Alert Calls of Male Red-Winged Blackbirds: Do Females Listen?
Author(s): Les D. Beletsky
Source: *Behaviour,* Vol. 111, No. 1/4 (Dec., 1989), pp. 1-12
Published by: Brill
Stable URL: https://www.jstor.org/stable/4534803
Accessed: 24-11-2022 21:43 UTC

REFERENCES

ALERT CALLS OF MALE RED-WINGED BLACKBIRDS: DO FEMALES LISTEN?

by

LES D. BELETSKY[1])

(Department of Zoology, NJ-15, University of Washington, Seattle, WA 98195, U.S.A.)

Introduction

Two approaches used for investigating the function of animal signals have proved especially productive. In one, the environmental contexts in which particular signals are generated are recorded, and correlational relationships are used to infer function (SMITH, 1977). Vocalizations given by animals only when they detect potential predators are thought, for example, to serve as anti-predation signals. The other approach is to identify the intended receivers of an animal's signals. Determining, for example, that a male's call is directed at female conspecifics permits at least a preliminary assessment that the call has some function in inter-sexual communication. I used this latter approach to investigate alert calls of male red-winged blackbirds (*Agelaius phoeniceus*).

Breeding male redwings use a communal vocal alert system to warn about predators that incorporates several unusual features. Foremost is that communication is achieved in part by "call switching" (BELETSKY *et al.*, 1986). An individual broadcasts a series of the same brief call and transmits alerting information by switching call types after, for instance, detecting an approaching predator. Most territory owners in small breeding "colonies" give the same call type at the same time, as a common background signal. After one male changes call types during alerting behavior, other males quickly switch to the same type, resetting the alert system to a new baseline. Many call types are interchangeably used as background signals (BELETSKY *et al.*, 1986).

Another novel feature is that male redwings give "alert" calls during most of the day throughout the breeding season. The alert system is always operating, in contrast to alarm systems of most other animals that have been studied, in which calling starts only after predators are detected (*e.g.*, great tits, *Parus major*, CURIO & REGELMANN, 1985; California ground squirrels, *Spermophilus beecheyi*, OWINGS *et al.*, 1986; reviewed by KLUMP & SHALTER, 1984). Furthermore, the number of different alert calls used, between 10 and 15 in various populations (ORIANS & CHRISTMAN, 1968; SIMMERS, 1975; BELETSKY, unpubl. data), and the vocal barrage resulting from the high rate of calling and call switching of many males on crowded breeding marshes, suggests levels of complexity to this alerting system that are not yet fully understood.

In a preliminary study (BELETSKY *et al.*, 1986), I used contextual analysis and other methods to provide a basic description of this alert system and to suggest that males use their alert calls to warn each other about predators and other potentially dangerous environmental disturbances. By call-matching and call switching, in natural and experimental situations, males demonstrated their perception of predator-evoked call switches and, presumably, reception of alerting information. The system appears to be intra-sexually cooperative because neighboring males match call types and switch types together. The initial study did not address the question of whether females breeding on a male's territory, and perhaps their young, also listen to and benefit from alert calls. In fact, mates and young may be the primary intended receivers of male alert calls. My objective in the present study was to test the hypothesis that males direct their alert calls to their mates. Because the two hypotheses of the function of these alert calls, that males use them to warn other males (BELETSKY *et al.*, 1986) or to warn their mates (this study) are not mutually exclusive, the results of the current study cannot discriminate between these hypotheses. They can only provide support for the mate-warning hypothesis.

Female redwings build nests in the dense vegetation of their mates' marsh territories. They incubate unassisted by their mates and do most of the provisioning of young. Females spend much of their time foraging for themselves and their young, both on and near territory. Males in my study area spend about two-thirds of their daylight hours on their territories during most of the breeding season, calling about 80% of the time (see below). Females could benefit by attending to their mates' steady streams of calls and receiving information about predator detection and movements because they could reduce their expenditure of time

and energy devoted to anti-predator vigilance. Similarly, while incubating, a female listening to her mate's calls could tell where her mate is and, when call types change, that potential danger exists.

I conducted three investigations to determine whether females listen to and benefit from male alert calls. First, I performed playback experiments in which calls were presented to nesting females. I predicted that if females listened to male calls, they would tend to remain on or near their nests when placed "on alert" by repeated call switches. A female leaving her nest in this situation might reveal its exact location to a predator. A female off but near her nest when alerted should remain nearby to protect the nest. Second, I observed calling males during the course of the breeding season to determine if the rate at which males call is dependent on breeding chronology. Specifically, if males direct their calls to their mates to alert them about potential nest predators, then call rates and call type switch rates should increase as the primary (first to breed) female on each territory initiates incubation. Because females incubate for 10-12 days, during which time they have limited abilities to perceive approaching danger, alert signals could be most advantageous during this period. Third, I assessed vigilance of nesting females. One measure of redwing vigilance is "time up", the proportion of time an individual spends on territory in exposed, usually elevated positions, where its ability to detect predators is maximized. For females, being vigilant conflicts with activities such as incubating and feeding. Thus, reduction in vigilance time should be advantageous. I tested if females are more vigilant when males are not calling by monitoring "time up" for females when their calling mates were present and absent.

Methods

I studied redwing calling from 1986 through 1988 on freshwater marshes in the Columbia National Wildlife Refuge, in eastern Washington state. The area supports a large, polygynously-breeding population of redwings, whose ecology and behavior are described by ORIANS & CHRISTMAN (1968) and ORIANS (1980). Each territorial male and most females were banded with unique combinations of colored legbands. Nest locations were marked with colored tape. Predation on redwing nests in the area by birds, mammals, and snakes is heavy, but few breeding adults are taken (ORIANS & BELETSKY, 1989).

Observations of calling behavior were conducted from March through June 1986 and 1987. Twenty-one males with territories on three separate marshes were each observed for various numbers of 15-min periods (range 2 to 10) during each of four breeding phases: 1) pre-incubation (the period before the primary female had arrived on territory, or after she arrived but before she initiated incubation); 2) incubation of the primary nest on the territory; 3) the period of the first nestlings on the territory; and 4) the period of the first fledglings on the territory. I could not separate early observations into those conducted before or after female arrival on male territories because I was often uncertain whether females had settled on some territories. Secondary and later-settling females

often began their nests only a few days after primary females and there was much renesting after nest predation. Therefore, by mid-season, there were normally nests in all stages of the breeding cycle on each territory. During each observation period, all calls given by the focal male were recorded. Observations were conducted during the early morning or late afternoon. Only those periods when males called were used for analysis (75.4% of 7770 min of observations; Table 1). Analysis of variance was used to determine among-breeding phase differences in call rates and switching rates.

Call playback experiments directed at breeding females were conducted from 24 April to 5 May 1986 and 28 April to 16 May 1988. All females were in the incubation stage at the time of stimulus presentation. In one experiment, male calls were played through a loudspeaker to females perched on top of vegetation in their territories. The loudspeaker was placed in the dry grass that bordered many territories in the area. Males regularly foraged and called there. Fourteen females were each presented with one experimental and one control playback, separated by 24 or 48 h. Presentation order was random. The experimental playback consisted of 4 alert call types given commonly by males in the region (chonk, cheer, check, chink; see BELETSKY et al., 1986 for sonagrams), each repeated 10 times in succession at a rate of one call every 4 to 5 s, for a total of 200 s. The tape, therefore, contained 3 call type switches: chonk to cheer, cheer to check, and check to chink. Each of these switches occurs in nature (BELETSKY et al., 1986). The experimental switch rate of 1/50 s (1.2/min) is greater than the average switch rate for the population (usually between 0.6 and 0.8 switches/min), but well below the high switch rates that sometimes occur. The experimental call rate, approximately 12 calls/min, is about average for males during the breeding season (see below), but when nests are directly threatened, rates of 45 or more calls/min are common. Control presentations consisted of repeated checks, the most frequently given alert call, 1 every 4 to 5 s, for 200 s, with no switches. Thus, the experimental tape imitated a male changing call types when detecting a predator, whereas the control tape imitated a male giving unchanging background calls.

Playback calls were recorded in 1984 from a territorial male who was no longer present in the study area during my experiments. Therefore, females could have identified the playback calls as originating with a male other than their mate or neighbor. However, it is unknown whether female redwings can identify individual males by their vocalizations. They do "answer" the advertising songs of both mates and non-mates with their own songs, suggesting a lack of discrimination (BELETSKY & CORRAL, 1983). Because both experimental and control vocalizations were recorded from a stranger, any effect on female behavior due to their hearing unfamiliar vocalizations would have been the same for both presentations.

At least five minutes after placement of the loudspeaker, the playback tape was started when I spotted the focal female in an exposed position in the territory, usually near her nest. Females were usually either in vigilant postures, i.e., they were "looking around", or they were preening. To minimize interference from resident males, each playback was initiated when the focal female's mate was off territory and out of sight; however, several returned before the presentation ended. The following female behaviors were recorded during playback: all vocalizations, including Type 1 and Type 2 songs, combination songs (BELETSKY, 1983), and chet calls (HURLEY & ROBERTSON, 1984), flights down to and up from the nest, other flights, and approaching the loudspeaker. Type 1 songs are used for communication with mates and Type 2 songs are usually given in aggressive contexts (BELETSKY, 1983). Type 2 and combination songs were pooled for analysis because previous field observations suggested combination songs are given in aggressive contexts. The function of chet calls is less certain.

Thirty other females were exposed to the same two playback tapes, in random presentation order, while they were on their nests. Incubating females typically intersperse short foraging trips among periods of 5 to 15 minutes on their eggs. After I observed the focal

female return to her nest, I waited at least 60 s before starting a playback. Female activities recorded included those listed above and whether they left their nests during playback. Vocalization rates (total number of vocalizations/presentation) of females during experimental and control presentations were compared using non-parametric matched pairs tests.

Female vigilance was evaluated in 1987 and 1988 by monitoring individuals during 15-min periods. I noted continuously whether the male territory owner was on territory ("on") or off territory and out of sight ("off"). Males within sight near their territories were considered to be "on". I also noted continuously whether the focal female was "up", on top of the marsh vegetation, or "down", out of sight. When females were at water level at the marsh edge, they were considered to be "down", although they presumably had good visibility in some directions. Twenty-three different females were observed for a total of 210 15-min periods on multi-male marshes. Eight females nesting on territories isolated from other male territories, i.e., having no adjacent neighbors, were observed for a total of 51 periods. Males with isolated territories called repetitively in the same manner as males that had adjacent neighbors. To assess whether female vigilance was influenced by male absence, I totaled the time each female was "up" or "down" and the time each male was "on" or "off" during each 15-min period (times when females were off territory were excluded) and then used regression analyses to determine if duration of female vigilance varied as a function of male presence.

Results

1. Male call rate and breeding chronology.

Males called at their lowest rates and switched call types less often during the pre-incubation phase of breeding (Table 1). Call rates increased as incubation began and remained elevated throughout the remaining breeding phases. There were significant differences in call rates among breeding phases (ANOVA, $F = 22.76$, $P < 0.001$); a Student-Newman-Keuls procedure (SNK) assigned the pre-incubation call rate to one statistically homogeneous group and the incubation, nestling and fledgling-phase call rates to another. There were also significant dif-

TABLE 1. Average calling and call switching rates of 21 male redwings during various breeding phases

Breeding phase	$\bar{X} \pm$ S.D. calls/min	$\bar{X} \pm$ S.D. switches/min	n (min)[a]	Total n[b]	% of time calling
Pre-incubation	9.6 ± 7.3	0.6 ± 1.2	1762	2760	63.8
Incubation	11.6 ± 8.0	0.9 ± 1.6	1398	1680	83.2
First nestlings	11.3 ± 7.5	1.0 ± 1.8	1362	1650	82.5
First fledglings	11.3 ± 8.0	0.7 ± 1.3	1334	1680	79.4
Seasonal $\bar{X}$	10.8 ± 7.7	0.8 ± 1.5			
Total			5856	7770	

[a] Number of minutes males called, used to calculate seasonal averages. [b] Total number of minutes of observation.

ferences among breeding phases in switching rates (Table 1; ANOVA, F = 12.95, P < 0.001); SNK assigned the pre-incubation and fledgling-phase switch rates to one statistically homogeneous group, the incubation phase rate to another group, and the nestling phase rate to a third. The prediction that male calling behavior, including call rates and switch rates, varies with female breeding activity, is supported by these data.

2. Call playbacks to females.

Females near their nests.

Female attentiveness during playbacks was difficult to evaluate because they seldom interrupted their activities or approached the loudspeaker. However, females vocalized significantly more often during experimental playbacks ($\bar{X}$ number of vocalizations given/playback = 3.8 ± 2.7 during controls and 8.8 ± 7.2 during experimentals; Wilcoxon matched pairs test, z = -1.69, 1-tailed P = 0.008, n = 14). Type 2 songs, and combination songs containing Type 2 songs, were given infrequently by females during these presentations (Table 2), but the percentage of vocalizations that were Type 1 songs was significantly greater during experimental playback (Table 2; t-test of the equality of 2 percentages (SOKAL & ROHLF, 1969; t = -3.70, 1-tailed P < 0.001). Significantly more females remained on their territories during experimental playbacks than during control playback (71.4% *vs* 28.6%, $\chi^2 = 5.14$, P = 0.02), supporting the prediction that females placed ''on alert'' by call switching would remain near their nests. Other behavior recorded during playbacks showed little or no difference between experimentals and controls. For example, all females flew at least once during control presentations, while 12 of 14 flew during experimental broadcasts.

TABLE 2. Vocal responses of female redwings to playback of male alert calls

	No. of Type 1 songs	No. of Type 2 songs	No. of Combination songs	No. of Chet calls	Total vocalizations	% Type 1	% Type 2/ combination
Females near nests							
Control (n = 14)	28	0	1	19	48	58.3	2.1
Experimental (n = 14)	108	0	4	14	126	85.7	3.2
Females on nests							
Control (n = 30)	38	4	6	16	64	59.4	15.6
Experimental (n = 30)	66	20	22	44	152	43.4	27.6

Females on their nests.

Response of females on their nests to call playback was more ambiguous. They vocalized significantly more often when played the experimental tape ($\bar{X}$ number of vocalizations given/playback = 2.3 $\pm$ 1.6 during control and 5.3 $\pm$ 5.1 during experimentals; Wilcoxon z = -1.50, 1-tailed P = 0.02, n = 30). These females gave a significantly greater percentage of Type 1 songs during control presentations (Table 2; t-test of the equality of 2 percentages; t = 2.16, 1-tailed P = 0.015) and a significantly greater percentage of Type 2 and combination songs during experimental presentations (Table 2; t = -1.97, P = 0.024). Experimental broadcasts, however, did not affect the females' decisions to leave nests: 53.3% (16 of 30) left nests during control broadcasts, as did 60.0% (18 of 30) during experimental broadcasts (χ^2 = 0.07, P = 0.79). Thirty-three percent (10 of 30) of females departed their territories to feed during control playbacks, as did 20% (6 of 30) during experimental playback. Furthermore, females left their nests during all portions of the 200-s playbacks, suggesting that the various call types and timing of call switches did not influence decisions to leave.

3. Female vigilance.

On marshes supporting more than one territory (range 3 to 15), I found positive significant relationships between the amount of time females were "up" and the duration their mates were off territory ($\bar{X}$ time "up" for females = 155 $\pm$ 163 s *vs* $\bar{X}$ time "off" for males = 319 $\pm$ 243 s/900 s period; r^2 = 0.032, P < 0.005, n = 210 periods), and the amount of time females spent "down" in the vegetation and the duration their mates were "on" territory ($\bar{X}$ time "down" = 674 $\pm$ 193 s *vs* $\bar{X}$ time "on" = 516 $\pm$ 242 s; r^2 = 0.058, P < 0.001, n = 210).

On isolated territories, where females are unable to listen to neighboring males for alerting information, the relationship between female vigilance and mate presence was somewhat stronger ($\bar{X}$ time "up" for females = 256 $\pm$ 194 s *vs* $\bar{X}$ time "off" for males = 239 $\pm$ 230 s, r^2 = 0.155, P < 0.005, n = 51 periods; $\bar{X}$ time "down" = 607 $\pm$ 203 s *vs* $\bar{X}$ time "on" = 647 $\pm$ 231, r^2 = 0.270, P < 0.0001, n = 51).

Discussion

Several results of this study indicate that male redwings direct their alert calls at least partly to their mates. First, as predicted, average call rates rose significantly when primary females started incubating. These

females settled on male territories usually two to three weeks before start-
ing their nests. Therefore, this significant increase in call rate was not
simply associated with female arrival, which could be interpreted in
several ways (*e.g.*, with increased male-male interaction when females
arrive), but with already resident females initiating their 10 to 12 day
incubation periods. The slight rise in average call rate between pre-
incubation and incubation phases could result either from a slightly
higher baseline call rate after females lay, or greater increases in call rates
when males are alarmed. Whether the relationship between the onset of
incubation by females and increased male call rates is causal cannot be
certain without experimental manipulation of breeding activity, but it
does support the idea that alert call rates and breeding activity are depen-
dent. Furthermore, the percentage of time males gave alert calls while on
territory increased significantly from 63.8% to 83.2% (Table 1) between
their pre-incubation and incubation phases (t = 14.43, P ≪ 0.001), also
suggesting that male calling was influenced by female breeding activity.

The absolute increase in average call rates as incubation began was
small, about two calls/min. Larger increases in average call rates were
not expected because males apparently signal the close approach of
predators by elevating their call rates high above the average values
reported here, for example, to rates of about 25 or more calls/min.

If individual males switch call types only when they detect potentially
dangerous changes in their surroundings or to match their neighbors'
disturbance-induced switches, then changes in average switching rates
could indicate either changing frequencies of dangerous disturbances or,
more likely, changing male sensitivities to them. Males may be more sen-
sitive to disturbances (*e.g.*, appearances of predators, startling splashes in
the marsh) when they have active nests on their territories. The most
important nest predator in the study area, the black-billed magpie (*Pica
pica*), poses no threat to adult redwings, and therefore may not affect
male calling prior to incubation. If so, a possible interpretation of the
average switching rates given in Table 1 is that male sensitivity to poten-
tial nest predators rose significantly after the pre-incubation phase, again
after the first incubation phase, and then declined significantly after the
first nestling phase. It should be noted, however, that there were ususally
other active nests on each territory by the time the first nest fledged
young.

The results of the playback experiments to nesting females demon-
strate that they listen to male calls; however, their responses were context
dependent and, thus, difficult to interpret. Females on or near their nests

vocalized more frequently when exposed to repetitive male calls containing call type switches. Females perched near their nests gave a higher percentage of Type 1 songs during experimental playback, whereas females on nests gave more Type 1 songs during control playback. Because Type 1 songs are thought to be directed at mates (BELETSKY, 1983, 1985; YASUKAWA et al., 1987), it is difficult to understand the differing responses of females in these two situations. Type 2 songs, directed aggressively at conspecific females and at predators (BELETSKY, 1983; YASUKAWA et al., 1987), were very rarely given in response to playback when females could see their surroundings, i.e., when they were in positions where they could ascertain that danger was not imminent, but were given regularly from their hidden nests, especially during broadcasts containing call type switches. These females may have responded differently because they were unsure of the extent of potential danger, but at this point, the relationship between male calls and female vocalizations is unclear.

The prediction that females would stay on or near their nests after hearing call type switches was partially supported. Females off their nests when exposed to call changes tended to remain on territory, but females on their eggs departed their nests at the same rates during experimental and control playback. This ambiguity suggests that whereas females may be alerted by a call type change, they do not necessarily remain at their nests. In fact, females that remained on their nests whenever males switched calls might rarely be able to leave, because their mates change call types, on average, every 1 to 2 min (Table 1; see below). Thus, although females may receive information from male call changes, a single call type switch might be insufficient to alter their movements. It is plausible that normal female responses to call switches are increased states of alertness. More substantive changes in male calling patterns, such as large increases in call rate or switch rate, may be more likely to affect female movements. The prediction that a few call switches would influence female behavior may, therefore, have been naive.

The amount of time females spent in elevated, vigilant positions varied as a function of male presence, suggesting that females may need to be less vigilant themselves when their calling mates are nearby. This relationship supports the contention of PEEK (1971) that male redwing calls serve as an early-warning system for nesting females in their concealed nests. PEEK found that he could approach incubating females in their concealed nests much closer without their flushing when their mates had been surgically muted. Female redwings may, therefore, use their mates as vocal sentinels.

The rate that males switch call types may be a key to understanding the overall function of repetitive alert calling in this species. High average switch rates appear inconsistent with the initial hypothesized function of call switching, *i.e.*, alerting conspecifics about the detection of predators or other potentially dangerous events (BELETSKY *et al.*, 1986). Of what utility is an alert system to females when their mates switch call types every two minutes? Several factors must be considered. First, two minutes is an average value. Highly alarmed males, near a potential nest predator, change call types very rapidly, whereas some males give a single call type during an entire 15-min observation period. However, the colonial nature of the redwing breeding situation may best explain high switch rates. Individual males and females may receive alerting information from many nearby calling males. An initial call type switch by Male A detecting a predator may provide information about detection, but also, by the position of Male A, relative information about the predator's location. The next call switch could arise with neighboring Male B, as the predator moves into *his* view. Thus, individuals listening to call type switches but also determining the spatial positions of the callers, may receive information about predator movements. Indeed, information about subtle and changing conditions in and around the marsh may be encoded in the ''web'' of sound broadcast by the males in a local breeding neighborhood. Call rates, call type switches, and positions of calling males, taken together, could be a rich source of anti-predator information for listeners, both male and female.

To summarize, direct and indirect evidence from several sources indicates that nesting female redwings respond to male alert calls. Because neighboring males are known to listen to each other's calls (BELETSKY *et al.*, 1986), it is now evident that both sexes listen to and probably benefit from these calls. Nevertheless, the evolution of this complex alert system is obscure. Female responses during breeding to male calls may have led to the use of the calls in a seasonal, territorial, antipredator system. However, observations of males calling before female arrival each spring in the study area, while off territory during the breeding season, and also during non-breeding periods of the year, suggest that the call alert system, at least in some form, operates whenever males are in proximity to one another. Studies of male redwing calling during the non-breeding season as well as comparative studies of the calling behavior of other icterine species, are required to elucidate the development of this alert system.

Summary

Male red-winged blackbirds (*Agelaius phoeniceus*) have an unusual vocal alert system that operates throughout the breeding season. Territory owners give alert calls repetitively during most of their activities and transmit information about potential predators when they switch call types. Males are known to listen to each other's alert calls, presumably benefiting by receiving anti-predator information. Results of three separate tests supported the hypothesis that nesting female redwings also listen to and benefit from male alert calls. 1) Average call rates of males monitored through the breeding season increased significantly when their first mates started to incubate. Alerting information about predators may be especially important to females during this period because their ability to detect approaching predators is reduced while they are incubating in dense vegetation. 2) Nesting females gave different responses to playback of repetitive calls without call type changes ("background" calls) and with call type changes (which mimic a male changing call types after detecting a predator). Females were more vocal during broadcast of the tape containing call type changes, and, in some cases, they were also more likely to remain near their nests. 3) Females were more vigilant when their calling mates were absent from their territories, and less vigilant when their mates were present, suggesting that territory owners act as vocal sentinels.

References

BELETSKY, L. D. (1983). Aggressive and pair-bond maintenance songs of female red-winged blackbirds (*Agelaius phoeniceus*). — Z. Tierpsychol. 62, p. 47-54.

—— (1985). Intersexual song answering in red-winged blackbirds. — Can. J. Zool. 63, p. 735-737.

—— & CORRAL, M. G. (1983). Lack of vocal mate recognition in female red-winged blackbirds. — J. Field Ornithol. 54, p. 200-202.

——, HIGGINS, B. J. & ORIANS, G. H. (1986). Communication by changing signals: call-switching in red-winged blackbirds. — Behav. Ecol. Sociobiol. 18, p. 221-229.

CURIO, E. & REGELMANN, K. (1985). The behavioural dynamics of great tits (*Parus major*) approaching a predator. — Z. Tierpsychol. 69, p. 3-18.

HURLY, T. A. & ROBERTSON, R. J. (1984). Aggressive and territorial behaviour in female red-winged blackbirds. — Can. J. Zool. 62, p. 148-153.

KLUMP, G. M. & SHALTER, M. D. (1984). Acoustic behaviour of birds and mammals in the predator context. — Z. Tierpsychol. 66, p. 189-226.

ORIANS, G. H. (1980). Some adaptations of marsh-nesting blackbirds. — Princeton University Press, Princeton.

—— & BELETSKY, L. D. (1989). Red-winged blackbird. — In: Lifetime reproduction in birds (I. NEWTON, ed.). Academic Press, New York.

—— & CHRISTMAN, G. M. (1968). A comparative study of the behavior of red-winged, tricolored, and yellow-headed blackbirds. — Univ. Calif. Publ. Zool. 84, p. 1-85.

OWINGS, D. H., HENNESSY, D. F., LEGER, D. W. & GLADNEY, A. B. (1986). Different functions of "alarm" calling for different time scales: A preliminary report on ground squirrels. — Behaviour 99, p. 101-116.

PEEK, F. W. (1971). Seasonal change in the breeding behavior of the male red-winged blackbird. — Wilson Bull. 83, p. 383-395.

SIMMERS, R. W. (1975). Variation in the vocalizations of male red-winged blackbirds (*Agelaius phoeniceus*) in New England and New York. — Unpubl. Ph.D. dissertation, Cornell University, Ithaca, NY.

SOKAL, R. R. & ROHLF, F. J. (1969). Biometry. — W. H. Freeman, San Francisco.

SMITH, W. J. (1977). The behavior of communicating. — Harvard University Press, Cambridge, MA.

YASUKAWA, K., BOLEY, R. A. & SIMON, S. E. (1987). Seasonal change in the vocal
    behaviour of female red-winged blackbirds, *Agelaius phoeniceus*. — Anim. Behav. 35,
    p. 1416-1423.

Zusammenfassung

Männliche Rotschulterstare (*Agelaius phoeniceus*) haben während der Brutsaison ein unge-
wöhnliches vokales Warnsystem. Gebietsinhaber zeigen wiederholte Wachsamkeitsrufe
während der meisten ihrer Aktivitäten und vermitteln Informationen über mögliche
Feinde, indem sie ihre Ruftypen ändern. Offensichtlich schenken die Männchen ihren
gegenseitigen Wachsamkeitsrufen Aufmerksamkeit; wahrscheinlich benutzen sie diese
Feindinformationen als weitere Vorsichtsmassnahme. Die Ergebnisse von drei verschie-
denen Untersuchungen bestätigen die Annahme dass Rotschulterweibchen, die ihr Nest
im Gebiet der Männchen haben, ebenfalls zuhören und von den Rufen Nutzen ziehen.
1) Die beobachteten durchschnittlichen Ruffrequenzen der Männchen stiegen merklich
an, sobald die ersten Partner zu brüten begannen. Der Wachsamkeit dienende Informa-
tionen über Feinde könnten für brütenden Weibchen besonders wichtig sein, da sich ihre
Nester in dichtem Gewächs befinden und daher die Möglichkeit, sich nähernde Feinde
zu erspähen stark eingeschränkt ist. 2) Nistende Weibchen reagierten verschieden auf das
Abspielen von sich wiederholenden männlichen Rufen ohne Ruftypenänderungen
(,,Hintergrundrufe'') und mit Ruftypenänderungen (die ein Männchen nachahmen, das
seine Rufe ändert nachdem es einen Feind entdeckt hat). Der Gesang der Weibchen ver-
stärkte sich während des Abspielens des Tonbandes das alle Ruftypen enthielt; in einigen
Fällen blieben sie auch in der Nähe ihrer Neste. 3) Weibchen zeigten grössere Wachsam-
keit, wenn ihre Partner sich ausserhalb ihrer Gebiete befanden: sie waren weniger wach-
sam, wenn ihre Partner nah waren. Dies führt zu dem Schluss, dass die Gebietsinhaber
als vokale Wachen funktionieren.