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RESPONSES OF NESTING BOBOLINKS (*DOLICHONYX ORYZIVORUS*) TO HABITAT EDGES

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ABSTRACT.—Avoidance of habitat edges may be contributing to reduced densities of grassland birds in small habitat patches. Nest densities for grassland-nesting Bobolinks (*Dolichonyx oryzivorus*) were much lower than expected within 25 m of forest edges at three sites in New York, and that pattern (“edge avoidance”) extended to 100 m at one site. Nests located within 50 m of forest or wooded hedgerow edges had lower daily survival rates, compared with nests >100 m from any habitat edge. Bobolinks tended to move away from forest edges when re-nesting after nest failure; that pattern was especially evident in females that placed their first nest within 50 m of a forest or wooded hedgerow edge. Second nests of all seven of those females were farther from that edge type than their first nests. However, nest placement in relation to wooded edges did not vary significantly between years for those philopatric females nesting at our study sites for more than one year. Bobolinks also avoided nesting near road edges, even though nest survival rates were not lower near that edge type. However, Bobolinks did not appear to avoid nesting near edges adjacent to old fields or pastures. Nest survival near those edge types was higher than near wooded edges and similar to or higher than survival of nests >100 m from any edge. Thus, responses of Bobolinks to habitat edges were inconsistent, and nest success was dependent on type of edge. Received 16 February 2003, accepted 28 March 2004.

RESUMEN.—El hecho de evitar los hábitats de borde puede estar contribuyendo a reducir las densidades de aves de pastizal en parches de pequeño tamaño. Las densidades de nidos de *Dolichonyx oryzivorus* fueron mucho menores dentro de los 25 m desde el borde del bosque en tres sitios en Nueva York y este patrón (“de evitar el borde”) se extendió hasta 100 m en un sitio. Los nidos ubicados a menos de 50 m del borde del bosque o de setos arbolados tuvieron tasas de sobrevivencia diaria menores que los nidos que se ubicaron a más de 100 m de cualquier borde. Los individuos de *D. oryzivorus* tendieron a alejarse de los bordes en sus intentos de re-nidificación luego de un intento de nidificación fallido. Este patrón fue especialmente evidente para hembras que pusieron su primer nido a menos de 50 m del borde del bosque o de un seto arbolado. Los segundos nidos de estas siete hembras estuvieron más alejados de ese tipo de borde que sus primeros nidos. Sin embargo, la ubicación del nido en relación con los bordes boscosos no varió significativamente entre años para las hembras filopátricas que nidificaron por más de un año en nuestros sitios de estudio. *D. oryzivorus* también evitó nidificar cerca del borde de los caminos, aunque la sobrevivencia de los nidos no fue menor cerca de este tipo de borde. Sin embargo no parecieron evitar nidificar cerca de otros tipos de borde como de campos de cultivo abandonados o pastizales. La sobrevivencia de los nidos ubicados cerca de esos tipos de borde fue mayor que la de aquellos ubicados cerca del borde de bosques, y similar o mayor que la sobrevivencia de nidos ubicados a más de 100 m de cualquier borde. Por estas razones las respuestas de *D. oryzivorus* a los bordes de hábitat no fueron consistentes y el éxito de nidificación dependió del tipo de borde.

NEGATIVE EFFECTS OF habitat edges have been known in forest-nesting birds for >20 years (Gates and Gysel 1978). Those effects include elevated predation rates (Gates and Gysel 1978) and increased rates of brood parasitism by cowbirds (Brittingham and Temple 1983) for nests near forest edges or in small forest fragments (Paton 1994, Donovan et al. 1995, Robinson et al.

1995). Many forest-nesting species apparently avoid edges by restricting their distribution to interior areas of large fragments (i.e. “area-sensitive” species; Whitcomb et al. 1981, Robbins et al. 1989).

The same effects occur in grassland-nesting birds (Johnson and Temple 1986, 1990; Winter et al. 2000; Walk 2001; Herkert et al. 2003) and may be contributing to the well-documented declines of those species (Bollinger and Gavin 1992, Knopf 1994, Herkert 1997, Helzer and Jelinski

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1999, Vickery and Herkert 1999). For example, Winter et al. (2000) reported greater activity by mid-sized mammalian carnivores in grasslands within 50 m of forest edges, and lower survival of artificial nests within 30 m of those edges (see also Burger et al. 1994; but see Davison 1998). Natural nests of grassland species may also experience elevated predation rates near forest edges (Johnson and Temple 1990, Winter et al. 2000) or in smaller fragments (Herkert et al. 2003). In addition, both Johnson and Temple (1986, 1990) and Walk (2001) reported higher rates of Brown-headed Cowbird (*Molothrus ater*) parasitism in grasslands near forest edges (but see Herkert et al. 2003). Finally, many grassland birds exhibit area sensitivity in that they are absent from or have reduced densities in small grassland patches (Herkert 1994, Vickery et al. 1994, Bollinger 1995, Helzer and Jelinski 1999, Johnson and Igl 2001).

Edge avoidance—defined here as having lower-than-expected density near an edge—has been detected by some investigators (Wiens 1969, Lima and Valone 1991, Delisle and Savidge 1996, Helzer 1996, O'Leary and Nyberg 2000, Winter et al. 2000, Fletcher and Koford 2003), and that phenomenon can produce area sensitivity ("distributional edge-sensitivity"; Winter et al. 2000). However, the degree to which edge avoidance extends to edge types other than forest edges is unclear, and recent work by Kershner (2001) and Walk (2001) suggests that edge avoidance may not occur in many grassland birds at row-crop agricultural edges.

Edge avoidance in grassland birds may result from any combination of a variety of factors. It may be a learned response to poor reproductive success near edges or simply an innate requirement for open habitat. Vegetation or microclimatic differences near edges (Mesquita et al. 1999) could also be involved either directly or indirectly (e.g. through reduced insect densities; see Burke and Nol 1998). Birds could also be competitively excluded from edge habitat by other species.

Bobolinks (*Dolichonyx oryzivorus*) have consistently been reported to be area sensitive (e.g. Herkert 1994, Bollinger 1995, Johnson and Igl 2001) and to avoid wooded (O'Leary and Nyberg 2000, Fletcher and Koford 2003), road (Fletcher and Koford 2003), and suburban edges (Bock et al. 1999). They were also among the species reported by Johnson and Temple

(1986, 1990) to experience elevated predation and parasitism rates near forests. However, most of those studies were based on small sample sizes (e.g. <50 nests) or they did not have marked populations to distinguish re-nesting attempts and limit pseudoreplication. Here, we report responses of Bobolinks to habitat edges in intensive studies of marked populations, with data on >300 nests at three sites in New York. We address the following questions: (1) Do Bobolinks avoid nesting near forest edges? (2) If such behavioral edge avoidance (or distributional edge-sensitivity; Winter et al. 2000) exists, does it occur at all types of edges? (3) Do reduced nest success and increased brood parasitism near forest edges, as found in Bobolinks by Johnson and Temple (1990), occur at our sites? (4) Is nest success reduced near other types of edges? (5) Do individual females change their nest location, relative to forest edges, when they re-nest after a nest fails, or return to nest in a subsequent year?

METHODS

Study sites.—We studied Bobolinks at three sites in New York. Sites were hayfields and meadows dominated by cool-season grasses, such as timothy (*Phleum pratense*). Sites consisted of up to four nearby or adjacent fields and were studied for 3 to 8 years, producing data on 71–169 nests per site (Table 1). Edge types (edge is defined here as a "junction between two dissimilar habitat types"; Faaborg et al. 1993) included forests (trees >12 m tall, habitat ≥10 m wide), wooded hedgerows (trees >8 m tall, habitat <5 m wide), old fields (vegetation dominated by goldenrod [*Solidago* spp.] and aster [*Aster* spp.], with scattered shrubs [e.g. *Viburnum* spp.] <2 m tall), pastures (heavily grazed, grass-dominated, with vegetation mostly <0.5 m tall), and roads (paved or graveled two-lane county roads with mowed fescue borders). None of those habitats supported nesting bobolinks. However, Bobolinks were sometimes seen in those habitats (e.g. foraging in pastures and old fields, singing from trees in hedgerows and forest).

Capture, marking, nest location, and monitoring.—At each site, we captured adults in mist nets, banded them (federal bands), and uniquely marked them by painting stripes on their tails (see Gavin 1984, Bollinger and Gavin 1989). We captured many males using playback of song near a mist net; others (and some females) were captured incidentally in nets placed in their territories. Females were often captured in nets adjacent to their nests. In all years at all sites, >90% of territorial males and nesting females were captured and marked.

TABLE 1. Description of study sites including locations, years studied, edge types, nest densities, and reproductive success.

	Bald Hill	Moore Road	Shackelton Point
Location	43°21'N, 76°23'W	43°08'N, 75°55'W	43°10'N, 75°56'W
Description	Four adjacent hayfields	One hayfield	Two adjacent meadows
Years studied	1982–1985	1984–1986	1981–1985, 1990–1992
Total size (ha)	21.5	19	26
Edge types	Forest, wooded hedgerow	Forest, wooded hedgerow, old field, pasture	Forest, road
Number of nests	71	169	135
Mean annual nest density (ha ⁻¹)	0.83	3.57	0.64
Exposure days	763	2,033	2,025
Daily survival rate	0.944 ^a	0.983 ^b	0.980 ^b

^{a,b} Daily survival rates with the same letter are not significantly different ($P < 0.05$, z -test; Johnson 1979).

All sites were gridded with permanent, color-coded metal stakes at either 40- or 50-m intervals to facilitate mapping of territories and nest locations. At all sites in all years, all or virtually all Bobolink nests were found during intensive daily searches by two or more biologists per site. Most nests (>70%) were found early in incubation. However, it is possible that a few nests that failed during egg laying or early in incubation were not found. Each nest was checked every 1–3 days until it was no longer active. A nest was considered successful if it fledged at least one nestling. It was considered depredated if all or some of the eggs disappeared between nest checks and the nest was no longer active. We considered a nest abandoned if it was not depredated yet was inactive (i.e. no adults seen at the nest site) for three successive nest checks. In addition, a few nest losses were attributed to weather (e.g. hail storms). Daily nest survival rates (DSR) were calculated using the Mayfield (1975) method (see also Johnson 1979).

Nest densities near edges.—Edge avoidance was tested for each edge type at each site, independent of other edge types, with chi-square tests using Bonferroni's correction for multiple tests. We tallied numbers of nests in the following distance categories (in meters from edge): 0–25, 26–50, 51–100, and >100. We then compared those observed nest numbers with numbers expected by chance given the area of fields at each site in the same four distance intervals. For that analysis, all re-nesting attempts were omitted, as were nests (in subsequent years) of philopatric females. We analyzed each edge type separately because we had no *a priori* predictions concerning how one edge type might influence another. However, we recognize that other edge types can influence nest locations relative to the edge type in question, especially at field corners.

In addition, we determined the average distance of each nest at each site to the nearest three neighboring nests. Mean nearest-neighbor distance was then used as the dependent variable in a stepwise multiple-

regression analysis in which distances of each nest to each edge type (at that site) were the independent variables (PROC GLM; SAS Institute 1995). We predicted that distances to avoided edge types would be negatively correlated with mean nearest-neighbor distance because nests located near avoided edge types would have few neighboring nests nearby.

Nest success near edges.—We used two approaches to determine effect of field edges on nest success. First, we used the z -test of Johnson (1979) to compare daily survival rates for nests at various distance intervals from habitat edges. Sample sizes were often small, especially close to forest edges, which necessitated combining data across years and sites. Typically, we compared survival rates for nests within 50 m of an edge with those >100 m from any edge. Only sites containing nests in both distance categories were included in those analyses, and we omitted nests abandoned because of human activities (e.g. nest abandoned immediately after being found or immediately after female was captured at nest). Second, we used stepwise logistic regression (PROC LOGISTIC, SAS Institute 1995; see also Winter et al. 2000) to determine which explanatory variables (see below) were most important in influencing nest success. For those analyses, nest success was a binary (1 if nest fledged ≥ 1 young, 0 if nest failed) dependent variable. Independent variables were (1) exposure days—number of days a nest was active (Mayfield 1975); (2) site—one of our four study sites; (3) first egg date—date when first egg in a clutch was laid (1 = 1 May, 32 = 1 June, etc.); (4) forest edge—distance (m) to edge of nearest forest; (5) forest or hedgerow edge—distance (m) to edge of nearest forest or wooded hedgerow; and (6) nearest edge—distance (m) to nearest field edge, regardless of edge type. Renests and nests in subsequent years of philopatric females were omitted from logistic regression analyses, as were human-caused nest abandonments. Exposure days were included to correct for nests found at different stages in the nesting cycle.

To determine whether females associated the proximity of their nest to a forest or wooded hedgerow edge with nest failure, we compared distances of first nests and re-nests from those edge types using paired *t*-tests. We first compared all females known to have re-nested (i.e. within the same breeding season) at our study sites. Then we restricted analysis to include only those females whose first nests were within 50 m of a wooded edge type.

We also looked at whether females modified their nest location relative to edges from one breeding season to the next. Paired *t*-tests were used to compare distances to various edge types for nests of the same female in two consecutive years. Females returning for three or more years were included only once in those analyses.

Finally, to determine if females nesting near edges were the later-nesting ones, we examined correlations between distances of nests from edge types and date the first egg was laid. Locations in interiors of fields were perhaps taken first, leaving only areas near edges for later-nesting females. Correlations were run separately for each year at each site.

RESULTS

General breeding biology.—Male Bobolinks returned to our grassland sites from South America in late April or early May to establish contiguous territories averaging 0.33–0.75 ha (Bollinger and Gavin 1992); females returned about one week later. Females built open-cup nests on the ground, laid clutches of 4–7 eggs, and incubated the eggs alone for 11–13 days. Both sexes typically fed nestlings for 9–10 days in the nest and for more than a week after fledging (see also Martin 1974; Wittenberger 1982; Bollinger and Gavin 1991, 1992; Martin and Gavin 1995).

We found 375 nests at our three study sites; sample sizes ranged from 71 at the Bald Hill site (BH) to 169 at the Moore Road site (MR). Forty-three of the 375 nests were either re-nests ($n = 37$) or second broods ($n = 6$; Gavin 1984), and 62 were nests of philopatric females from their second (or later) year at our sites. Yearly nest densities varied from 0.3–1.1 nests ha^{-1} at Shackleton Point (SP) to 3.3–3.9 nests ha^{-1} at MR. Daily nest survival rates (for all years combined) were significantly lower (0.94) at BH than at MR (0.98) or SP (0.98) (Table 1). Only 1 nest (0.2%) was parasitized by a cowbird (at BH).

Edge avoidance.—Bobolinks consistently avoided forest edges at all three sites (chi-square tests, $df = 3$, $P < 0.01$; Fig. 1). Observed

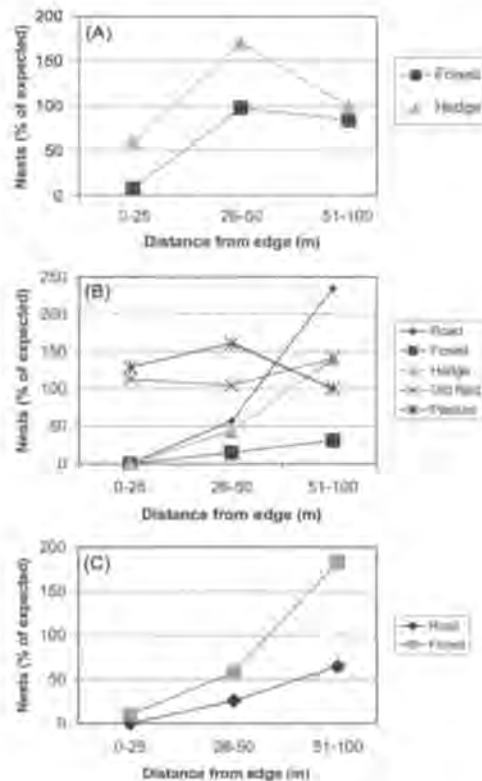


FIG. 1. Relationships between observed nest numbers and those expected on the basis of field area at various distances from habitat edges at three grassland sites in New York. Vertical axis was calculated as (observed number of nests/expected number of nests) $\times 100$. Thus, values markedly below 100% suggest edge avoidance, whereas those near 100% suggest that edge avoidance does not exist. (A) Bald Hill, (B) Moore Road, and (C) Shackleton Point.

nest numbers within 25 m of forest edges were 0–8% of those expected on the basis of field area. Beyond 25 m, however, extent of avoidance of forest edges varied. At MR (Fig. 1B), very few nests were found 50–100 m from any forest edge; whereas at BH (Fig. 1A), observed nest numbers were 98% of numbers expected 26–50 m from forest edges. Wooded hedgerows were also avoided at MR ($\chi^2 = 8.7$, $df = 3$, $P < 0.05$; Fig. 1B) but not at BH (Fig. 1A; though nest numbers were lower than expected within 25 m of that edge type; $\chi^2 = 3.1$, $df = 3$, $P > 0.25$).

Bobolinks avoided road edges; that pattern occurred at both MR and SP (chi-square tests, $df = 3$, $P < 0.01$; Fig. 1B, C). Nest densities were lower than expected for both the 0–25 m and

26–50 m intervals at MR (0% and 57%, respectively; Fig. 1B) and much higher than expected 50–100 m from road edge (235%). At SP (Fig. 1C), however, avoidance of road edges appeared to extend to 100 m. Numbers of nests in the 50–100 m interval at that site were less than expected (65%).

The other two edge types (old field and pasture) were not avoided. In each case, observed nest numbers within both the 0–25 m and 26–50 m intervals were greater than expected (i.e. >100%). Those edge types were present only at MR.

Stepwise multiple-regression models of nearest-neighbor distances consistently corroborated those patterns. At all three sites, distance to forest edge was a significant ($P < 0.05$) negative correlate of mean nearest-neighbor distance, as was distance to road edge at SP and MR. At MR, distance to old field edge was included as the last variable and was positively correlated with nearest-neighbor distance. However, predictive ability of models was fairly low ($25\% < r^2 < 35\%$).

Nest success versus distance to edge.—Daily survival rate of nests within 50 m of forest edges was significantly lower than DSR of nests at distances >100 m from all edges (years and sites combined, 0.95 vs. 0.98; $z = 2.61$, $P < 0.05$;

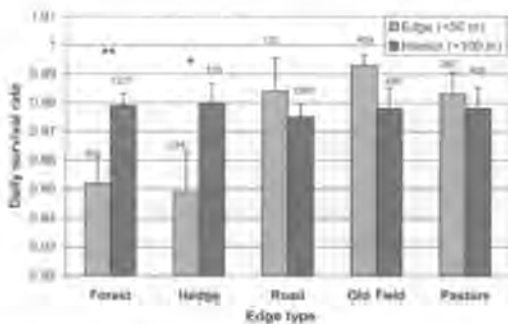


Fig. 2. Daily survival rates (DSR; Mayfield 1975) for nests ≤ 50 m from various edge types ("Edge"), compared with DSRs for nests >100 m from all edge types ("Interior"). In each case, DSRs for edge nests were compared only with interior nests at the same sites. Thus, because nests near forest edges occurred at all three sites, the overall forest DSR was compared with interior DSR for all sites combined. For old field and pasture edges, only interior nests at Moore Road were used (because those edge types occurred only at that site). Sample sizes (exposure days) and standard error bars are included above each bar. For each paired comparison: * $P < 0.10$; ** $P < 0.05$ based on z-test (Johnson 1979).

Fig. 2). Furthermore, patterns of nest survival were similar at each of the sites (though z-tests for individual sites were not significant; $P > 0.05$). Survival appeared to be particularly low within 25 m of forest edges (Fig. 3). Nest survival within 50 m of wooded hedgerows was also lower than in the interior (>100 m from all edges), though the difference was marginally significant (0.95 vs. 0.98; $z = 2.04$, $P < 0.10$; Fig. 2). Nests within 50 m of other edge types survived at rates similar to those for nests >100 m from all edges (Fig. 2).

Stepwise logistic-regression analyses generally corroborated survival-rate comparisons between distance categories (Table 2). With all sites included, nest exposure (Mayfield 1975, Johnson 1979) was the first variable entered, followed by distance to nearest forest or wooded hedgerow edge. Nest exposure, as expected, was positively correlated with a nest's probability of success (i.e. nests with more "exposure days" tended to be the nests that fledged young). Distance to forest or hedgerow edge also was positively correlated with success (i.e. nests at greater distances from wooded edges tended to have higher survival). When sites were analyzed separately, results were similar (Table 2). Exposure followed by distance to nearest forest or wooded hedgerow were the variables included in each model.

Nest locations for renesting and philopatric females.—Females renesting after nest failure (with both nests at our study sites) tended to move farther from forest edges for their second attempt (mean = 137 m, first attempt; mean = 149 m, second attempt; paired $t = 2.22$; $df = 31$, $P = 0.034$). No such difference was found

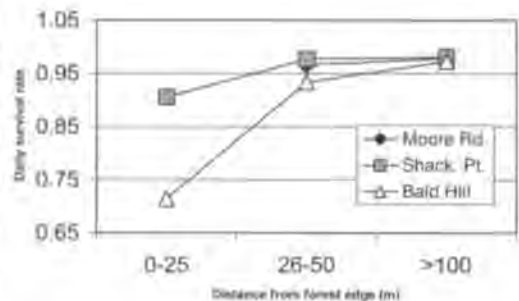


Fig. 3. Daily survival rates (DSR, Mayfield 1975) for nests at various distances from forest edges at our three sites.

TABLE 2. Results of stepwise logistic regression analyses, in which nest success (1 if nest successful, 0 if nest failed) was the dependent variable and exposure days, site, first egg date, distance (m) to forest edge ("Forest edge"), distance (m) to nearest forest or hedgerow edge ("Forest or hedgerow edge"), and distance (m) to nearest edge of any type were the potential independent variables. Only variables explaining a significant amount of variation in nest success ($P < 0.05$) are shown.

Study sites included	Number of nests ^a	Variable entered ^b	Fraction of concordant pairs ^c
All sites	277	+Exposure days, +forest or hedgerow edge, -egg date	83%
Bald Hill only	47	+Exposure days, +forest edge	87%
Moore Road only	128	+Exposure days, +forest or hedgerow edge	83%
Shackelton Point only	102	+Exposure days, +forest edge ^d	81%

^aRenests, nests in subsequent years of philopatric females, and nests failing because of human disturbance are omitted.

^bVariables are listed in the order they were entered into the model. A "+" indicates a positive correlation with the dependent variable.

^cSimilar to the percentage correctly classified, fraction of concordant pairs is calculated by considering all possible pairs of observations with different values of the dependent variable. Concordant pairs are those for which the observation with the larger observed value of the dependent variable has higher predicted probability than does the other observation.

^dNo wooded hedgerow edges occurred at this site (thus, forest and forest and hedgerow edge are the same).

for distance to wooded hedgerows (first nests, mean = 84 m; second nests, mean = 86; $df = 31$, $P > 0.50$). When we restricted analyses to only those females whose first (failed) nest was within 50 m of a forest edge ($n = 7$), those females, on average, more than doubled their distance from forest edge for their second attempt (36 vs. 75 m); all seven increased their distance from forest edge ($P = 0.016$, sign test).

Nest locations of philopatric females relative to forest edges were very similar between their first and second years at our study sites. Nests were located, on average, 174 m from forest edge in the first year and 169 m in the second ($t = 0.06$, $df = 51$, $P > 0.50$). Furthermore, distance to forest edge was consistent for individual females between years ($r = 0.84$, $df = 50$, $P < 0.01$). The pattern was similar if we restricted our analyses to consider only females that were unsuccessful their first year (yet still returned the next). Here, distances to forest edge averaged 208 m in the first year and 186.3 in the second ($t = 1.35$, $df = 9$, $P > 0.20$).

Nest locations versus date.—We ran correlations between the various "edge variables" used in logistic regression analysis (see above) and first egg date for each year at each site (total of 19 "site-years"). Overall, those analyses failed to detect any temporal pattern in nest locations relative to habitat edges. For example, only 1 of the 15 correlations (that for distance to forest edge) was statistically significant ($P < 0.05$). Furthermore, only 6 of those 15 correlations were negative. Results were very similar for distance to nearest edge (of any type; 1 of 15 statistically significant, 6 of 15 negative).

DISCUSSION

Avoidance of forest edge.—Bobolinks rarely nested near forest edges. That result was consistent across all three sites. Helzer (1996), O'Leary and Nyberg (2000), and Fletcher and Koford (2003) also reported avoidance of forest edges by Bobolinks, but that was based primarily on locations of males' territories and not nests. However, avoidance of forest edges by other species of grassland birds based on nest locations has been reported (e.g. Delisle and Savidge 1996, O'Leary and Nyberg 2000, Winter et al. 2000). Edge avoidance, therefore, is likely to be partially responsible for the consistent area sensitivity of Bobolinks and perhaps of other grassland species (e.g. Bollinger 1995, Helzer and Jelinski 1999, Johnson and Igl 2001).

There are at least six possible explanations for edge avoidance of (or distributional edge-sensitivity to) forest edges, as found here and in the other studies mentioned above. (1) Reduced nest densities near forest edges may be attributable to competition with dominant species for edge habitat, which may have excluded Bobolinks from nesting near forest edges. It is possible that Red-winged Blackbirds (*Agelaius phoeniceus*), a species that is dominant over Bobolinks (E. K. Bollinger pers. obs.), excluded them from edge habitat. However, there were only two or three male Red-winged Blackbirds per year at two of our sites (MR and BH), yet Bobolinks still avoided forest edges at those sites. (2) Vegetation near forest edges may have been different from that of grassland interiors and less appropriate habitat for Bobolinks.

Unfortunately, we have no data to address that question at our New York sites, but data from an Illinois site suggest that it is unlikely to be a major factor (E. K. Bollinger et al. unpubl. data; see also Fletcher and Koford 2003). (3) Microclimatic differences created by forest might contribute to markedly reduced nesting density near forest. Certainly, shade at forest edges could reduce temperatures experienced at edges relative to interiors. (4) Indirect edge effects may be important (e.g. Murcia 1995); microclimatic differences near forest edges may indirectly affect Bobolinks by leading to reduced populations of insects that are eaten or fed to nestlings. (5) Bobolinks may have an innate preference for open habitats or an innate avoidance of forest, being a species of the tallgrass prairie ecosystem (Cody 1985). If so, that innate avoidance may be the product of natural selection, given that the present study and others (e.g. Gates and Gysel 1978, Johnson and Temple 1990, Winter et al. 2000) have found increased predator activity and nest predation rates near forest edges. Individuals nesting near edges would tend to leave fewer offspring than those nesting in the grassland interior. (6) Finally, Bobolinks may learn to avoid nesting near forest edges. That explanation is supported by our detection of movement of re-nesting Bobolinks away from forest edges. Females that initially nested within 50 m of a forest edge more than doubled their distance from that edge type for their second nest. However, it is unclear whether that potentially learned edge avoidance is retained through the next breeding season, because nest locations for philopatric females (relative to distance from forest edges) were similar between years. Unfortunately, few unsuccessful females returned to our sites, and only one of those built her first nest within 50 m of a forest edge; that female increased her distance from the edge from 31 to 45 m. That Bobolinks may learn to avoid nesting near forest edges is also supported by the higher predation rates near that edge type found here as well as in other studies (Johnson and Temple 1990, Winter et al. 2000). Although they were virtually absent from our sites, higher parasitism rates by Brown-headed Cowbirds near forest edges (Johnson and Temple 1990, Walk 2001; but see Herkert et al. 2003) would also provide impetus for re-nesting Bobolinks to increase their distance from forest edges.

Those six explanations are not mutually exclusive. However, we feel that competition with other species for edge habitat and vegetative and microclimatic differences near edges are all, at most, minor influences on the patterns of edge avoidance we found. Thus, we are left with both innate and learned avoidance of forest edges, resulting from elevated predation and parasitism rates, as our best explanation for avoidance of nesting near forest edges. It is unclear, however, why magnitude of edge avoidance varied among sites. Perhaps, at sites like BH, where regional Bobolink populations are high, nesting females are making the best of a bad situation. However, that does not explain why avoidance was fairly pronounced at MR, where both regional and site densities were high. Furthermore, if edge-nesting Bobolinks were merely making the best of a bad situation, then we should have detected more consistent and stronger negative correlations between first egg date and distance to forest edge. Instead, magnitudes of those correlations were small and mostly positive, which suggests that the females that nested near forests had not been forced to do so by earlier nesters.

Wooded hedgerows were not as strongly avoided as forests (though they were present only at two sites). In fact, observed nest numbers were not significantly different from expected numbers at one of the sites (BH). Hedgerows at BH, however, separated hayfields used by nesting Bobolinks and were only a few meters wide. Nevertheless, the lack of strong avoidance was surprising given relatively high rates of nest predation for nests near that edge type.

Other edge types.—Bobolinks consistently avoided edges with roads (see also Fletcher and Koford 2003). It is unclear why that occurred, especially given that nest success near that edge type appeared to be as high as in interior areas. One possibility was that Bobolinks were avoiding not the road, but rather habitat on the other side of the road (e.g. forest). However, that explanation seems unlikely, because only one road edge (at SP) was bordered on the opposite side by forest. Other road edges were bordered by pasture (at SP) or old field (at MR). Edges directly adjacent to those two habitat types (i.e. without a road in between) were not avoided by nesting Bobolinks, yet the road edges were. Thus, it may be that vehicular traffic was responsible for the avoidance, even

though those county roads were lightly traveled. Alternatively, chemical runoff from the road or pesticides applied to road edges may have reduced insect populations near roads.

Bobolinks did not appear to avoid nesting near edges of old fields and pastures. Those habitat types were not used by Bobolinks for nesting, and territory borders often ran along the edges. Observed nest numbers in all cases were greater than those expected on the basis of field areas, which suggests that Bobolinks may be somewhat attracted to those edges. However, Bollinger and Switzer (2002) have shown that such a pattern (higher nest densities near edges) can occur even when edges are not attractive (if nests are uniformly dispersed). It is noteworthy that nest success was as high along each of those edge types as in interior areas. Similar results regarding row-crop edges have been found by Davison (1998), Kershner (2001), and Walk (2001) for artificial nests, Eastern Meadowlarks (*Sturnella magna*), and Dickcissels (*Spiza americana*), respectively. Furthermore, we have also found a lack of avoidance of row-crop edges by Bobolinks nesting in Conservation Reserve Program fields in Illinois (and similar nest success as found for interior nests; E. K. Bollinger et al. unpubl. data). Those results suggest not only that grasslands embedded in an agricultural matrix may provide habitat for grassland birds, but that the birds enjoy relatively high reproductive success in such habitat.

Conservation implications.—Bobolinks responded to habitat edges in both expected and unexpected ways. They predictably avoided forest (and to a lesser extent wooded hedgerow) edges where reproductive success was low, displaying both distributional and demographic edge-sensitivity (Winter et al. 2000). Thus, small grasslands (especially those <10 ha) surrounded by forest are poor habitat for Bobolinks. Even sites that are larger, such as BH (with a total grassland area of 21.5 ha), if dissected by wooded hedgerows, may be unlikely to support self-sustaining populations. Bobolinks may (at least within a year) “learn from their mistakes” if they choose to nest within 50 m of a forest edge, and more than doubled their distance from that edge type when renesting. Also, they avoided edges with roads, though it is unclear (given high reproductive success) why they did so. Surprisingly, however, Bobolinks showed no avoidance of pasture and old field edges. The

fact that nest success was as high near those edges as in interior habitats is good news from a conservation perspective; it suggests that grassland fragmentation may not be as detrimental as forest fragmentation unless sites are fragmented by roads or trees. Those results also suggest that grasslands created in agricultural regions, such as the midwestern U.S. (where population declines have been especially severe; Herkert 1997), may be beneficial to Bobolinks, even if the areas are relatively small. Finally, the lack of avoidance of nonwooded edges suggests that factors other than edge avoidance may be contributing to the consistent area sensitivity found in Bobolinks.

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