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Sex-specific differences in site fidelity and the cost of dispersal in yellow-headed blackbirds

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Abstract Male migratory birds tend to be more faithful than females to previous breeding sites, suggesting sex differences in costs or benefits of dispersal. In Illinois, greater site fidelity by male yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) was associated with reduced reproductive success the following year for dispersers relative to non-dispersers. Dispersing females suffered no reduction in reproductive success the following year. Males that attracted few social mates, and thus had low reproductive success, were more likely to disperse, whereas females dispersed in response to low-patch reproductive success, regardless of their individual performance. Males that dispersed appeared to be successful acquiring territories because none was observed as a floater. The rate of dispersal by males in this low-density population was greater than in more dense populations where dispersing males may be less successful at acquiring territories. Despite success at obtaining territories, males that dispersed acquired territories on the periphery of wetlands where fewer females nested, resulting in lower reproductive success. In the second year after dispersing, however, males moved onto more central territories where they acquired larger harems. Thus, disper-

sal by males may be a long-term strategy requiring at least 2 years for benefits to be realized. Long-term success was enhanced because dispersing males moved to wetlands on which reproductive success was higher than on the wetlands they left. In addition to demonstrating that both individual and patch reproductive success affect dispersal decisions, these data indicate that when evaluating costs and benefits of dispersal, researchers should use a time frame beyond 1 year.

Keywords Dispersal · Site fidelity · Site dominance · Site familiarity · Reproductive success · Patch reproductive success · Yellow-headed blackbird · *Xanthocephalus xanthocephalus*

Introduction

Breeding site fidelity in migratory birds often differs between the sexes (Clarke et al. 1997). Among a diverse group of species occupying a variety of habitats, males are generally more likely than females to return to the site where they bred the previous year, although there are exceptions (Greenwood and Harvey 1982; Clarke et al. 1997). Abandoning a breeding site could allow a bird to breed at a superior site, but alternatively, the bird could fail to find a new site, fail to compete for access to the site, or the new site could prove to be inferior to the old site. Individual differences in these costs and benefits should explain why some individuals are site faithful, while others in the same population are not (Weatherhead and Boak 1986). Thus, when one sex regularly exhibits higher site fidelity than the other, it suggests that costs or benefits of dispersal differ predictably between the sexes such that the sex that is more site faithful should have a greater cost of dispersal than the sex more likely to disperse. Here we use data from yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) to test this hypothesis and to identify the proximate factors used by males and females in deciding whether or not to disperse.

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Studies of numerous avian species have found higher breeding site fidelity among individuals with higher reproductive success (e.g., Nolan 1978; Harvey et al. 1979, Dow and Fredga 1982; Weatherhead and Boak 1986; Bollinger and Gavin 1988; Hoover 2003). As long as past success predicts future success, this “win-stay, lose-shift” strategy will be effective. Boulinier and Danchin (1997) extended the cues used in this strategy to include patch reproductive success (the success of all birds breeding in the same patch), because future success might be predicted more reliably by mean success on a patch than by a bird’s individual success. Although we consider how both individual and patch success affect dispersal decisions, neither factor predicts that one sex should be more site faithful.

A proposed explanation for sex-specific differences in site fidelity is familiarity with attributes of a site that are relevant to reproductive success (Hilde 1956; Greenwood 1980; Bensch and Hasselquist 1991). Knowing where to find food and good nest sites should make a familiar site more valuable than an unfamiliar site (Pärt 1994). If males have to compete for high-quality territories to attract mates, familiarity with a site should be advantageous (Paton and Edwards 1996; Schjöring et al. 2000). In a socially polygynous species such as the yellow-headed blackbird (Willson 1966; Lightbody and Weatherhead 1987a), where competition among males for resource-based territories is often intense, fidelity to a familiar site should be particularly advantageous for males (Greenwood 1980). If familiarity with resources is advantageous, then females should also benefit from site fidelity. Unlike males, however, female yellow-headed blackbirds appear not to compete for resources (Lightbody and Weatherhead 1987b), or at least competition is dramatically less than between males, so the relative advantage of site fidelity to females may be lower. On the basis of site familiarity we therefore predict higher male site fidelity.

Another factor that should favor site fidelity by males is site dominance (Davies 1978; Krebs 1982; Desrochers and Hannon 1989). Independent of familiarity with specific attributes of a territory, males that have held a territory previously are generally successful in acquiring it again (Rowher 1982; Lanyon and Thompson 1986; Shutler and Weatherhead 1992). The success of residents appears to be unrelated to their competitive ability (e.g., Eckert and Weatherhead 1987; Beletsky and Orians 1989; Shutler and Weatherhead 1991, 1992; Veiga et al. 2001), but rather to an increased willingness to fight for the territory (Tobias 1997). Although the explanation for site dominance remains elusive (Shutler and Weatherhead 1992; Searcy and Yasukawa 1995; Veiga et al. 2001), the phenomenon clearly favors site fidelity in males because dispersing individuals forfeit this advantage. Simultaneously, social polygyny should make it relatively easy for a dispersing female to find a good breeding opportunity, particularly because female yellow-headed blackbirds breeding on the same territory do not negatively affect one another’s nesting success and females do not inhibit settlement by other females (Lightbody and Weatherhead 1987b). On this basis we expect males to be more site faithful than females because the

relative reproductive success of dispersing males should be lower than that of females, primarily because dispersing males will have less success competing for breeding opportunities.

Although familiarity with neighbors appears unrelated to site dominance (Shutler and Weatherhead 1992), familiarity has been proposed to provide other advantages for site-faithful individuals. Familiar neighbors may compete less (Eason and Hannon 1994), or even cooperate. For example, Beletsky and Orians (1989) found that female red-winged blackbirds (*Agelaius phoeniceus*) preferred to nest on territories of males with familiar neighbors, because cooperative nest defense by those males increased nest success. In a different population of red-winged blackbirds, however, (Weatherhead 1995) found no evidence that familiar males cooperated in nest defense and that females were more successful on territories of males with new neighbors. Different nest predators in the two populations may account for this difference in effects of neighbor familiarity (Weatherhead 1995), making it difficult to predict how familiarity among site-faithful yellow-headed blackbirds should affect nest success. In this study we determine if site fidelity is influenced by the effect of individual familiarity on nest success.

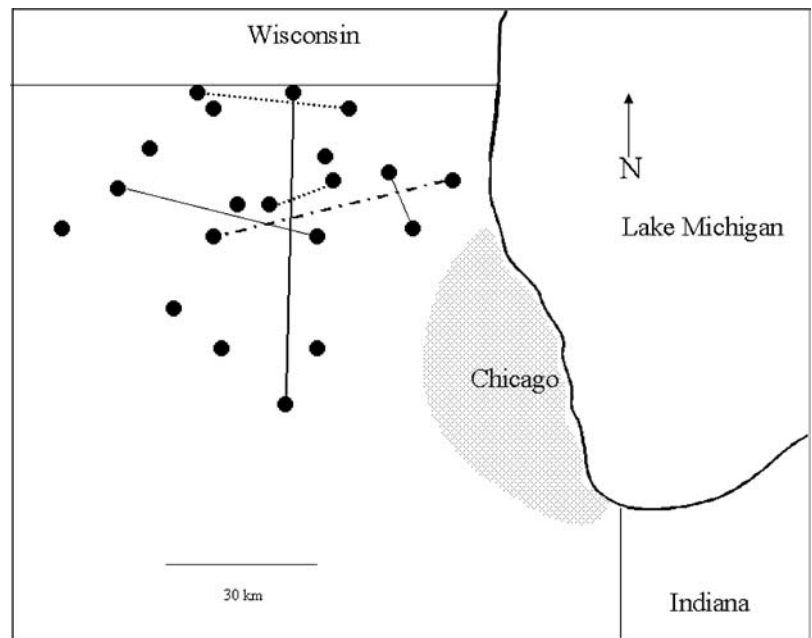
Despite the importance of dispersal to many aspects of avian biology, our understanding of the phenomenon remains poor. Although many studies have determined why individuals disperse, in most field studies, an individual that disperses leaves the study area. Therefore, not only can its reproductive success following dispersal not be determined, dispersal is often indistinguishable from mortality. This makes it difficult to estimate post-dispersal success unambiguously. Here we take advantage of an isolated population of yellow-headed blackbirds that allowed us to track the fate of birds before and after dispersal, as well as to determine the consequences of dispersal.

Methods

Yellow-headed blackbirds are polygynous, migratory passerines that breed in deep-water wetlands in western North America and winter in west-central Mexico (Twedt and Crawford 1995). From 1998 to 2004, we studied an isolated, low-density population located primarily in Lake and McHenry Counties in northeastern Illinois, an area of approximately 160 km² (Fig. 1). Our study population is approximately 200 km from the nearest isolated population in Wisconsin and approximately 630 km from a larger population in Iowa (Ward in press a). There were 32 wetlands in the study area suitable for yellow-headed blackbirds. Of these, yellow-headed blackbirds occupied 12–18 sites in any given year, and the same suite of sites was not occupied each year (Ward 2004).

Beginning in April of each year, before the onset of nesting, we surveyed all wetlands at least once a week to determine if yellow-headed blackbirds were present and monitored sites with blackbirds through early July. We used Potter walk-in traps baited with corn to capture breeding adults. Each individual was given a unique combination

Fig. 1 Map of the study area showing wetlands occupied by yellow-headed blackbirds during the study. Dispersal histories for three males (*broken lines*) and three females (*solid lines*) illustrate typical patterns of dispersal



of color bands. On each visit we surveyed the wetland for color-marked individuals. We used the conspicuous territorial behavior of males to map territories. We also identified banded male floaters, defined as males present but not defending a territory. We categorize territories as central (interior 1/3 of the wetland), intermediate, or peripheral (outer 1/3 of the wetland). We used the maximum number of territories at a site to estimate the adult male population. We estimated the female population as the maximum number of females observed at a site during a single visit or the maximum number of simultaneously active nests, whichever was greater. The number of females and territorial males observed seldom varied between visits.

On each visit we searched emergent vegetation for nests. We monitored nests until they failed or fledged young. When nestlings disappeared between visits we assumed the nest was successful if it remained intact and nestlings would have reached at least 11 days of age since the previous visit. Because we color banded most nestlings and they remained close to the nest for several days after fledging, we could usually confirm the young had fledged. For analyses of reproductive success we attribute all fledglings in a territory to the resident male. Given the high rate of extra-pair fertilizations in many birds, this assumption is unlikely to be correct. However, in another polygynous blackbird, both harem size and apparent reproductive success significantly predicted a male's genetic reproductive success (Weatherhead and Boag 1997). Thus, we assume these measures are reasonable indices of male reproductive success (this also may be the best information available to the males themselves). We determined a male's harem size as the maximum number of simultaneously active nests in his territory. We also determined patch reproductive success as the mean number of young per breeding attempt for all nests at a wetland (e.g., Boulinier and

Danchin 1997; Doligez et al. 1999, 2002; Serrano et al. 2001).

We considered an individual to have dispersed if it bred in a wetland other than where it bred the previous year, and site faithful if it bred at the same wetland in consecutive years. To avoid confounding effects of mortality, we estimated dispersal rates using only birds known to have survived between years. We excluded several cases of individuals not observed for a year and then seen again. There was no reason to assume these birds behaved differently from birds we did observe each year, but even if they did, their numbers were so small that excluding them should not bias our results. We also excluded several cases of dispersal where alteration of the habitat between years could have affected dispersal. We used a general linear model (GLM) controlling for individual, year, and site to determine correlates of dispersal or site fidelity. We controlled for individual because some birds contributed more than one data point and we wanted to determine if individuals were predisposed to be site faithful or disperse. Factors of interest included individual reproductive success, patch reproductive success, patch population size and density, and harem size (for males only). We used program MARK (White and Burnham 1999) to estimate annual adult survival rate by applying the variance component function of the program. To determine the average life span of breeding-age male yellow-headed blackbirds we assumed a constant survival rate throughout their adult life. Using a hypothetical cohort of 100 adults, we multiplied the number alive each year by the survival rate until all individuals were dead. We then divided the total number of individuals over all years by the combined age of all individuals over all years to estimate mean life span of adult males (Verner 1978). For analyses assessing neighbor familiarity we considered a returning male to have familiar neighbors if at least one adjacent territory was held by the owner from the previous year.

Table 1 Results of GLM analyses assessing factors associated with dispersing vs. site fidelity in yellow-headed blackbirds in Illinois

	Males		Females	
Overall model	$F_{8,58}=5.84$	$P<0.01$	$F_{7,64}=3.49$	$P<0.01$
Individual	$F_{1,58}=0.18$	$P=0.68$	$F_{1,64}=0.35$	$P=0.56$
Site	$F_{1,58}=0.54$	$P=0.46$	$F_{1,64}=0.28$	$P=0.60$
Harem size	$F_{1,58}=4.37$	$P=0.04$	–	–
Year	$F_{1,58}=2.41$	$P=0.13$	$F_{1,64}=0.72$	$P=0.41$
Number of yellow-headed blackbirds	$F_{1,58}=0.31$	$P=0.58$	$F_{1,64}=1.07$	$P=0.31$
Density of yellow-headed blackbirds	$F_{1,58}=0.48$	$P=0.49$	$F_{1,64}=1.36$	$P=0.25$
Individual reproductive success	$F_{1,58}=1.05$	$P=0.31$	$F_{1,64}=0.32$	$P=0.58$
Patch reproductive success	$F_{1,58}=1.51$	$P=0.23$	$F_{1,64}=10.13$	$P<0.01$

All variables were quantified in year 1 (i.e., prior to dispersal or site fidelity)

Results

From 1998 to 2004 we monitored an average of 58 territories each year and followed the fate of 551 nests. Over the course of the study we banded 304 breeding males and 332 breeding females, constituting between 50 and 67% of the Illinois population in a given year. We observed 123 females and 131 males in at least two successive years. Consistent with our general prediction that males should be more site faithful than females, overall 63% of 131 males known to be alive were site faithful compared to 43% of 123 females ($\chi^2=895.02$, $P<0.01$). In the following analyses we refer to year 1 as the year preceding either dispersal or site fidelity, and year 2 as the year following dispersal or fidelity. Thus, reproductive success of a dispersing male in year 1 for example, refers to his success in the year prior to dispersing.

The overall model comparing males that dispersed with those that were site faithful in year 1 was significant (Table 1). The only factor associated with whether or not males dispersed was harem size—dispersing males had fewer social mates than site-faithful males. There was no effect of individual, site, year, or the number or density of yellow-headed blackbirds (Table 1). Neither individual reproductive success nor patch reproductive success influenced whether a male was site faithful. There were also no significant interactions. Although reproductive success was not a significant factor in the model, harem size was significantly correlated with reproductive success ($R^2=0.60$, $n=67$, $P<0.01$). Thus, harem size may have concealed the effect of reproductive success. When we reran the model excluding harem size, the model remained significant ($F_{7,58}=6.51$, $P<0.01$) and individual reproductive success was the only significant independent variable ($F_{1,58}=4.73$, $P<0.01$).

Dispersing males produced fewer young than males that were site faithful ($t=-1.78$, $df=40$, $P=0.04$; Fig. 2). Patch reproductive success did not differ between males that were site faithful and those that dispersed ($t=-1.46$, $df=40$, $P=0.09$; Fig. 3). For males that dispersed, however, success in year 1 on the patch they moved to was substantially higher than on the patch they left (mean = 1.99 vs. 1.46, paired $t=4.51$, $df=25$, $P<0.01$).

The overall model comparing females that dispersed with those that were site faithful in year 1 was also significant (Table 1). Individual, site, and year did not have signifi-

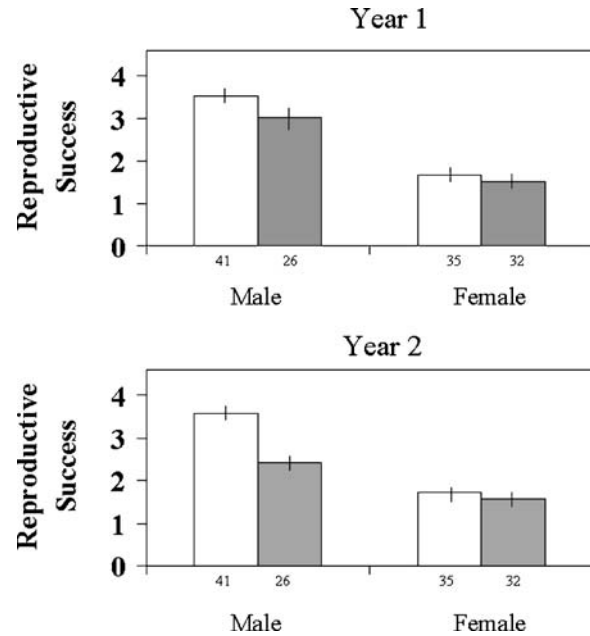


Fig. 2 Mean (\pm SE) reproductive success (young fledged per individual) of male and female yellow-headed blackbirds prior to dispersing or being site faithful (year 1) and after dispersing or being site faithful (year 2). Site-faithful individuals are shown as open bars and dispersers as shaded bars

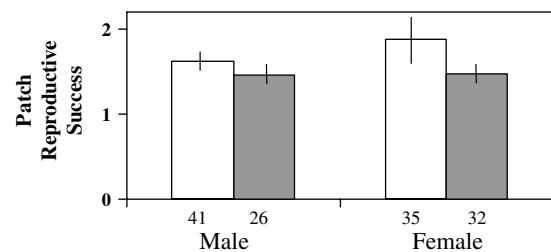


Fig. 3 Mean (\pm SE) patch reproductive success (mean number of young fledged per nest at a wetland) for male and female yellow-headed blackbirds prior to dispersing or being site faithful (year 1)

cant effects. Similarly, individual reproductive success, the number of yellow-headed blackbirds at a site and the density of birds at a site were not associated with the decision to disperse. As with the model for males, there were no significant interactions. Females did differ from males in that patch reproductive success affected whether a female was site faithful or dispersed (Table 1). Reproductive success

in year 1 did not differ between dispersing and site-faithful females ($t=1.11$, $df=34$, $P=0.27$; Fig. 2), but patch reproductive success in year 1 was greater for site-faithful females ($t=4.63$, $df=34$, $P<0.01$; Fig. 3). Consistent with patch success providing females with reliable information on future nesting success, patch success in year 2 was significantly correlated with success in year 1 ($r^2=0.58$, $df=30$, $P<0.01$), for 31 wetlands for which we had patch success estimates for two successive years.

Males that dispersed paid a cost, producing fewer young in year 2 compared to year 1 (paired $t=-2.17$, $df=25$, $P=0.01$; Fig. 2), whereas site-faithful males had similar success in year 1 and year 2 (paired $t=0.14$, $df=40$, $P=0.89$; Fig. 2). For females, there was no difference in the number of young produced in year 2 compared to year 1 for individuals that dispersed (paired $t=0.21$, $df=31$, $P=0.83$) and those that were site faithful (paired $t=0.13$, $df=34$, $P=0.90$; Fig. 2).

We never observed a male known to have held a territory in year 1 as a floater in year 2, indicating that most males that dispersed acquired territories. We regularly observed subadult male floaters, so failure to see adults as floaters was not due to lack of opportunity. Despite success at acquiring territories, there were qualitative differences in the territories males acquired relative to those they left behind. In year 1 territories of dispersing and site-faithful males were equally distributed across central, intermediate and peripheral positions (dispersers: $\chi^2=0.73$, $P=0.69$; site faithful: $\chi^2=2.10$, $P=0.35$). In year 2, however, dispersing males were less likely to have an interior territory (i.e., intermediate or center) ($\chi^2=17.1$, $P<0.01$), whereas site-faithful males were more likely to have an interior territory ($\chi^2=27.6$, $P<0.01$).

Although the mean number of young fledged per nest in year 2 for males that dispersed was similar to that for site-faithful males ($\bar{x}=1.54$, $n=26$ and $\bar{x}=1.59$, $n=41$, respectively; $t=0.41$, $df=40$, $P=0.41$), the number of mates obtained differed. Overall, mean harem size increased from peripheral to central territories (= 1.57, 2.17, 3.10, respectively; ANOVA: $F_{1,65}=8.75$, $P<0.01$), and because dispersing males acquired peripheral territories, their mean harem size in year 2 was smaller than that of site-faithful males ($\bar{x}=1.86$ and 2.52, respectively; $t=-2.19$, $df=12$, $P=0.05$). These differences account for the lower reproductive success of dispersing males in year 2.

Familiarity with neighbors appeared not to affect harem size. Among site-faithful males, individuals with familiar neighbors acquired as many social mates as individuals with unfamiliar neighbors ($\bar{x}=2.45$ vs. 2.58, respectively; $t=0.51$, $df=11$, $P=0.62$). The small sample size might suggest that this result should be interpreted cautiously. Alternatively, however, the fact that we observed only 12 males with familiar neighbors in the course of the study suggests that neighbor familiarity must be relatively unimportant. Otherwise movement between and within marshes from year to year should have been much less extensive.

We were able to follow the reproductive success of 19 males for three consecutive years, allowing us to assess longer-term consequences of dispersal and site fidelity. For

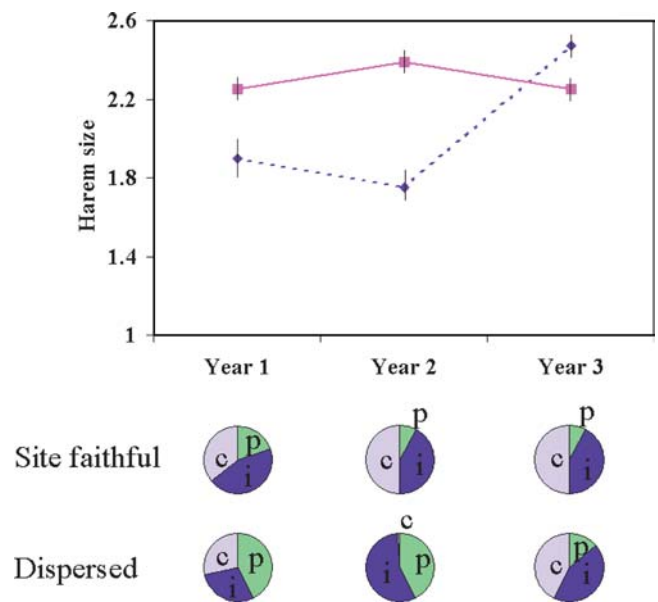


Fig. 4 Mean (\pm SE) harem sizes and territory positions in wetlands (p = peripheral, i = intermediate, c = central) of male yellow-headed blackbirds that dispersed (broken line, $n=7$) or were site faithful (solid line, $n=12$) for years 1, 2, and 3. All males were site faithful in years 2 and 3

these males we found the same pattern in years 1 and 2 that we observed in the overall analysis – dispersing males had smaller harems, associated with their acquisition of peripheral territories (Fig. 4). In year 3, however, that pattern was reversed. Dispersing males substantially increased their harems from year 2 to 3 (paired $t=1.99$, $df=6$, $P=0.05$), although their harems in year 3 were not significantly bigger than those of site-faithful males ($t=0.53$, $df=6$, $P=0.08$; Fig. 4). Although we lacked complete nesting data for these males, the strong overall association between male reproductive success and harem size suggests that dispersing males would have improved their reproductive success in year 3. Survival data indicate an average longevity for males of 3.26 years after reaching adulthood, giving dispersing males a reasonable probability of living long enough to realize the longer-term benefits of dispersal.

Discussion

Male yellow-headed blackbirds were less likely to disperse than females, consistent with costs and benefits of dispersal differing between the sexes (Greenwood 1980; Weatherhead and Boak 1986). Relative to site-faithful individuals of the same sex, males that dispersed realized reduced reproductive success following dispersal, whereas female success appeared unaffected by dispersal. Despite equivalent reproductive success before and after dispersing, females may have improved their reproductive success by dispersing relative to what their success would have been had they stayed. Females dispersed in response to low-patch success (Boulinier and Danchin 1997), and patch success

was consistent between years. Unlike females, males dispersed in response to low individual success, associated with having few social mates. The benefit of dispersing for males was not realized until the year following dispersal.

In the polygynous mating system of yellow-headed blackbirds, females on the same territory appear not affect one another's success (Lightbody and Weatherhead 1987b), allowing females freedom to settle where they choose. The same is true for red-winged blackbirds (Searcy and Yasukawa 1995). This suggests that all a dispersing female must do to be successful is find a new breeding population. Both male and female yellow-headed blackbirds from this population have been observed during the breeding season visiting wetlands other than those on which they bred that year (Ward, in press b). Such "prospecting" behavior should provide those individuals with information on the locations of alternative breeding sites, and even information on site quality, because males and females that disperse preferentially settle in more productive patches (Ward, in press b).

We had expected that competition for territories would inhibit male dispersal. However, male yellow-headed blackbirds that dispersed always appeared to acquire territories because we never saw a former territory holder behaving as a floater. The success of dispersing males at acquiring territories may be unusually high in our study population because the density of the population is low relative to available habitat (Ward 2004). If so, then male site fidelity should be greater in denser populations. Also, because population density should affect female dispersal less, the sex bias in dispersal should be greater in denser populations. We are unaware of any data relevant to the latter prediction, but three studies have quantified male site fidelity in denser populations of yellow-headed blackbirds. In Washington State, 51–52% of males were site faithful (Searcy 1979; Beletsky and Orians 1994) and in Manitoba, 43% of males were site faithful (Picman and Isabelle 1995). These studies did not control for mortality. The comparable estimate (i.e., not controlling for mortality) of site fidelity for males in Illinois is 27%. Higher site fidelity in the other studies supports the prediction that greater costs of dispersal in denser populations promote greater site fidelity.

Higher dispersal in our population did not result from higher nest predation. Yellow-headed blackbirds in Illinois are among the most productive populations studied (Ward, in press a). Nest predators such as marsh wrens (*Cistothorus palustris*), that can be important in some locations (Picman and Isabelle 1995), were rare in our study and accounted for only a few instances of nest predation (Ward 2004).

Familiarity with neighbors and with a territory have both been proposed to provide advantages to site-faithful individuals (Hilde 1956; Greenwood 1980; Pärt 1994; Beletsky and Orians 1989). We found no benefit to males from having one or more familiar neighbors, suggesting that familiarity does not promote cooperation among males. We could not directly test the hypothesis that familiarity with a territory is advantageous. However, given the high rate of dispersal we observed, and a previous study showing that relaxation of competition for territories promotes greater dispersal (Weatherhead and Boak 1986),

it seems reasonable to conclude that if familiarity with a territory provides any advantages, they must be small.

Despite their success at acquiring territories, dispersing males realized a reduction in reproductive success because the territories they acquired tended to be on the periphery of wetlands, where fewer females nested. However, those males subsequently (in year 3) acquired central territories, resulting in their harems being comparable to, or larger than, those of site-faithful males. Improved success in year 3 helps explain why these males dispersed, given their reduced success in year 2. Thus, it is possible that dispersal is a longer-term strategy for males, requiring at least 2 years to pay off. Given that dispersing males were able to acquire central territories and improve their reproductive success in year 3, they should have been able to do that on their original wetland and not disperse. The patches those males left, however, were less successful than the patches to which they moved. Therefore, longer-term prospects for dispersing males were increased by dispersing.

If dispersal is a long-term strategy for male yellow-headed blackbirds, there are parallels with patterns reported for lekking species. In black grouse (*Tetrao tetrix*), males gradually acquire central lek positions and greater mating success through competition spread over several years (Kokko et al. 1999). In the discussion above, we discounted the importance of familiarity with neighbors in the context of cooperative behavior. However, familiarity with neighbors may help males recognize when vacancies occur on superior territories. Thus, when returning for his second year on a wetland, a male can compete for those territories not defended by returning males, given that returning males generally prevail through the convention of site dominance.

Any test of the hypothesis that male yellow-headed blackbirds pursue a long-term strategy when dispersing must consider survival as well as reproductive success. Some males that disperse will not survive to year 3, and thus will not realize the improved reproductive success we observed, whereas males that survive beyond year 3 could realize higher success for several years. Because we estimated the average life span of male yellow-headed blackbirds reaching adulthood to be 3.26 years, a sufficient proportion of dispersing males should live long enough for dispersal to be beneficial. It remains to be determined whether delayed benefits of dispersal occur in other species. Our results indicate, however, that any analysis of the consequences of dispersal that considers only the year before and the year after dispersal may miss important information regarding the costs and benefits of dispersal.

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