

THE EFFECTS OF SITE QUALITY ON BREEDING-SITE FIDELITY IN BOBOLINKS

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ABSTRACT.—We compared breeding-site fidelity of Bobolinks (*Dolichonyx oryzivorus*) at two low-quality sites (Bald Hill and Shackelton Point, BH+SP) with that at one high-quality site (Moore Road, MR) in central New York. Yearly density of fledglings at Moore Road was more than six times the density at Bald Hill and Shackelton Point. Furthermore, individual residents fledged 50–70% more young at the high-quality site. At Moore Road, 70% of the males and 49% of the females returned one or more times, compared with 44% of the males and 25% of the females at the low-quality sites. Successful residents (i.e. those fledging one or more young the previous year) were equally likely to return at all sites. However, the return rates of unsuccessful residents were more than three times higher at the high-quality site. Neither overall return rates nor intrasite dispersal of returning residents differed between individuals that had been successful or unsuccessful the previous year at the high-quality site. At the low-quality sites, individuals unsuccessful the previous year were much less likely to return than were successful individuals (55% vs. 19% for males, 41% vs. 9% for females). Those unsuccessful individuals that did return tended to move farther between nest sites than successful individuals. Overall, site productivity was the best predictor of yearly, site-specific return rates. For females (but not for males), individuals that were resident in one or more years previous were more likely to return than were novice residents (47% vs. 20%). Individuals that had nests experimentally destroyed by hay-cropping returned at similar rates to those of naturally unsuccessful residents. We believe that the patterns of breeding-site fidelity in Bobolinks are primarily the result of experience-based choices by the birds and do not simply reflect patterns of mortality. Bobolinks appear to use both their own reproductive success and that of others at their site to influence their decision to return to a breeding site. Received 18 October 1988, accepted 22 April 1989.

STRONG site fidelity has been documented in many avian species (Greenwood 1980, Greenwood and Harvey 1982). There is, however, little consensus concerning the ultimate cause of this behavior. The balance between breeding dispersal (Greenwood 1980) and natal dispersal has been interpreted as the result of group selection (Howard 1960, Johnston 1961), inbreeding avoidance (Greenwood and Harvey 1976, Greenwood et al. 1978, Koenig and Pitelka 1979), intraspecific competition (Murray 1967, Moore and Ali 1984), optimal outbreeding (Bateson 1978, 1982; Shields 1982), and physiological constraints (Ligon et al. 1988).

Although ultimate causes of breeding-site fidelity have been difficult to study, its proximate correlates have been more easily managed. In a wide variety of avian taxa, higher return rates or shorter dispersal distances are observed for individuals successful in hatching or fledging

young the previous year (e.g. Delius 1965, Nolan 1978, Harvey et al. 1979, Newton and Marquiss 1982, Oring and Lank 1982, Dow and Fredga 1983, Gratto et al. 1985, Weatherhead and Boak 1986), although this pattern is not always found (Austin 1949, Bédard and LaPointe 1984, Haig and Oring 1988a). In some species, philopatry increases with age of breeding adults (e.g. Austin 1949, Newton and Marquiss 1982, Oring and Lank 1982, Harvey et al. 1984, but see Darley et al. 1977, Bédard and LaPointe 1984, Atwood and Massey 1988) and with territory quality (Baeyens 1981, Newton and Marquiss 1982). However, the fate of nonreturning individuals is generally not known, and their disappearance could be due either to dispersal (Weatherhead and Boak 1986, Drilling and Thompson 1988), mortality (Nol and Smith 1987), or both.

Few investigators have examined patterns of breeding-site fidelity at more than one site. Those that have studied multiple sites either have not considered explicitly (e.g. Soikkeli 1970, Lessells 1985) or did not have (e.g. Gavin

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and Bollinger 1988, Drilling and Thompson 1988) differences among sites in philopatry patterns. Furthermore, there have been very few experimental studies of philopatry (but see Berndt and Sternberg 1968, Haukioja 1971).

Previously (Gavin and Bollinger 1988), we examined the relative importance of various reproductive parameters that influence breeding-site fidelity of Bobolinks (*Dolichonyx oryzivorus*) at two low-quality sites. We found large differences in reproductive success the previous year between returning and nonreturning individuals. The number of young fledged was the strongest positive correlate of whether or not an individual returned. Subsequently, we tested the generality of these patterns by examining breeding-site fidelity of Bobolinks at a high-quality site and by experimentally manipulating nest success. Our objectives were to compare patterns and reproductive correlates of breeding-site fidelity of Bobolinks between high- and low-quality sites and to determine the influence of Bobolink age or experience on philopatry. We examined the effects of an experimental manipulation of nest success on breeding-site fidelity and determined the relative importance of mortality and dispersal in influencing patterns of breeding-site fidelity in Bobolinks.

METHODS

Study areas.—The majority of this study was conducted at three sites in central New York: Bald Hill (BH), Shackelton Point (SP), and Moore Road (MR). Moore Road and Shackelton Point were 3.8 km apart; both were ca. 95 km from Bald Hill. Nesting habitat consisted of four contiguous hayfields (22 ha) at BH (42°21'N, 76°23'W), two meadows (22 ha) at SP (43°10'N, 75°56'W), and two contiguous hayfields (19 ha) at MR (43°8'N, 75°55'W). We studied BH and SP from 1982–1985 and MR from 1984–1987, although only briefly in 1987 (see Gavin 1984, Gavin and Bollinger 1985, Wootton et al. 1986 for details). Prior to the 1986 breeding season, 8 ha of MR were converted to pasture and this area became unsuitable as nesting habitat for Bobolinks. Only males with a territory in the section that was not pasture, and females with nests in this nonpasture section in 1985, were considered in the sample of individuals used to calculate return rates for 1986. In 1985, nest success was manipulated experimentally by hay-cropping at both MR and a fourth site, Lestina Road (LR). Nesting habitat at LR (43°9'N, 75°54'W) consisted of two hayfields (8.5 ha). This site was studied from 1985–1987.

Capture and marking.—At each site, we captured, banded (USFWS bands), and individually marked adults by painting stripes on their tails. Many males and females were captured in nets placed in males' territories. Females were also captured in nets adjacent to their nests. In all years and at all sites, >90% of territorial males and nesting females were captured and marked. Most unmarked males were unpaired birds that abandoned the sites after holding a territory for 1–3 weeks. Most unmarked females disappeared immediately after their nests were destroyed by predators early in the nesting cycle. Some of these females may have been captured at a later date when re-nesting. Captures began in early May when males arrived, and most individuals of both sexes were captured by late May. We continued mist-netting, however, until early July because new birds arrived, possibly from other sites. All nestlings were banded at 7–9 days after hatching.

Procedures and definitions.—We recorded the presence or absence of each marked individual every 2–3 days beginning with the arrival of the first birds. Territory boundaries of males were mapped using a combination of Wiens' (1969) flush technique and aggressive encounters between adjacent males. Each site (except Lestina Road) was gridded with color-coded metal stakes at either 40- or 50-m intervals to facilitate mapping of territories, nests, and behaviors. Courtship, copulations, and nest attendance, as well as the territory on which a female nested, allowed us to determine which birds were paired. Each nest was checked every 1–2 days to record clutch size, number of eggs hatched, and number of young fledged.

A male was defined as a *resident* if he was territorial ≥ 7 days; a female was defined as a *resident* if she built a nest. All nonresidents were considered *transients*. Most individuals either disappeared the same day they were captured or became residents. After the initial year of study at each site, residents were classified as either *former residents* (resident in a previous year at the same site) or *novice residents* (never before classified as a resident at that site). We considered that a bird returned in year $t + 1$ if it was resident at the same site in year t and $t + 1$. We defined a *successful* bird as one that fledged ≥ 1 young from its nest or territory.

We used data collected at Bald Hill and Shackelton Point in 1982–1985 and Moore Road in 1984–1986 to determine which residents returned from the previous year, and to compare reproductive parameters between MR and BH+SP. Data from 1983–1985 (BH+SP) and 1985–1986 (MR) were used to compare former residents with novice residents. A total of 9 females (5 at BH+SP and 4 at MR) disappeared from our sites immediately after being captured at their nests. These females were excluded from analyses. Eighty-five males (59 different individuals) and 86 females (71 individuals) were resident at BH and SP during 1982–1984. At MR, 79 males (56 individuals)

TABLE 1. Variables used in analyses of the relationship of reproductive success to site fidelity in Bobolinks. All variables refer to one breeding season.

Males	
MATE	Total number of mates acquired on territory
NEST	Total number of nests built on territory
EGG	Total number of eggs laid in nests on territory
HATCH	Total number of eggs hatched on territory
FLEDGE	Total number of young fledged from nests on territory
FLEGG	Total number of young fledged on territory divided by the total number of eggs laid on territory
Females	
NEST	Total number of nests built by a female
EGG	Total number of eggs laid by a female
HATCH	Total number of eggs hatched by a female
FLEDGE	Total number of young fledged by a female
FLEGG	Total number of young fledged by a female divided by total number of eggs laid by that same female
LFLEDGE	Total number of young fledged by a female on her last nesting attempt*

* LFLEDGE = FLEDGE except for 6 females at Bald Hill that attempted a second nest after fledging young from their first (Gavin 1984).

and 85 females (68 individuals) were resident during 1984–1985.

Statistical analyses.—We used stepwise logistic regression (Harrell 1986) to determine which reproductive variables were the most effective at explaining the variation in the return behavior of birds at our sites the following year. We used six sex-specific variables in these analyses (Table 1). Chi-square tests ($df = 1$ unless noted otherwise), Fisher's exact tests, Mann-Whitney U -tests, and t -tests were used for other comparisons.

As elsewhere (Gavin and Bollinger 1988), we combined data from Bald Hill and Shackleton Point (denoted BH+SP) for all subsequent analyses. These 2 sites had overall return rates similar to each other for each sex ($\chi^2 < 0.80$, $P > 0.30$), and they did not differ significantly (χ^2 and Fisher's exact tests, all $P > 0.20$, mean $P = 0.60$) in any of the more specific categories of return rates discussed below. In addition, BH and SP had similar Bobolink densities (residents/ha; $t = 1.22$, $df = 6$, $P = 0.28$) and yearly site productivities (fledglings/ha; $t = 1.42$, $df = 6$, $P = 0.21$), although each differed from Moore Road for both variables ($P < 0.05$).

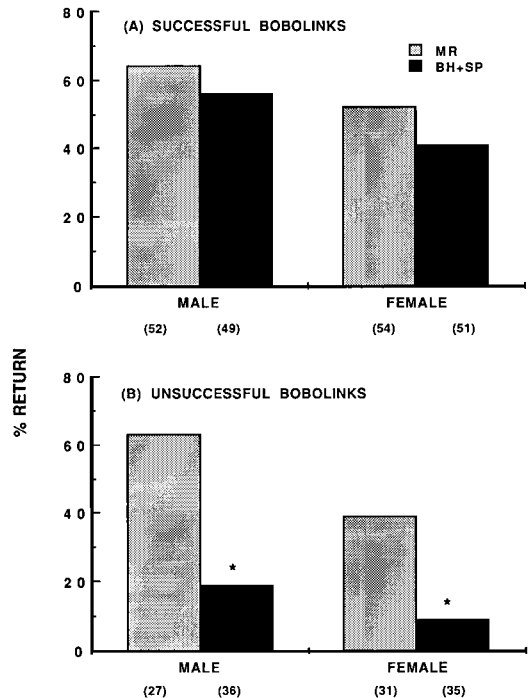


Fig. 1. Return rates (% of residents returning) in year $t + 1$ for Bobolinks that were (A) successful in year t and (B) unsuccessful in year t at a high-quality site (Moore Road) compared with rates at low-quality sites (Bald Hill & Shackleton Point). An asterisk indicates significant difference ($P < 0.01$, χ^2 tests); only within-sex comparisons were made. No significant differences existed for successful residents ($\chi^2 < 1.25$, $P > 0.25$). Sample sizes are in parentheses.

RESULTS

Comparison of return rates and reproductive success between sites.—A higher proportion of both males (70%) and females (49%) returned at least once to Moore Road than to Bald Hill and Shackleton Point (44% for males, 25% for females, $\chi^2 > 7.50$, $P < 0.01$). For residents that were successful in year t , there were no significant differences in return rates in year $t + 1$ between MR and BH+SP for either sex ($P > 0.25$, Fig. 1A). However, unsuccessful residents at MR were 3–4 times more likely to return the next year than at BH+SP for both sexes ($P < 0.005$, Fig. 1B). Males returned more frequently than females at both MR and BH+SP ($\chi^2 > 5.00$, $P < 0.025$).

At Moore Road, successful and unsuccessful residents returned at similar rates the next year ($\chi^2 = 0.00$, $P > 0.95$ for males; $\chi^2 = 1.37$, $P >$

TABLE 2. Comparison of reproductive variables ($\bar{x} \pm 1$ SD) in year t for Bobolinks that returned to a high-quality site (Moore Road) in year $t + 1$ with those for Bobolinks that did not return in year $t + 1$. Successful Bobolinks fledged ≥ 1 young from their territory (males) or nests (females) in year t . P values are for Mann-Whitney U -tests.

Variables	All residents			Successful residents		
	Returned ($n = 50\delta, 40\varphi$)	Did not return ($n = 29\delta, 45\varphi$)	P	Returned ($n = 33\delta, 28\varphi$)	Did not return ($n = 19\delta, 26\varphi$)	P
Males						
MATE	1.28 \pm 0.70	1.24 \pm 0.69	0.90	1.39 \pm 0.66	1.53 \pm 0.61	0.32
NEST	1.44 \pm 0.79	1.34 \pm 0.81	0.57	1.55 \pm 0.71	1.58 \pm 0.77	0.90
EGG	7.46 \pm 4.06	6.97 \pm 4.13	0.59	8.18 \pm 3.64	8.16 \pm 3.91	0.77
HATCH	5.18 \pm 3.06	5.34 \pm 3.37	0.72	5.79 \pm 2.87	6.79 \pm 2.68	0.24
FLEDGE	3.12 \pm 2.58	3.34 \pm 2.79	0.83	4.73 \pm 1.55	5.11 \pm 1.63	0.63
FLEGG ^a	—	—		0.66 \pm 0.27	0.71 \pm 0.25	0.44
Females						
NEST	1.17 \pm 0.38	1.07 \pm 0.25	0.13	1.11 \pm 0.31	1.04 \pm 0.20	0.35
EGG	6.27 \pm 1.97	5.47 \pm 1.56	0.02	5.93 \pm 1.56	5.50 \pm 1.39	0.25
HATCH	4.65 \pm 1.61	4.38 \pm 1.69	0.49	4.82 \pm 1.31	4.72 \pm 1.06	0.90
FLEDGE ^b	3.02 \pm 2.26	2.49 \pm 2.37	0.35	4.32 \pm 1.25	4.32 \pm 1.28	0.91
FLEGG	0.54 \pm 0.41	0.45 \pm 0.44	0.41	0.77 \pm 0.24	0.80 \pm 0.23	0.75

^a FLEGG not included for all males because several had 0 eggs.
^b FLEDGE = LFLEDGE at Moore Road; no double-brooded females.

0.20 for females). In addition, all but one of the measured reproductive variables were similar for returning and nonreturning individuals of each sex at this site ($P > 0.10$, Table 2). Females that returned had laid more eggs the previous year than those that did not return. No reproductive variables for either sex were entered into stepwise logistic regression models as ex-

plaining significant variability ($P < 0.05$) in the return patterns of Bobolinks at MR. In contrast, variables associated with fledging success (FLEDGE for males, LFLEDGE for females) were highly significant ($P < 0.001$) predictors of the sex-specific return patterns at Bald Hill and Shackelton Point (BH+SP), and successful residents were 3–5 times more likely to return than unsuccessful residents. Among successful residents only, there were no significant differ-

TABLE 3. Comparison of reproductive variables ($\bar{x} \pm 1$ SD) for Bobolinks at two low-quality sites (BH + SP)^a with those for Bobolinks at a high-quality site (MR)^b. P -values are for Mann-Whitney U -tests.

Variables	BH + SP ($n = 111\delta,$ 108 φ)	MR ^c ($n = 111\delta,$ 122 φ)	P
	Males		
MATE	1.05 \pm 0.92	1.23 \pm 0.73	0.04
NEST	1.22 \pm 1.18	1.33 \pm 0.80	0.07
EGG	5.65 \pm 5.51	6.89 \pm 4.04	0.004
HATCH	3.56 \pm 3.66	5.31 \pm 3.34	<0.001
FLEDGE	2.26 \pm 2.65	3.90 \pm 2.68	<0.001
Females			
NEST	1.18 \pm 0.45	1.07 \pm 0.25	0.03
EGG	5.60 \pm 2.23	5.61 \pm 1.46	0.55
HATCH	3.60 \pm 2.47	4.62 \pm 1.61	<0.001
FLEDGE	2.33 \pm 2.21	3.48 \pm 2.08	<0.001
FLEGG	0.43 \pm 0.41	0.64 \pm 0.38	<0.001
LFLEDGE	2.08 \pm 2.19	3.48 \pm 2.08	<0.001

^a Bald Hill and Shackelton Point.
^b Moore Road.
^c Males (9) and females (13) at Moore Road (MR) who were unsuccessful because of hay-cropping operation in 1985 were excluded.

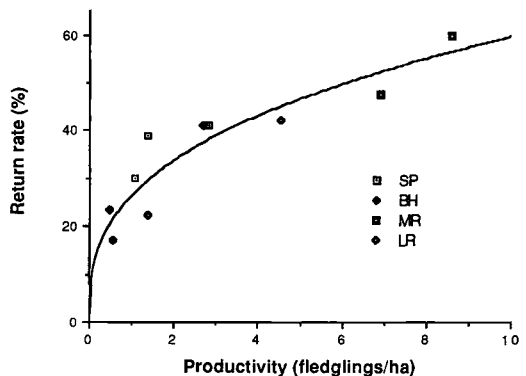


Fig. 2. Relationship between Bobolink return rate (% of residents returning) in year $t + 1$ and yearly site productivity in year t (fledglings/ha) for Shackelton Point, Bald Hill, Lestina Rd., and Moore Rd. The equation for the curve is $y = 27.8 + 12.3 \cdot \ln(x)$ ($r^2 = 0.85, P < 0.001$). Each point represents one year; males and females were combined.

TABLE 4. Wing chord measurements (mm, $\bar{x} \pm 1$ SD) of Bobolinks for all sites combined. Residents were compared with transients and former residents were compared with novice residents (2-way ANOVA, * = $P < 0.001$).

Category	Males		Females	
	$\bar{x} \pm$ SD	<i>n</i> ^a	$\bar{x} \pm$ SD	<i>n</i> ^a
Residents	97.4 \pm 2.8	301	87.5 \pm 2.6	261
Transients	96.0 \pm 2.5	90*	87.7 \pm 2.2	52 ^b
Former residents	98.3 \pm 2.5	118	88.5 \pm 2.4	74
Novice residents ^c	96.8 \pm 2.9	84*	87.0 \pm 2.7	114*

^a Sample sizes include individuals from all sites (BH, LR, MR, SP, and several other nearby locations).

^b $P > 0.50$.

^c For males, novice residents had longer wing chords than transients ($P < 0.05$).

ences between returning and nonreturning individuals of either sex at MR for these reproductive variables (Table 2). At BH+SP, successful males that returned the next year ($t + 1$) had fledged more young (year t) than those that did not return. Successful females that returned had built fewer nests and laid fewer eggs (Gavin and Bollinger 1988).

Resident males at MR had, on average, more mates, more eggs laid, more eggs hatched, and more young fledged on their territories than males at BH+SP ($P < 0.05$, Table 3). Similarly, resident females at MR averaged more eggs hatched, more young fledged, more young fledged per egg laid, and more young fledged on the last brood than females at BH+SP ($P < 0.001$, Table 3). In addition, *yearly site productivity* (defined as the number of fledglings produced per ha of nesting habitat each year) was significantly higher at MR than at BH+SP: an average of 9.4 ± 3.0 fledglings/ha were produced at MR compared with 1.5 ± 1.1 fledglings/ha at BH+SP ($t = 4.50$, $df = 3$, $P < 0.05$).

Relationship between site productivity and return rate.—There was a nonlinear increase in return rate (percentage of residents returning the next year, sexes combined) with increased site productivity with all sites and years included ($r^2 = 0.85$, $P < 0.001$, Fig. 2). Return rate was more

highly correlated with \ln (site productivity) ($r = 0.92$) than with the percentage of successful residents ($r = 0.84$), average individual productivity (total number fledging divided by number of residents, $r = 0.79$), % nest success ($r = 0.67$), or density of residents (residents/ha, $r = 0.70$). Site productivity was the only variable of this group that appeared to have a nonlinear relationship with return rate. Nevertheless, the linear correlation between site productivity and return rate was still the highest ($r = 0.89$).

Comparison of wing chords.—Wing chords increased in length for both males and females in both the second and third season that those individuals were present (paired t -tests, $n = 21-65$, $P < 0.05$, all sites combined). The average yearly increase was 1.1 mm for males and 1.0 mm for females. Wing chords of former residents were ca. 1.5 mm longer than those of novice residents ($P < 0.001$, Table 4) for each sex. For males, both residents overall and novice residents had longer wing chords than transients (Table 4).

Wing chords of residents at Moore Road were longer than those at Bald Hill and Shackleton Point for both males ($P < 0.001$, Table 5) and females ($P < 0.05$, Table 5). This difference was relatively greater for males (1.7%) than for females (0.8%). For males, both former residents

TABLE 5. Comparison of mean wing chord measurements (mm) for Bobolinks at low-quality sites (BH + SP)^a with those at high-quality site (MR).^b P values are for t -tests; sample sizes are in parentheses.

Category	Males			Females		
	BH + SP	MR	P	BH + SP	MR	P
All residents	96.5 (92)	98.1 (124)	<0.001	87.1 (78)	87.8 (143)	0.03
Former residents	97.3 (42)	98.5 (56)	0.04	88.1 (26)	88.7 (43)	0.24
Novice residents	95.9 (46)	97.9 (19)	0.002	86.7 (49)	87.1 (44)	0.37

^a Bald Hill and Shackleton Point.

^b Moore Road.

TABLE 6. Comparison of reproductive variables ($\bar{x} \pm 1$ SD) for former resident and novice-resident Bobolinks. Data from all sites¹ are combined. Individuals that were unsuccessful because of hay-cropping operations at Moore Road and Lestina Road in 1985 are excluded. *P*-values are for Mann-Whitney *U*-tests.

Variables	Former residents (<i>n</i> = 85♂, 61♀)	Novice residents (<i>n</i> = 63♂, 87♀)	<i>P</i>
Males			
MATE	1.32 ± 0.89	0.86 ± 0.80	0.002
NEST	1.45 ± 1.10	0.86 ± 0.80	0.001
EGG	7.24 ± 5.27	4.11 ± 3.84	<0.001
HATCH	5.48 ± 4.01	3.03 ± 3.27	<0.001
FLEDGE	3.49 ± 2.98	2.30 ± 2.73	0.01
Females			
NEST	1.13 ± 0.39	1.02 ± 0.21	0.04
EGG	6.02 ± 1.67	5.00 ± 1.38	<0.001
HATCH	4.90 ± 1.88	3.83 ± 2.00	0.003
FLEDGE	3.62 ± 2.15	2.51 ± 2.32	0.005
FLEGG	0.63 ± 0.38	0.50 ± 0.43	0.05

¹ Bald Hill, Lestina Road, Moore Road, and Shackelton Point.

(*P* < 0.05) and novice residents (*P* < 0.005) had longer wing chords at MR than at BH+SP. For females, neither of these differences was evident (*P* > 0.20).

Former residents vs. novice residents.—Former residents had higher reproductive success than novice residents. Former resident males had more mates, nests, eggs, eggs hatching, and young fledging from their territories than novice residents (*P* < 0.05, Table 6). For females, former residents built more nests, laid more eggs, hatched more eggs, fledged more young, and fledged more young/egg than novice residents (*P* < 0.05, Table 6).

For males there were no significant differences between return rates for former residents and novice residents at either Moore Road or Bald Hill and Shackelton Point (*P* > 0.75, Fig. 3A). However, for females, former residents appeared more likely than novice residents to return the next year at both MR and BH+SP (*P* < 0.10, but *P* < 0.01 with all sites combined, Fig. 3B). This pattern was evident only for unsuccessful females ($\chi^2 = 4.82$, *P* < 0.05); successful former residents and successful novice residents were equally likely to return the next year (*P* > 0.20).

Return rates (sexes combined) of both unsuccessful former residents and unsuccessful novice residents were higher at MR than at BH+SP.

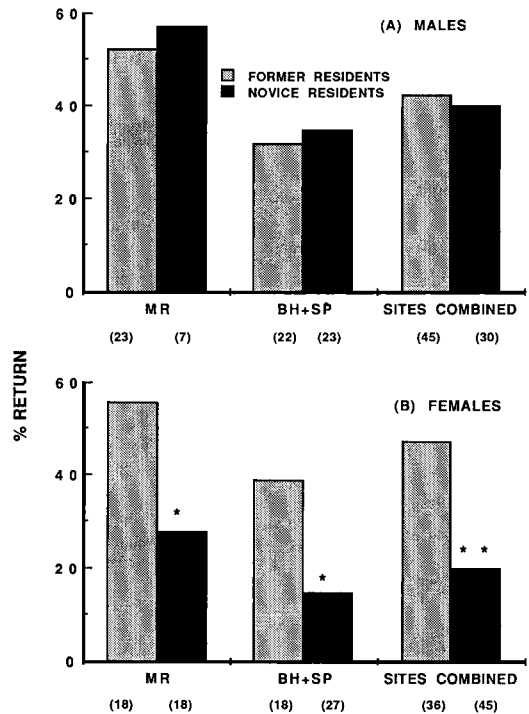


Fig. 3. Comparison of Bobolink return rates (% of residents returning) between former residents and novice residents for (A) males and (B) females at a high-quality site (Moore Road), 2 low-quality sites (Bald Hill & Shackelton Point), and with all 3 sites combined. Asterisks indicate significant differences (* = *P* < 0.10, ** = *P* < 0.01, χ^2 tests). Sample sizes are in parentheses.

At MR, 63% (12 of 19) of unsuccessful former residents and 33% (5 of 15) of unsuccessful novice residents returned, compared with 25% (6 of 24) and 7% (2 of 27) at BH+SP ($\chi^2 = 6.34$, *P* < 0.02 for former residents; Fisher's exact test, *P* < 0.05 for novice residents). Similar comparisons with successful individuals were not significant (*P* > 0.75).

Movement of marked adults.—Returning males at Moore Road dispersed a median distance of 37 m (between territory centers; $\bar{x} = 46$ m, *n* = 50) between successive years. Females dispersed a median distance of 55 m (between nest sites; $\bar{x} = 65$ m, *n* = 40). The difference between the sexes is significant (Mann-Whitney *U*-test, *P* < 0.01). There were no significant differences, however, in dispersal distances (Mann-Whitney *U*-tests, *P* > 0.70) between successful and unsuccessful individuals of either sex returning to MR (males: successful, median = 38 m; un-

successful, median = 37 m; females: successful, median = 53 m; unsuccessful, median = 62 m).

At Bald Hill and Shackelton Point (BH+SP), returning males dispersed farther (median = 74 m, \bar{x} = 93 m) than those at MR (Mann-Whitney *U*-test, $P < 0.01$). The unsuccessful males that returned tended to disperse greater distances (n = 7, median = 134 m) than successful males (n = 23, median = 65 m, $P = 0.10$). Returning females at BH+SP dispersed a median distance of 110 m (\bar{x} = 138 m), greater than MR females (Mann-Whitney *U*-test, $P < 0.01$). Although only three unsuccessful females returned to BH+SP, they dispersed farther (median = 300 m) than the 23 successful females that returned (median = 101 m, $P < 0.05$).

Six individuals (5 males, 1 female) that were resident at SP were resident at another site in a later year. All of these birds moved to sites of higher Bobolink density. The wing chords of 83% (5/6) of these individuals were longer than the average wing chord for former residents at SP. Another male, a previous resident at BH, was captured 2.5 km from BH at a site with a denser Bobolink population. This male attempted to obtain a territory at this site, but later that day it was territorial at BH, where it became a resident. This situation also occurred once at SP. One male that was a transient at Moore Road was later discovered as a resident at a site of lower density 3.6 km away. In addition, one female whose nest was destroyed by hay-cropping at Lestina Road in 1985 was a resident at Moore Road in 1986 (2.6 km from LR).

Effects of haying on return rates.—From 10 June to 4 July 1985, Moore Road was hayed; 22 of 61 nests were destroyed. Lestina Road was hayed between 12–25 June 1985; 10 of 12 nests were destroyed. The adults associated with these nests were not injured by the mowing. At MR, return rates for males that were unsuccessful because of mowing (67%, 6 of 9) were similar to those for naturally unsuccessful males (61%, 11/18, Fisher's exact test, $P > 0.90$). Five of 13 (38%) females that were unsuccessful because of mowing returned, compared with 7 of 18 (39%) naturally unsuccessful females ($\chi^2 = 0.00$, $P > 0.95$ for females). However, return rates of birds unsuccessful because of mowing at MR were also not significantly different from those of successful individuals ($\chi^2 = 0.03$, $P > 0.75$ for males; $\chi^2 = 0.75$, $P > 0.25$ for females). At LR, 33% (3/9) of males and 0% (0/10) of females that were unsuccessful because of mowing returned the

next year. We have few data at this site on the return rates of naturally unsuccessful individuals (1 of 3 males and 0 of 2 females returned). However, return rates of all residents (successful and unsuccessful) at LR with nests not destroyed by haying were higher for both sexes than those for individuals with nests destroyed by haying (50%, 6/12 males; 40%, 4/10 females). The difference was significant for females (Fisher's exact test, $P < 0.05$) but not for males (Fisher's exact test, $P = 0.20$).

DISCUSSION

Age/experience differences.—Patterns of wing chords (e.g. former residents had longer wing chords than novice residents) suggested that novice residents were, on average, younger birds than former residents. It is also possible that novice residents were not younger but that smaller residents were less likely to survive. However, the increase in wing chord for birds caught in multiple years (see also Bédard and LaPointe 1984, Smith et al. 1986) supports the conclusion that novice residents were also younger. They had, to our knowledge, no breeding experience at our sites. The combined effects of age and experience probably affected reproductive success for both sexes (Harvey et al. 1985); former residents fledged more young than novice residents. Increased reproductive success with age is common among long-lived birds (e.g. Coulson 1966, Fisher 1969, Thomas 1980), but appears less pervasive in shorter-lived species (e.g. Bédard and LaPointe 1985). Alternatively, the higher reproductive success of older birds could be at least partially due to high mortality rates of poor-quality individuals among the younger birds (Nol and Smith 1987).

Return rates increased with age for female Bobolinks (i.e. the return rate of former residents was higher than that of novices) in our study (see also Thomas 1980, Newton and Marquiss 1982, Harvey et al. 1984), but did not increase for males. This difference may be a result of the resource-defense mating system of Bobolinks. Territory acquisition appears critical to a male's reproductive success, and wing-chord data suggest that smaller (and probably younger) males often failed to obtain territories. Thus, philopatry may not increase with age for males because the youngest males, which are most likely to disperse (or die), often are nonterritorial transients.

Site differences in philopatry patterns.—Moore Road had the highest productivity (fledglings \cdot ha⁻¹ \cdot yr⁻¹) and Bald Hill and Shackelton Point had the lowest productivity of published Bobolink studies (Martin 1971, 1974; Wittenberger 1978). Bobolinks were approximately two times as likely to return to the high-quality site (MR) as to the two low-quality sites (BH+SP). This difference was due primarily to the much higher return rate for unsuccessful residents at MR. High return rates regardless of breeding experience can occur if breeding habitat is limited and alternative sites are rare or far away (Haig and Oring 1988b). However, this was not the case for Bobolinks in our study areas. For example, >200 Bobolink territories were present each year within 5 km of MR (Bollinger unpubl. data). Thus, unsuccessful birds at MR had numerous alternative sites but still did not usually disperse.

Explanations for patterns of return take two extremes. First, patterns of return may be solely the result of mortality patterns. All adults that survive until the next breeding season return to the site where they bred the year before. With regard to our results, this "mortality hypothesis" implies that most unsuccessful individuals die, at least at low-quality sites. Any increase in return rate with age is the result of natural "culling" of poor-quality individuals after their initial nesting attempt, or increased survival with age independent of a bird's quality. The alternative option is that mortality patterns are independent of site and reproductive success, and patterns of return result from experience-based choices by birds. This "choice hypothesis" suggests that most unsuccessful individuals at the poor-quality sites choose not to return and that the increases in return rate with age for female Bobolinks might be the result of previous experience at the site. For example, females unsuccessful in one year may return the next year if they have been successful at the site in an earlier year. It is likely that neither hypothesis is completely correct. The important question is whether mortality or choice is the dominant determinant of breeding-site fidelity.

Wing-chord data provide some support for the mortality hypothesis, at least for males. The longer wing chords at MR indicate that these birds were older, more dominant, or both, than those at BH+SP. This pattern was especially evident among male novice residents. Males appeared to be older and larger before they first

became residents at the high-quality site. These "high-quality" birds might be expected to have high survival rates regardless of reproductive success. Thus, the high return rate for unsuccessful males at MR might be due to the presence of high-quality individuals at this site. Females did not appear to be older or larger before they first became residents at MR, as wing chords were not different between MR and BH+SP for novice females. The fact that wing chords of females were, overall, larger at MR may be simply due to the higher proportion of former residents at MR.

We feel that our data are more consistent with the choice hypothesis than the mortality hypothesis for several reasons. First, in 7% (11/160) of the instances in which a bird did not return, we knew it was alive, because it was either captured at another site ($n = 7$) or at the same site in a subsequent year ($n = 4$). Because we spent little time at other sites in all but one year (1984), it is probable that there were many more birds that dispersed.

Second, results of the haying experiment support the choice hypothesis, at least for females. If birds that fail naturally are "poor-quality" individuals that are more likely to die, as predicted by the mortality hypothesis, then individuals that fail artificially (some of which are "high-quality" individuals) should return at higher rates than naturally unsuccessful birds. The return rates for these two groups of birds were virtually identical at MR for both sexes. On the other hand, because naturally unsuccessful residents had relatively high return rates at this site, then the mortality hypothesis would also predict equivalent return rates for naturally and artificially unsuccessful individuals because MR birds were all of "high-quality." At Lestina Road, however, no females (0/10) that were unsuccessful because of hay-cropping returned the following year. Their return rate must have been less than or equal to that for naturally unsuccessful residents and was lower than that for all nonmanipulated females at this site. The mortality hypothesis predicts similar return rates for manipulated and all nonmanipulated birds, because similar proportions of high- and low-quality individuals could be expected in both groups. Furthermore, we know that at least 1 of the 10 "disturbed" females changed sites (to MR). For males at LR, 3 of 9 that were unsuccessful because of mowing returned. This frequency was lower, but not sig-

nificantly lower, than all nonmanipulated males (50%, 6/12). Thus, no firm conclusion for males can be drawn from the mowing experiments.

Third, unsuccessful former residents were more likely to return the next year to MR than to BH+SP. These individuals at BH+SP, returned after a successful breeding season, had already shown that they were "high-quality" individuals according to the mortality hypothesis. Thus, the return rates at MR and BH+SP for this category should have been nearly equal if mortality were the primary determinant of philopatry patterns. Alternatively, if unsuccessful individuals choose whether or not to return, they may use site quality to influence their decision. Experienced breeders moved between sites, generally to sites of higher quality. These birds tended to have relatively large wing chords, suggesting that older, dominant individuals may look for a better site. This movement pattern may explain why males at MR had longer wing chords than at BH+SP.

Fourth, nesting success seemed to influence intrasite dispersal at the poor-quality sites but not at the high-quality site. Birds often move greater distances between nest sites after an unsuccessful attempt than after a successful attempt, both within (e.g. Shields 1984, but see Greig-Smith 1982) and between breeding seasons (e.g. Harvey et al. 1979, Newton and Marquiss 1982, Dow and Fredga 1983). When suitable habitat is found in discrete patches (as is the case for Bobolinks in New York), this greater movement after an unsuccessful year could result in intersite dispersal and a lack of return to the poor-quality sites. We feel our results more strongly support the choice hypothesis but that more extensive experimental tests of philopatry are needed.

We concluded previously that fledging success was the primary determinant of whether a bird returned (Gavin and Bollinger 1988), but no difference in return rate between successful and unsuccessful birds occurred at Moore Road. The observed patterns of return at this site imply that individuals may include an assessment of site quality (Weatherhead and Boak 1986, Beletsky and Orians 1987 but see Korpimäki 1988) or use breeding experiences for years other than the most recent one when deciding whether or not to return. Bobolinks may be able to judge the overall productivity of a site when adults and fledglings gather into large flocks at the end of the breeding season. The return of

unsuccessful birds to a high-quality site may be adaptive because the probability of breeding success the following year is high.

Finally, we believe that patterns seen at one site may not generalize to the same species at other sites (Haig and Oring 1988b). The common practice of selecting the densest and most convenient aggregation of a species for research (as we did in choosing Moore Road) may lead to patterns and measurements markedly different from other sites with average or low densities.

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LITERATURE CITED

- ATWOOD, J. L., & B. W. MASSEY. 1988. Site fidelity of Least Terns in California. *Condor* 90: 389-394.
- AUSTIN, O. L. 1949. Site tenacity, a behaviour trait of the Common Tern (*Sterna hirundo* Linn.). *Bird-Banding* 20: 1-39.
- BAEYENS, G. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* 69: 145-166.
- BATESON, P. P. G. 1978. Sexual imprinting and optimal outbreeding. *Nature* 273: 659-660.
- . 1982. Preferences for cousins in Japanese Quail. *Nature* 295: 236-237.
- BÉDARD, J., & G. LAPOINTE. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. *Wilson Bull.* 96: 196-205.
- , & ———. 1985. Influence of parental age and season on Savannah Sparrow reproductive success. *Condor* 87: 106-110.
- BELETSKY, L. D., & G. H. ORIANS. 1987. Territoriality among male Red-winged Blackbirds I. Site fidelity and movement patterns. *Behav. Ecol. Sociobiol.* 20: 21-34.
- BERNDT, R., & H. STERNBERG. 1968. Terms, studies

- and experiments on the problem of bird dispersion. *Ibis* 110: 256-269.
- COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *J. Anim. Ecol.* 35: 269-279.
- DARLEY, J. A., D. M. SCOTT, & N. K. TAYLOR. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. *Bird-Banding* 48: 145-151.
- DELIUS, J. D. 1965. A population study of Skylarks, *Alauda arvensis*. *Ibis* 107: 446-492.
- DOW, H., & S. FREDGA. 1983. Breeding and natal dispersal of the Goldeneye, *Bucephala clangula*. *J. Anim. Ecol.* 52: 681-695.
- DRILLING, N. E., & C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *Auk* 105: 480-491.
- FISHER, H. I. 1969. Eggs and egg-laying in the Laysan Albatross *Diomedea immutabilis*. *Condor* 71: 101-112.
- GAVIN, T. A. 1984. Broodedness in Bobolinks. *Auk* 101: 179-181.
- , & E. K. BOLLINGER. 1985. Multiple paternity in a territorial passerine: the Bobolink. *Auk* 102: 550-555.
- , & ———. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* 69: 96-103.
- GRATTO, C. L., R. I. G. MORRISON, & F. COOKE. 1985. Philopatry, site tenacity, & mate fidelity in the Semipalmated Sandpiper. *Auk* 102: 16-24.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- , & P. H. HARVEY. 1976. The adaptive significance of variation in breeding area fidelity of the blackbird (*Turdus merula* L.). *J. Anim. Ecol.* 45: 887-898.
- , & ———. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13: 1-21.
- , ———, & C. M. PERRINS. 1978. Inbreeding and dispersal in the Great Tit. *Nature* 271: 52-54.
- GREIG-SMITH, P. W. 1982. Dispersal between nest-sites by Stonechats *Saxicola torquata* in relation to previous breeding success. *Ornis Scandinavica* 13: 232-238.
- HAIG, S. M., & L. W. ORING. 1988a. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105: 268-277.
- , & ———. 1988b. Distribution and dispersal in the Piping Plover. *Auk* 105: 630-638.
- HARRELL, F. E., JR. 1986. The LOGIST procedure. Pp. 269-294 in *SUGI supplemental library user's guide, version 5* (R. P. Hastings, Ed.). Cary, North Carolina, SAS Institute, Inc.
- HARVEY, P. H., P. J. GREENWOOD, & C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). *J. Anim. Ecol.* 48: 305-313.
- , ———, B. CAMPBELL, & M. J. STENNING. 1984. Breeding dispersal of the Pied Flycatcher (*Ficedula hypoleuca*). *J. Anim. Ecol.* 53: 727-736.
- , M. J. STENNING, & B. CAMPBELL. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (*Ficedula hypoleuca*). *J. Anim. Ecol.* 54: 391-398.
- HAUKIOJA, E. 1971. Short distance dispersal in the Reed Bunting *Emberiza schoeniclus*. *Ornis Fennica* 48: 45-67.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* 63: 152-161.
- JOHNSTON, R. F. 1961. Population movements of birds. *Condor* 63: 386-389.
- KOENIG, W. D., & F. A. PITELKA. 1979. Relatedness and inbreeding avoidance in the communally nesting Acorn Woodpecker. *Science* 206: 1103-1105.
- KORPIMAKI, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *J. Anim. Ecol.* 57: 97-108.
- LESSELLS, C. M. 1985. Natal and breeding dispersal of Canada Geese *Branta canadensis*. *Ibis* 127: 31-41.
- LIGON, J. D., C. CAREY, & S. H. LIGON. 1988. Cavity nesting, philopatry, and cooperative breeding in the Green Woodhoopoe may reflect a physiological trait. *Auk* 105: 123-127.
- MARTIN, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Ph.D. dissertation, Corvallis, Oregon, Oregon State Univ.
- . 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. *Am. Zool.* 14: 109-119.
- MOORE, J., & R. ALI. 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.* 32: 94-112.
- MURRAY, B. G., JR. 1967. Dispersal in vertebrates. *Ecology* 48: 975-978.
- NEWTON, I., & M. MARQUISS. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. *J. Anim. Ecol.* 51: 327-341.
- NOL, E., & J. N. M. SMITH. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *J. Anim. Ecol.* 56: 301-313.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* No. 26.
- ORING, L. W., & D. B. LANK. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behav. Ecol. Sociobiol.* 10: 185-191.
- SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. Albany, State Univ. New York Press.
- . 1984. Factors affecting nest and site fidelity

- in Adirondack Barn Swallows (*Hirundo rustica*). Auk 101: 780-789.
- SMITH, J. N. M., P. ARCESE, & D. SCHLUTER. 1986. Song Sparrows grow and shrink with age. Auk 103: 210-212.
- SOIKKELI, M. 1970. Dispersal of Dunlin *Calidris alpina* in relation to sites of birth and breeding. Ornis Fennica 47: 1-9.
- THOMAS, C. S. 1980. Certain aspects of the breeding biology of the Kittiwake (*Rissa tridactyla*). Ph.D. dissertation. Durham, Univ. of Durham.
- WEATHERHEAD, P. J., & K. A. BOAK. 1986. Site infidelity in Song Sparrows. Anim. Behav. 34: 1299-1310.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8.
- WITTENBERGER, J. F. 1978. The breeding biology of an isolated Bobolink population in Oregon. Condor 80: 355-371.
- WOOTTON, J. T., E. K. BOLLINGER, & C. J. HIBBARD. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledge costs, and random settlement. Am. Nat. 128: 499-512.