J. Field Ornithol., 72(1):106–112

THE "PREDATOR EARLY WARNING SYSTEM" OF RED-WINGED BLACKBIRDS

NICOLE BURTON AND KEN YASUKAWA
Beloit College
Department of Biology
Beloit, Wisconsin 53511 USA

Abstract.—Male Red-winged Blackbirds (*Agelaius phoeniceus*) are known to give alarm calls in response to the approach of a predator, and to encode information about the level of threat in their calling behavior. To determine whether such sentinel males alert females, we conducted a simple field experiment in which we measured the distances at which incubating females flushed from their nests in response to the approach of a human observer. Using a matched-pairs design, we measured flushing distances with a sentinel male present (mean 19.8 m), and when the same male was absent from his territory (mean 10.4 m). Female Red-winged Blackbirds flushed from their nests at significantly greater distances when males were present than when males were absent. These results and those of other studies support the existence of a "predator early warning system" in the Red-winged Blackbird.

SISTEMA DE ALARMA TEMPRANA CONTRA DEPREDADORES POR PARTE DE *AGELAIUS PHOENICEUS*

Sinopsis.—Los machos de *Agelaius phoeniceus* responden con llamadas de alarma a la presencia de depredadores. Además éstas aves incluyen información en sus llamadas sobre el nivel de peligro. Para determinar si los machos de éstas aves alertaban a las hembras, se condujo un experimento en donde se midió la distancia a la cual la hembra dejaba el nido en respuesta al acercamiento de un observador humano. Utilizando un sistema de pareo medimos la distancia a la cual la hembra dejaba el nido cuando había como sentinela e un macho (19.8 m), y cuando el macho estaba ausente del territorio (10.4 m). Las hembras de la especie se salieron del nido a una distancia significativamente mayor cuando el macho estaba presente que cuando éste estaba ausente. Estos resultados, al igual que el de otros trabajos, apoyan la existencia de un "sistema de alarma contra depredadores" en la especie estudiada.

Numerous field studies of Red-winged Blackbird (*Agelaius phoeniceus*) reproductive success have identified predation as the single most important source of mortality of eggs and nestlings (Searcy and Yasukawa 1995; Yasukawa and Searcy 1995; Beletsky 1996). For example, during their 16-yr field study, Beletsky and Orians (1996) observed annual nest predation rates of 35–75%. Many reptiles, birds, and mammals are known to prey on redwing eggs and nestlings, and on average they produce nest failure at nearly one-third of all nests in this species (Beletsky 1996).

Given the impact that predators have on nest success, it is not surprising that Red-winged Blackbirds have evolved anti-predator behavior (Searcy and Yasukawa 1995; Yasukawa and Searcy 1995; Beletsky 1996). Nests are concealed in vegetation, placed in proximity to each other, and initiated synchronously. Males and, to a lesser extent females, vigorously defend nests against predators. Finally, males use prominent perches within their territories and have an "alert system" of calls with which they can signal the presence of a nest predator (Beletsky 1996). Male redwings clearly communicate with each other using this call system (Beletsky et al. 1986).

There is also evidence that males signal nesting females as well (Beletsky 1989). Thus, male Red-winged Blackbirds appear to have an anti-predator sentinel system (Searcy and Yasukawa 1995) that could provide nesting females with information about predators. Such information is potentially important because a female on her nest, which is concealed in the vegetation, is unable to see an approaching predator at a distance. As a result, in the absence of a sentinel male, a predator is more likely to approach the nest undetected (Peek 1972). Perhaps for this reason, when a sentinel male is not present, the female spends time in anti-predator vigilance at the expense of incubating or brooding (Beletsky 1989).

Peek's (1972) observation that, in response to his approach, females of surgically muted male Red-winged Blackbirds flushed from their nests at closer distances than females mated to intact, calling males suggested a simple, experimental test of the hypothesis that the call system and perching behavior of males functions as an anti-predator sentinel system. If this sentinel hypothesis is correct, then in response to the approach of a predator, incubating females should flush from their nests at greater distances when a male is perched prominently on the territory (i.e., "on sentinel") than when the male is absent from the territory. We tested this prediction by measuring flushing distances of female Red-winged Blackbirds in response to the approach of a human observer.

METHODS

We conducted our experiment at Newark Road Prairie, a 13-ha wet-mesic prairie in south central Rock County, Wisconsin (42°32′N, 89°08′W; see Yasukawa et al. 1987a). This study area supported approximately 20 territorial males and about 50 nests in 1999. All territorial males and about one-third of nesting females were banded with numbered aluminum bands and unique color combinations of plastic bands. We performed our experiment from 21 May through 9 June 1999 on 14 territories as nests were available.

Nests were located by observing females and systematically searching suitable habitat. Once a nest was located, it was marked with vinyl flagging tied to nearby vegetation. We visited each nest daily to note its contents until it produced fledglings or failed. These nest chronologies enabled us to identify primary (most advanced) and secondary (later) nesting attempts on each territory. We noted nest status because previous studies at this site have shown that male Red-winged Blackbirds are more likely to feed nestlings of primary nests than those of secondary nests (Yasukawa et al. 1990).

We measured flushing distances for female Red-winged Blackbirds that were incubating complete clutches. For nests discovered during egg laying, we attempted to make our measurements during the first 3 d of incubation following clutch completion. For nests discovered after clutch completion, we made measurements as soon as possible during the incubation stage. In many cases, however, nests failed or eggs hatched before we could measure flushing distances.

To measure a flushing distance, we observed the focal male and female until we were certain that the female was on the nest and the male was either perched nearby, within sight of the nest, or off territory. Then one of us slowly (about one step per second) approached the focal nest in a straight line until the female left the nest. We then measured the distance to the nest with a tape measure, and noted whether the male was present (on sentinel) or absent (off territory). We next left the focal territory to a safe distance and waited for the female to return to the nest and for the male to return to or leave the territory, as appropriate. We then repeated the approach from the same initial point and measured flushing distance a second time under the other male (present or absent) condition. The order of measurements was randomly determined.

Flushing distances measured by the two authors, and of primary and secondary females were compared with two-sample *t*-tests. Distances with and without males present were compared with a matched-pairs *t*-test. The assumption of normality was tested with a Shapiro-Wilk goodness of fit test. All statistical tests were performed with JMP v 3.2.2 and statistical significance was accepted at the 0.05 level.

RESULTS

We measured female Red-winged Blackbird flushing distances with males present and absent at 12 primary (most advanced) and 12 secondary (later) nests. Mean (±SE) distances measured by the two authors (male present: 17.7 ± 2.5 vs. 22.4 ± 2.8; male absent: 9.7 ± 2.2 vs. 11.4 ± 2.3) did not differ significantly ($P > 0.20$); distances of primary and secondary females (male present: 21.6 ± 2.8 vs. 18.1 ± 2.6; male absent: 11.4 ± 2.1 vs. 9.5 ± 2.4) did not differ significantly ($P > 0.30$); and the distribution of distance differences used in the matched-pairs *t*-test did not differ significantly from normality (Shapiro-Wilk $W = 0.95$, $P > 0.25$).

Female Red-winged Blackbirds flushed from their nests at significantly greater distances when males were present (19.8 m ± 1.9) than when males were absent (10.4 m ± 1.6; paired $t = 6.30$, $P < 0.01$).

DISCUSSION

Given the impact of predators on nest failure in the Red-winged Blackbird, it is not surprising that Red-winged Blackbirds have evolved an elaborate set of adaptations to reduce the risk of nest predation. Like the North American "distant early warning system" of the early cold war, we might call these adaptations a "predator early warning system" (PEWS). This system consists of four components: (1) male sentinel behavior, (2) female nest-associated calling, (3) the male alert call system, and (4) female response to an alert. Once alerted, male and female Red-winged Blackbirds can then attempt to deter the predator or take other appropriate action. We describe the components of the redwing PEWS below.

Male sentinel behavior.—Male Red-winged Blackbirds spend considerable amounts of time scanning from prominent perches within their territories. Such vigilance has been attributed to territory defense (Peek

1971), but once nesting begins, vigilance could also serve a nest defense function. Yasukawa et al. (1992) studied the vigilance of male Red-winged Blackbirds during the nesting season, and concluded that male vigilance was, in part, anti-predator sentinel behavior (Searcy and Yasukawa 1995), and that the presence of a sentinel male reduced the risk of predation. In addition, they presented experimental evidence that males increase sentinel behavior in response to the presence of predators, and that female Red-winged Blackbirds prefer nest sites near sentinel perches. Anti-predator sentinel behavior might explain why male redwings continue to allocate large portions of their time budgets to territorial vigilance even though trespassing by conspecific males may become less frequent and less consequential once nesting begins.

Female nest-associated calling.—A curious aspect of female Red-winged Blackbird behavior (and of other species; see McDonald and Greenberg 1991) is their habit of calling when leaving the nest (almost always), when arriving at the nest (less often), and even when on the nest (Beletsky and Orians 1985; Yasukawa et al. 1987a). Yasukawa (1989) provided experimental evidence that such "nest-associated calling," in which females utter loud and easy-to-locate sounds (Beletsky and Orians 1985), increases the risk of predation, but also seems to facilitate male anti-predator vigilance. Beletsky and Orians (1985) suggested that nest-associated calling by female redwings functions as a component of an intrapair communication system by which males gather information about female activity and reproductive states. Males appear to use this information to focus their anti-predator vigilance, among other things.

Male alert call system.—A well developed sentinel system is characterized by elements in addition to vigilance. Wickler (1985) described such an element as the "watchman's song," by which a sentinel uses vocalizations to inform its companions of its watchfulness. Male Red-winged Blackbirds have a variety of brief calls, which they give frequently while on their territories (Orians and Christman 1968; Beletsky et al. 1986). This frequent calling appears to provide a background against which changes in call type can be detected and located (Beletsky 1996), but it may also inform conspecifics of the sentinel's watchfulness. Males on neighboring territories tend to match call types, so that the background (or watchful) situation is a single call type given by all males. If one of these males detects a predator, he immediately switches to a different call, and the new call type spreads contagiously among the males (Beletsky et al. 1986). Males also encode information about the risk of predation in their calling rates (Beletsky 1991). For example, call rates were higher in response to a nest predator (Black-billed Magpie, *Pica pica*) or a predator of adults (Great Horned Owl, *Bubo virginianus*), than they were to a nonpredator (muskrat, *Ondatra zibethica*), and call rates increased as a human observed approached a territory, peaked when the observer was within 10 m of the territory, and declined as the observer stood motionless at the boundary (Beletsky 1991). Finally, call and switching rates increased sig-

nificantly when females began to incubate (Beletsky 1989), suggesting that males were directing their alert calls to their mates.

Female response to alert.—Female Red-winged Blackbirds appear to respond to male alert calling. Females were more likely to remain near their nests and to vocalize in response to playback of a sequence of four different call types (i.e., three call switches) than in response to a similar playback with only one call type (Beletsky 1989). In addition, females spent more of their own time perched above the nesting vegetation when their mates were absent from their territories than when they were present (Beletsky et al. 1986). Finally, as we have shown in this study, females flush from their nests at greater distances when their males are on sentinel than when they are absent from their territories. Flushing from nest when the predator is still relatively distant may reduce the risk of cueing the predator to the location of the nest, and may also reduce the risk of predation on the female as well.

Once the male has alerted the female to the risk of predation, the most appropriate actions probably depend on the type and location of the predator. If the predator is far from the nest or does not represent great risk, continued vigilance may be sufficient. It may also be advantageous for the female to avoid the immediate vicinity of the nest while the predator is nearby, especially given the cueing effect of nest-associated calling (Yasukawa 1989). If the nest is in immediate danger, more overt action may be appropriate. Male and female Red-winged Blackbirds mob predators, although the effectiveness of such anti-predator behavior varies (Knight and Temple 1988). Mobbing is probably effective when directed at avian nest predators (e.g., Black-billed Magpie or American Crow, *Corvus brachyrynchos*), but seems to be ineffective against snakes and mammalian predators such as mink (*Mustela vison*) and raccoons (*Procyon lotor*). In contrast, mobbing may be disadvantageous if the predator represents a risk to the adults. For example, in our experience, male and female Red-winged Blackbirds do not mob accipiters, which could catch them in flight. If the hawk is detected early, adult redwings take flight and circle above it until it leaves the area. If the hawk is not detected early enough for a flight to a safe altitude, however, then adult redwings crouch under cover until the hawk departs (see also Nero 1984).

Although we focused on the interaction between a male and his mates, it is also possible for the females mated to a male to gain cooperative anti-predator benefits (e.g., Searcy and Yasukawa 1989). There is no evidence that females coordinate their departures from their nests and the male's territory with each other or with the male (Beletsky and Orians 1985), but Knight and Temple (1988) and Yasukawa et al. (1987b) found a positive correlation between group size and the effectiveness of nest defense against predators, and Picman et al. (1988) and Westneat (1992) observed cooperative nest defense by female Red-winged Blackbirds. In addition, when we measured flushing distances on territories with two active nests, both females would flush nearly simultaneously if both were incubating. Further study of such interactions and the most appropriate

responses to predators would enhance our understanding of the Red-winged Blackbird's predator early warning system.

ACKNOWLEDGMENTS

We are grateful to Sondra Fox and two anonymous reviewers for their comments on earlier drafts of our manuscript. We also thank Jody Urish for her help in locating nests. The authors gratefully acknowledge the support of the J. Carl and Susan Welty Fund of Beloit College.

LITERATURE CITED

BELETSKY, L. D. 1989. Alert calls of male Red-winged Blackbirds: do females listen? Behaviour 111:1–12.

———. 1991. Alert calls of male Red-winged Blackbirds: call rate and function. Can. J. Zool. 69:2116–2120.

———. 1996. The Red-winged Blackbird: the biology of a strongly polygynous songbird. Academic, London, United Kingdom.

———, B. HIGGINS, AND G. H. ORIANS. 1986. Communication by changing signals: call-switching in Red-winged Blackbirds. Behav. Ecol. Sociobiol. 18:221–229.

———, AND G. H. ORIANS. 1985. Nest-associated vocalizations of female Red-winged Blackbirds. Z. Tierpsychol. 69:329–339.

———, AND ———. 1996. Red-winged Blackbirds: decision-making and reproductive success. University of Chicago Press, Chicago, Illinois.

KNIGHT, R. L., AND S. A. TEMPLE. 1988. Nest defense behavior in the Red-winged Blackbird. Condor 90:193–200.

MCDONALD, M. V., AND R. GREENBERG. 1991. Nest departure calls in female songbirds. Condor 93:365–373.

NERO, R. W. 1984. Redwings. Smithsonian Institution Press, Washington D.C.

ORIANS, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. Univ. Calif. Publ. Zool. 84:1–81.

PEEK, F. W. 1971. Seasonal change in the breeding behavior of the male Red-winged Blackbird. Wilson Bull. 83:383–395.

———. 1972. An experimental study of the territorial function of vocal and visual display in the male Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20:112–118.

PICMAN, J., M. LEONARD, AND A. HORN. 1988. Antipredation role of clumped nesting by marsh-nesting Red-winged Blackbirds. Behav. Ecol. Sociobiol. 22:9–15.

SEARCY, W. A., AND K. YASUKAWA. 1989. Alternative models of territorial polygyny in birds. Am. Nat. 134:323–343.

———, AND ———. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton University Press, Princeton.

WESTNEAT, D. F. 1992. Nesting synchrony by female Red-winged Blackbirds: effects on predation and breeding success. Ecology 73:2284–2294.

WICKLER, W. 1985. Coordination of vigilance in bird groups. The "watchman's song" hypothesis. Z. Tierpsychol. 69:250–253.

YASUKAWA, K. 1989. The costs and benefits of a vocal signal: the nest-associated "chit" of the female Red-winged Blackbird, *Agelaius phoeniceus*. Anim. Behav. 38:866–874.

———, R. A. BOLEY, AND S. E. SIMON. 1987a. Seasonal change in the vocal behavior of female Red-winged Blackbirds, *Agelaius phoeniceus*. Anim. Behav. 35:1416–1423.

———, R. L. KNIGHT, AND S. K. SKAGEN. 1987b. Is courtship intensity a signal of male parental care in Red-winged Blackbirds? Auk 104:628–634.

———, J. L. MCCLURE, R. A. BOLEY, AND J. ZANOCCO. 1990. Provisioning of nestlings by male and female Red-winged Blackbirds, *Agelalus phoeniceus*. Anim. Behav. 40:153–166.

———, AND W. A. SEARCY. 1995. Red-winged Blackbird (*Agelaius phoeniceus*). No. 184, *in* A. Poole and F. Gill, eds. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania and The American Ornithologists' Union, Washington, D.C.

———, L. K. WHITTENBERGER, AND T. A. NIELSEN. 1992. Anti-predator vigilance in the Red-winged Blackbird (*Agelalus phoeniceus*): do males act as sentinels? Anim. Behav. 43:961–969.

Received 26 October 1999; accepted 1 March 2000.