

EFFECTS OF PRIOR NESTING SUCCESS ON SITE FIDELITY AND BREEDING DISPERSAL: AN EXPERIMENTAL APPROACH

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ABSTRACT.—Based on more than 300 individually marked American Robins (*Turdus migratorius*) and Brown Thrashers (*Toxostoma rufum*), I tested three hypotheses to explain low return rates of birds whose nesting attempts are unsuccessful: (1) birds with low reproductive success are low-quality individuals that are more likely to suffer mortality between breeding seasons; (2) nesting failure increases reproductive effort by causing birds to renest, and this energetic stress increases the probability of mortality; and (3) birds use a “decision rule” based on prior experience to select nesting sites, such that individuals that experience low reproductive success are more likely to move to an alternate breeding site, whereas birds that nest successfully are more likely to breed in the same site again. Birds subjected to experimental nesting failure returned at a significantly lower rate (robins 18%, thrashers 12%) than birds that nested successfully (robins 44%, thrashers 29%). Birds that nested more than once in a season returned at rates (robins 43%, thrashers 21%) indistinguishable from birds that nested only once in a season (robins 36%, thrashers 23%). These results, as well as supplementary data, were inconsistent with hypotheses 1 and 2 and consistent with hypothesis 3. This study provides strong evidence that low return rates result from dispersal in response to nesting failure. Received 11 August 1997, accepted 12 March 1998.

DESPITE THE OBVIOUS AND IMPORTANT DIFFERENCES between dispersal and mortality, we are unable to distinguish between them in many natural populations (e.g. Delius 1965, Harvey et al. 1985). Dispersal is difficult to study, and data on immigration and emigration largely are lacking for bird populations (Greenwood and Harvey 1982, Clobert and Lebreton 1991, Brawn and Robinson 1996). Birds that breed successfully in one year are more likely to return to the same site the following year than are those that fail to fledge young (e.g. Harvey et al. 1979, Gratto et al. 1985, Drilling and Thompson 1988, Gavin and Bollinger 1988, Pärt and Gustafsson 1989, Thompson and Hale 1989, Haas 1990, Payne and Payne 1993, Murphy 1996; but see Bollinger and Gavin 1989). When marked birds are not resighted on a study area, however, we generally do not know whether they have dispersed or died.

Some authors have attributed low return rates of banded birds to mortality (e.g. Askenmo 1979, Harvey et al. 1985, Johnson and Marzluff 1990), whereas others have invoked dispersal (e.g. Högstedt 1981). Although evi-

dence suggests a link between reproductive success and survivorship (Pugesek and Diem 1990) and between reproductive success and breeding dispersal (Harvey et al. 1979, Drilling and Thompson 1988, Jakobsson 1988, Nur 1988a), a causal relationship between an individual bird's failure to produce young and an increased probability of that bird's subsequent dispersal or mortality has not been demonstrated experimentally.

In this study, I examine three hypotheses to explain low return rates by birds that nest unsuccessfully. The low quality hypothesis posits that birds with low reproductive success are low-quality birds that are more likely to suffer mortality between breeding seasons and therefore are less likely to return to their previous breeding site (Coulson 1968, Lambrechts and Dhondt 1986, Pugesek and Diem 1990). The re-nesting stress hypothesis states that nesting failure increases reproductive effort by causing birds to renest; this energetic stress increases the probability of mortality. Lastly, the prior experience hypothesis states that birds use a “decision rule” based on prior experience to select nesting sites. Individuals that experience low reproductive success are more likely to disperse to another breeding site, whereas those that fledge young are more likely to breed again in the same site (Darley et al. 1977, Gratto

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TABLE 1. Responses of birds (centered in bold) in three experimental categories of nesting outcome (successful, natural failure, experimentally induced failure) as predicted by three alternative hypotheses.

Hypothesis	Predicted outcome			Test
	Successful	Natural failure	Induced failure	
	Return rate			
Low quality (LQH)	High	Low	High	Reject LQH if return rates of induced-failure birds are lower than those of successful birds
Renesting stress (RSH)	High	Low	Low	
Prior experience (PEH)	High	Low	Low	
	Body condition			
Low quality	Good	Poor	Good	Reject RSH and PEH if body condition early in season is lower in adults that fail
Renesting stress	Good	Good	Good	
Prior experience	Good	Good	Good	
	Dispersal distance			
Low quality	Equal	Equal	Equal	Reject LQH and RSH if dispersal distance between nests is longer after nesting failure
Renesting stress	Equal	Equal	Equal	
Prior experience	Short	Long	Long	

et al. 1985, Gavin and Bollinger 1988). I tested predictions of these hypotheses (see Table 1) using two species of passerines that breed in a habitat that was easy to census completely. I chose to work with tree- and shrub-nesting birds in a prairie habitat so that I could identify and search all potential nest sites within the study area.

I looked at additional parameters that could support or challenge one or more of the hypotheses. I measured two indices of condition of breeding birds (fat score and a ratio of body mass to body size) to determine whether birds starting the season in poorer condition would be more likely to experience natural nesting failure, because low energy stores often appear to limit reproduction in birds (see Martin 1987). I also examined dispersal distance between subsequent nests (both within and between years) to determine whether birds moved different distances between nest sites after different outcomes of their first nesting attempts. In addition, I compared return rates of birds that nested only once per season with those of birds that nested multiple times per season to determine whether renesting effort resulted in reduced return rates.

METHODS

My field assistants and I monitored the nesting success and movements of marked individuals of two species of migratory passerines, American Rob-

in (*Turdus migratorius*) and Brown Thrasher (*Toxostoma rufum*), breeding in shelterbelts and woody draws in Sioux and Morton counties, south-central North Dakota. Because trees were planted in well-spaced rows, it was possible to search every tree for a nest, completely censusing the study area. The study was conducted during the breeding seasons (April to August) of 1984 to 1989. The study area encompassed 52 shelterbelts at 16 sites and the woody draws within an 8 × 11 km block of agricultural land. The most common woody species planted in shelterbelts included exotic species (Siberian elm [*Ulmus pumila*] and Russian olive [*Eleagnus angustifolia*]) as well as native species (green ash [*Fraxinus pennsylvanica*] and boxelder [*Acer negundo*]). Tree species occurring in wooded creeks included American elm (*Ulmus americana*), boxelder, and green ash. For a more detailed description of the study area, see Haas (1990, 1997) and Titus and Haas (1990).

From 1984 to 1988, we captured 209 adult robins and 282 adult thrashers in mist nets and marked each bird with a unique combination of three colored plastic bands and one aluminum U.S. Fish and Wildlife Service band. From 1986 to 1989, we also painted the tails with Testors model paint for easy identification within a season. Sex was determined by brood patch or cloacal protuberance, or (robins only) by plumage and wing chord. We estimated body condition using the ratio of body mass to tarsus length (Murphy 1980) and interclavicular fat scores. We scored fat on a scale from 0 (no visible fat) to 2 (fat filling the cavity) at intervals of 0.5.

We conducted regular searches of every tree in the 52 shelterbelts and numerous wooded creeks for nests and marked birds. We located nests weekly by

visual searches as we walked on both sides of each row of every shelterbelt or by following adults to nests. Most nests were found during laying or incubation. Because we rarely encountered a marked bird without a nest, and because nests generally were easy to locate, we believe that we found almost all of the nests of banded birds that nested in shelterbelts in the study area. Each nest was visited at least once a week (most more frequently) to identify both parents and to determine the nest's fate. We returned to band young when they were seven to eight days old and checked the area subsequently to determine whether the young had survived to fledging. A nest or adult that produced at least one young to fledging was defined as successful. To determine the number of young fledged, we used the number of young that were banded in nests known to have produced fledglings. Fledging usually occurred within two to four days of banding. Only adults that failed to produce any young in a given season (adults for whom all nesting attempts failed) were defined as unsuccessful for that season.

In 1987, we randomly selected one out of every three pairs of banded thrashers and robins nesting on the study area for nest manipulations, during which we removed all eggs or nestlings from every nest of these pairs during that season. We continued these manipulations for thrashers in 1988, selecting one out of every two pairs for nest manipulations. Most nests were subjected to experimental predation at the egg stage. When we removed nestlings from the nest, nestlings more than two days old were hand-reared, banded, and released. Nestlings younger than two days old were euthanized by thoracic compression or by cervical dislocation following published guidelines (AOU 1988). Collecting and hand-rearing were conducted under federal and state permits and were approved by the University Animal Care and Use Committee.

We measured the distance between consecutive nests of marked birds that bred more than once on the study area with a meter tape, by pacing, or, for distances >500 m, by mapping the locations of the nests on a U.S.G.S. topographic map and measuring the distance between those two points. Within the study area, resighting probability was not related to distance moved because all sites in the 8 × 11 km area were searched uniformly. Because distances moved between nests of a male and female that remained paired were not independent, I did not analyze between-nest dispersal distances separately for each sex. I lumped data for both sexes, but when both members of a pair moved together, I calculated inter-nest distance for only one bird. I calculated between-season return rates by dividing the number of banded birds that returned to breed on the study site in year $n + 1$ by the total number of banded birds breeding on the study site in year n .

I compared the proportions of returning birds in

different classes of reproductive success using 2 × 3 contingency tables. If I found significant differences in the 2 × 3 tables, I partitioned each table into two independent 2 × 2 subtables (Siegel and Castellan 1988) and tested them using Fisher's exact tests. I used two-tailed *t*-tests to compare body-condition indices of birds that nested successfully with birds that failed naturally. When testing the effect of re-nesting on return rate, I included all birds (successful single-brooded and multiple-brooded birds and unsuccessful birds) in the analysis for the following reasons. It was not possible to test only birds whose nests had failed, because almost all birds that failed re-nested within the season. Testing only successful birds would have ignored the population of interest (birds that failed). If repeated nesting is stressful, its effects should be visible in both successful and unsuccessful birds.

RESULTS

Return rate relative to nesting success and nesting attempts.—Resighting probabilities were high, so the observed return rates approximated actual rates of survival and return with minimal bias (Martin et al. 1995). Out of 100 resightings of each species, only 7 were of robins not located in an intervening year (93% resighting probability), and only 8 were of thrashers not located in an intervening year (92% resighting probability). Some missing observations of robins (43%, 3/7) and thrashers (25%, 2/8) occurred when birds moved between sites on the study area.

For both robins and thrashers, return rate in any given year was related to an individual's nesting success in the previous year (Table 2). Return rates differed among birds that nested successfully, experienced natural nest failure, and experienced experimental nest failure for both robins ($\chi^2 = 9.80$, $df = 2$, $P = 0.006$) and thrashers ($\chi^2 = 12.45$, $df = 2$, $P = 0.002$). Return rates of birds that failed experimentally were almost identical to those of birds that failed naturally, both for robins (Fisher exact test, $P = 0.999$) and thrashers (Fisher exact test, $P = 0.999$). Return rates of birds that nested successfully were significantly higher than those of birds whose nests failed (natural and induced failure combined; Fisher exact tests, robins, $P = 0.002$; thrashers, $P = 0.0005$). When sexes were compared separately, the trends remained the same, but differences in return rates depending on previous reproductive success were not significant for female thrashers.

TABLE 2. Observed return rates of American Robins and Brown Thrashers relative to nesting success in the previous year. Values in parentheses are the number of birds that returned/total number.

Sex	Nesting outcome		
	Successful	Natural failure	Induced failure
American Robin			
Males	46% (33/72)	12% (2/16)	20% (1/5)
Females	43% (39/90)	27% (8/30)	17% (1/6)
Sexes combined	44%	22%	18%
Brown Thrasher			
Males	36% (31/87)	17% (5/30)	12% (4/32)
Females	24% (22/90)	9% (3/32)	12% (4/32)
Sexes combined	30%	13%	12%

For robins and thrashers, the tendency to return to the study area in a given year was not related to the number of nesting attempts made in the previous year (Table 3).

Body condition.—During the years when nest manipulations were performed (1987 and 1988), fat scores and ratios of body mass to tarsus length did not differ among birds with different nesting outcomes (Table 4). The only comparison of body condition that approached significance was for female thrashers: mean fat scores were slightly higher for females that nested successfully than for those that failed naturally (1.0 vs. 0.7, respectively; *t*-test, *P* = 0.18; Table 4).

Distance moved between nests.—Observed dispersal distances between nests on the study area ranged from 4 to 1,200 m within seasons and from 0 to 1,300 m between years. No thrashers were observed to move more than

500 m within a season. For both species, dispersal distances between nests tended to be shorter within a given breeding season than between breeding seasons, and tended to be farther after experimental and natural nesting failures than after successful nesting attempts (Figs. 1A–D). The relationship between nesting outcome and dispersal distance was significant, however, only for movements of American Robins within a season. Robins that re-nested after successfully raising one brood moved shorter distances between nests (median = 42 m) than did robins that were relaying after natural nesting failure (median = 71 m;

TABLE 3. Observed return rates of American Robins and Brown Thrashers relative to number of nesting attempts in the previous year. Values in parentheses are the number of birds that returned/total number. *P*-values are from χ^2 tests.

Sex	Number of nesting attempts		<i>P</i>
	One nest	> One nest	
American Robin			
Males	38% (25/65)	39% (11/28)	1.00
Females	35% (31/89)	46% (17/37)	>0.10
Sexes combined	36%	43%	>0.50
Brown Thrasher			
Males	27% (31/113)	29% (8/28)	1.00
Females	19% (24/125)	12% (3/25)	>0.25
Sexes combined	23%	21%	>0.50

TABLE 4. Indices of body condition (ratio of body mass to tarsus length, and fat score) of American Robins and Brown Thrashers relative to nesting success. Data for 1987 and 1988 combined. Values are $\bar{x} \pm SD$, with *n* in parentheses. *P*-values are from two-tailed *t*-tests.

Variable	Nesting outcome		<i>P</i>
	Successful	Natural failure	
American Robin			
Mass/tarsus			
Males	2.1 \pm 0.09 (22)	2.1 \pm 0.10 (8)	0.24
Females	2.3 \pm 0.25 (29)	2.2 \pm 0.22 (7)	0.70
Fat score			
Males	0.6 \pm 0.49 (20)	0.6 \pm 0.80 (6)	0.98
Females	0.8 \pm 0.62 (26)	0.9 \pm 0.56 (7)	0.78
Brown Thrasher			
Mass/tarsus			
Males	1.8 \pm 0.12 (21)	1.8 \pm 0.10 (17)	0.45
Females	1.8 \pm 0.13 (24)	1.9 \pm 0.15 (21)	0.21
Fat score			
Males	0.6 \pm 0.58 (21)	0.6 \pm 0.52 (17)	0.80
Females	1.0 \pm 0.77 (25)	0.7 \pm 0.66 (21)	0.18

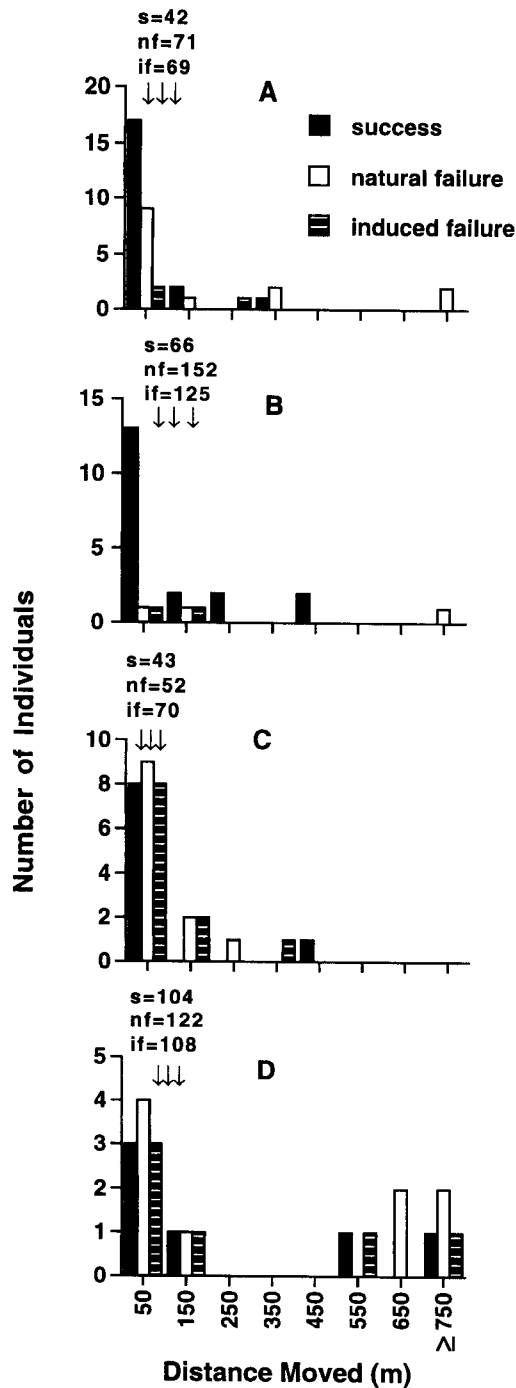


FIG. 1. Number of individual birds moving various distances between successive nests on the study area, in relation to outcome of the first nest. Successful nests produced at least one fledgling, natural failure nests failed naturally, and experimentally induced failure nests were randomly selected and then

Mann-Whitney $U = 281.5, P = 0.017$) or that were relaying after either natural or experimental nesting failure combined (median = 69 m; $U = 303.5, P = 0.020$).

DISCUSSION

Experimental manipulations of reproductive success demonstrate a causal relationship between an individual's failure to reproduce successfully in a season and its failure to return the next year. Randomly selected pairs subjected to experimental nesting failure returned to the study area in lower proportions than did pairs that fledged young and in proportions indistinguishable from those of pairs that experienced natural nesting failure (Tables 2 and 3). These findings allow rejection of any noncausal explanations, such as the low quality hypothesis. Bollinger and Gavin (1989) reached this same conclusion for Bobolinks (*Dolichonyx oryzivorus*) after experimentally causing nests to fail by mowing the entire field in which the birds were nesting. Elsewhere, I have shown that the probability of Brown Thrashers returning to a site is significantly related to the proportion of thrashers nesting at that site successfully in the previous year (Haas 1997), but the results reported here demonstrate that birds also select breeding sites based on their own previous nesting success at a breeding site.

Low quality hypothesis.—The results of the experimental nest manipulation allowed me to reject this hypothesis. Depending on the proportion of low-quality birds existing in the population (and therefore, in the randomly selected

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caused to fail. Values on x-axis represent medians of distance categories (e.g. 150 represents values between 101 and 200 m). Distances ≥ 701 m are lumped in the final category. (A) Distances moved by American Robins between successive nests within a breeding season. (B) Distances moved by American Robins between successive nests between years (between the last nest of the first year and the first nest of the following year). (C) Distances moved by Brown Thrashers within a breeding season. (D) Distances moved by Brown Thrashers between years. Values above bars are median dispersal distances (m) for birds whose previous nest outcome was success (s), natural failure (nf), or induced failure (if).

lected sample), it would be possible to interpret the results of the experimental manipulation differently. Assuming that all surviving birds are site faithful, by definition any bird that is successful is a high-quality bird, and all low-quality birds fail to produce young. (However, not all birds that fail to produce young are low-quality birds.) Specifically, the difference in return rate between successful birds and birds that fail naturally should reflect the proportion of low-quality birds existing in the population if: (1) 100% of the high-quality birds that are alive return; (2) some high-quality birds lose their nests but survive to return (this is the proportion of failed birds that return); and (3) all low-quality birds lose their nests and fail to return. Thus, the argument that my results are dependent on the proportion of low-quality birds in the population can be tested with my data.

For thrashers, the proportion of allegedly low-quality birds was 17% (i.e. 30 – 13; Table 2). The remainder (83%) allegedly are high-quality birds and would return at a rate of 30% (24.9 birds). Therefore, we would expect an overall return rate of 24.9% in a randomly selected group of thrashers. However, the observed return rate, 12%, was less than half of the expected value ($\chi^2 = 5.60$, $P < 0.028$). Similarly, for robins, 22% of the birds (i.e. 44 – 22) allegedly are of low quality (Table 2). The remainder (78%) allegedly are high-quality birds and would return at a rate of 44% (34.3 birds). Therefore, we would expect an overall return rate of 34.3% in a randomly selected group of robins. However, the observed return rate, 18%, was significantly lower than the expected value ($\chi^2 = 6.65$, $P < 0.015$). Even after correcting for the estimated proportion of low-quality birds in the population, then, my results allow me to reject the low quality hypothesis.

Data on body condition also fail to support the hypothesis that birds with low nesting success are low-quality birds, at least as measured by my indices (i.e. fat score and the ratio of body mass to tarsus length).

Renesting stress hypothesis.—The hypothesis that nesting failure induces parental mortality by causing an energetic stress associated with renesting has not been emphasized in the literature, but it is a logical explanation for the relationship between nesting failure and the subsequent failure to return to a site. Although a

tradeoff between reproductive effort and survival of parents has been suggested for some species (Pugesek 1987, Nur 1988b, Jacobsen et al. 1995), the influence of renesting on survival is not clear. This hypothesis actually is just one of a set that composes a larger hypothesis, that nesting failure causes adult mortality. General knowledge of the biology of breeding passerines provides little to suggest that nesting failure causes mortality of adult birds (Biedenweg 1983, Finch 1984, Bryant 1988, Weathers and Sullivan 1989, Ricklefs 1996). The only possibility that seemed plausible enough to warrant testing was that adults are subjected to increased risk of mortality if they deplete their energy reserves by renesting after a nesting failure.

This hypothesis predicts that birds that nest more than once would have lower return rates than birds that nest only once within a season (assuming that this index of reproductive effort is correlated with reproductive cost). However, renesting had no effect on subsequent return rate (Table 3). Thus, my results do not support the hypothesis that the energetic stress of renesting causes increased mortality in adults.

Prior experience hypothesis.—Results of the experimental nest manipulation indicate that nesting failure caused breeders to fail to return to their previous breeding sites, either by causing mortality or dispersal. Because we have rejected the hypothesis that nesting failure increases the probability of mortality of breeders (renesting stress hypothesis), we conclude that nesting failure must increase the probability of dispersal of breeders. The results of the experiment therefore provide strong support for the prior experience hypothesis.

For robins renesting within a season, there was a significant difference in dispersal distances between individuals that were successful versus those that failed. These results again suggest that individual birds responded to nesting failure by moving longer distances to breed. The low overall return rate of birds that failed suggests that much of the movement occurred on a scale greater than that encompassed by the study area (i.e. more than 5 to 10 km). Observations of Wood Thrushes (*Hylocichla mustelina*) moving more than 4 km between nests within seasons and up to 7 km between nesting and molting sites suggest that this

range of movement is not unusual for small passerines (Vega Rivera 1997).

CONCLUSIONS

This is the first study to demonstrate experimentally in migratory passerines that failure of an individual nest causes that bird to disperse. The extent to which this relationship holds in other birds and other vertebrates will be an important avenue for future study. Obviously, many birds that fail to return to a study area are dead, and my results do not rule out a weaker relationship between nesting failure and mortality.

This work has important implications for our understanding and management of bird populations. Although many studies of avian population dynamics assume that immigration balances emigration, and therefore that dispersal is unimportant, the result that breeding dispersal may be linked to another demographic parameter, the production of young, suggests that more attention to detail is required. Protected populations may decline in reserves small enough to undergo cross-population reproductive failure in a given year not only (or even primarily) because of the lack of recruitment, but because of the dispersal of much of the breeding population. Learning more about typical distances and timing of dispersal movements, as well as about the tendency of landscape features to direct these movements (e.g. Villard et al. 1992; Haas 1995, 1997; Matthysen et al. 1995; Machtans et al. 1996), would add greatly to our knowledge of and ability to manage populations of migratory birds.

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