IS COURTSHIP INTENSITY A SIGNAL OF MALE PARENTAL CARE IN RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*)?

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ABSTRACT.—We studied Red-winged Blackbird (*Agelaius phoeniceus*) behavior in marsh and prairie habitats to determine whether courting males provide cues of their nest defense, whether females prefer males that defend nests vigorously, and whether male nest defense affects nest success. We found no evidence that courtship behavior provides cues of male nest defense, or that females prefer males that court intensely. We found evidence that females nesting in marshes prefer males that defend nests intensely, but no evidence that intensely defending males in the prairie habitat achieve high nest success. We found differences, however, between marsh and prairie habitats that suggest a coarse-grained relationship between male parental quality and female choice of mate in this species. *Received 31 October 1986, accepted 20 March 1987.*

THERE have been numerous attempts to identify the parameters by which females choose their mates (e.g. Halliday 1978, 1983; Janetos 1980; Wittenberger 1981a; Parker 1983). In territorial species of birds, these parameters include territory quality, male parental quality, and male genetic quality (e.g. Searcy 1979, 1982). One territorial species of bird commonly used to study female choice of mate is the Red-winged Blackbird (*Agelaius phoeniceus*). While there is general agreement on the importance of territory quality in influencing female mate choice in this species (e.g. Searcy 1979, Orians 1980, Weatherhead and Robertson 1981, Yasukawa 1981), there is considerable disagreement about the role of male quality (Weatherhead and Robertson 1979, 1981; Heisler 1981; Searcy and Yasukawa 1981; Wittenberger 1981b; Weatherhead 1984; Kirkpatrick 1985; Alatalo et al. 1986; Muldal et al. 1986; Eckert and Weatherhead 1987).

It has been hypothesized that females should choose mates so as to maximize their own fitness, and that the choice should be based on characteristics that affect female reproductive success (e.g. Searcy 1979, Halliday 1983, Parker 1983). One set of male characteristics that could affect female choice is parental quality. Females might be expected to appraise paternal quality if it increases female reproductive success, and if males provide reliable cues of their parental quality (Yasukawa 1981). Two potentially important aspects of male parental care are feeding young and defending young against predators. Male feeding behavior is an important component of parental investment in some populations of Red-winged Blackbirds; in these populations, females appear to benefit by choosing males that are good providers (Patterson 1979, Fiala 1981, Yasukawa 1981, Searcy and Yasukawa 1981, Yasukawa and Searcy 1982, Muldal et al. 1986). Despite the potential importance of male nest-defense behavior (Andersson et al. 1980), relatively few studies have attempted to investigate its importance in female choice (see Searcy 1979, Eckert and Weatherhead 1987). We attempted to determine whether courting male Red-winged Blackbirds provide cues of their nest-defense behavior to potential mates, whether females prefer males that are vigorous defenders of nests, and whether male nest defense affects nest success.

METHODS

Our study was conducted during March through May 1985 in three cattail (*Typha* spp.) marshes (Kettle, Redwing, and Cloverleaf) in Madison, Wisconsin, and

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The Auk 104: 628–634. October 1987

in a prairie (Newark Road) near Beloit, Wisconsin. Kettle and Redwing were deep-water (>30 cm) marshes with high nest success (>60%) during the preceding 2 yr. Cloverleaf was a shallow-water (<10 cm) marsh and had low prior nest success (<10%). Newark Road Prairie was wet in early spring but dry at the height of the nesting season. Red-wings nested in grey dogwood (*Cornus racemosa*), willow (*Salix* spp.), sedge (*Carex* spp.), cordgrass (*Spartina pectinata*), and cattail (*Typha latifolia*). Nest success in the preceding 2 yr on the prairie was intermediate (<40%).

Many of the male Red-winged Blackbirds were recognized individually by unique color combinations of plastic bands. To identify unbanded males we recorded songs during courtship and nest-defense trials, and then compared sound spectrograms of the recorded songs. Sound spectrograms were prepared with a Kay Elemetrics 7800 Digital Sona-Graph using flat input and 300 Hz (wide band) analysis. Male Red-wing song types are consistent and distinct (Yasukawa et al. 1980).

Courtship intensity.—Pair formation in Red-winged Blackbirds begins as soon as a female enters a male's territory (Nero 1956). Once pair bonding has occurred, and long before copulation occurs, the female repeatedly performs precopulatory, "soliciting" behavior. The male's response to the female's solicitation gradually intensifies, and progresses from approach through a crouched posture to full precopulatory display, and ultimately to copulation. We used Nero's (1956) descriptions of courtship to estimate the intensity of a male Red-wing's response to a simulated potential mate.

Male courtship intensity was measured by presenting a taxidermic mount of a female Red-winged Blackbird in a precopulatory, "soliciting" posture (Nero 1956: fig. 4I; see also Eckert and Weatherhead 1987) to territorial males from 27 March through 8 April 1985. These dates corresponded to the period just before females arrived on the breeding grounds in spring. A courtship-intensity trial consisted of placing the female mount on a 1.5-m pole approximately in the center of a male's territory. Once the male oriented toward the mount we recorded the number and degree of wing extension (display intensity) used in song spread displays (see Nero 1956: fig. 1, Peek 1971); the number and intensity of crouching precopulatory displays (see Nero 1956: fig. 4A); the occurrence of walking precopulatory display (Nero 1956: fig. 4D, E); the occurrence of, and latency to, attempted copulation; and the closest approach (measured after the trial was completed). Each courtship-intensity trial was terminated when the male attempted to copulate, or after 5 min if the male did not attempt to copulate.

These responses were then used to rank males in courtship intensity. Males that attempted to copulate were assigned to the most responsive group and ranked according to latency to copulate (shortest latency = highest rank). Males that performed the walking precopulatory display, but that did not attempt to copulate, were assigned to the next most responsive group and ranked according to closeness of approach (closest approach = highest rank). Males that performed the crouching precopulatory display were next ranked according to intensity and number of displays and closeness of approach. Males that gave only song spread displays after their initial approaches were assigned to the next group and ranked according to closeness of approach. Males that did not approach during a female mount presentation were assigned to the least responsive group; all such males received tied ranks.

Nest-defense intensity.—Male Red-winged Blackbirds aggressively defend their nests against predators (Bent 1958), and the intensity of this behavior varies among males (Siglin and Weller 1963, Knight and Temple 1986a, Eckert and Weatherhead 1987). We estimated nest-defense intensity by presenting a crow (*Corvus*) model at the nest of each male's primary (first to begin incubation) female during day 5–7 of the incubation period. We used an inflatable rubber crow decoy, which is otherwise used to attract crows. The decoy was realistic and elicited apparently normal responses from our subjects. The crow was mounted on a pole, which was placed 0.5 m from the nest. The height of the pole was adjusted so that the head of the crow model was level with and facing the nest. During placement, the model was covered with a cloth attached to a string. The model remained covered until the start of the observation period. Observations were made from outside the subject male's territory and were not begun until the male and his females had resumed "normal" behavior. We conducted 3-min observations of male antipredator behavior.

During each crow presentation we noted the number of alarm calls (Orians and Christman 1968), the number of dives toward the crow, and the number of times the male struck the crow (see also Knight and Temple 1986a, b; Eckert and Weatherhead 1987). We used these responses to rank the nest-defense intensity of males. Males that struck the crow were assigned to the most responsive group and ranked according to number of strikes (most strikes = highest rank). Males that dove at, but did not strike, the crow were assigned to the next most responsive group and ranked according to the number of dives. Males that gave only calls were assigned to the least responsive group and were ranked according to the number of calls.

Pairing success.—Harem size is a commonly used estimate of male pairing success, and therefore of female mate preferences (Searcy and Yasukawa 1983). Although harem size does not necessarily reflect preferences of individual females (e.g. Lenington 1980), it is the most useful index of sexual selection on characteristics of males in polygynous species (see Arnold

TABLE 1. Response of male Red-winged Blackbirds to a soliciting female mount. Each male was categorized according to his most intense response. Percentages (with sample sizes in parentheses) are shown.

Habitat		No response	Approach to <5 m	Precopulatory display		Attempted copulation
				Crouching	Walking	
Deep-water marsh	(16)	0	18.8	12.5	0	68.7
Shallow-water marsh	(4)	0	75.0	0	0	25.0
Prairie	(20)	45.0	5.0	10.0	25.0	15.0

1983). While choice experiments would provide useful information on the preferences of individual females, they are complicated by individual differences in cues used. Estimates of pairing success based on harem size are less affected by individual differences, and can produce consistent patterns despite such differences (e.g. Yasukawa and Searcy 1986).

We determined harem size by periodically searching the territories of all males and constructing a nesting chronology for each nesting attempt. Harem size was then calculated as the maximum number of simultaneously active nests within a male's territory (Yasukawa 1981).

Nest success.—It is often assumed that nest defense reduces predation (e.g. Andersson et al. 1980, Greig-Smith 1980, Blancher and Robertson 1982, Knight and Temple 1986c; but see Searcy 1979, McLean et al. 1986). One estimate of the effect of predation is nest success, which is defined as the proportion of nests that produce at least 1 fledgling. In addition to factors such as nest-site quality (McLean et al. 1986), nest success should reflect the effect of defense against predators because depredated nests would most likely lose all nestlings, while starvation, brood parasitism, and other sources of mortality are more likely to cause partial brood losses (Ricklefs 1969, Patterson 1979, Ritschel 1985). We determined nest success by examining nest chronologies and noting whether nests that received at least 1 egg produced at least 1 fledgling. We measured nest success only in the prairie habitat, and we ranked the nest success of prairie-nesting males by calculating the proportion of all nesting attempts on the territory of each male that was successful.

Statistical analysis.—Data from the two deep-water marshes (Redwing and Kettle) were combined for analysis because these two areas were similar in water depth, harem size, and prior nest success. We calculated Spearman rank correlation coefficients to determine the relationships among courtship intensity, nest-defense intensity, pairing success, and nest success. Differences among habitats were examined by applying the Kruskal-Wallis test to the ranked responses of all males in the study. Statistical significance was accepted at the 0.05 level.

TABLE 2. Response of male Red-winged Blackbirds to a crow model. Each male was categorized according to his most intense response. Percentages (with sample sizes in parentheses) are shown.

Habitat		Call	Dive	Strike
Deep-water marsh	(16)	12.5	12.5	75.0
Shallow-water marsh	(4)	0	50.0	50.0
Prairie	(18)	44.4	16.7	38.9

RESULTS

Courtship intensity.—We estimated courtship intensity for 40 male Red-winged Blackbirds. Of these, 15 (38%) attempted to copulate with the soliciting female mount, and 9 (23%) performed precopulatory behavior without attempting to copulate (Table 1). Males that crouched in response to the soliciting female mount performed a mean of 4.0 crouching precopulatory displays (SE = 3.0) during the 5-min presentations. Males that performed walking precopulatory display gave a mean of 1.6 displays (SE = 0.6) during the presentations. Males that attempted to copulate with the mount did so with a mean latency of 26 s (SE = 9 s). Responses to the mount varied significantly among habitats (Kruskal-Wallis $H = 12.22$, $P < 0.01$). Responses of males in the prairie were significantly weaker than those of males in the deep-water marshes ($H = 10.83$, $P < 0.01$). Responses of males in the shallow-water marsh did not differ significantly from those of prairie males ($H = 3.61$, $P > 0.10$).

Nest-defense intensity.—We estimated nest-defense intensity for 38 of the 40 male Red-winged Blackbirds. Twenty-one (55%) struck the crow model, and 7 (18%) dove toward, but did not strike, the crow. The remaining males (26%) gave alarm calls but did not strike or dive at the crow (Table 2). Males that only called gave a mean of 25.9 alarm calls (SE = 10.1) during the 3-min presentation. Males that dove but never struck did so 12.0 times (SE = 3.5) on average. Males that struck the crow did so 36.9

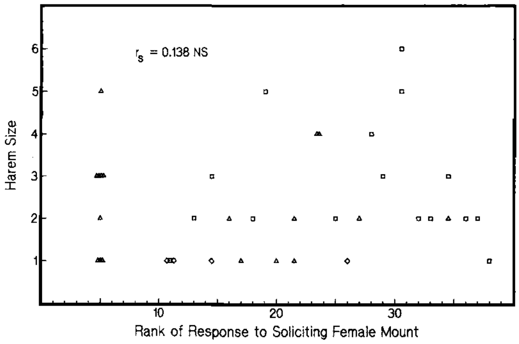

Fig. 1. Scattergram of courtship intensity and harem size of male Red-winged Blackbirds in three habitats. Squares = deep-water marsh, diamonds = shallow-water marsh, and triangles = prairie ($n = 38$).

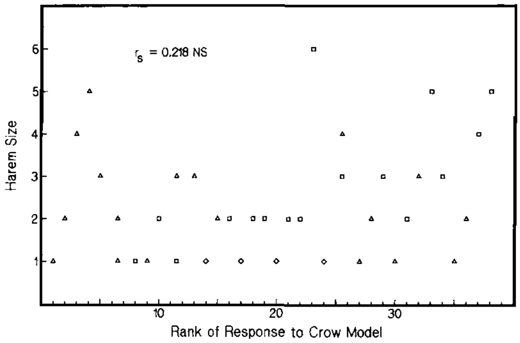

Fig. 2. Scattergram of nest-defense intensity and harem size of male Red-winged Blackbirds in three habitats. Squares = deep-water marsh, diamonds = shallow-water marsh, and triangles = prairie ($n = 38$).

times (SE = 8.1) on average. Male response to the crow did not vary significantly among habitats ($H = 3.76$, $P > 0.1$).

Pairing and nest success.—We measured the harem sizes of the 38 males for which we estimated nest-defense intensity. The mean harem size of males in the deep-water marshes was 2.8 (SE = 0.3). Each male in the shallow-water marsh acquired 1 female. The mean harem size of males in the prairie was 2.3 (SE = 0.4). Harem sizes differed significantly among habitats ($H = 7.70$, $P < 0.05$); males from the shallow-water marsh attracted significantly fewer females than did males in the prairie ($H = 8.07$, $P < 0.01$). Harem sizes of prairie and deep-water marsh males did not differ significantly ($H = 1.11$, $P > 0.10$).

We estimated the nest success of each of the 18 prairie males for which we measured harem size. Of the 56 nests that received at least 1 egg, 19 produced at least 1 fledgling (34% nest success). This estimate was similar to that for the previous 2 yr (38%; Yasukawa unpubl. data).

Female choice and male behavior.—Courtship intensity was not significantly correlated with harem size when analysis included all male Red-winged Blackbirds for which we had both estimates (Fig. 1). Nest-defense intensity also was not significantly correlated with harem size for these males (Fig. 2), nor was courtship intensity significantly correlated with nest-defense intensity (Fig. 3). When results were examined within habitat types (Table 3), harem size was significantly correlated with nest-defense intensity in marsh habitat, but all other correlation coefficients were nonsignificant ($P > 0.1$). The significant correlation between harem size and nest-defense intensity in the marsh habitat could have been an artifact of our combining data from deep-water and shallow-water marshes. When we examined this relationship using only data from the deep-water marshes ($n = 16$), however, the correlation was again positive and statistically significant ($r_s = 0.798$, $P < 0.01$).

DISCUSSION

To be adaptive, female choice of mate ultimately should be based on characteristics that vary and affect female reproductive success. In addition, reliable proximate cues of the char-

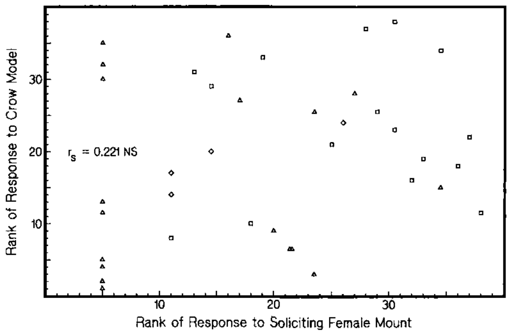

Fig. 3. Scattergram of courtship intensity and nest-defense intensity of male Red-winged Blackbirds in three habitats. Squares = deep-water marsh, diamonds = shallow-water marsh, and triangles = prairie ($n = 38$).

TABLE 3. Spearman rank correlation coefficients of male Red-winged Blackbird behavior and pairing success in marsh (above the diagonal) and prairie (below the diagonal) habitats. Asterisk indicates $P < 0.01$.

	Courtship intensity	Nest-defense intensity	Harem size
Courtship intensity	—	0.210 NS	0.274 NS
Nest-defense intensity	0.077 NS	—	0.719*
Harem size	0.003 NS	−0.186 NS	—
Nest success	0.297 NS	−0.329 NS	−0.025 NS

acteristic must be available to females when they are choosing (Searcy 1979). In populations where males provision young, female choice based on male ability to feed young seems to meet the criteria for an adaptive mate-choice system (Searcy and Yasukawa 1981, Muldal et al. 1986; cf. Weatherhead 1984). We attempted to determine whether male nest defense also meets these criteria.

If female mate choice is to be based on male nest defense, then male nest defense must vary, affect female fitness, and be assessable (Searcy 1979). Male Red-winged Blackbird nest defense clearly varies among individuals (Siglin and Weller 1963, Searcy 1979, Ritschel 1985, Knight and Temple 1986a, Eckert and Weatherhead 1987, this study), and females in the deep-water marshes appeared to prefer intensely defending males. An alternative explanation for the correlation between nest-defense intensity and harem size in the deep-water marshes is that males with large harems defended their nests most intensely because predation on one nest placed their other nests at risk. In the populations we studied this explanation is unlikely. We tested the responses of males at their primary nests during the incubation period, but harem sizes usually did not reach their maxima until well after we assessed nest-defense intensity. We found no evidence that male nest defense affected female reproductive success in the prairie, and we could not demonstrate that courtship behavior provides cues of male nest-defense intensity.

Although we did not show that male nest defense affects female reproductive success in the prairie habitat, Ritschel (1985) demonstrated that nest defense by male Red-winged Blackbirds reduces predation by Marsh Wrens (*Cistothorus palustris*). Marsh Wrens did not reduce nest success on our study areas (Marsh Wrens were present only on unstudied portions of Redwing Marsh), but are important predators of Red-wing eggs in other populations (Picman 1977, 1980a, 1983; Ritschel 1985). Ritschel (1985) also found that male Red-wings with large harems defended their nests more vigorously than did males with small harems. Although Ritschel (1985) did not attempt to determine whether male Red-wings provide cues of their nest-defense intensity, her results provide support for the hypothesis that female Red-winged Blackbirds prefer males that vigorously defend their nests against predators.

Although we did not demonstrate that male courtship provides cues of nest-defense intensity (see also Eckert and Weatherhead 1987), prospecting female Red-winged Blackbirds could use other cues to assess male nest-defense intensity. For example, male Red-wing epaulet size and tendency to attack an intruding male conspecific both correlated significantly with the intensity of a male's response to a crow model (Eckert and Weatherhead 1987). A female could base her choice of mate on such morphological and behavioral cues if they are also reliable predictors of female reproductive success.

Although our evidence did not support all predictions of the hypothesis that female choice is based on male nest defense in the Red-winged Blackbird, there are several reasons to continue to test this hypothesis. First, other aspects of male parental quality, such as male feeding of young, seem to provide an adaptive basis for female choice of mate. Second, although we attempted to control many sources of variance in male nest defense (e.g. number of times the model was presented to a male, stage of the nesting cycle and status of the female at whose nest the model was presented, and the model's distance from and orientation toward the nest), there were two potentially important factors that were not controlled: male age and previous experience. Age and experience have been shown to affect other aspects of male Red-winged Blackbird reproductive behavior (Yasukawa et al. 1980, Yasukawa 1981), and to affect nest defense (Knight and Temple 1986a, b; Eckert and Weatherhead 1987) and female reproductive success (Picman 1980b). There is evidence, for example, that repeated "successful" interactions with a simulated predator cause male Red-wings to become more aggressive toward the predator (Knight and Temple 1986a, b). We attempted to control for this effect by presenting the crow model only once to each male, but we could not control the previous experience of the males with real crows and other potential predators. Successful encounters with real predators could reinforce antipredator behavior, while unsuccessful or damaging encounters could inhibit nest-defense behavior. Third, we chose the crow model because male Red-wings often mob crows and respond readily to crow models, but we have no information about the actual impact of crows on Red-wing nest success. Perhaps crows represent little actual risk to both the adults and the young in this species. Future studies could examine the relationships among male experience, feeding of young, and defense of young, as well as the relationship between nest defense and risk of predation.

Raccoons (*Procyon lotor*) and snakes were important predators in the habitats studied. In addition, Brown-headed Cowbirds (*Molothrus ater*) frequently parasitized nests in the shallow-water marsh and the prairie. We do not have information on the relative impact of these and other predators (see Bent 1958), and the use of a stimulus model of another species might have produced different results. Despite the potential differences in relative predator impact, however, individual male Red-winged Blackbirds have been shown to respond similarly to a crow, raccoon, Red-tailed Hawk (*Buteo jamaicensis*), and human (R. L. Knight and S. A. Temple unpubl. data).

Finally, the between-habitat differences demonstrate the importance of habitat quality in female choice of breeding situation (Wittenberger 1976). Mean harem sizes were larger in two habitats with higher nest success than in one with lower nest success. These between-habitat differences suggest that high-quality males are overrepresented in superior habitats. Female preferences for high-quality males could thus be coarse grained and expressed as between-habitat differences in male pairing success. Further empirical study of the relative importance of male and habitat quality on female mate choice in the Red-winged Blackbird may resolve these issues.

ACKNOWLEDGMENTS

It is a pleasure to thank the following individuals and organizations for their help and support. Rebecca A. Boley, Patty D. McIntire, Clint K. Miller, and Sue E. Simon helped with fieldwork. Jack P. Hailman, Stanley A. Temple, and Sooil Kim provided logistical support. William A. Searcy, Jaroslav Picman, and two anonymous reviewers criticized earlier drafts of this paper. Permission to work in the marshes was granted by the Director of the University of Wisconsin Arboretum and Si Widstrand of Madison's Conservation Parks Department. Our work was supported by grants from the Friends of the Arboretum, University of Wisconsin, and the National Science Foundation (BNS 84-05221).

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