

Anti-predator vigilance in the red-winged blackbird, *Agelaius phoeniceus*: do males act as sentinels?

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Abstract. During the nesting season, male red-winged blackbirds frequently scan from prominent perches near active nests. Males engaged in such behaviour appear to be acting as sentinels, guarding their nests against predators. The sentinel hypothesis was tested in three ways. (1) Male response to a simulated predator was observed. On average, males spent significantly more time within 10 m of their nests following predator presentations than at other times during the same day, and many males looked into their nests immediately after the simulated predator was removed. (2) The height and distance distributions of putative sentinel perches near nests that successfully fledged young were compared with those near nests that failed as a result of predation. Successful nests were associated with significantly closer and higher perches than were depredated nests. (3) The effect of artificial sentinel perches on female choice of nest location in a prairie habitat lacking tall perches was observed. Females were more likely to place their nests in areas with nearby artificial perches than in similar areas lacking such perches. These results support the sentinel hypothesis. There was no evidence, however, that more vigilant male red-winged blackbirds were more aggressive in nest defence, or experienced higher pairing and reproductive success than less vigilant males.

Parental care, defined as care-giving by a parent that is likely to increase the survival and reproductive success of offspring, is thought to have evolved as an evolutionary trade-off between the benefit to the parent in increased offspring fitness and the cost to the parent in reduced reproductive potential (Wittenberger 1979; Clutton-Brock 1991). Parental care is also viewed as an important component of the breeding system of a species because the amount, type and timing of parental care is related to the intensity of competition for mates (Trivers 1972; Clutton-Brock 1991).

Parents can provide many forms of care, including guarding and provisioning offspring. At one extreme, food is often provided to one offspring at a time because the benefits of provisioning depreciate if the food is divided among several offspring. Trivers (1972) focused attention on this depreciable, or non-shareable parental care with his definition of 'parental investment' as behaviour by a parent that increases the offspring's expected reproductive success at the cost of the parent's ability to invest in other offspring. As a result, much is now known about the costs and benefits of depreciable parental care (Clutton-Brock 1991).

At the other extreme, a parent can often guard several offspring simultaneously because the benefits of guarding do not depreciate as the number of guarded offspring increases (Clutton-Brock 1991). Such cases of non-depreciable, or shareable parental care are also presumed to evolve through natural selection (Wittenberger 1979; Clutton-Brock 1991). In this paper, we examine a non-depreciable form of parental care, anti-predator vigilance.

Parental Behaviour in the Red-winged Blackbird

Aspects of parental care have been analysed in most groups of animals, but birds have been especially well studied, and much attention has been focused on male parental care (e.g. Kendeigh 1952; Skutch 1976; Silver et al. 1985). The red-winged blackbird is a species of bird ideally suited to a study of male parental (paternal) care for several reasons. First, we would expect relatively little paternal care because, as a result of the polygynous mating system, males should benefit more from attempts to acquire additional mates than from investment in existing offspring (Trivers 1972;

Mock 1983). Advantages of paternal care, therefore, can be analysed in terms of the trade-off between mate attraction (sexual selection) and nest success (non-sexual selection), and the conflict between the evolutionary 'best interests' of males and females. Second, paternal care provided to nestlings varies both between populations and between individuals within populations (e.g. Fiala 1981; Muldal et al. 1986; Patterson 1991). Finally, male red-winged blackbirds engage in several forms of paternal behaviour. They (1) defend territory, (2) feed young, (3) actively defend young against predators and (4) maintain vigilance against predators. We have focused on anti-predator vigilance because little is known about this form of paternal care.

Anti-predator Vigilance

Maintaining vigilance against predators is generally thought to enhance reproductive success, and might be one advantage of group-breeding in birds (e.g. Gaston 1977; McGowan & Woolfenden 1989). In the group-breeding Florida scrub jay, *Aphelocoma coerulescens coerulescens* (McGowan & Woolfenden 1989) and several species of babblers (Andrews & Naik 1970; Gaston 1977; Wickler 1985), individuals appear to coordinate their vigilance into a sentinel system. Coordinated vigilance is unlikely in most systems, however, because the benefit is usually not sufficient to pay the cost of coordination (Ward 1985).

There also have been reports of one member of a breeding pair acting as a sentinel for the other (Morton & Shalter 1977; Wickler 1985), and parents acting as sentinels for their young (D'Agostino et al. 1981; Knopf & Knopf 1983). Vigilance could enable a watchful parent to detect predators and subsequently to distract, harass or deter them, thus reducing an offspring's risk of predation. Vigilance appears to be a function of the conspicuousness of the vigilant individual (Lendrem 1983), the visibility in the habitat (Metcalf 1984), and the hunting style of the predator (Hart & Lendrem 1984).

Red-winged Blackbird Vigilance

Observations of red-winged blackbirds in our study population indicate that males with active nests spend considerable amounts of time engaged in what appears to be anti-predator vigilance.

Vigilant males scan and call from high, exposed perches and they are very responsive to potential predators. From this position, males might communicate information about predators (Beletsky et al. 1986), which could be used by females (Beletsky 1989). Females are responsive to males perched near their nests and they frequently call in response to the songs of males perched nearby (Yasukawa et al. 1987a; Yasukawa 1989). An experimental study of calling from the nest by female red-winged blackbirds showed that one potential function of this behaviour is to facilitate the male's anti-predator vigilance (Yasukawa 1989).

We observed male red-winged blackbirds to determine whether they guard their active nests. In our initial observations, we also examined whether the status of the female affects the behaviour of the male because previous studies of paternal care in our population have demonstrated such effects (Yasukawa et al. 1987a, 1990; Yasukawa 1989).

We tested the hypothesis that male red-winged blackbirds engage in anti-predator guarding of offspring by examining three predictions of this sentinel hypothesis. First, the sentinel hypothesis predicts that males should respond to an increased risk of predation with an increase in vigilance. According to this prediction, males should increase the amount of time they attend nests once the nest is threatened by a predator. We tested this prediction by presenting a model crow, *Corvus* sp., at nests during the incubation stage and observing male attendance. Second, the hypothesis predicts that the presence of a nearby male 'on sentinel' should decrease the likelihood of predation. Thus, successful and depredated nests should differ with respect to the presence of prominent, nearby (sentinel) perches used by the males. We tested this prediction by examining the distance and height distributions of 'sentinel perches' associated with successful and depredated nests. And finally, the hypothesis predicts that females should prefer nest sites near prominent (sentinel) perches. We tested this prediction by placing artificial perches in portions of our study area that lacked tall perches and comparing the number of nests constructed in control (no artificial perch) and experimental (artificial perch) plots.

Parental behaviour is a potentially important component of male quality (Eckert & Weatherhead 1987; Yasukawa et al. 1987b). Females could benefit from choosing males that are good at guarding nests and deterring predators if they can identify

such males and if their reproductive success is enhanced by this form of male parental behaviour (Searcy 1979). We therefore attempted to determine whether male red-winged blackbird sentinel behaviour affects mating and reproductive success.

METHODS

Our study was conducted at Newark Road Prairie in Rock County, Wisconsin, U.S.A. Newark Road Prairie is a designated Scientific Area, and is owned and managed by Beloit College in cooperation with the Nature Conservancy. The study area is a 13-ha prairie and sedge meadow habitat on which approximately 35 male red-winged blackbirds defend territories. As a result of 7 years of previous field work, nearly all of the males and many of the females have been colour-banded for individual recognition, and all nestlings reaching day 9 of the nestling period have been banded with U.S. Fish and Wildlife numbered aluminium bands. A map of the study area was prepared from an aerial photograph, and the study area marked with a 20-m grid system to facilitate accurate plotting of male and female activity and nest locations.

Initial Observations

During the nesting seasons (late April to mid-July) of 1988 and 1989, we observed the behaviour of male red-winged blackbirds from blinds placed 5–20 m from active non-experimental nests (not used in the artificial perch experiment), which we found by watching and following females. We conducted daily 30-min observations between sunrise and noon at nests in the incubation stage. We used these observations to construct time budgets for males associated with focal nests. Time budgets were constructed by calculating the mean amount of time each male spent in three locations: (1) within 10 m of the nest ('in attendance'), (2) on the territory but more than 10 m from the nest ('on territory'), and (3) off the territory.

There was some evidence that time budgets of males observed in 1989 at primary and secondary nests were not independent (the sample size from 1988 was too small for analysis). The amounts of time males ($N=15$) spent off territory in 1989 during observations at primary nests were significantly correlated with those observed at secondary nests (Spearman rank correlation $r_s=0.625$, $P=0.019$).

Time spent within 10 m ($r_s=0.396$) and on territory beyond 10 m ($r_s=-0.218$) were not significantly correlated ($P>0.05$ for both), however. We report results of statistical tests for independent comparisons using mean amounts of time from observations at all primary and secondary nests in 1988 and 1989 (Mann-Whitney U -test) and tests for paired comparisons using mean amounts of time from observations at one primary and one secondary nest only for each of 15 males in 1989 (Wilcoxon signed-ranks test).

Crow Presentation and Male Attendance

In 1989 we conducted predator presentations between 0600 and 1100 hours at all nests found prior to the end of the incubation period. Our predator stimulus was a model crow mounted on a 2-m-high metal pole. We used a model crow because American crows, *Corvus brachyrhynchos*, are known to depredate red-winged blackbird nests (Bent 1958), and because male red-winged blackbirds attack both real and model crows (Eckert & Weatherhead 1987; Yasukawa et al. 1987b). In each presentation we waited until the female left the territory. We then placed the pole 1 m from the nest and positioned the model crow so that it appeared to be looking at the nest. We observed the behaviour of the male from a blind for 5 min with the crow in place, and then removed the crow and pole. We continued to observe the behaviour of the male for 30 min after the crow presentation (experimental period). In addition, we conducted a similar 30-min observation (control period) using the same nest at a randomly selected time (i.e. either before or after the experimental period) between sunrise and noon on the day the crow was presented.

To determine whether males increased their attendance in response to an increased risk of predation, we compared the amounts of time males spent within 10 m of focal nests (attendance time) during control and experimental periods. We used a Wilcoxon signed-ranks test to determine whether males spent more time near nests after predator presentations than during control periods. We presented the model crow at all 38 non-experimental nests on the territories of 22 males. It was clear, however, that a male responded similarly to presentations of the crow at several nests on his territory. As repeated presentations were not independent, we analysed only the first presentation to each male.

Pairing Success and Nest Success

In 1989 we visited each non-experimental nest daily to construct nest chronologies and to determine the fate of each nesting attempt. Pairing success of males was measured by counting the maximum number of nests that were active simultaneously on each territory. This number, called the male's harem size, is an estimate of the minimum number of females necessary to account for all nesting activity within each territory. Nests that produced at least one fledgling were classified as successful, and the number of fledglings produced by all successful nests on each male's territory was used to estimate male reproductive success. Nests from which all eggs or nestlings disappeared were considered to have failed as a result of predation. Nesting attempts that failed for other reasons (e.g. those abandoned by the female or in which all nestlings starved) were eliminated from our analysis.

Perch Distance and Perch Height

For each successful and depredated nest, we measured the distance to the nearest prominent (sentinel) perch used by the male, and the height above the nest of that perch. The distance and height distributions were then used to compare perches associated with the two categories of nests. We used a Mann-Whitney *U*-test to compare perch distance and height distributions of successful and depredated nests. To ensure that nests constructed on a single male's territory were independent, we used Spearman rank correlation analysis to estimate the correlation in perch distance and height from first and second nests measured on each territory. As distance and height from first and second nests were not significantly correlated (distance $r_s = -0.15$, $N = 16$, $P > 0.50$; height $r_s = 0.379$, $N = 16$, $P > 0.10$), we used all nests to characterize the perch distance and height distributions.

Artificial Perches and Nest Site Selection

Much of our study area is relatively homogeneous prairie habitat with very little vertical stratification. There are no prominent perches from which the male can see the nest and be seen by the female from the nest in these non-stratified, grassland portions of the study area. To determine whether females prefer nest sites near potential sentinel perches, we placed artificial perches on the

study area as follows. Once females had settled on our study area, but before they had begun to nest, we identified 14 blocks, each measuring 40×80 m, in non-stratified portions of our study area. Each block was then randomly divided into control and experimental halves, each containing four grid squares measuring 20×20 m. A 2.4-m high pole was then placed by the grid marker at the centre of the experimental half in each block.

Preliminary studies in 1988 showed that males in non-stratified portions of our study area readily used artificial perches, from which they scanned and advertised normally. Once the artificial perches were in place, we observed the 14 blocks from blinds throughout the nesting season to locate nest sites. For each nest that received at least one egg, we determined whether it was located within an experimental or control grid square, and plotted its position on the map of the study area. We used a chi-squared test of independence to determine whether nest site location was independent of presence of an artificial perch.

RESULTS

In 1988 and 1989 we observed male red-winged blackbirds associated with 27 and 38 non-experimental nests, respectively. Weather conditions were very different in the 2 years (there was a severe drought in 1988), so we analysed the years separately. In 1988 we observed males associated with 15 primary (first within a male's territory) and 12 secondary (later) nests. In 1989 we observed 20 primary and 18 secondary nests.

On average (\pm SE), male red-winged blackbirds spent more time perched within 10 m of primary than secondary nests (1988: 12.0 ± 1.8 min versus 9.2 ± 2.1 min; 1989: 8.2 ± 2.2 min versus 3.5 ± 0.9 min) but the difference was not statistically significant (Mann-Whitney *U*-tests, Wilcoxon signed-ranks test, all $P > 0.05$). On some territories, the apparent preference for primary nests may have resulted from the placement of primary nests near preferred perches, but in most cases males used different perches to attend primary and secondary nests. In any case, there was no evidence that the vigilance of male red-winged blackbirds varied with status of the nest. In all subsequent analyses, therefore, we combined data from primary and secondary nests.

Our results demonstrated that males spent considerable amounts (25–35%; Fig. 1) of time within

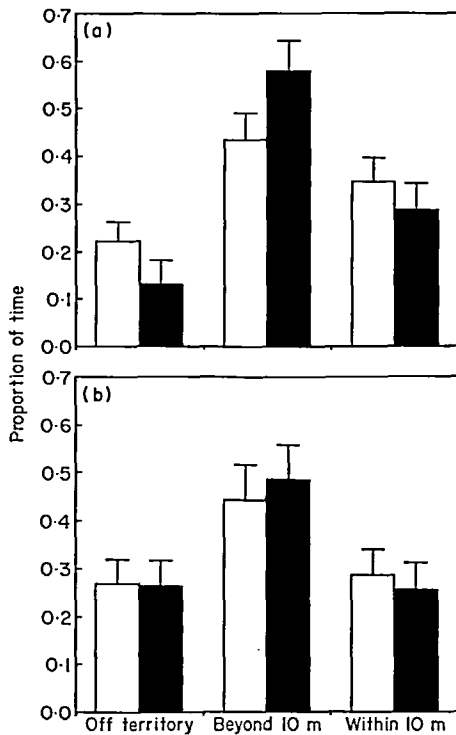


Figure 1. Time budgets of male red-winged blackbirds. Mean (\pm SE) proportions of time in three locations are shown for primary (□) and secondary (■) nests during the incubation stage. (a) 1988: primary $N=15$; secondary $N=12$. (b) 1989: primary $N=20$; secondary $N=18$. None of the differences in time budgets of males with primary and secondary nests was statistically significant (Mann-Whitney U -test, all $P>0.05$).

10 m of nests containing eggs. During these times 'in attendance', males perched at prominent locations from which they could see their nests and be seen by the females on the nests. Males maintained an alert posture (Nero 1956; Orians & Christman 1968) and scanned continuously. In addition, males gave calls that convey information about predators (Beletsky et al. 1986; Beletsky 1989) and sang songs that were frequently answered by females (Yasukawa et al. 1987a; Yasukawa 1989).

We measured the distance to, and height of the nearest prominent perch used by the male for each of 38 non-experimental nests on our study area in 1989. In some cases, males seemed to ignore potential perches that were closer, especially if their preferred perches were higher. We did not, however, attempt to identify the differences between used and unused perches. On average (\pm SE), the nearest

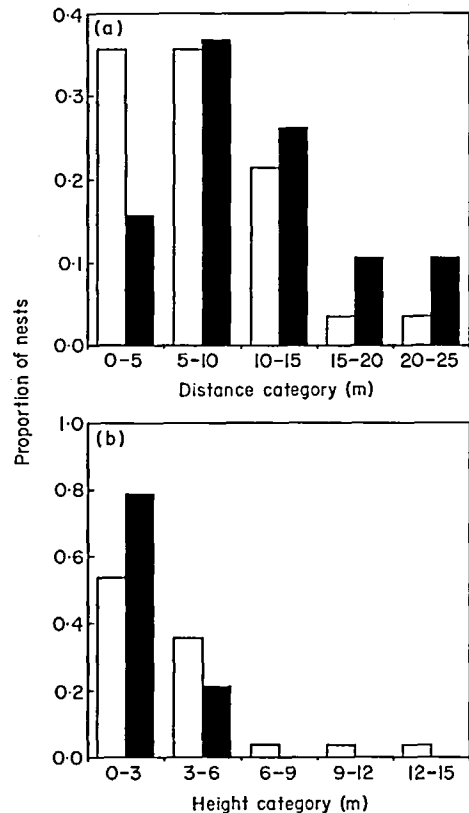


Figure 2. (a) Distance and (b) height distributions for the nearest prominent (sentinel) perches associated with red-winged blackbird nests. Proportions of nests in each distance and height category associated with successful (□, $N=25$) and depredated (■, $N=13$) nests are shown. Prominent perches associated with successful nests were significantly closer (Mann-Whitney U -test, $U=94$, $P=0.004$) and higher (Mann-Whitney U -test, $U=94$, $P=0.004$) than those associated with depredated nests.

perch used by the male was 9.1 ± 0.8 m from, and 3.0 ± 0.3 m above the nest (Fig. 2). Perch distance and height distributions of primary and secondary nests did not differ significantly (Mann-Whitney U -test, both $P>0.10$). Prominent perches were 10.0 ± 1.4 m from and 3.0 ± 0.6 m above primary nests ($N=20$), and were 8.1 ± 0.9 m from and 2.9 ± 0.4 m above secondary nests ($N=18$).

Crow Presentation and Male Attendance

Presentation of the model crow at nests elicited strong responses from males. All males gave alarm calls, and males attacked by striking the crow with their feet in 26 of 38 presentations. The male looked

directly into the nest after we removed the crow in 14 cases. We measured the amount of time each of the 22 males perched within 10 m of its nest during the 30 min immediately after the crow was removed (experimental period), and during a 30-min control period on the day the first presentation was performed on each territory. On average (\pm SE), males spent significantly more time in attendance during experimental (10.9 ± 1.8 min) than during control periods (5.6 ± 1.5 min; Wilcoxon matched-pairs signed-ranks test, $T_5 = 50$, $P = 0.023$, $N = 21$ non-tied pairs). These 'attendance' times are conservative with respect to the sentinel hypothesis because the preferred sentinel perches were more than 10 m from many of the nests (Fig. 2). In several cases involving nests lacking prominent perches within 10 m, males used perches within 10 m of the nest during experimental periods that they never used otherwise.

Nest Success, Perch Distance and Perch Height

We observed 38 non-experimental nests that were either successful ($N = 22$) or depredated ($N = 16$) in 1989. For successful nests (Fig. 2), the mean (\pm SE) distance to the nearest prominent perch used by the male was 6.8 ± 1.0 m; the mean height of the nearest prominent perch was 3.6 ± 0.7 m. The mean distance for depredated nests (Fig. 2) was 10.9 ± 1.2 m; the mean height was 2.0 ± 0.3 m. Prominent perches associated with depredated nests were significantly more distant (Mann-Whitney U -test, $U = 94$, $P = 0.004$) and lower (Mann-Whitney U -test, $U = 94$, $P = 0.004$) than those associated with successful nests.

Artificial Perches and Nest Site Selection

We analysed the effect of prominent perches on nest site selection by females in two ways. When analysed according to individual grid squares of 20×20 m, females constructed nests in 23 of the 112 grid squares in our 14 blocks (Fig. 3). Seven of 56 control grid squares and 16 of 56 experimental grid squares attracted at least one nesting attempt. This difference was statistically significant (chi-squared test, $\chi^2 = 4.43$, $df = 1$, $P = 0.035$). When analysed by block, 7 of 14 control areas and 13 of 14 experimental areas attracted at least one nesting attempt, a statistically significant difference (chi-squared test, $\chi^2 = 6.30$, $df = 1$, $P = 0.012$).

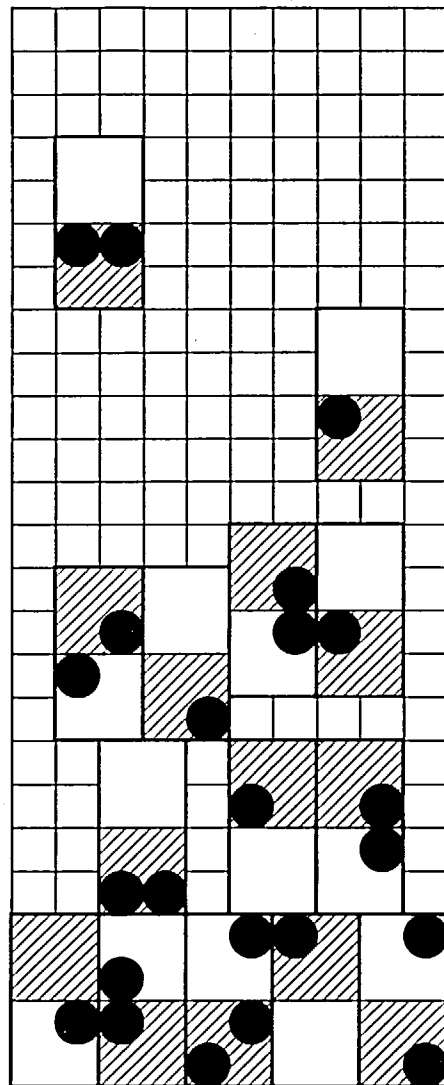


Figure 3. Effect of artificial perches on nest site selection by female red-winged blackbirds. Control blocks (\square) contained no artificial perches. Each experimental block (hatched) contained an artificial perch at the centre. Grid squares (20×20 m) in which at least one nest was constructed are indicated by solid circles. Experimental blocks were significantly more likely to attract at least one nest than were control blocks (chi-squared test, $\chi^2 = 6.30$, $df = 1$, $P = 0.012$).

Anti-predator Vigilance, Pairing Success and Reproductive Success

The mean percentages of time our males ($N = 25$) spent within 10 m of their nests during the incubation stages were not significantly correlated (all

$P > 0.05$) with harem sizes ($r_s = 0.235$), numbers of fledglings ($r_s = -0.344$) or proportions of their nesting attempts that were successful ($r_s = -0.182$). The correlation between time within 10 m and number of fledglings was marginally non-significant ($P = 0.092$), but the coefficient was negative, showing that 'attendance time' tended to decline as the number of fledglings produced increased. There is thus no evidence that more vigilant males acquired more females or had higher reproductive success than less vigilant males.

DISCUSSION

Male red-winged blackbirds spend considerable amounts of time scanning, singing and calling from prominent perches (Nero 1956; Orians & Christman 1968). Early in the breeding season, such vigilance is clearly an aspect of territory defence (Peek 1971). Male red-winged blackbirds are very responsive to conspecific males, and will direct song, visual display and overt aggression at intruders (Nero 1956; Orians & Christman 1968; Peek 1971). Rates of intrusion by conspecific males are especially high before females settle and begin to nest (Peek 1971). Once nesting begins, male red-winged blackbirds continue to devote considerable amounts of time to vigilance and to respond to conspecific male intruders, although pressure from intruders declines once nesting begins (Peek 1971). Male red-winged blackbirds also begin to respond specifically to potential predators as nesting begins (Nero 1956; Orians & Christman 1968). Detection of predators could therefore be a second function of vigilance by male red-winged blackbirds during the nesting season. Our results suggest that male red-winged blackbirds may guard their nests and females against predators.

Male red-winged blackbirds responded to the simulated predator by increasing the amount of time they spent within 10 m of threatened nests. Many of the males increased nest attendance by using perches within 10 m of their nests that they did not otherwise use. In addition, many of the males looked directly into their nests immediately after we removed the predator. These results are consistent with the sentinel hypothesis, but are also consistent with hypotheses that propose advantages of nest defence regardless of whether males act as sentinels.

When we compared the distance and height distributions of successful and depredated nests, we

found that successful nests were associated with nearby, prominent perches, from which males perform what appears to be anti-predator vigilance. These results are consistent with the sentinel hypothesis, but an alternative hypothesis cannot be eliminated. It is possible that the females that are most likely to nest successfully are also most likely to acquire preferred nest sites near high prominent perches. Previous studies of our population have shown, for example, that nest success depends on the female's status within the male's harem, and on whether she receives assistance from the male in feeding nestlings (Yasukawa et al. 1987a, 1990). In addition, males in our population have been shown to be more attentive toward nestlings in primary nests than they are of those in secondary nests (Yasukawa 1989; Yasukawa et al. 1990). Finally, our artificial perch experiment (see below) demonstrated that female red-winged blackbirds prefer to nest near prominent perches. Experimental studies of the effect of sentinel perches on nest success, in which the quality of the nest site is controlled, are clearly needed to discriminate between these two alternative explanations of our results.

Our final test of the sentinel hypothesis employed artificial perches in an attempt to affect nest site selection by female red-winged blackbirds. We were able to isolate nest site selection from choice of mate and territory because we placed our perches on the study area after females had already settled. Females were more likely to nest in otherwise non-stratified habitats when an artificial perch was available than when no such perch was present. Thus, females appear to prefer nest site locations near perches from which males can maintain vigilance against predators.

A vigilant male red-winged blackbird might be effective in detecting and subsequently harassing or deterring avian predators such as crows, jays, magpies and wrens (see Bent 1958; Picman 1983; Knight & Temple 1988). Vigilance might also reduce the risk of brood parasitism by brown-headed cowbirds, *Molothrus ater*. We were unable to demonstrate a correlation between vigilance and nest defence intensity, however, so it seems unlikely that more vigilant males are more aggressive toward predators, although it is possible that a vigilant male could detect a predator sooner and distract or divert it, or alert the female and silence the young (Beletsky et al. 1986; Knight & Temple 1988; Beletsky 1989). In addition, it is not clear how vigilance could reduce the risk of predation by

snakes, which were common on our study area, or mammals. Much of the predation on nests in our population probably occurred at night, and the major nocturnal predators were probably mink, *Mustela vison*, and raccoon, *Procyon lotor*. Neither vigilance nor active nest defence would seem to be effective against such predators (Yasukawa et al. 1987b; Knight & Temple 1988; Yasukawa 1989). Vigilance could enable a watchful individual to detect and avoid a predator, but how could a vigilant male red-winged blackbird reduce the risk to eggs or nestlings, which cannot escape, from a predator it cannot deter?

A second question that remains is whether males and females coordinate their anti-predator vigilance. In a perfectly coordinated sentinel system, the male and female would avoid simultaneous absences from the territory, and each would depart when the other was present. Such coordination might explain some aspects of the vocal behaviour of male and female red-winged blackbirds. Males frequently vocalize as they depart and return to their territories, and females give nest-departing and nest-arriving calls (Nero 1956; Orians & Christman 1968; Beletsky & Orians 1985). Neither males nor females, however, seem to coordinate their absences from their territories (Beletsky & Orians 1985). Would benefits of vigilance be increased by coordination between the male and his mates?

A final question to be answered is whether male anti-predator behaviour is a component of female choice of mate. Can females identify and choose males that are vigilant or aggressive in defending nests? Neither this study nor a previous one (Yasukawa et al. 1987b) demonstrated significant correlations between male vigilance, nest defence and pairing success in our population of red-winged blackbirds. While we believe that our results support the sentinel hypothesis, further observational and experimental studies are clearly needed.

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