

# Familiar neighbors enhance breeding success in birds

(social behavior/reproductive success/red-winged blackbird/cooperation)

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**ABSTRACT** We tested the hypothesis that long-term familiarity with neighbors is advantageous by determining whether male red-winged blackbirds (*Agelaius phoeniceus*) breeding adjacent to familiar neighbors have better reproductive success than other males. Using data gathered during a 10-yr study of breeding success, we found that males with familiar neighbors fledged, on average, significantly more offspring annually than males without familiar neighbors. We also found that the same males, breeding in different years on the same territories, had significantly larger harems in the years they had familiar neighbors. Improved reproductive success was due to the males' abilities to attract more females to nest in their territories. Alternative hypotheses to explain the positive relationship between familiar neighbors and breeding success were not supported by our data. Relatively high reproductive success for breeders with long-term neighbors may provide a basis for the evolution of cooperative behavior in this and other species.

Individuals of many species are known or presumed to benefit from familiarity with their physical and social environments (1-4). Experience in a habitat should increase the store of information available to individuals concerning the location and quality of foraging and breeding sites and the habits of local predators. Individuals familiar with their neighbors or with other members of their social groups could potentially benefit by having prior information about, for example, dominance statuses and fighting abilities of competitors, probabilities for reciprocal actions during cooperative behaviors, and the relative quality of potential mates. These benefits would be expressed as improved survival and reproductive success, but direct evidence in natural populations of benefits from familiarity is scarce. Here we test the hypothesis that social familiarity is advantageous by evaluating the prediction that male red-winged blackbirds (*Agelaius phoeniceus*) with familiar neighbors produce more offspring, on average, than males lacking familiar neighbors.

Social relations between adjacent neighbors are probably the most common type of interaction among territorial males of many species of birds. Neighbors are potential competitors for food and mates, but they are also potential deliverers of cooperative assistance. For this reason, zoologists characterize neighbor interactions as "dear enemy" relationships (5-7). Familiarity with territorial neighbors could be beneficial to males in several ways. For example, in migratory species, familiarity with previous neighbors may facilitate year-to-year territory reestablishment (8-10) by reducing time and energy allocated to disputes over boundaries. Also, for species with small contiguous territories, such as the redwing, long association among males could increase cooperation in alarm systems or in nest defense.

Male redwings are sometimes aggressive toward neighbors but, as in other territorial songbirds, they also recognize them

as individuals (10, 11) and tolerate them in the vicinity of their territories; boundary disputes are relatively rare among long-established neighbors (personal observations). Return rates of territorial redwings are high enough in our study area and elsewhere that groups of males breeding on particular marshes often have been neighbors for several years. If long association reduces costs of territorial defense and/or increases anti-predator cooperation, then males with long-term familiarity with their neighbors should experience better reproductive success than those with new neighbors. We tested this prediction, using data from a 10-yr study of redwing territoriality and breeding success.

## METHODS

Redwings breed polygynously over much of North America. Males defend territories in most marsh habitats and many upland ones within their range. At our study site, the Columbia National Wildlife Refuge in Washington State, males occupy their territories starting in February, females arrive and settle in March and April, and breeding continues through June. Females build nests, incubate, and feed young unassisted by their mates. Males at the study site bred for an average of  $2.1 \pm 1.4$  yr (range 1-9) during the years of the study and attracted an average of  $4.1 \pm 2.4$  females per year (range 1-14;  $n = 729$  male breeding years). Average annual reproductive success for male territory owners was  $5.0 \pm 5.9$  young fledged (range 0-38;  $n = 729$  breeding years). All breeding males and most females carried unique combinations of colored aluminum legbands for individual identification.

On each of the eight marshes we monitored, territories were contiguous, and males established well-defined and seasonally stable boundaries with their neighbors. Cooperative mobbing of nest predators by males and females occurred regularly, but its effectiveness in reducing predation on eggs, nestlings, and fledglings is unknown. The males holding territories on each marsh were very rarely closely related because most breeders on our study area were born elsewhere. The few males born on our marshes that also bred there dispersed an average of  $\approx 1000$  m (L.D.B. and G.H.O., unpublished data).

For these intensively studied marshes, containing a total of 65-80 territories each year, we plotted territorial boundaries several times during each breeding season from 1977 through 1986. Most males occupied their territories throughout a breeding season, but there were a few within-breeding season territorial takeovers. Males were strongly site faithful; most bred on the same territories each year (12). They remained in the study area all year but spent most of their time in flocks during nonbreeding periods. Marshes in the area were of two types. In strip marshes, the emergent vegetation bordered lakes in thin patches only one territory wide. Territory owners in strip marshes had, at most, two neighbors. In pocket marshes, with broad expanses of vegetation, males had up to five neighbors.

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We classified territorial males *breeding for their second or subsequent years* into those with familiar and those with unfamiliar neighbors, based on whether or not they shared a territorial boundary with at least one of their adjacent neighbors from the previous year. We compared reproductive success of males with familiar and unfamiliar neighbors with respect to harem size, total number of nests built, and total number of young fledged. Harem size (Table 1) is the total number of females that build nests on a male's territory during one breeding season. Total number of nests includes second clutches and nests built to replace ones destroyed by predators. The number of young fledged is the total number of offspring fledged from all nests located on a male's territory. Paternity is assumed to be 100%.

## RESULTS AND DISCUSSION

For all marshes combined, males with familiar neighbors had larger harems and fledged significantly more offspring than males with all new neighbors (Table 1). Average territory sizes for the two groups did not differ significantly. The enhancing effect of familiar neighbors on reproductive success was highly significant in pocket marshes but not significant in strip marshes (Table 1). Although our study site includes a number of strip marshes, most redwings in North America breed in marshes in which they have more than two neighbors; thus, our pocket marsh results should apply to most breeding situations.

Harem size and annual fledging success per male are strongly correlated in this population (12, 13). Indeed, the data in Table 1 suggest that attracting more females is the mechanism by which males with familiar neighbors achieve better reproductive success. To test the hypothesis that males attract larger harems *because* they have familiar neighbors, while controlling for differences among the males or their territories, we compared the harem size of individual males that bred *three or more years* during the years they had familiar neighbors with those during the years they had all new neighbors. When males had more than one breeding year in one or both categories, their average harem sizes in those categories were compared. Males had significantly larger harems when they had familiar neighbors (26 males had larger harems when they had familiar neighbors, 9 had smaller harems, and 7 had harems of equal size; Wilcoxon matched pairs test,  $z = -3.30$ ,  $P < 0.001$ ). The probability that a male did or did not have familiar neighbors was not correlated with age—i.e., males did not have familiar neighbors more often in later years than in early years (24 males had no familiar

neighbors, whereas 18 males had familiar neighbors during their second breeding year). Furthermore, age differences did not affect our results because males did not, on average, improve their annual breeding success as they got older (males of ages 2–6 *breeding for at least their second year*,  $n = 374$  breeding years, Kruskal–Wallis test,  $\chi^2 = 1.87$ ,  $P = 0.76$ ). Territory quality does not affect these results because we used each male as his own control and analyzed only those males that did not change territories between years. Therefore, this result strongly suggests that having familiar neighbors accounted for the significant differences in harem sizes in Table 1.

Although the preceding analysis eliminates age and territory quality as causes of the correlation, it does not exclude interannual differences in survival as a factor. The probability of having familiar neighbors must be positively correlated with over-winter survival of males. If female over-winter survival is positively correlated with male survival and if breeding success were better after a mild winter, then a positive relationship between breeding success and having familiar neighbors could result, but the improved success could not be attributed to a "familiar neighbor" effect. However, this plausible hypothesis can be rejected by our data. (i) Male and female return rates each year were not positively correlated, as required by the hypothesis. The average male return rate for 1977–1986 was  $53.1 \pm 8.8\%$  (range, 35.4%–64.2%); the average female return rate was  $52.3 \pm 6.3\%$  (range, 40.7%–61.5%). Although there was a trend for male and female return rates to covary, the correlation was not significant (Spearman  $r = 0.47$ ,  $P = 0.10$ ,  $n = 9$ ). (ii) The hypothesis requires breeding success to be below average in years of low male returns and above average in high-return years. However, males had above average breeding success in two of four low-return years [defined as years in which the percentage of males returning to breed was less than the average (53.1%) during the 10-yr study period]—1978, 1979, 1982, and 1986—and in only two of five high-return years ( $>53.1\%$ )—1980, 1981, 1983, 1984, and 1985. Thus, no clear relationship existed between return rates and reproductive success. (iii) The familiar-neighbor effect should disappear when high- or low-return years are analyzed separately. However, males in pocket marshes had significantly higher reproductive success when they had familiar neighbors in both low- and high-return years [low years, pooled: average fledging success for males with familiar neighbors equaled  $11.0 \pm 9.3$  ( $n = 27$  breeding years) and without familiar neighbors equaled  $5.6 \pm 5.5$  ( $n = 25$ ,  $t = 2.39$ ,  $P$  (one-tailed) = 0.01]; high years, pooled: average success of

Table 1. Breeding success of male redwings with and without familiar neighbors

	Males without familiar neighbors		Males with familiar neighbors		<i>t</i>	<i>P</i> (one-tailed)
	$\bar{X} \pm SD$	<i>n</i>	$\bar{X} \pm SD$	<i>n</i>		
All marshes						
Harem size	$3.9 \pm 1.9$	148	$5.0 \pm 2.4$	169	4.28	0.000
Nests, no.	$6.4 \pm 3.6$	148	$8.1 \pm 4.3$	169	3.71	0.000
Young fledged, no.	$5.0 \pm 5.3$	158	$6.6 \pm 7.3$	175	2.38	0.009
Territory size, m <sup>2</sup>	$160 \pm 89$	143	$154 \pm 77$	159	-0.69	0.25
Pocket marshes						
Harem size	$4.4 \pm 2.1$	56	$6.0 \pm 2.8$	68	3.70	0.000
Nests, no.	$7.0 \pm 3.7$	56	$9.3 \pm 4.7$	68	3.09	0.001
Young fledged, no.	$6.4 \pm 5.3$	59	$10.3 \pm 8.7$	71	3.10	0.001
Territory size, m <sup>2</sup>	$140 \pm 82$	58	$143 \pm 71$	68	0.25	0.40
Strip marshes						
Harem size	$3.6 \pm 1.8$	92	$4.3 \pm 1.9$	101	2.42	0.008
Nests, no.	$6.1 \pm 3.6$	92	$7.3 \pm 3.9$	101	2.19	0.02
Young fledged, no.	$4.1 \pm 5.2$	99	$4.2 \pm 4.8$	104	0.05	0.48
Territory size, m <sup>2</sup>	$174 \pm 91$	85	$162 \pm 81$	91	-0.97	0.17

males with familiar neighbors equaled  $9.8 \pm 7.7$  ( $n = 44$ ) and with no familiar neighbors,  $7.0 \pm 5.1$  ( $n = 34$ ,  $t = 1.91$ ,  $P = 0.03$ ).

Improved reproductive success for males with familiar neighbors was mainly due to their larger harems. To determine what factors might lead females to settle preferentially on their territories, we compared the reproductive success of females breeding on pocket marshes, where the familiar neighbor effect was strong, between territories where their mates had familiar neighbors ( $n = 71$ ) and where they did not ( $n = 59$ ); females fledged more young per nest (total number of young fledged divided by total number of nests;  $\bar{X} = 1.1 \pm 0.7$  vs.  $0.9 \pm 0.7$ , respectively) and more young per individual (total number of young fledged divided by harem size;  $\bar{X} = 1.5 \pm 1.0$  vs.  $1.4 \pm 1.0$ ) on territories with familiar neighbors, but the differences between averages were not significant for this sample [ $t = 1.06$ ,  $P$  (one-tailed) = 0.14 and  $t = 0.75$ ,  $P = 0.23$ , respectively].

Breeding success on one of the four pocket marshes was consistently very poor, due to especially heavy nest predation and extensive use of the marsh by breeding yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), which are interspecifically territorial with redwings (male yellow-heads are aggressive toward female redwings and often drive them from or damage their nests). When data from this marsh were excluded, females on the remaining three marshes fledged significantly more young per nest [ $\bar{X} = 1.2 \pm 0.7$ ,  $n = 55$  vs.  $0.9 \pm 0.8$ ,  $n = 45$ ;  $t = 1.76$ ,  $P$  (one-tailed) = 0.04] and more young per individual ( $\bar{X} = 1.7 \pm 0.9$  vs.  $1.4 \pm 1.0$ ,  $t = 1.79$ ,  $P = 0.04$ ) on territories with familiar neighbors. After fledging, young are fed by their parents for  $\approx 2$  weeks either in the marsh or in adjacent uplands. Postfledging survival may also be enhanced by having familiar neighbors, but we lack survival data to test this idea.

Because most females return to the same breeding areas each year (13), they could identify males with familiar neighbors by memory (the average number of breeding years per female during the study was 2; range 1–10). Also, females could recognize males with familiar neighbors behaviorally. To test whether females use the degree of male familiarity in a local area as a preference cue for deciding where to nest, we assessed whether the percentage of males that bred on a given marsh in year  $X$  that returned in year  $X + 1$  influenced female settling decisions. We computed for each marsh each year a

male familiarity value,  $MF$ , defined as the number of males who returned in year  $X + 1$ , divided by the total number of males breeding on the marsh in year  $X$ . We then determined whether  $MF$  values—i.e., male familiarity, correlated with the probability that females changed marshes between breeding years. Among females that were unsuccessful at fledging offspring from their last nest in year  $X$ ,  $MF$  values were significantly lower for females that changed marshes in  $X + 1$  than for females that did not change marshes. This is true both for the entire data set and for the subset of females whose mate in year  $X$  did not survive to year  $X + 1$  (Table 2). Females that were unsuccessful at previous nests were more likely than females with successful last nests to change marshes between years (Table 2; L.D.B. and G.H.O., unpublished data). Thus, females making breeding location decisions may respond positively to the presence of familiar males at past breeding sites, irrespective of the survival of their former mates.

Our initial prediction, that male redwings with familiar neighbors would, on average, produce more offspring, is supported by our data. However, we do not suggest that having familiar neighbors is a prime determinant of reproductive success or that the familiar-neighbor effect always operates. Rather, we have presented several lines of evidence that together suggest long-term familiarity among breeding males (*i*) may be recognized by females, (*ii*) may be beneficial, on average, to female breeding success, (*iii*) may influence female settling behavior, and therefore (*iv*) may contribute to male breeding success. The presence of familiar males on their former breeding sites, however, is just one of a complex array of factors that influence female settling decisions. For example, a female's previous nesting success, familiarity with her physical surroundings and with her harem mates, genetic factors, as well as chance events, all contribute to female nesting decisions (ref. 14; L.D.B. and G.H.O., unpublished data). The major determinants of annual reproductive success for males in the population are harem sizes and nest predation rates (13).

The mechanism by which having familiar male neighbors increases female breeding success is unknown. A clue is provided by the observation that the familiar-neighbor effect was strong on pocket but not on strip marshes. Because these marshes differ in relative numbers of nearby individuals available to mob predators, mobbing efficiency may be better

Table 2. Number of female redwings changing breeding marshes between years as a function of the proportion of familiar males present on their previous marshes

	$MF$ , $\bar{X} \pm SD$	$n$	$U^*$	$P$ (two-tailed)
All cases				
Year $X + 1$ behavior of females that had a successful last nest in year $X^\dagger$				
Changed marsh	$0.54 \pm 0.20$	67		
Did not change marsh	$0.55 \pm 0.17$	363	12179.0	0.98
Year $X + 1$ behavior of females that had an unsuccessful last nest in year $X$				
Changed marsh	$0.48 \pm 0.18$	90		
Did not change marsh	$0.55 \pm 0.16$	241	13507.5	0.001
Cases in which year- $X$ mate does not survive to year $X + 1$				
Year $X + 1$ behavior of females that had a successful last nest in year $X$				
Changed marsh	$0.45 \pm 0.17$	32		
Did not change marsh	$0.50 \pm 0.17$	140	2693.5	0.074
Year $X + 1$ behavior of females that had an unsuccessful last nest in year $X$				
Changed marsh	$0.40 \pm 0.17$	47		
Did not change marsh	$0.49 \pm 0.17$	94	2840.5	0.006

\*Mann-Whitney  $U$  test statistic (nonparametric ranks test).

†A successful nest is defined as one from which at least one chick is known to have fledged.

in the densely packed pocket marshes. We have observed groups of 20 or more male and female redwings mobbing a black-billed magpie (*Pica pica*) raiding nests on pocket marshes, but we have never seen such large concentrations on the more sparsely settled strips. Both males and females participate in mobbing, but males, being 40% larger than females, are probably more effective at repelling nest predators. Long-term neighbors may be more likely or quicker to mob their neighbors' territories, or they may repel predators more efficiently together. Also, redwing females engage in extra-mate copulations with neighboring males (ref. 15; G.H.O. and E. Davies, unpublished data). This behavior could influence the willingness of those males both to mob predators at their nests and to permit those females to forage on their territories, both of which could increase reproductive success. Additional studies are needed to explore these ideas empirically.

The value of familiar neighbors to males may explain why male redwings trespass onto their neighbors' territories to chase off intruding nonterritorial males when their neighbors are temporarily absent (ref. 16; personal observations; see also ref. 11). Greater reproductive success of males with long-term neighbors may also provide a basis for the evolution of redwing cooperative behavior, such as predator mobbing and group alert calling (17). The improved success of males with familiar neighbors suggests that genes for cooperative behaviors with neighbors may be favored by natural selection. The applicability of our conclusions to other species remains to be demonstrated, but the positive effects of neighbor familiarity could influence site fidelity and other forms of social behavior.

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