1.90	2.02		
	yes, new adult	37	2.19	2.07		
Niles	no	90	2.03	2.07	0.29	NS
	yes, within study area	30	2.30	1.78		
	yes, new adult	19	2.32	2.21		

^a All males first arriving as adults from 1980 through 1985, including males banded as yearlings from 1979 through 1984.

TABLE 10. Adult lifetime breeding success of male buntings in relation to dispersal history.^a

Area	Dispersal	<i>n</i> fledglings				
		<i>n</i> males	Mean	SD	<i>F</i>	<i>P</i>
George Reserve	no	64	4.81	4.93	0.97	NS
	yes, within study area	29	4.59	5.42		
	yes, new adult	37	3.49	3.55		
Niles	no	90	4.14	3.85	2.58	NS
	yes, within study area	30	5.93	4.59		
	yes, new adult	19	5.94	6.49		

^a "Adult lifetime breeding success" is the total number of offspring that fledged, from all years in which the bird was an adult (lifetime success minus the breeding success of the male as a yearling).

returned to the same site, $n = 87$, $\bar{y}_1 = 2.07$, $\bar{y}_2 = 1.83$, $SD = 2.69$, $t = 0.84$, NS; males dispersed, $n = 24$, $\bar{y}_1 = 1.33$, $\bar{y}_2 = 2.33$, $SD = 2.47$, $t = 1.99$, $P = 0.059$). At the George Reserve, neither the males that settled on their old territory or the males that dispersed to a new site significantly improved their success in their second year (2c, 2d); while at Niles the dispersing second-year males had a marginally significant higher success in the year following dispersal (2d).

The cumulative breeding success of males banded as first-year birds or as adults was compared over their adult years in relation to their dispersal histories. The new adults may have been unsuccessful as yearlings, yet we observed some successful yearlings settle on a new territory in their second breeding season (Table 3). For this reason, we compared "adult lifetime success" for only the adult years of each male. Adult lifetime success did not differ significantly among males with different dispersal histories (Table 10). Males first appearing as adults tended to have lower cumulative adult success at the George Reserve, but not at Niles, where the males banded as yearlings that changed sites in their second year had a marginally significant higher adult lifetime success than the males that resettled on their first-year breeding site (pairwise Scheffé test, $F = 3.64$, $P = 0.058$, NS). In our comparisons of the breeding success of individuals in consecutive years, we found little difference either in breeding success before and after dispersal, or in breeding success before and after returning to the previous territory, so we did not find support for dispersal having an effect on breeding success.

Males disperse less often than females, and as a result of limited dispersal the males with the same song types often remain as neighbors. We found a higher annual breeding success for adult males with neighbors with the same song types

than for adults with no matching neighbors (Payne 1982, Payne et al. 1988), suggesting that song matching is associated with breeding success, though the mechanisms leading to the difference in success have not been determined (Payne 1983b). Song matching depends both on a male returning to the area where his adult neighbors have the old song, and on the social transmission of his song to new yearlings; the first of these is involved in the present test. We note that some song types remain present for many years in the same part of the study area (Payne et al. 1981, 1988), and the local persistence is due to the return of males to the site where they were present in the previous season. The results are consistent with predictions from the social constraints hypothesis (3c, 3d). The results also showed that both returning and dispersing males were often successful in the following year, and that dispersers were not unsuccessful, so are consistent with predictions of all four adaptive hypotheses (1–4); i.e., dispersal is not a losing behavior.

Females. Female buntings provide most of the parental care to the young, and nearly all the care while the young are still in the nest. Finding food for their brood might be enhanced if a female were familiar with the breeding site from an earlier year. To test the consequences of dispersal on breeding success, we compared the breeding success in females that returned to their old territory and in females that moved to a new site. We also compared the breeding success of individual females that dispersed with females that did not disperse.

Females were equally likely to breed successfully when they were on a new territory as when they settled on their old site (Table 11). The mean number of young fledged in their second year and in subsequent years did not differ between

TABLE 11. Incidence of breeding success of females and their breeding site in the previous year.

Area	Breeding success	Female breeding site		χ^2	<i>P</i>
		Old	New		
George Reserve	yes	40	37	0.22	NS
	no	16	12		
Niles	yes	77	57	0.15	NS
	no	44	29		

females on a new territory and females that returned to their old one (Table 12). Breeding success did not differ between females on an old or new site in their second year, in contrast to the predictions of increased success with dispersal (2b, 2c).

To test the effect of dispersal on the breeding success of individual females, the number of young fledged by each returning female in a year was compared with her success in the following year. All females were included in the comparison regardless of their age at banding for as many years as the females returned. The grouping is supported by the lack of variation of breeding success in females with age and by the lack of a correlation across years in their breeding success (Payne 1989). A female that dispersed from her first year to a new breeding territory in her second year and returned to that site in the third year comprises one case of dispersal and one case of returning to the same site. A female not seen in the second year then appearing in the third year was not counted unless she also returned for a fourth year. We compared breeding success for individual females in consecutive years with

paired *t*-tests. Mean success \bar{y} did not differ between years y_1 and y_2 (George Reserve, females returned to same site, $n = 56$, $\bar{y}_1 = 2.68$, $\bar{y}_2 = 2.41$, $t = 0.70$, NS; females dispersed, $n = 49$, $\bar{y}_1 = 2.53$, $\bar{y}_2 = 2.63$, $t = 0.28$, NS; Niles, females returned, $n = 119$, $\bar{y}_1 = 2.60$, $\bar{y}_2 = 2.22$, $t = 1.49$, NS; females dispersed, $n = 85$, $\bar{y}_1 = 2.36$, $\bar{y}_2 = 2.13$, $t = 0.80$, NS). We conclude that females did not increase their breeding success either when they returned to the same territory or when they dispersed to a new breeding site, so we failed to find evidence in support of the adaptive consequences of dispersal (2c, 2d). However, the results showed that dispersing females often were successful in the next year, so dispersal appears to be an adaptive behavior.

POPULATION EFFECTS OF BREEDING SUCCESS IN RELATION TO DISPERSAL

Dispersing adults contributed to the production of offspring in both areas. At the George Reserve, 254 resident males were banded between 1979 and 1984 as yearlings, or between 1980 and 1985 as new adults. The breeding success of each male was determined for each year it was on the study area, including their first year; the sample includes the banded males that were present only as yearlings as well as those that bred as older adults. The 254 males had a total of 848 young that survived to fledge. Of the total fledglings, 129 (15.2%) were produced from nests on territories defended by males that immigrated as adults (Table 13). At Niles, 214 resident males had 952 fledglings, and 113 (11.9%) of all young that fledged were produced from nests on territories defended by males that first appeared as adults. We combined the resident males that

TABLE 12. Breeding success of females that returned to the same territory and females that settled on a different territory after their first year banded.

Area	Dispersal	<i>n</i> fledglings				
		<i>n</i> females	Mean	SD	<i>t</i>	<i>P</i>
Second-year breeding success						
George Reserve	no	34	2.09	2.19	0.81	NS
	yes	37	2.49	1.94		
Niles	no	73	2.17	2.03	0.09	NS
	yes	61	2.14	1.98		
Lifetime breeding success						
George Reserve	no	34	6.32	3.82	0.05	NS
	yes	37	6.27	3.27		
Niles	no	72	5.84	4.11	0.27	NS
	yes	61	5.63	4.78		

TABLE 13. Dispersal history of the male parents of fledgling buntings.

Area	Age at banding	Males ^a		Fledglings	
		Dispersal history	<i>n</i>	<i>n</i>	%
George Reserve	first-year	no dispersal	188	556	44.7
	first-year	breeds before dispersal	29	30	3.5
	first-year	breeds after dispersal	29	133	15.7
	adult	breeds after dispersal	37	129	15.2
Niles	first-year	no dispersal	165	629	66.1
	first-year	breeds before dispersal	30	32	3.4
	first-year	breeds after dispersal	30	210	22.1
	adult	breeds after dispersal	19	113	11.9

^a A male appears twice if it was banded as a yearling and settled on a new territory in a later year, occurring once before dispersal and once after dispersal. Each offspring is counted once, in the year appropriate to the parent's dispersal history at the time. Birds banded as adults were not seen on the study area as yearlings and presumably dispersed into the area in their second breeding season. Dispersal refers only to movement between consecutive breeding seasons, and some birds with no dispersal were present on the study area in one year only.

moved from one territory to another between years, either within the study area or into it, to estimate the proportion of fledglings produced after their parent had dispersed. A total of 30.1% of the fledglings on the study area were produced by a male after he had dispersed at the George Reserve, and 33.9% at Niles.

Because only half of the local females were banded, we were uncertain that an unbanded female had dispersed when we caught her. The proportion of returning banded females that dispersed from one year to the next was higher than for males (Table 6), so the proportion of their offspring born after the females dispersed is higher than in the males. Some females did not disperse until their second year or later, exaggerating the proportion of offspring produced after female dispersal. On the other hand some females changed breeding sites within a season (Payne 1992) and returned to one of them in the next year, biasing downward the proportion that we counted as produced after nondispersal.

The proportion of fledglings produced when neither of its parents had dispersed is less than the proportion produced when only one parent had dispersed, as the probability of simultaneous occurrence of events is less than each component probability. The probability that neither parent had dispersed is described by the last term of expansion of a binomial expression,

$$(1 - P \text{ of male dispersal}) \\ \cdot (1 - P \text{ of female dispersal}),$$

or 0.30 at the George Reserve and 0.34 at Niles. In other words, at least 70% of the young buntings produced have one or more parents with a history of breeding dispersal, where most dispersals were on a scale of a few hundred meters.

In comparison, the proportion of fledglings produced by buntings that were banded as nestlings within the study area was calculated over the lifetimes of the birds that returned and bred on their natal area, not including cases where the breeding male was of unknown adult age when it was banded off the previous year's study area (Payne 1991). At the George Reserve, 20 of 848 fledglings (2.35%) were produced by males that originally were banded as nestlings on the study area. At Niles, 76 of 952 fledglings (8.0%) were due to males banded as nestlings. Mean lifetime breeding success did not differ significantly between males banded as nestlings on the area and males born elsewhere (George Reserve, $F_{1,253} = 0.12$, $P = 0.72$, NS; Niles, $F_{1,214} = 1.70$, $P = 0.19$, NS). The proportion of fledgling buntings produced by parents born off the study area was greater than the proportion produced by parents that dispersed between years from one breeding site to another. Also, the distances moved by birds born on the study area and that settled elsewhere (two birds were recovered in the breeding season at distances of 52 km and 350 km from their natal site, Payne 1991) were two orders of magnitude greater than any known distances of breeding dispersal. The distribution of natal dispersal distances outside the study area is unknown. By comparing birth and survival rates of adults in the relatively stable populations of buntings with the low proportion of locally-born birds that returned to breed in the study areas, we infer that most survivors among the birds we banded as nestlings returned to breed somewhere outside the study area (Payne 1990, 1991).

The number of buntings that were resident as yearlings and bred elsewhere in later years was

presumably balanced by the number resident elsewhere that settled inside the study area in later years, at least during the years when the number of breeding birds was stable. The observed values of offspring produced averaged 3.34 ± 4.24 SD for the George Reserve and 4.47 ± 4.67 SD for Niles, where bunting numbers were stable over most years of observation. The lifetime breeding success of all males was considerably lower than the lifetime adult success for birds followed as adults (Table 10) due to the low success of the yearling males.

EFFECTIVE POPULATION SIZE

Wright (1931) introduced the concept of a neighborhood or "population number" as an ideal population with the same genetic variance properties as an actual population, to calibrate the amount of random genetic drift in actual populations (Crow 1954, Lande and Barrowclough 1987). The effective population number is equivalent to the ideal number of breeding males and females. It may be less than the census number of individuals in a closed population, in part due to loss of genetic variation through inbreeding. However it is much greater than the census number of individuals in a local population that is open to immigration (Crow 1954). Wright (1943) developed the concept of neighborhood size from the effect of immigration. Later (Wright 1946) he developed the concept of a genetically equivalent population size N_e in a model that included the statistical parameter of variance among individuals in breeding success. Crow (1954) clearly distinguished the two models of effective population size. One model gives an estimate, N , sometimes called the "inbreeding effective number," based on the number of ancestors of the breeders in a local census population. This "inbreeding" effect "is not due to consanguineous mating in the usual sense but rather is the result of approximately random mating in a population of restricted size" (Crow 1954:545). N is the size of the population from which the parents of a given individual may be considered to be drawn at random (Wright 1943). The other estimate, the "variance effective number," or N_v , is based on the number of offspring of the breeders (Crow 1954:552, Wright 1969:220).

The appropriate model for a population depends on its spatial distribution and dispersal pattern. In species with an approximately uniform distribution over a wide range, in a meta-

population as in the Indigo Bunting, effective population size is appropriately described by a "continuous model" (Barrowclough 1980) which uses the dispersal distances traced by the breeding individuals from their natal sites and breeding sites in earlier seasons. In other species with discrete, isolated demes, as on islands where a local population might be closed to immigration, indirect demographic measures of reproductive success may be used for parameter estimation (Barrowclough 1980, Rockwell and Barrowclough 1987, Grant and Grant 1992a). Because the terms have sometimes been used otherwise in the avian literature (Grant and Grant 1992a: 774, 776), and because both models use an estimate of "variance" (either of dispersal distance or of reproductive success), we refer to the first, the "inbreeding effective number," as the "dispersal effective number," to indicate its operational nature in estimation from dispersal data, and to distinguish it from the second, the "reproductive variance effective number," as estimated from variance in breeding success.

Because of the difficulty in detecting birds that settle far from their site of birth or capture, dispersal distances are not sufficiently well known for an estimate of dispersal-effective population size N with a known small, defined confidence interval. Dispersal of individuals becomes increasingly difficult to observe with distance from their place of origin. Rockwell and Barrowclough (1987) suggest, however, that "even knowing the order of magnitude of a parameter . . . will represent a major advance" in estimating the genetic structure of avian populations.

In general, the dispersal effective population size is

$$N = (4\pi\rho\sigma_\eta^2) + (4\pi\rho\sigma_\beta^2),$$

where ρ is the density of birds per km², σ_η^2 is the variance of the natal dispersal distances, and σ_β^2 is the variance of the breeding dispersal distances (Crow 1954, Barrowclough 1980:789, 790). The effect of long-distance dispersal on N is proportional to the sum of the squares of the distances dispersed, so the long-distance movements bring about a disproportionate increase in N .

A dispersal estimate of effective population size is $N = 4\pi\rho\sigma^2$, where σ is the root mean squared dispersal distance, summed separately for natal η and breeding β dispersal. Including the two buntings recovered beyond their natal area, for

all 117 yearlings $\sigma_n = 32.7$ km and $\sigma^2 = 1.07 \times 10^4$ km². For the 115 local returns of yearling buntings, $\sigma_n = 1.004$ km and $\sigma^2 = 1.01$ km². Breeding densities near the study areas were 2.89 pairs/km² at the George Reserve and 6.7 pairs/km² at Niles (Payne 1992), an average ρ of 9.6 breeding buntings in southern Michigan. For all yearlings, $4\pi\rho\sigma_n^2 = 1.29 \times 10^6$ breeding birds. This estimate is an order of magnitude less than the total number of breeding Indigo Buntings in North America, as estimated from continental survey data (Robbins et al. 1986, Payne 1992). In contrast, the estimate for local returns without the two long-distance recoveries is only 1.22×10^2 , which is several orders of magnitude less than the nontruncated estimate.

The second term for dispersal, breeding dispersal, was much smaller both in frequency and in the distances involved. Only 25% of the cases of a breeding bunting returning from one year to the next involved a change in territory (Table 6). Barrowclough (1980) included a term λ for the expected lifetime of adult birds. We have estimated this parameter for buntings ($\lambda = S_0$, Payne and Payne 1990, Payne 1992); here the data are included in our statistics of cases by the season (rather than of individuals), which also include the age-related component of breeding dispersal, and (by the similar numbers of males and females) also include the differential breeding dispersal by sex. For breeding dispersal between years, $\sigma_\beta = 0.53$ km, and $\sigma_\beta^2 = 0.28$ km². The effect of breeding dispersal was negligible compared with that of natal dispersal, as natal dispersal involved five orders of magnitude greater effect on N . Combining the terms for natal and breeding dispersal, $N = 1.29 \times 10^6 + 3.02 \times 10^1 = 1.29 \times 10^6$ breeding buntings.

Other possible effects on population size N include a bias for underestimate of distances seen within a finite sample area (Barrowclough 1978), a non-normal distribution of distances (Wright 1969), and fluctuations of population size from year to year (Wright 1969, Gillespie 1989). These effects either are small when compared with the importance of long-distance natal dispersal in general, or they are not important in bunting populations. First, Barrowclough (1978) estimated an increase in σ^2 of 23% from Kendeigh's (1941) study due to a finite size of the study area, where the area and local dispersal distances were comparable to those of the bunting study. When the long-distance recoveries of birds banded as

nestlings are also included, the estimate of N increases nearly 20-fold (Payne 1990). In banding studies of other small songbirds, typically no young are found in the breeding season unless they return to the study area, so the estimates of population size based on local returns are minimal. Second, in the buntings the two distant recoveries are responsible for a leptokurtic distribution ($\gamma^2 = 107.2$) of dispersal distances, which would decrease the estimate of N relative to a normal distribution of distances by only about 43% (Wright 1969:304). Third, the number of breeding Indigo Buntings remained nearly constant during 10 years of observation at Niles and dropped by about half at the George Reserve. Both regional numbers over time and local genetic variability were compared for evidence of possible bottleneck effects of small population size in buntings. The population density over the breeding range of the species in North America remained unchanged through a 15-year period (Robbins et al. 1986:109). The genetic heterozygosity of buntings at Niles did not differ significantly from that predicted from a random assortment of alleles (Westneat 1987b). We conclude that there is no census or genetic evidence of a recent history of small effective population size.

Reproductive variance effective population size N_e is a function of the variance among individuals in breeding success. In order to estimate the effect of variation among individuals in leaving offspring on N_e , we determined the lifetime reproductive success from the number of nestlings that survived to fledge for all Indigo Buntings captured as resident yearling males and as yearling females and females of uncertain age from 1979 to 1983. We observed the fledging success of all birds in these five cohorts over their lifetimes through 1987. The mean success and variance in success did not differ significantly between the sexes, areas, or cohorts (Payne 1989). Sex ratio, mating systems, and survival affect N_e through the variance in lifetime reproductive success (Wright 1969); the combined effect was determined directly in the buntings. Variance is reasonably assessed from fledging success in females, though genetic success in males is less certain due to extra-pair copulation and fertilization (Payne 1983a; Westneat 1987b, 1990; Payne and Payne 1989).

The reproductive variance effective population size was estimated from the expression,

$$N_e = (N\bar{k} - 1)/(\bar{k} - 1 + \sigma_k^2/\bar{k}),$$

where N is the dispersal estimate of N_e , \bar{k} is mean lifetime reproductive success, and σ_k^2 is the variance in lifetime success (Wright 1969: model 8.16). With the dispersal estimate $N = 1.29 \times 10^6$, and the observed values of mean lifetime reproductive success ($\bar{k} = 3.77$) and mean variance in success ($\sigma_k^2 = 17.25$) (Payne 1989), the lifetime reproductive variance $N_e = 288,092$. This estimate of N_e is only 22% of the estimate N based on variance in dispersal distance. The relative difference would be the same if it were based on the local census size, an average of 80–100 pairs per breeding season. The comparison shows that unequal lifetime reproductive success may affect the estimate of N_e . As with the estimate N , reproductive variance effective population size N_e is much larger than the size at which local chance events would determine genetic change (Wright 1969).

The effect of variance in reproductive success is several orders of magnitude less than the effect of variance in dispersal distance. When dispersal was first included in the model for estimating N , and N_e was then calculated from the variance in lifetime reproductive success, N_e was 3–4 orders of magnitude greater than the local census size. This was true whether local size was based on regional data, 9.6 birds/km times the area, for an average of 67 birds for an area the size of that in our study, or on counts of birds on the study areas themselves.

Effective population size is sensitive to dispersal distance, and our data on natal dispersal are notably incomplete, because natal returns are more detectable within a local study area than are movements beyond it. The two long-distance recoveries increased by several orders of magnitude the variance in dispersal distances over the local returns. Including these long-distance recoveries, which account for only a small proportion of the birds banded as nestlings, is more realistic than excluding them. Most buntings breeding in the study area were born elsewhere, with locally born birds (banded as nestlings, in the years before the source of the breeding birds was estimated) comprising 1.6% and 13.0% of the breeding population in two areas of 10 km² and 4 km² (Payne 1991). By this reasoning, it is likely that the same proportion of birds born in the study area and returning to breed as yearlings settle further than 1 km from their natal area

(Payne 1991). Wright (1969) and Crow (1954: 553) have emphasized that N can be infinitely greater than local estimates of N_e due to dispersal and immigration.

DISCUSSION

PROXIMATE CAUSES OF BREEDING DISPERSAL AND SITE FIDELITY

For the hypotheses of breeding dispersal considered here (mate choice, site choice, social constraints, and heritability of behavior differences), the predictions of the site choice and social constraints hypotheses appear to be most strongly supported in the Indigo Buntings. A social constraints hypothesis appears best to explain the pattern of dispersal of males, and a site choice hypothesis accounts for the dispersal of females.

In males, only one of seven tests of predictions of the site choice model was supported (2a, return to the old territory after a successful season and disperse after an unsuccessful season). However, whether a male dispersed was more closely related to his age than to his prior success. The other predictions about the adaptive significance of dispersal concerned the consequences. Because none of the predicted consequences of dispersal were supported, the model does not explain the breeding dispersal of male buntings. In contrast, the age difference in dispersal of males is explained by the social constraints hypothesis, and the consequences of males returning to a neighborhood where their neighbors have similar songs and the association of song matching in adult males with their breeding success (Payne 1982, Payne et al. 1988) provide support for a proximate and ultimate explanation of breeding dispersal in the males. Social familiarity among males may be a general reason for males to return to their previous site in other species as well, though the importance of song matching and song familiarity will vary among species.

In females, the fidelity to their old territories was lower than in males, and it was independent of their breeding success in the previous year. The fidelity of females to their old breeding site was stronger than their fidelity to their old mate, even when he also returned to the study area or to the old territory. For the mate choice hypothesis, the differences between males and females were in the direction predicted (1b). However, within the females none of the comparisons were as predicted. In particular, dispersal did not vary

significantly with breeding success of the female in the previous season. For the site choice model, two of the five tests of predictions were supported in females. Both of those were of a stronger association of a female with her previous breeding site than with her mate, and both associations were loosely based on prediction (2a). On the other hand, the predictions of the association of a social constraints model were supported in only one of five tests: females were more likely than males to disperse, though they did not disperse further. This prediction (3a) is based on an assumption of intersexual conflict, and we have no observational evidence for any such conflict in the buntings, except perhaps for forced copulations (Payne 1983a), but this lies outside the field of seasonal dispersal. In its other assumptions, the greater incidence of breeding dispersal of females than of males is consistent with the social constraints model. Females have less social interaction with other conspecifics than do males, and females survive less well between years so fewer of their neighbors would return. The difference between male and female social interactions is consistent with the greater incidence of dispersal in females than in males, since females are unlikely to benefit from prior familiarity with other females, whereas male buntings may benefit from familiarity with their neighbors in setting up their territories and in matching their song types.

Male buntings are more likely to return to an old territory than are females; the females are nearly as likely to disperse as to return. The difference in breeding dispersal of males and females may be due to their survival as well as to their social behavior. Male survival is reasonably high (52% to 59%; Payne and Payne 1990, Payne 1992), and buntings live in local groups of territories with several neighbors within 200 m (Payne et al. 1988). The probability P_0 that none of a male's former neighbors will return is very low. For example, where the number of neighbors $n = 8$, which is our mean value of territorial males within 200 m of a male's territory, P_0 [where P_0 is the last term in the expansion of the binomial expression, $(1 - P_n)^n$] = 0.04. Because of annual survival and local neighborhood densities of buntings, a returning male is likely to have at least one returning neighbor near his old territory, and the cost of establishing social relationships may be lower for a male returning to an old territory than for a male settling on a new

one. Returning females also may have an advantage in recalling sites to feed and nest. But females do not interact socially in the same conspicuous manner as the males that chase, sing, and countersing with their neighbors (Payne 1983a, 1983b). Also, the lower survival rate in females suggests less advantage from social familiarity for a returning female, for the following reason. Although a female may be familiar with the nesting habitat at a site, she has no obvious social incentive to return to her old breeding site, as she is unlikely to encounter a familiar neighboring female from an earlier year.

The proportion of buntings and other species that re-unite with the returning partner is low ($\leq 50\%$) in seasonally migratory songbirds in North America, compared with many seabirds (Rowley 1983) that mate "for life." In studies of songbirds where more than 20 cases of both male and female were known to return from a previous year, Song Sparrows, *Melospiza melodia*, reunited with the old mate in 27% of 30 cases (Nice 1937), House Wrens in 42% of 26 cases (Ken-deigh 1941) and 4% of 84 cases (Drilling and Thompson 1988), Barn Swallows, *Hirundo rustica*, in 28% of 25 cases (Shields 1984), and Red-winged Blackbirds, *Agelaius phoeniceus*, in 38% of 52 cases (Picman 1981). The proportion of rematings is higher in Indigo Buntings (49.5%) than in these other species. Remating in buntings is notable since the males have uncertain paternity (Westneat 1987a, 1987b, 1990; Westneat et al. 1987; Payne and Payne 1989) and they provide little parental care (Westneat 1988, Payne 1992), and so we might expect little re-uniting with the previous mate. If females are not restricted to their mate's territory and can gain the resources and attention of males on neighboring territories, then their return to a site suggests that the site is more important than which male is there. The blackbirds and wrens also have a high proportion of extrapair fertilization, and the blackbirds like buntings provide little paternal care (Price et al. 1989, Whittingham 1989, Gibbs et al. 1990). Remating in the Indigo Buntings and perhaps the other species may be an indirect effect of the male and female independently returning to the same territory that they occupied in the previous year.

Breeding dispersal was related to age in male buntings. Older males arrive earlier than first-year males on average (Payne 1991). Males in their second year sometimes settle near their pre-

vious territory, from where they may have assessed other sites, as suggested for blackbirds by Beletsky and Orians (1987). Male buntings appear on their neighbors' territories during the period of sexual activity of the neighbors' females (Westneat 1987a). On the other hand, breeding dispersal is not related to age in the females. The costs in time to assess a number of males and breeding sites with a loss of time for nesting (Janetos 1980, Wunderle 1984, Wootton et al. 1986, Slagsvold et al. 1988, Slagsvold and Dale 1991) may limit the searching behavior of females, so that most return to their previous nesting site regardless of their breeding success in the previous year.

Other species may return to a site as a result of an advantage of social familiarity, including Red-winged Blackbirds, where adult males return to the same territory (Picman 1981, Beletsky and Orians 1987), and females may be familiar with each other (Picman 1981) as well as with the neighboring males (Beletsky and Orians 1991). Female blackbirds usually return to their old territory whether their previous mate is present (67% of 32 females) or absent (62% of 53 females; data in Picman 1981); the difference is not significant ($\chi^2 = 0.001$, NS). In this species remating may be a consequence of females returning to the same territory and mating with the resident male independently of their mating status in previous years. Female blackbirds may be more affiliative than are the female Indigo Buntings, which show no common defense of a nesting area. Also, the breeding success of females affects whether they return to the old site or settle on a new one in some other migratory songbirds (Shields 1984, Beletsky and Orians 1991, Lindén 1991). The buntings are more like House Wrens, *Troglodytes aedon*, as the return of females to the old site does not depend on their breeding success in the previous year (Drilling and Thompson 1988).

Even though their social behavior may explain the pattern of breeding dispersal in the male Indigo Buntings, we note that the range and permanence of social interactions in these migratory songbirds is less than in many resident birds and mammals with persistent social bonds (Chepko-Sade and Halpin 1987, Stacey and Koenig 1990). The occurrence of other buntings near a territory may affect the settlement of buntings, as neighbors affect breeding opportunities through extra-pair copulations. Social cohesion or coercion may

account for sex differences of dispersal in a resident species, but not in seasonally migratory species. We note the need for studies of different species of birds as a basis for any general or comparative statements on the adaptive significance of breeding dispersal.

CONSEQUENCES OF BREEDING DISPERSAL

We found little difference in the breeding success of birds that dispersed and those that did not, or in the breeding success of individual birds in the years before and after they dispersed. Breeding dispersal was not followed by a significant increase in the success of dispersing buntings, either in comparison with the success of the dispersing birds in an earlier year, or in comparison with nondispersing birds that returned to the same breeding site as in the earlier year. Dispersing birds tended to do better in their second year after they settled on a new territory, but the effect appears to be explained by the low success of these birds in the earlier year. To the extent that the behavior of dispersing and not dispersing lead to equivalent breeding success in later years, we found no evidence that breeding dispersal increased the fitness of dispersing birds.

On the other hand, dispersal is adaptive in the Indigo Buntings in the sense that birds are successful breeders after they disperse. Much of their breeding success follows their dispersal from the site where they bred in one year to the site used in the next year. In fact, most young were born after a parent had dispersed from an earlier breeding territory. We estimate that 70% of all young in the study areas were produced after a parent dispersed from one year to the next, mainly from a first breeding season to the next one.

Breeding dispersal may lead to closely-related birds moving apart and contribute to avoiding close inbreeding. The breeding site of buntings that return to their natal study area as yearlings is on the average six territories removed from their natal territory, and we estimate that most buntings move further, since the proportion of locally-born breeding birds is lower than necessary to maintain population numbers (Payne 1989, 1991). In buntings with known genealogies, inbreeding is rare and is close to the degree expected (1–2%) with random mating (Payne 1991). Considering the low degree of kinship during their first breeding season, breeding dispersal in later years has a negligible effect on the degree of relatedness of mates and neighbors. We

observed no breeding dispersal in buntings that bred with a close relative. The lack of an association of first-to-second-year dispersal between Indigo Buntings whose natal history was known and their parents of the same sex indicates no simple heritability of behavior differences for dispersal. In this the buntings are similar to most other birds and mammals where heritability has been tested (Johnson and Gaines 1990).

In other social vertebrates the proportion of breeders that disperse from their natal area is high. In mammals the males are more likely to disperse than females, and the reverse is true in many birds. The fate of these dispersers is critical to the evaluation of the consequences of dispersal, but the consequences have not been determined in detail, either whether they breed or what proportion of the offspring they produce. In several species of cooperatively breeding birds and mammals the proportion of breeders that have immigrated has been determined, and the observations usually indicate a bias for one sex to immigrate more than the other, males in mammals and females in birds, as in Greenwood (1980). In a few species the natal dispersal history of breeding individuals in a population has been determined (Arcese 1989, Rood 1990, Johnson and Gaines 1990, Payne 1991).

Although individual lifetime reproductive success has been described in several species, the reproductive success of dispersers and nondispersers following dispersal has not often been compared (Rubenstein and Wrangham 1986, Chepko-Sade and Halpin 1987, Newton 1989, Johnson and Gaines 1990, Stacey and Koenig 1990), so no strong inference can be made about the adaptive consequences of dispersal. In a few species, the reproductive success of birds has been compared with their dispersal history. In Pied Flycatchers, *Ficedula albicollis*, Pärt and Gustafsson (1989) found that breeding success was positively correlated with distance moved in females that were unsuccessful in the previous year, and negatively correlated with distance moved in females that were successful. They did not compare the later success of dispersing and non-dispersing birds. The data are consistent with the view that dispersal itself has little if any effect on later success. In Galápagos finches, *Geospiza* species, immigrants of one species had breeding success as high as or higher than the resident island birds (of two other species) with which they interbred, as did their hybrid offspring (Grant and

Grant 1992a, 1992b). The prior breeding success of the immigrants was unknown. Finally, in resident, cooperatively-breeding Red-cockaded Woodpeckers, *Picoides borealis*, the breeding success of dispersers and nondispersers was compared for the year following dispersal and for later years. In this species the dispersers were yearlings that had not previously attempted to breed, and the movement was natal dispersal in response to territory quality (Walters et al. 1992b), rather than a decision to abandon or to remain on a site where they bred in a previous year, or breeding dispersal. In these woodpeckers, the lifetime reproductive success of birds that dispersed did not differ from the success of birds that remained on their natal territory, either when individual fitness was measured or when inclusive fitness also was considered (Walters et al. 1992a). The results in all these studies, like those of the buntings, suggest that dispersers do as well as nondispersers, at least when they are able to establish themselves on a territory. We encourage further studies for a comparative approach within species to the adaptive function or fitness consequences of breeding dispersal.

In observations of marked birds in a small area, dispersal and mortality both can contribute to the disappearance of a bird in a later season, and the relative importance of dispersal and mortality in a local population cannot be resolved without additional information (Nur 1988, Sherry and Holmes 1991). Estimates of survival and lifetime breeding success are uncertain to the extent that individuals may disperse and breed elsewhere. The uncertainty is a matter of micro-geographic scale. Comparison of the proportion of breeders that returned show a higher proportion returning in the larger areas (Shields 1984). If a population were monitored on a continental scale, then failure to observe a bird in a later year would be due to mortality. In contrast, if the area were limited to a few territories, then estimates of survival and lifetime breeding success would be reduced due to local dispersal. In the buntings, the study area was large in relation to the size of a territory, and local dispersal was unlikely to have been overlooked in many instances. Continent-wide banding recoveries of Indigo Buntings and observations of marked buntings returning in Michigan give similar estimates of adult survival (Payne and Payne 1989). Loss to dispersal would lead to lower observed values of lifetime breeding success, to the same extent that

values increase when birds entering the breeding population as two-year-old adults are included in estimates of survival and breeding success (Tables 9, 12).

The genetic effect of breeding dispersal within or among local populations is small compared with effects of natal dispersal. In the buntings, 2% of the breeding birds were born in the same area at the George Reserve, and 10% bred in their natal area at Niles, whereas the remainder immigrated from outside this area (Payne 1991). In contrast, more than half of the breeding birds return to the area where they bred in the previous year. Also, 70% of all fledglings had at least one parent that had dispersed from one breeding site to another across years. Dispersal at this level is sufficient to prevent chance extinction of local populations (Goodman 1987, Lande 1988, Stacey and Taper 1992) or loss of genetic diversity (Barrowclough 1980, 1983; Lande and Barrowclough 1987; Rockwell and Barrowclough 1987; Koenig 1988). In the buntings, the proportion of young produced after their parents disperse within the area or into it is an order of magnitude less than that produced after the parents disperse from their natal area into a local population. A large proportion (30%) of lifetime success comes after a male disperses from his first-year territory to his adult breeding site. Nevertheless, more than 90% of all fledglings were produced by parents that dispersed from another natal area. The comparison indicates that natal dispersal is more effective in maintaining the genetic cohesion of a biological species (Mayr 1963) than is the more local behavior of breeding dispersal.

A greater effect of natal dispersal on effective population size has also been reported in analyses of banding recoveries and returns in other species of songbirds (Barrowclough 1980, Moore and Dolbeer 1989, Payne 1990). Banding recoveries show that dispersal effective population size in birds may be greater by several orders of magnitude over local census size due to natal dispersal (Payne 1990). It also is increased by breeding dispersal which involves fewer birds and shorter distances. The extent of natal dispersal in Indigo Buntings suggests an N with an order of magnitude of 10^6 . Breeding dispersal adds only slightly to the estimate, and not to the order of magnitude. In birds with an open population structure that is continuous across a broad region and connected through local immigration, as in the Indigo Buntings, we suggest that estimates of

population structure account for the effects of dispersal, and not be based simply on local reproductive success.

ACKNOWLEDGMENTS

We thank our research assistants for help in the field. Banding was carried out under a U.S. Fish and Wildlife Service Banding Permit and a permit from the Michigan Department of Natural Resources. Amtrak and landowners allowed access to their lands at Niles. The University of Michigan Museum of Zoology made available the facilities of the E. S. George Reserve. For comments on the manuscript we thank E. A. Lacey, S. Meagher, and the reviewers. Research was supported by a University of Michigan Faculty Research Grant and NSF grants (BNS78-03178, BNS81-02404, BSR83-17810).

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