

## INTERSEXUAL VOCAL COMMUNICATION IN THE RED-WINGED BLACKBIRD

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**Abstract.**—Intersexual vocal communication in Red-winged Blackbirds (*Agelaius phoeniceus*) was investigated in this study. Females gave two basic vocalizations that either overlapped or followed their mates' songs in time. As males got farther from the center of the territory, females tended to shift from answering with type-1 songs to answering with type-2 songs and from overlapping to following male songs. As the distance between singing males and their mates increased, the incidence of answering decreased, and the answers shifted from type-1 to type-2 songs and from overlapping to following. Finally, as the orientation of singing males relative to females changed from facing toward the females to facing away, the incidence of answering decreased, and female answers shifted from type-1 to type-2. These findings indicate that intersexual vocal communication in redwings is affected by the spatial association of the male with the female and with the territory.

### COMUNICACIÓN VOCAL INTERSEXUAL EN *AGELAIUS PHOENICEUS*

**Sinopsis.**—Se investigó la comunicación vocal intersexual en *Agelaius phoeniceus*. Las hembras mostraron dos tipos básicos de vocalización que solapan o prosiguen, el canto de su pareja. Entre más se alejan los machos del centro del territorio, las hembras tienden a cambiar su respuesta de canto tipo 1 a canto tipo 2 y de solapar el canto a ofrecer una respuesta luego que el macho ha terminado su canto. Según fue incrementándose la distancia entre la pareja, la incidencia de respuesta al canto se redujó y la respuesta en canto por parte de la hembra cambió de 1 a 2, y de solapar a canto subsiguiente. Finalmente, según fue cambiando la orientación relativa del macho de estar de frente a la hembra hasta estar de espalda, la incidencia de canto de respuesta se redujó, y el canto de la hembra fue cambiando de tipo 1 al 2. El estudio demuestra que la comunicación intersexual en esta especie es afectada con la asociación espacial del macho con respecto a la hembra y con el territorio.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a common polygynous North American icterine possessing a well-studied vocal repertoire. Orians and Christman (1968) detailed 18 male and 6 female vocalizations including, however, only one male and one female song and a male flight song. Beletsky (1983) described two types of female song, a type-1 song used predominately intersexually in pair-bond maintenance and a type-2 song used intrasexually in aggression among females (this terminology was followed in this study; see also Beletsky and Corral 1983b, Hovekamp 1988, and Yasukawa et al. 1987 for sonagrams and descriptions of songs and song-answers).

Female redwings respond to many of their mates' songs by singing either a type-1 or type-2 song immediately following or even overlapping the male song (Beletsky 1985; Beletsky and Corral 1983a,b). In this study, a song-answer is defined as a male song immediately followed (less than 1 s later) or overlapped by a female song, while an answer refers just to the female contribution to the song-answer. Finally, a solo is defined as a male or female song that is not part of a song-answer.

Several studies have proposed that the type of vocal interaction repre-

sented by these song-answers could maintain pair-bonds and convey information to the mate concerning location, motivation, or physiological state (Armstrong 1963, Farabaugh 1982, Thorpe 1961). Beletsky and Corral (1983a) suggest that the loudness and direction of the male song might mediate the female answer. I tested the hypothesis that locational context affects the song-answer. Specifically, I attempted to determine whether females answer their mates and whether they change the type or timing of their answers when singing males are in different locations relative to the territories, at different distances from the females, and facing in different directions relative to the females.

#### METHODS

The study was conducted at the Class of 1918 Marsh (approximately 8.1 ha at 43°05'00"N, 89°25'50"W) on the campus of the University of Wisconsin-Madison. The marsh was monitored from 26 Feb.-26 Jun. 1988. Male redwings were first seen on 5 March; females arrived 1 April. Observations were conducted usually between 0500-1000 h and between 1600-2000 h. Binoculars (7 × 35) were used to identify and observe birds, and a Sony TCM-5000EV portable cassette-corder with a Sony Electret ECM-23F remote condenser microphone was used to record redwing songs on TDK high bias SA60 tape for analysis on a Multigon Industries, Inc. model 4600 Uniscan II with FFT real time sonogram spectral display.

Subjects were captured and banded to facilitate individual identification. Most were caught using 61-mm-mesh mist nets set in or near the cattails at the marsh's edge, others using 26 × 36 × 72-cm wire mesh traps placed on the ground and baited with cracked corn. Seven males and nine females were banded with U.S. Fish and Wildlife Service bands and unique combinations of two color bands. The unique band combinations, particular territorial occupancy and, sometimes, certain vocal peculiarities, allowed individual identification.

Initial observations focused on determining the territorial boundaries of the males. The marsh was mapped with the aid of aerial photographs, and territories were determined by marking perches from which males sang, noting the location of confrontations with other males (such as aggressive displays [Nero 1956, 1984] or fights), and then delineating as the territory's boundary the line connecting the outermost of these points. Females that nested and spent much of their time within these territories, and copulated with and sang in answer to the territorial male, were assumed to be mated to him and associated with his territory.

After territories had been mapped, observations focused on vocal behavior. Every song given in an interval of continuous singing by a particular male and by all of his associated females was recorded. For each male song, I noted whether or not there was an answer, what type of song (1 or 2) the female answered with, the timing of the answer (overlapping or following the male's song), the location of the male relative to his territory (on it, at the edge, or off of it), and the position of the male

TABLE 1. Sampling dates and observation time for Red-winged Blackbirds at the Class of 1918 Marsh, Madison, Wisconsin.

Male	Dates observed	No. of study bouts	Total time observed (hr : min)	No. of females on the territory
6	8 Apr–26 May	4	0:24	2
RW	16 Apr–4 May	6	0:38	2
GR	16 Apr–3 Jun	10	1:29	2
YR	9 Apr–31 May	11	1:51	1
1A	23 Apr–3 Jun	12	1:56	1
4	9 Apr–31 May	10	1:57	2
WG	24 Apr–3 Jun	14	2:05	4
7	9 Apr–24 May	14	2:50	2

relative to his mate (the distance between them and whether he was facing her, facing toward the side, or facing away from her).

The female song was classified as type-1 or type-2 depending upon the components present in the song. The type-1 song consists exclusively of a rapid series of relatively brief, sharp song components, each sounding like “chit” (Hurly and Robertson 1984). The length of the song depended upon the number of chits. The type-2 song is composed of a lesser number of relatively longer components, each usually at least twice the duration of a chit (Beletsky 1983) and sounding like “teer” (Hurly and Robertson 1984). The two song components are often combined in many different ways, the females switching from one to the other sometimes more than once in individual songs (“combinations” of Beletsky 1985). However, due to the distinctiveness of the type-2 song component, any song containing at least one “teer” was classified in this study as type-2, type-1 song being defined as containing only chits (following Beletsky 1989). Armstrong (1992) has suggested a more complex system involving several female note types which can be variously combined.

The position of the male relative to the female was recorded by noting the distance between them and the orientation of the male in relation to the female. The distance was estimated as being <10, 10–20, or >20 m, an assessment aided by reference to four on-site, measured distance “standards.” The orientation of the male was defined as (1) toward the female ( $0 \pm 45^\circ$ ), (2) to the side ( $90 \pm 45^\circ$ ), or away from the female ( $180 \pm 45^\circ$ ).

Data were collected from eight adjoining territories along the northwest corner of the marsh. Table 1 presents information concerning the dates, study bouts (individual continuous observation sessions), the total amount of time spent watching each of the eight males and their associated females, and the number of females on each territory. In those instances where a male had more than one female on his territory, the females’ answer data were pooled. The length of study bouts depended on when males arrived upon or departed from their territories and varied

TABLE 2. Male and female solos and the effect of male song on the female answers.

Male	Female			Total
	No song	Type-1	Type-2	
No song	—	106	180	286
Song	599	403	174	1176
Total	599	509	354	1462

from 1–35 min; most, however, were about 10 min in duration. Male RW disappeared after 4 May and the territory of male 6 was in a particularly difficult location for data collection.

### RESULTS

*Effects of male song.*—A total of 1462 songs (solos) and song-answers was observed (Table 2). Male songs were unanswered and answered about equally (599 vs. 577,  $P = 0.27$ , binomial test), and females sang more answers than solos (577 vs. 286,  $P < 0.001$ , binomial test). Females sang type-1 song more often than type-2 song (509 vs. 354,  $P < 0.001$ , binomial test), but song type depended on whether the song was a solo or an answer to the male ( $\chi^2 = 85.8$ ,  $df = 1$ ,  $P < 0.005$ ; Table 2). This interaction is explained by the fact that as a solo, type-1 song was less frequent than type-2 (106 vs. 180,  $P < 0.001$ , binomial test); as an answer, type-1 was more frequent (403 vs. 174,  $P < 0.001$ , binomial test).

Song type also depended on the timing of the female answer ( $\chi^2 = 72.6$ ,  $df = 1$ ,  $P < 0.005$ ; Table 3). Overlapping answers were predominantly type-1 (281 vs. 55,  $P < 0.001$ , binomial test), whereas answers that followed the male song were equally frequent in type (122 vs. 119,  $P = 0.45$ , binomial test).

*Effects of male location relative to the territory.*—The location of the male relative to the territory appeared to have no effect on the female's type of solo ( $\chi^2 = 5.2$ ,  $df = 2$ ,  $0.1 > P > 0.05$ ; Table 4). However, there was significant interaction ( $\chi^2 = 31.3$ ,  $df = 2$ ,  $P < 0.005$ ) between the singing male's location and the female's answer type and between male location and the timing of the female answer ( $\chi^2 = 39.9$ ,  $df = 2$ ,  $P < 0.005$ ; Table 4). As the male's distance from the center of his territory increased, the female's answers shifted from type-1 to type-2 song and from overlapping to following his song.

TABLE 3. Relationship between female answer type and the timing of the answer.

Answer timing	Answer type		Total
	Type-1	Type-2	
Overlapping	281	55	336
Following	122	119	241
Total	403	174	577

TABLE 4. Effect of male location relative to the territory on female solos and answers.

Male location	Female solo		Female answer			
	Type-1	Type-2	Type-1	Type-2	Overlap	Follow
On territory	77	109	308	93	266	135
At edge	16	47	87	71	67	91
Off territory	13	24	8	10	3	15
Total	106	180	403	174	336	241

*Effects of male distance and orientation with respect to the female.*—Frequency of song-answering decreased significantly as distance ( $\chi^2 = 6.0$ ,  $df = 2$ ,  $P < 0.05$ , Friedman ANOVA) and angle ( $\chi^2 = 6.0$ ,  $df = 2$ ,  $P < 0.05$ , Friedman ANOVA) between mates increased (Table 5). Also as the angle got larger, the distance at which the female tended to answer the male decreased ( $\chi^2 = 24.3$ ,  $df = 4$ ,  $P < 0.005$ ; Table 5).

The type and timing of the female's answer was also influenced by the distance between her and her mate (Table 6) Type-2 answers became more common as the distance between the male and female increased ( $\chi^2 = 54.5$ ,  $df = 2$ ,  $P < 0.005$ ), regardless of the direction category. Females shifted from overlapping to following answers as the distance between the male and female increased ( $\chi^2 = 85.1$ ,  $df = 2$ ,  $P < 0.005$ ). This shift as distance increased was observed at  $0 \pm 45^\circ$  and  $90 \pm 45^\circ$  but not at  $180 \pm 45^\circ$ .

Finally, as the angle at which the male sang relative to the female increased, the proportion of type-2 songs increased ( $\chi^2 = 7.5$ ,  $df = 2$ ,  $0.05 > P > 0.02$ ), but answer timing was unaffected ( $\chi^2 = 0.9$ ,  $df = 2$ ,  $0.7 > P > 0.5$ ) (Table 6).

Two unusual types of song-answers were noticed. Males very often sang while flying into or within their territories about 1 sec or less before perching or landing. There were 99 such "flight songs" (Orians and Christman 1968) noted during this study, 53 (53.5%) of which were answered by females. Also, in 39 instances, two females answered the same male song; this represents 6.8% of all the answered songs recorded. No pattern of female song type or timing in either answering the male flight songs or double-answering was detected.

TABLE 5. Effect of distance between male and female, and direction male faces relative to female, on the frequency of female answers.

Distance	Direction			Total
	$0 \pm 45^\circ$	$90 \pm 45^\circ$	$180 \pm 45^\circ$	
<10 m	127	102	52	281
10–20 m	106	77	23	206
>20 m	65	20	5	90
Total	298	199	80	577

TABLE 6. Effect of male distance and direction (relative to the female) on female answer type and timing.

Male distance	Male direction	Female answer			
		Type 1		Type 2	
		Overlap	Follow	Overlap	Follow
<10 m	0 ± 45°	99	18	4	6
	90 ± 45°	69	13	7	13
	180 ± 45°	29	7	4	12
10–20 m	0 ± 45°	43	29	11	23
	90 ± 45°	23	22	12	20
	180 ± 45°	4	4	10	5
>20 m	0 ± 45°	8	21	4	32
	90 ± 45°	4	8	2	6
	180 ± 45°	2	0	1	2

## DISCUSSION

Beletsky (1985) found that 46% of 3727 male songs were answered; I counted 49.1% answered of 1176. However, he totalled 93.5% answered by type-1 and 6.5% by type-2 or a combination, whereas I found 69.8% and 30.2%, respectively. I also found a relatively high (53.5%) frequency of answers to male flight songs, and Beletsky found an even higher (62%) proportion of what he considered a sort of female “greeting” to her returning mate. He too noted instances of more than one female answering the same male song. Beletsky (1985) also found that female answers became less frequent with the appearance of nestlings. In this study, most females were observed to have nestlings by the end of May, at which time their answering decreased.

It appears that the nature of the female Red-winged Blackbird’s response to the song of her mate is influenced by aspects of their respective locations, including her mate’s location relative to the territory, the distance between her and her mate, and the direction in which the male delivers his song. The female answers a greater number of male songs directed toward her or sung at closer range. A shift in answer from type-1 toward type-2 song and from overlapping to following the male song is seen as the male gets farther from the territory center and as the distance between the male and female increases. Also, the female tends to answer with type-1 song when the male song is directed toward her and shifts toward type-2 song when his song is directed away from her.

This system of song-answering in redwings may indicate a relation between male location and female motivational state. Beletsky and Corral (1983b) propose that the timing of the female answer relative to the male song may convey information about her identity, physiological state, and/or other pair-bond information. The type of song the female employs in answering the male song also appears to send important signals, with

type-1 song functioning in maintaining the pair-bond and type-2 song functioning in female aggression (Beletsky 1983, Yasukawa 1990).

These relations between female answer and motivation, and results of this study linking type and timing of the female answer to locational context, may denote a motivational shift on the part of the female as the male position relative to her or the territory changes. The female may sing a type-1 answer to her mate's song in order to identify herself as one of his females and to specify her location while maintaining the pair-bond. If this is the primary function of the song-answer, the predominance of the type-1 answer over type-2 (Table 2) may be explained. The female may sing type-2 answers when the male sings at the edge or away from the territory, farther from her, or in directions away from her, again to associate herself with her mate but to do so while sending an aggressive message toward other females. The timing of the female answer is correlated with the type of answer (Table 3) and may emphasize the difference between the two types.

The explanation for the occurrence and nature of these song-answers among Red-winged Blackbirds is probably related to the dense vegetation characteristic of their nesting habitat and their polygynous mating system (Beletsky 1983, Yasukawa and Searcy 1982). In thick stands of cattails, information contained in the song-answers may compensate for difficulty in visually communicating. Also, with several females potentially occupying the same male territory, it may be advantageous if female answers convey information to other females as well as to the male (Yasukawa 1990). Furthermore, it may be that the acoustically crowded environment of a marsh densely populated with redwings makes a song-answer coordinated between male and female imperative to locating one another, maintaining the pair-bond, and perhaps as a quick assessment of female motivational state. Future research combined with the results of this study could lead to more detailed conclusions concerning the function and origin of song-answers in redwings and to a better understanding of intersexual vocal communication.

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### FIFTH INTERNATIONAL CONGRESS OF VERTEBRATE MORPHOLOGY

The Fifth Congress of the International Society for Vertebrate Morphologists will be held at the University of Bristol, UK, 12–17 Jul. 1997. All those interested in vertebrate morphology and related areas are invited to attend.

The Congress aims to bring together all those with an interest in vertebrate morphology and related subjects. It will be a meeting place for professional zoologists, morphologists, and anatomists from throughout the globe. Suitable topics for discussion at the meeting include all aspects of vertebrate morphology, such as anatomy, evolution, development, biomechanics and locomotion; vertebrate palaeontology; ecological morphology; morphological aspects of behavior; cell structure and function; neurobiology and neuro-anatomy; and morphometric and other methods.

The call for papers and details of booking arrangements and costs will be published in September 1996; the closing date for submission of papers will be 16 Dec. 1996. For further information, contact:

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