

Effects on female reproductive success of familiarity and experience among male red-winged blackbirds

PATRICK J. WEATHERHEAD

Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6 Canada

*(Received 14 December 1993; initial acceptance 26 December 1993;
final acceptance 18 March 1994; MS. number: A6929R)*

Abstract. Evidence from a long-term study of red-winged blackbirds, *Agelaius phoeniceus*, in Washington has indicated that females preferentially nest in territories of males that are familiar with their neighbours, perhaps because familiar males cooperate in nest defence. Data presented here from a long-term study in Ontario indicated that an average of 55% of territorial males returned from one year to the next, and of those, 81% reoccupied their former territories, so males were often familiar with their neighbours. Also 40% of breeding females returned to the study area between years (76% of those individuals returned to the same marsh), allowing the possibility of females recognizing males that were familiar with each other. However, no advantage to females, or preference by females, for familiarity among male neighbours was found. In fact, females were more successful on territories with one or more new neighbours because of reduced nest predation. These results, in conjunction with observations of male interactions with their neighbours during focal observations and model predator presentations, provided no evidence that familiarity among males was advantageous to females or facilitated cooperative nest defence by males. The effect of familiarity among neighbours may vary geographically (in Washington and Ontario) because the principal species of nest predators differ geographically and these predators may respond differently to variation in nesting density. Having new males as neighbours may be advantageous in Ontario because new neighbours are inexperienced and attract fewer females. In turn, local nest density is reduced, resulting in lower predation. When neighbours do help defend nests on their neighbour's territory, they may be defending young they have sired through extra-pair copulations, so it may be prudent to continue regarding territorial neighbours as adversaries, even when their behaviour appears cooperative.

When two male birds hold neighbouring territories their relationship can be thought of as adversarial. By definition, both males actively exclude each other from their respective territories and compete with each other for access to females, including each other's mates. None the less, relative to other territorial males in the population, neighbours are 'dear enemies' (Fisher 1954) in that they can potentially benefit from their association, despite their conflicting reproductive interests. Recently, Beletsky & Orians (1989a) presented data from a long-term study of red-winged blackbirds, *Agelaius phoeniceus*, showing that females preferentially nested on territories of males with familiar neighbours and may have realized higher reproductive success by doing so. In this study I use data from a long-term study of another red-winged blackbird population to determine the generality of the patterns reported

by Beletsky & Orians (1989a) and explore the basis for those patterns.

Familiarity among neighbours occurs regularly in red-winged blackbirds. Although on average, males hold territories for only slightly more than 2 years, some males can return for as many as 8 or 9 years (Beletsky & Orians 1989a). Because males usually occupy the same territory each time they return, long-term familiarity among neighbours can be established. There is also evidence suggesting that males pay attention to what transpires on their neighbours' territories. Freeman (1987) found that males were more likely to trespass on territories of neighbours that failed to attack a simulated intruder, and Metz & Weatherhead (1991) found that harassment by neighbours appeared to be the cause of territory loss by males given red colour bands. Finally, neighbours have the clear potential to

influence each other's reproductive success both positively and negatively. The alert calls of male red-winged blackbirds can provide information on the proximity of predators (Beletsky 1991) which could be beneficial to neighbours, whereas it is a male's neighbours that are most likely to sire young on his territory through extra-pair copulations (Gibbs et al. 1990; Westneat 1993). My first aim was to document the extent of site fidelity in my population to assess the opportunity for familiarity to develop among males.

From a female's perspective, familiarity among neighbouring males should influence her decision of where to nest only if that familiarity affects her reproductive success. For example, Beletsky & Orians (1989a) proposed that cooperative nest defence by familiar neighbours might account for the higher reproductive success of females in those territories and their preference for those territories. My next two aims in this study were to determine whether female nesting success was higher in territories of males with familiar neighbours and whether females preferentially nest on those territories.

For familiarity among neighbours to play a major role in where females choose to nest, females must be able to recognize males that are familiar with each other. Females that have bred on a marsh previously could conceivably recognize returning males. Therefore, my fourth aim was to document site fidelity by females between years to assess the potential for females to recognize returning males.

Given that site fidelity by females could be low, and that females breeding for the first time obviously do not know any of the males from previous years, if familiarity among males is to influence where those females nest, then some method of distinguishing males that are familiar with each other from those that are not would be necessary. Therefore, my fifth aim was to determine how females might recognize males that had shared a territory boundary in previous years (i.e. familiar neighbours) based on the males' behaviour at the time females settle.

Finally, Beletsky & Orians (1989a) suggested that the advantage derived by females from nesting in territories of males with familiar neighbours may be cooperative nest defence by the males. Therefore, my last aim was to determine whether the response of males and their neighbours to a

predator differed when the males were familiar with each other.

In this study I consider only the implications of familiarity among males for females' nesting success. The high rate of extra-pair paternity in red-winged blackbirds (Gibbs et al. 1990; Westneat 1993) makes it conceivable that familiarity among males could influence a female's decision of which male to copulate with, in addition to where to nest. Although an interesting question, it is separate from that dealt with here. Throughout the paper I refer to female preferences for territories in which to nest, but recognize that female settlement may be influenced by a variety of attributes of males and their territories. I assume that the number of females that settle in a territory (i.e. harem size) is an index of female preference for that territory.

METHODS

Breeding Data

I collected data on where females nested and their reproductive success as part of a long-term study of red-winged blackbirds at the Queen's University Biological Station in eastern Ontario. Some males were banded on these areas prior to 1986, but from 1986 through to 1991 (the last year included here), nearly all males holding territories were banded. I also banded nearly all females that nested on the study area, although each year there were some females that had nests fail before they could be banded. All birds were banded with anodized aluminium bands that do not appear to cause band-colour effects (Beletsky & Orians 1989b; Weatherhead et al. 1991) of the sort reported by Metz & Weatherhead (1991).

I considered two males to be familiar if they had a shared territory boundary for at least one previous breeding season. Therefore, only males known from banding records to have been neighbours in previous years were considered familiar. Similarly, only males that replaced a previous territory holder that was banded were considered new (i.e. their first year on the territory). By this criterion, new males were necessarily unfamiliar with all their neighbours. For males breeding for at least their second year, strong site fidelity meant that most unfamiliar neighbours were new males.

The study areas were marshes along the shore of Lake Opinicon and four nearby beaver ponds.

In three of the beaver ponds and part of the lakeshore, the vegetation used by the birds was more extensive than just a strip along the shore, so most males had more than two neighbours (maximum of five). In the remaining areas the vegetation was only wide enough for a single territory, so males usually had one neighbour on either side. Thus, with respect to the spatial arrangement of territories, these two types of habitats corresponded to the 'pocket' and 'strip' marshes of Beletsky & Orians (1989a) and I use their terminology here. All males included in the analyses had at least one neighbour.

In each year of the study, marshes were monitored as males reoccupied their territories in April, and new males were banded. Nesting activity was followed from its inception in early May through its completion in mid-July. Most nests were discovered before egg laying began and were checked every other day until the nest was preyed on or the young fledged.

To determine whether the patterns of female settlement and nest success reported by Beletsky & Orians (1989a) also occurred in my population, I repeated their initial analysis using some of the same variables. However, I also used several different variables that better reflect the consequences of familiarity among males for female reproductive success. Beletsky & Orians (1989a) framed their study in terms of the effect of familiarity among neighbours on male reproductive success. To do so, they assumed all young fledged in a territory were sired by the territory owner. Because that assumption appears to be false (Gibbs et al. 1990; Westneat 1993), it is best to use fledging success only as a measure of female success and to ask whether familiarity among males affects where females nest and how successful they are.

I use harem size to denote the total number of individual females that nested in a male's territory in a given season. Note that this is different from the alternative use of harem size to denote the maximum number of females nesting simultaneously in a male's territory (e.g. Weatherhead 1990a). I considered a nest successful if it fledged at least one young. I use the proportion of nests that were successful as a measure of predation, because predation usually involves the loss of all the eggs of young. The number of young fledged per successful nest provides an indication of success controlling for predation, and the number of

young fledged per female measures female fledging success. For males to have familiar neighbours they must have been breeding for at least their second year on the study area. Therefore, I restricted the analysis of the effects of familiarity to males breeding for at least the second time (defined as experienced males), as did Beletsky & Orians (1989a). For males present for more than 2 years, I treat each year as an independent event (except where specified otherwise) because the status of a male's neighbours (familiar or unfamiliar) usually changes from one year to the next.

Because the analysis of female nesting performance involved multiple statistical testing, some adjustment of probabilities was required (Rice 1989). I chose as my 'family' of tests, all tests within a marsh type (overall, pocket, strip). My principal interest was in whether familiarity among neighbours had any overall effect on female nesting performance. The separate analysis of pocket and strip marshes was simply to assess whether the patterns from the overall analysis were consistent in both marsh types. Therefore, probabilities were adjusted for the number of analyses within each marsh type for each general question addressed (i.e. within each table of results).

Focal Observations

To determine whether I (and by implication, female red-winged blackbirds) could recognize familiar from unfamiliar neighbouring males by their behaviour, I collected time-budget information on 22 territorial males in 1990. Of these males, eight were first-time breeders on my study area, four were returning males without familiar neighbours, and 10 were returning males with familiar neighbours. All time-budget observations were made between 27 April and 22 May, which is the period when females are settling on territories and initiating their first nests. Each male was observed on 4 days for 15 min each day, with two observations made before 0800 hours and two between 0800 and 1000 hours. To avoid influencing the males' behaviour, all observations of a focal male were made from the edge of the study area in a location that was not part of any male's territory.

During observations, an assistant watched males continuously and recorded the amount of

time they spent interacting (chasing or being chased) with their neighbours, chasing females and chasing floaters (non-territorial males). They also recorded the numbers of song-spread displays and flight-song displays given by the focal male and calculated the total duration of trespasses by neighbours. Finally, for the six focal males that had both familiar and unfamiliar neighbours, the assistant recorded the position of the focal male relative to its neighbours' boundaries. To do this, the assistant first mentally divided the male's territory into a central and peripheral portion, with the dividing line falling half-way between the boundary and the central point of the territory. A male was considered to be spending time near a particular neighbour if he was in the peripheral portion of his territory adjacent to the neighbour's territory. The centre of the territory and peripheral areas not adjacent to neighbours were considered to be neutral with regard to neighbours. For all analyses of time budgets I summed the data for the four observation periods for each male.

I used arcsine transformation on all the proportion variables (e.g. proportion of time spent interacting with neighbours) for use in parametric analyses.

Nest Defence

To determine whether familiar neighbours cooperated more in nest defence than unfamiliar neighbours, I presented a model crow to 19 experienced males, 11 of which had at least one familiar neighbour and eight of which did not. All trials were conducted between 31 May and 26 June 1990, which is the peak nesting period. The crow was placed 2 m from an active nest. Nests were not all at the same stage, so nest stage was recorded for use in analyses. After positioning the model, I retreated to neutral ground (not on any male's territory) and recorded the response of the resident male and his neighbours for 5 min. Although in previous studies of nest defence I have simply recorded the response of birds to a human observer at the nest (e.g. Weatherhead 1989, 1990b), this approach would not have allowed simultaneous observation of both the resident male and his neighbours. During these trials I recorded the rate of alarm calls and dives at the crow and the proportion of time spent within 5 m of the crow by the resident male, as

well as the amount of time neighbours spent trespassing (i.e. within the territory boundaries of the focal male). All values for the nest-defence variables were arcsine transformed for parametric analysis.

Even though all males were banded, it was difficult to keep track of all individual males simultaneously, so trespassing by neighbours could not be attributed to specific males. I predicted that, if familiar neighbours cooperate more in nest defence than unfamiliar neighbours, then I should observe higher rates of trespassing during model presentations on territories of males with familiar neighbours than on those without familiar neighbours. Furthermore, during nest-defence trials there should be clear evidence that trespassing neighbours are cooperating in nest defence (e.g. mobbing the predator) rather than taking advantage of the situation to trespass for other reasons.

RESULTS

Male Site Fidelity

To analyse site fidelity I first considered each year separately, so some males are included several times. Over 6 years the return rate of territorial males to the study area from one year to the next ranged from 49 to 62%, and overall 122 of 221 territory holders (55.2%) returned. This analysis is based on 123 individual males. Of these, 68 (55.3%) returned to the study area at least once. Of these 68 males, three (4.4%) switched marshes between years and 10 (14.7%) changed territories within marshes (no overlap between old and new territories) between years. Thus, 80.9% of males that returned reoccupied their previous territory. The high site fidelity in my study population meant that familiarity among males was a regular occurrence.

Reproductive Success

In contrast with Beletsky & Orians' (1989a) results, over all marshes I found no evidence that more females nested on territories of males with one or more familiar neighbours or that nesting success was higher on territories with familiar neighbours (Table I). In fact, while not significant, the differences were in the opposite direction.

Table I. Nesting performance on territories of experienced males with one or more familiar neighbours versus those without familiar neighbours

	With familiar neighbours			Without familiar neighbours			<i>t</i>	<i>P</i> *
	\bar{X}	SE	<i>N</i>	\bar{X}	SE	<i>N</i>		
All marshes								
Harem size	2.65	0.15	72	2.96	0.25	26	1.08	0.28
Proportion of nests successful	0.40	0.04	71	0.45	0.06	26	0.74	0.46
Young/successful nest	2.84	0.11	52	2.93	0.17	22	0.44	0.66
Young/female	1.41	0.16	71	1.82	0.25	26	1.36	0.18
Pocket marshes								
Harem size	2.73	0.16	62	3.00	0.36	14	0.73	0.47
Proportion of nests successful	0.43	0.04	61	0.47	0.06	14	0.40	0.69
Young/successful nest	2.85	0.11	48	2.70	0.22	13	-0.60	0.55
Young/female	1.52	0.17	61	1.83	0.31	14	0.79	0.44
Strip marshes								
Harem size	2.20	0.36	10	2.92	0.34	12	1.45	0.16
Proportion of nests successful	0.18	0.08	10	0.43	0.10	12	1.85	0.08
Young/successful nest	2.75	0.32	4	3.26	0.25	9	1.18	0.26
Young/female	0.73	0.33	10	1.81	0.41	12	2.00	0.06

Sample sizes are the number of territories from which data were available.

*Two-tailed.

Table II. Paired *t*-test analysis of nesting performance on the territories of the seven experienced males observed during breeding seasons when they had one or more familiar neighbours and when they had no familiar neighbours

	Males with familiar neighbours		Males without familiar neighbours		<i>t</i>	<i>P</i> *
	\bar{X}	SE	\bar{X}	SE		
Harem size	2.71	0.47	3.00	0.58	-0.44	0.67
Proportion of nests successful	0.38	0.09	0.47	0.10	-1.11	0.31
Young/successful nest	2.07	0.37	2.40	0.53	-1.01	0.36
Young/female	1.52	0.47	1.91	0.46	-1.39	0.21

*Two-tailed.

These results were similar on both strip marshes and pocket marshes.

Beletsky & Orians (1989a) confirmed that their results were a consequence of familiarity among males, rather than something specific to individual males or their territories, by comparing the same males (and territories) with and without familiar neighbours. I use the same approach here. To qualify for consideration, males must have bred for at least 3 years and, during the second and subsequent year(s), must have had at least one familiar neighbour in one year and no familiar neighbours in another. For the seven males that met these criteria, there was no significant difference in harem size or nesting success between

years with and without familiar neighbours (Table II).

Because the overall analysis suggested that if there were any differences in reproductive performance they favoured females on territories where the males had no familiar neighbours, I reclassified males according to whether or not they had any new neighbours. A comparison of these two classes of males over all marshes indicated that females were more successful when there was at least one new neighbour (Table III). That difference was the result of much lower predation, as indicated by the higher proportion of nests that were successful on territories with new neighbours. Interestingly, despite the

Table III. Nesting performance on territories of experienced males with one or more new neighbours versus those without new neighbours

	With new neighbours			Without new neighbours			<i>t</i>	<i>P</i>
	\bar{X}	SE	<i>N</i>	\bar{X}	SE	<i>N</i>		
All marshes								
Harem size	2.79	0.13	80	2.50	0.36	18	0.88	0.38
Proportion of nests successful	0.46	0.04	79	0.21	0.07	18	3.00	0.004*
Young/successful nest	2.83	0.10	65	3.15	0.08	9	-1.16	0.25
Young/female	1.69	0.15	78	0.79	0.23	18	2.69	0.008*
Pocket marshes								
Harem size	2.77	0.15	65	2.82	0.50	11	-0.12	0.91
Proportion of nests successful	0.47	0.04	64	0.27	0.09	11	1.90	0.06
Young/successful nest	2.78	0.11	54	3.12	0.08	7	-1.08	0.28
Young/female	1.69	0.17	64	0.95	0.29	11	1.76	0.08
Strip marshes								
Harem size	2.87	0.29	15	2.00	0.44	7	1.67	0.11
Proportion of nests successful	0.41	0.09	15	0.12	0.08	7	2.09	0.05
Young/successful nest	3.08	0.24	11	3.25	0.25	2	-0.30	0.77
Young/female	1.68	0.35	15	0.55	0.37	7	1.97	0.06

Sample sizes are the number of territories from which data were available.

*Two-tailed $P < 0.05$ with sequential Bonferroni adjustment (see text).

Table IV. Paired *t*-test analysis of nesting performance on the territories of the eight experienced males observed during breeding seasons when they had one or more new neighbours and when they had no new neighbours

	Males with new neighbours		Males without new neighbours		<i>t</i>	<i>P</i> *
	\bar{X}	SE	\bar{X}	SE		
Harem size	3.13	0.35	2.13	0.48	3.06	0.02
Proportion of nests successful	0.38	0.09	0.11	0.06	3.10	0.02
Young/successful nest	1.59	0.37	1.19	0.58	0.92	0.39
Young/female	1.05	0.37	0.48	0.29	2.13	0.08

*Two-tailed *P*; none of these differences was significant when Bonferroni adjustment was used.

advantage to females of nesting on territories with new neighbours, there was no significant difference in the harem sizes on territories with and without new neighbours (Table III). When I subdivided the territories into those in pocket marshes and those on strip marshes, I found the same general patterns on both (Table III).

Eight males met the criteria (see above) for a matched-pairs analysis of the effects of having a new neighbour. In years when these males had at least one new neighbour, nesting success on their territories was higher (Table IV). Moreover, more females nested on the territories of these males when they had at least one new neighbour. Although these patterns were the same as for the

analyses involving all males, the small sample size resulted in none of the differences being significant after a correction for multiple testing was applied.

Because I restricted all the preceding analyses to males breeding for at least their second year, and because of high site fidelity by males between years, new neighbours were nearly always males holding territories for the first time. Therefore, the results presented above indicate that there was an advantage to females that had an inexperienced male on an adjacent territory and in particular, that the presence of an inexperienced neighbour somehow reduced predation. One possible mechanism to account for this pattern could be that inexperienced males are less effective at defending

against predators, so predators spend more time on their territories and less on neighbours' territories. To gain insight into how the presence of inexperienced males might reduce predation on their neighbours' territories I compared the reproductive performance of females relative to the number of years the male had held the territory. Harem size varied significantly with male experience, with the fewest females nesting on territories held by males in their first breeding season (Table V). However, there was no evidence of higher nest failure on territories of new males and there was no significant difference in the number of young fledged per female.

Female Site Fidelity

Considering each return from one year to the next as a separate event, over 6 years 156 of 385 (40.5%) females that nested on the study area returned the following year. Annual variation was small, varying from 37.8 to 43.8%. These estimates are based on 269 individuals. Of these, 111 (41.3%) bred on the study area in more than 1 year. Among returning females, 84 (75.7%) nested on the same marsh as the previous year. When females had the opportunity to nest on the territory of the same male as the previous year (i.e. both the male and female returned to the same marsh), 58.7% of females did so. However, 87.5% of females that returned to the same marsh nested on or within one territory of where they had nested the previous year, so females appear more faithful to general areas of the marsh than to specific males, at least for nesting purposes. Note that these analyses only consider nests that persisted long enough for females to be caught or identified (if already banded), so many short-lived nesting attempts are not included. Overall, there appears to be ample opportunity for returning females to recognize males on the basis of the previous year's experience.

Time Budgets

Considering each behavioural variable separately by Mann-Whitney *U*-tests, there was no significant difference between males with one or more familiar neighbours and those without familiar neighbours in the proportion of time spent interacting with neighbours, floaters or females, the time that neighbours spent trespass-

ing, or the males' display rates (all $P > 0.20$). A discriminant function model using all of the behavioural variables failed to discriminate significantly between males with and without familiar neighbours. For the six males that had both old and new neighbours, the mean (\pm SD) time spent near the boundaries of familiar neighbours (299.2 ± 101.2 s) was not significantly different from the time spent near the boundaries of new neighbours (281.3 ± 209.0 s; Wilcoxon matched-pairs signed-ranks test: $z = 0.105$, $P = 0.92$). These data provide no evidence that females that did not recognize males from previous experience could distinguish familiar from unfamiliar neighbours on the basis of the males' behaviour.

Predator Model Presentations

Because nests used in the predator model presentations were not all at the same stage, I first determined whether nest stage accounted for significant variation in any of the response variables (see Weatherhead 1990b). None of the relationships was significant (all $r^2 < 0.07$, all $P > 0.28$), so I did not control for nest stage in subsequent analyses.

Analysis of individual variables by Mann-Whitney *U*-tests revealed no significant difference between males with and without one or more familiar neighbours in the time spent less than 5 m from the model ($z = 0.00$, $P > 0.99$), the rate of dives at the model ($z = -0.21$, $P = 0.84$), or the number of alarm calls ($z = -0.91$, $P = 0.36$). Although neighbours occasionally trespassed during predator model presentations, they never mobbed the model or approached within 5 m, so there was no evidence that neighbours trespassed to cooperate in nest defence. The mean (\pm SE) time that neighbours spent trespassing was higher on territories of males with familiar neighbours (27.82 ± 14.43 versus 0.0 ± 0.0 s), as was the time floaters spent trespassing (53.73 ± 19.57 versus 14.13 ± 10.30 s), but neither difference was significant ($P = 0.10$ and 0.19 , respectively). Finally, linear regression revealed no significant relationships between the proportion of time neighbours spent trespassing and any of the resident male's behaviour patterns. Thus, males did not vary their nest defence in accordance with whether they had familiar neighbours, neighbours did not actively participate in nest defence, and neighbours did not

Table V. Nesting performance relative to the number of years a male had held his territory

	1st year (N=99)		2nd year (N=47)		3rd year (N=28)		4th year (N=14)		5th (+) year (N=9)		F†	P
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE		
Harem size	2.03	0.11	2.77	0.20	2.57	0.23	2.57	0.31	3.33	0.33	5.37	<0.001*
Proportion of nests successful	0.38	0.04	0.42	0.05	0.43	0.06	0.41	0.09	0.32	0.10	0.31	0.87
Young/successful nest	2.72	0.96	2.85	0.76	3.13	0.69	2.21	0.80	3.10	0.60	2.42	0.05
Young/female	1.19	0.12	1.57	0.19	1.72	0.26	1.17	0.32	1.24	0.51	1.42	0.23

Males holding territories for the fifth or subsequent years were combined.

* $P < 0.05$ with Bonferroni adjustment.

†ANOVA.

coordinate this trespassing with any feature of a male's nest-defence behaviour.

DISCUSSION

Beletsky & Orians (1989a) found that more females nested on territories of males with familiar neighbours, and that females nesting on those territories were more successful. The same analysis of my data indicated neither a preference for territories of males with familiar neighbours, nor any advantage to females that nested on those territories. In fact, I found that females were more successful on territories of males with new neighbours relative to those without new neighbours, primarily because of lower nest predation. Because these analyses were restricted to experienced males (i.e. those breeding for at least the second time), new neighbours were mostly males holding territories for their first time. An analysis of harem size relative to the number of years a male had occupied his territory revealed that more females nested on territories of experienced males than on those of new males.

To assess how females might recognize familiarity (or lack thereof) between neighbouring males, I observed how males interacted with familiar and unfamiliar neighbours. My failure to detect any difference does not mean that there are not subtle cues available to females that I may have overlooked. However, there was sufficient site fidelity by females that simple recognition of returning males by females that returned would have allowed the possibility of discrimination between males on the basis of their familiarity with neighbours.

Beletsky & Orians (1989a) proposed that the advantages to familiarity that they observed among neighbouring males might be a consequence of cooperative nest defence. To test this hypothesis I compared the nest defence of males with and without familiar neighbours. I found no evidence that a male's neighbours trespassed more in response to the male's nest defence behaviour when at least some of the neighbours were familiar. However, in my study population, there was also no benefit from familiarity among neighbours. It would be informative to perform similar nest-defence trials in Beletsky & Orians' (1989a) study population where there was an advantage to neighbour familiarity.

Two issues are raised by the different effect of neighbouring males on where females nested and their reproductive success observed by Beletsky & Orians (1989a) and in the present study. First, what is the basis for this difference between studies, and second, what are the broader implications? It seems likely that differences in predators and predation patterns between the two study populations explain the differences in female preferences and reproductive success. In Washington, black-billed magpies, *Pica pica*, are the most important nest predators (Orians & Beletsky 1989). Beletsky & Orians (1989a) found that the advantage of having familiar neighbours was most pronounced in pocket marshes, where nesting densities were higher and thus, the opportunity for group mobbing of magpies was greatest. Magpies do not occur in eastern Ontario. In my study population, nocturnal mammalian predators such as raccoons, *Procyon lotor*, prey on a substantial number of nests. Nocturnal predators are not mobbed, which may explain why predation increases rather than decreases with nesting density in this population (Weatherhead & Robertson 1977). Because fewer females nested on territories of inexperienced males, the combined nesting density (and nest predation) on two neighbouring territories would be lower when an experienced male had a new (i.e. inexperienced) neighbour than a familiar (i.e. experienced) neighbour. This explanation could account for the different effect of neighbours in the two studies. However, it does not explain why females in my study preferred territories of experienced males but showed no overall preference for experienced males with new neighbours. In this study I have considered the consequences of where a female nests only on her success in fledging young. Where a female nests, however, will also influence with which males she is likely to have an opportunity to copulate, and it may sometimes be advantageous to females to compromise between the best place to nest and the best male(s) with which to mate (e.g. Weatherhead 1984). Complete understanding of the factors influencing where females choose to nest awaits comprehensive genetic analyses of mating patterns.

Finally, what are the implications of there being advantages to neighbour familiarity in Washington but not Ontario? Beletsky & Orians (1989a) suggested that the improved success of males with familiar neighbours could lead to

selection for cooperative behaviour among males. The effect of such selection would depend on whether the advantage of neighbour familiarity is the norm in red-winged blackbirds (i.e. my study population is atypical) and the extent of gene flow among populations. However, at least one line of evidence argues against Beletsky & Orians' hypothesis. If familiarity among neighbours is really important to reproductive success, then selection should favour extreme male site fidelity in their population. However, I found higher male site fidelity in Ontario, where, if anything, male familiarity is disadvantageous. Beletsky & Orians suggested that group mobbing of predators was consistent with their hypothesis that familiar neighbours are cooperative. However, as they also suggested, males may sometimes defend their neighbour's nests because they have some likelihood of having fathered the young. Recent genetic evidence suggests that males do defend nests in other males' territories when they have fathered young in those nests (Weatherhead et al. 1994). Therefore, apparent cooperation could really be simple self-interest. Until the effects of neighbour familiarity on paternity are assessed it seems prudent to continue viewing territorial neighbours as adversaries.

ACKNOWLEDGMENTS

I thank Drew Hoysak and Kit Muma for assistance in the field, Karen Metz and Drew Hoysak for assistance with data analysis, Gordon Orians, Ellen Ketterson, Ray Chandler and Kevin Dufour for helpful comments on the manuscript, Queen's University for the use of their facilities and the Natural Sciences and Engineering Research Council of Canada for financial support.

REFERENCES

- Beletsky, L. D. 1991. Alert calls of male red-winged blackbirds: call rate and function. *Can. J. Zool.*, **69**, 2116–2120.
- Beletsky, L. D. & Orians, G. H. 1989a. Familiar neighbors enhance breeding success in birds. *Proc. natn. Acad. Sci. U.S.A.*, **86**, 7933–7936.
- Beletsky, L. D. & Orians, G. H. 1989b. Red bands and red-winged blackbirds. *Condor*, **91**, 993–995.
- Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process* (Ed. by J. Huxley, A. C. Hardy & E. B. Ford), pp. 71–83. London: Allen & Unwin.
- Freeman, S. 1987. Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. *Behav. Ecol. Sociobiol.*, **21**, 307–311.
- Gibbs, H. L., Weatherhead, P. J., Boag, P. T., White, B. N., Tabak, L. M. & Hoysak, D. J. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by hypervariable DNA markers. *Science*, **250**, 1394–1397.
- Metz, K. J. & Weatherhead, P. J. 1991. Colour bands function as secondary sexual traits in red-winged blackbirds. *Behav. Ecol. Sociobiol.*, **28**, 235–241.
- Orians, G. H. & Beletsky, L. D. 1989. Red-winged blackbird. In: *Lifetime Reproduction in Birds* (Ed. by I. Newton), pp. 183–197. New York: Academic Press.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Weatherhead, P. J. 1984. Mate choice in avian polygyny: why do females prefer older males? *Am. Nat.*, **123**, 873–875.
- Weatherhead, P. J. 1989. Nest defence by song sparrows: methodological and life history considerations. *Behav. Ecol. Sociobiol.*, **25**, 129–136.
- Weatherhead, P. J. 1990a. Secondary sexual traits, parasites and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. *Behav. Ecol.*, **1**, 125–130.
- Weatherhead, P. J. 1990b. Nest defence as shareable paternal care in red-winged blackbirds. *Anim. Behav.*, **39**, 1173–1178.
- Weatherhead, P. J., Hoysak, D. J., Metz, K. J. & Eckert, C. G. 1991. A retrospective analysis of red-band effects on red-winged blackbirds. *Condor*, **13**, 1013–1016.
- Weatherhead, P. J., Montgomerie, R., Gibbs, H. L. & Boag, P. T. 1994. The cost of extra-pair fertilizations to female red-winged blackbirds. *Proc. R. Soc. Lond. B*, **258**, 315–320.
- Weatherhead, P. J. & Robertson, R. J. 1977. Harem size, territory quality, and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). *Can. J. Zool.*, **55**, 1261–1267.
- Westneat, D. F. 1993. Polygyny and extra-pair fertilizations in eastern red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol.*, **4**, 49–60.