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THE CONTEXT AND FUNCTION OF DUET AND SOLO SONGS IN THE RED-SHOULDERED BLACKBIRD

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ABSTRACT.—We examined the social and behavioral context of male and female duet and solo songs in Red-shouldered Blackbirds (*Agelaius assimilis*), formerly known as the Cuban race of the Red-winged Blackbird (*A. phoeniceus*). Songs were most common during intersexual interactions before birds were on breeding territories. In contrast to Red-winged Blackbirds, Red-shouldered Blackbirds sang relatively little and aggressive interactions were rare when they were on breeding territories. Our results suggest that duet and solo songs are important in pair bond formation and maintaining contact between mates. *Received 28 May 1996, accepted 15 Oct. 1996.*

The function of song has been studied in many species; however, studies have focused primarily on the function of male song. The study of female song has been restricted mostly to tropical species in which females sing frequently, usually in the form of a duet with her mate (Farabaugh 1982). Intraspecific studies of the function of both duetting and solo songs are rare; however, such studies are important for understanding the functions of duets and solo songs for both sexes. In this paper we present a study of the function of song in Red-shouldered Blackbirds (*Agelaius assimilis*) a species that is endemic to Cuba and was formerly considered a race of the Red-winged Blackbird (*A. phoeniceus*; Garrido and Kirkconnell 1996). In Red-shouldered Blackbirds, male and female songs are similar and occur as both duets and solo songs (Whittingham et al. 1992). This is particularly fascinating because it is unlike most other duetting species which have sex-specific songs, and it provides an interesting contrast to the well studied Red-winged Blackbird. The song of both male and female Red-shouldered Blackbirds is similar to the song of the male Red-winged Blackbird (Whittingham et al. 1992). However, Red-shouldered Blackbirds differ from Red-winged Blackbirds in morphology and social behavior. Red-shouldered Blackbirds are socially monogamous and both sexes feed young with equal frequency, unlike Red-winged Blackbirds. In addition, Red-shouldered Blackbirds are less sexually dimorphic in size and plumage than Red-winged Blackbirds (Whittingham et al. 1992, 1996).

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Several hypotheses for the function of avian song have been proposed and most apply to species that duet as well as to those in which individuals of either or both sexes sing solo songs. These include synchronization of reproductive activities, maintenance of contact between mates and mate location, territorial defense, mate guarding, mate attraction, and pair bond formation. Although these hypotheses are not mutually exclusive we can make specific predictions. (1) If song is important for the synchronization of reproductive activities, then songs by both sexes should be most frequent during the female's pre-fertile and fertile periods (Beletsky 1982, Ritchison 1986). (2) Song may be used to maintain contact between mates or to force a mate to be attentive (Wickler 1980, Hoelzel 1986, Kellner and Ritchison 1988, Smith 1994). This hypothesis predicts that songs should be most frequent in the presence of the mate and throughout the duration of the pair bond (i.e., potentially all year long in species with year-round or life long pair bonds). (3) Song may function in mate location, in which case we would expect songs to be most frequent when visual contact between pair members is occluded, perhaps in dense vegetation (Hooker and Hooker 1969, Thorpe 1972). (4) If territorial defense is a primary function of song then songs should be most frequent in response to territorial intrusions by conspecifics (Beletsky 1982, Kellner and Ritchison 1988, Arcese et al. 1988) and during territory establishment or during high risk of territory takeover (Baptista et al. 1993). If males and females cooperate in territory defense, then the similarity in the song and plumage of Red-shouldered Blackbirds may facilitate territory defense (e.g., Baptista 1978). (5) Song may function in mate guarding in which males or females attempt to deter their mate from attracting an additional partner (Sonnenschein and Reyer 1983, Montgomerie and Thornhill 1989, Møller 1991). In this case, we would expect song to be most frequent in response to intrasexual intruders during the fertile period. (6) A mate attraction and pair bond formation function suggests that song should be most frequent during courtship and pair formation and by unmated individuals early in the breeding season or in response to mate loss (Baptista et al. 1993, Hanski and Laurila 1993). In Red-shouldered Blackbirds, this function may apply to both sexes.

To investigate the function of duets and solo songs in Red-shouldered Blackbirds, we examined the social contexts in which songs were used and the behaviors associated with particular songs. Our results suggest that songs are important in pair bond formation and maintaining contact between mates.

METHODS

We studied Red-shouldered Blackbirds in the Zapata Swamp, Cuba, 162 km southeast of Havana. We observed the singing behavior of birds prior to the nesting period (5–17 April)

in 1992 and during the nesting period (25 May–4 June, 17–18 June, and 1–2 July) in 1993. During the pre-nesting period, birds were found only at Guama, a village of 12 small islands covered mostly by lawn, each with 6–8 cabins. Most islands have trees introduced from Australia, including bottlebrush (*Callistemon speciosus*) and *Eucalyptus* (spp.). During the pre-nesting period, Red-shouldered Blackbirds foraged throughout the islands, particularly in bottlebrush trees, but did not defend territories (see below). Guama is approximately 1 km via canal from the edge of Treasure Lake (16 km^2). During the nesting period we found birds only on their breeding territories which were established in the vegetation along the periphery of Treasure Lake. The vegetation consisted primarily of *Typha* spp., *Phragmites* spp. and *Sagittaria lancifolia.*

We caught 50 adult birds in mist nets, and all birds were banded with a unique combination of colored leg bands. We observed the singing behavior of second year (SY) and after second year (ASY; Pyle et al. 1987) adult males and females. The plumage of ASY males was entirely jet black except for the red-orange epaulet with a light yellow band along the distal edge of the epaulet. SY males were also black; however, the epaulet was orange interspersed with black feathers and lacked the distal yellow band. ASY females were also entirely jet black but lacked the epaulet. SY females had olivaceous feathers at the base of the lower mandible and whitish edges on the greater and middle wing coverts as well as on the under tail coverts (Whittingham et al. 1996).

Each morning between 07:30 and 11:00 h, we walked a circuit of four islands (in random order) on which foraging birds were found most commonly. A male and female were described as a pair if they were observed more than four times together and never observed separately. We observed each of 15 pairs during two to four independent observation periods. For data analysis, we used only observation periods which were $\geq$5 min in duration.

Singing behavior was observed until the pair flew away or until the group composition changed. In Red-shouldered Blackbirds, either sex sings solo songs or leads duets (a pair of songs, one song produced by each sex, overlapping or less than 1 s apart, and given repeatedly in sequence; Whittingham et al. 1992). During observations of singing behavior prior to nesting (April), we recorded (1) group size, (2) number of solo songs by males and females, and (3) number of duets led by male or led by female. We recorded the context of singing behavior as: (1) pair alone, (2) pair with additional female present, (3) pair with additional male present, or (4) pair with additional pair present. Additional birds were considered "present" when they were <2 m away from the focal pair. For each pair, the mean song rate from all observations was used so that each pair was represented only once in the data analysis.

We also observed singing behavior during the nest-building and incubation periods (May to July), and we recorded (1) number of solo songs or duets, (2) activity of male (perched, foraging), and (3) activity of female (collecting nesting material, building at nest, foraging). Observation periods during the nest-building and incubation periods were 30–240 min each, between 07:30–11:00 and 14:00–18:00 h.

During the pre-nesting and nesting periods, we recorded observations of aggressive behavior between individuals. Aggressive behaviors included bill tilting, flaring epaulets, and displacement of one individual by another (Nero 1956).

All birds observed as pairs were banded, and different pairs were observed in each year. Some unbanded individuals were included as "additional" birds present near pairs (see Table 2). Means were used when there was more than one observation period for each pair for each category. Means are presented with their standard errors.

RESULTS

During the pre-nesting season, birds were observed foraging around Guama either on the cabin lawns or in the bottlebrush trees. Of the 50

TABLE 1
NUMBER OF DUET AND SOLO SONGS/MIN (MEAN ± SE) OF RED-SHOULDERED BLACKBIRDS IN RELATION TO SEASON

		Duets		Solo songs	
Season[a]	N	Male leads	Female leads	Male	Female
Pre-nesting	15	0.23 ± 0.06	0.38 ± 0.06	0.93 ± 0.2	1.12 ± 0.2
Nest building	6	0.05 ± 0.01	0.01 ± 0.01	0.22 ± 0.04	0.14 ± 0.02

[a] Observations during the pre-nesting period were conducted in 1992 and observations during the nest building and incubation periods were conducted in 1993. N = number of pairs observed.

banded birds, 23 were ASY males, 10 were SY males, 9 were ASY females, and 8 were SY females. Birds were foraging either in pairs or in small groups (6.3 ± 0.6 birds). Of 22 foraging groups, 18 had an equal number of males and females. The remaining four groups had one or two additional birds present.

Aggression.—Red-shouldered Blackbirds singing at Guama during the pre-nesting period were not defending territories. Neither males nor females responded to duet or solo song playbacks conducted in the presence of both male and female taxidermic mounts (Whittingham, Kirkconnell and Ratcliffe, unpubl. data). In general, aggressive interactions were rare. We observed only five cases of aggressive behavior during the pre-nesting period at Guama: (1) bill tilting display (Nero 1956) between an SY male and an ASY male, (2) an ASY male supplanted two males singing near his mate, (3) a paired SY female supplanted and then chased another female, (4) an ASY intruder displayed his epaulets to a paired ASY male, and (5) a bill tilting display between two females. There was little evidence of overt aggression or territorial intrusions during the nesting period. Territorial boundaries on Treasure Lake were determined by monitoring the locations of males and females while they were foraging or singing. Throughout the nesting period, we observed only one male and one female on each territory (700 ± 128 m^2, N = 6). Unlike the territorial aggression commonly observed in Red-winged Blackbirds (Searcy and Yasukawa 1995), we observed only one instance where two males sang simultaneously at their common territorial border.

General vocal patterns.—Solo songs were more common than duets (Table 1). Both males and females sang solo songs more frequently than duets during the pre-nesting period (Student's t-test, males: $t = 9.89$, $P < 0.001$, females: $t = 7.68$, $P < 0.001$) and the nest building period (males: $t = 3.75$, $P = 0.001$, females: $t = 5.22$, $P < 0.001$). Duets and solo songs were more frequent during the pre-nesting period than during

TABLE 2

VOCAL BEHAVIOR OF RED-SHOULDERED BLACKBIRDS DURING THE PRE-NESTING SEASON[a]

Category	N	Duets		Solo songs	
		Male leads	Female leads	Male	Female
Pair type					
ASY male, ASY female	7	0.15 ± 0.1	0.23 ± 0.1	0	0.87 ± 0.5
ASY male, SY female	5	0.36 ± 0.1	0.67 ± 0.4	1.88 ± 0.1	1.05 ± 0.2
SY male, SY female	3	0.20 ± 0.1	0.47 ± 0.1	1.58 ± 0.3	0.85 ± 0.2
Social context					
pair alone	12	0.03 ± 0.03	0.33 ± 0.1	1.12 ± 0.3	0.18 ± 0.1
additional female	5	0	0.28 ± 0.2	0	3.13 ± 0.5
additional male	15	0.54 ± 0.2	0.58 ± 0.1	1.98 ± 0.3	1.23 ± 0.3
additional pair(s)	13	0.12 ± 0.05	0.24 ± 0.1	0.92 ± 0.3	1.07 ± 0.3

[a] Number of duets and solo songs/min (mean ± SE) were analyzed in relation to the type of pair members and the social context. Category refers to the factors used in one-way ANOVA tests (see text for results). N = the number of pairs observed.

the nest building period for both males and females (males: leading duets $t = 2.2$, $P < 0.05$, solo songs $t = 3.3$, $P = < 0.01$; females: leading duets $t = 5.3$, $P < 0.001$, solo songs $t = 4.2$, $P < 0.001$; Table 1).

Songs during pre-nesting.—During the pre-nesting period, singing behavior was analyzed according to the social context in which the song was given and pair type (N = 15 pairs; Table 2). The pair bond formation hypothesis predicts song will be more frequent during courtship or when pairs are newly formed. By definition, SY birds are in their first year after hatching (Pyle et al. 1987), and thus, SY individuals were most likely to be members of newly formed pairs participating in their first breeding season. We analyzed song in relation to pair type to see if pairs in which one or both members were SY individuals sang more frequently. Pair type refers to paired birds that were either (1) both SY individuals (N = 3 pairs), (2) an SY female and ASY male (N = 5 pairs), or (3) both ASY individuals (N = 7 pairs). Males led duets (one-way ANOVA, $F = 5.60$, df = 3, 41, $P < 0.01$; Table 2) and gave solo songs ($F = 4.49$, df = 3, 41, $P < 0.01$) more often when an additional male was nearby (<2 m away) than in other social contexts. Similarly, females gave solo songs most often when an additional female was nearby ($F = 11.12$, df = 3, 41, $P < 0.001$; Table 2); however, the rate of female duets was not affected by social context ($F = 2.37$, df = 3, 41, $P > 0.05$). Males paired to SY females sang more solo songs than males paired to ASY females ($F = 7.4$, df = 2, 12, $P < 0.01$; Table 2); however, pair type had little

TABLE 3

VOCAL BEHAVIOR OF RED-SHOULDERED BLACKBIRDS DURING THE NEST-BUILDING PERIOD[a]

Category	Duets		Solo songs	
	Male leads	Female leads	Male	Female
Female activity				
Collecting nesting material	0.04 ± 0.01	0.02 ± 0.01	0.39 ± 0.09	0.07 ± 0.02
Building at nest	0.05 ± 0.01	0.02 ± 0.02	0.17 ± 0.03	0.09 ± 0.02
Foraging	0.09 ± 0.04	0.02 ± 0.02	0.17 ± 0.03	0.09 ± 0.02
Male activity				
Perched	0.07 ± 0.02	0.01 ± 0.01	0.35 ± 0.03	0.20 ± 0.08
Foraging	0.05 ± 0.01	0.01 ± 0.01	0.15 ± 0.06	0.19 ± 0.04

[a] Number of duets and solo songs/min (mean ± SE) were analyzed in relation to male and female activity (see methods).

influence on the rate of duets or female solo songs (all $F < 1.29$, df = 2, 12, all $P > 0.3$).

Songs during the nesting period.—In all pairs of birds (N = 6) observed during the nesting period both individuals were ASY. Thus, we did not include pair type as a factor in analyzing song rate during this period. During the nest-building period, female song was observed during three main activities: foraging, collecting nesting material, or building the nest. Males were either foraging low in the vegetation or perched overlooking the territory. The rate at which males and females led duets was not related to male or female activities (all $F < 3.6$, all $P > 0.07$; Table 3). However, during the nest-building period, males sang significantly more solo songs when they were perched than when they were foraging ($F = 9.01$, df = 1, 10, $P < 0.02$). Males also sang more solo songs when females were collecting nesting material than when females were at the nest or foraging ($F = 9.04$, df = 2, 15, $P < 0.01$; Table 3).

DISCUSSION

Songs in Red-shouldered Blackbirds were most common prior to the nesting period when birds were not on breeding territories. Intrasexual interactions appeared to influence the rate at which males led duets and the rate at which both sexes sang solo songs in the pre-nesting period. Furthermore, the high rate of solo songs given by males paired to SY females suggests that the recency of the pair bond influenced male solo song rate. During the nesting period, intrasexual interactions were rare and male songs were most common when males were perched on their territory and females were collecting nesting material. We suggest that

duets and solo songs are important in intrasexual interactions and may function in pair bond formation during the pre-nesting period. In addition, songs may be important in maintaining contact between mates during the nesting period.

Our observations do not support the synchronization of reproductive activities or mate location hypotheses for the primary function of song. Contrary to the prediction of the synchronization hypothesis, the rate of duet and solo songs, for both sexes, was lower during the female's fertile period (i.e., nest building). In other species, singing prior to the female's fertile period stimulates hormones which may advance nesting (Kroodsma 1976, Morton et al. 1985, Cheng 1992). We do not know if song functions as a sexual stimulant in this manner in Red-shouldered Blackbirds, but this idea warrants further investigation.

A mate location function is likely to be important in tropical species nesting in dense vegetation where mates are often out of sight of each other (Hooker and Hooker 1969). It is unlikely that this is a primary function of song in Red-shouldered Blackbirds, because when songs were most frequent pairs foraged together in open lawn areas prior to the nesting season.

In many species, duets as well as male and female solo songs play an important role in intrasexual aggressive interactions associated with territorial defense (e.g., Payne and Skinner 1970, Baptista 1978, Farabaugh 1982, Sonnenschein and Reyer 1983, Beletsky 1983). Similarly, in Red-winged Blackbirds, male songs function primarily in intrasexual interactions associated with territorial defense and mate attraction (e.g., Searcy and Yasukawa 1990), and female songs appear to be important in intrasexual aggressive interactions (Beletsky 1983). Both sexes of Red-shouldered Blackbirds sang frequently during intrasexual interactions prior to the nesting period while foraging away from their breeding territories, suggesting that territorial defense was not a primary function of song at this time of year. Although territorial aggression may be rare and song rate was low during the nesting period, most male songs occurred when they were perched, suggesting that solo songs could be associated with advertising territory occupancy. Red-shouldered Blackbirds at Guama do not seem to defend territories year round, and as a result, it is possible that songs are more important in territorial defense when borders are first established or when borders change (e.g., when a neighboring male disappears). To investigate this possibility, it will be necessary to make observations of territory establishment and conduct experiments that temporarily remove males from territories during the nesting period.

Both duets and solo songs seem to be important in intrasexual interactions, suggesting that these songs may function in mate guarding.

Males may sing in response to the presence of additional males to deter extra-pair copulations and protect their paternity (e.g., Farabaugh 1982, Montgomerie and Thornhill 1989, Møller 1991). This is unlikely to be a primary function of male song in Red-shouldered Blackbirds because song rate was greater during the pre-nesting period and lower during the female's fertile period (i.e., nest building). In contrast, females may sing in response to the presence of conspecific females to deter their mates from pairing with additional females (i.e., polygyny; Sonnenschein and Reyer 1983). The risk of polygyny will not necessarily be limited to the female's fertile period because pair bonds are apparently formed well before the nesting period. Polygyny and the consequent loss of male parental care could be costly to females because male Red-shouldered Blackbirds contribute a substantial amount of parental care to nestlings (Whittingham et al. 1996). Polygynous male Red-winged Blackbirds often assist only one of several mates, and the lack of male parental care reduces fledging success (e.g., Whittingham and Robertson 1994). It is possible that females are singing more frequently prior to nesting to advertise their mate's mated status; however, it is unlikely that males are singing frequently at this time to protect their paternity and deter extra-pair copulations.

A role for song in mate attraction and pair bond formation is suggested in many species because unpaired individuals sing frequently, reducing the rate of songs after pairing (Quaintance 1938, Marshall 1964, Catchpole 1973). In addition, individuals of either sex that lose their mate (i.e., widowed) may increase their song rate while trying to attract another mate (Baptista et al. 1993, Hanski and Laurila 1993). Since SY individuals are more likely to be members of newly formed pairs, the high rate of solo songs by males paired to SY females suggests that these songs may play a role in pair bond formation in Red-shouldered Blackbirds. At present, we lack information on the vocal and social behavior of unpaired Red-shouldered Blackbirds, but natural and experimental (i.e., via temporary removals) observations of the mate attraction process will help clarify the important functions of song in this species.

In many species of birds, individuals do not stop singing once they become paired, although song rate may change. A combination of the pair bond formation and maintenance hypotheses predicts songs will be more frequent during pair formation and less frequent during the maintenance period (Arrowood 1988). In Red-shouldered Blackbirds, singing by both sexes continued throughout the nesting season at a significantly lower rate than during the pre-nesting season, consistent with a function in pair bond formation and maintenance. Furthermore, both sexes in this species sing during the winter (A. Kirkconnell, pers. obs.). Pair bond maintenance or

maintenance of contact between mates is often suggested as the primary function for year round singing in many duetting species (Hooker and Hooker 1969, Payne and Skinner 1970, Wickler 1980, Farabaugh 1982, Sonnenschein and Reyer 1983).

A comparison between Red-winged and Red-shouldered blackbirds reveals some differences and similarities in the function and context of their songs. Similar to Red-shouldered Blackbirds, the song of male Red-winged Blackbirds functions primarily in mate attraction and pair bond formation (Searcy 1988, Searcy and Yasukawa 1995); however, in Red-winged Blackbirds this occurs primarily on their breeding territories, whereas, in Red-shouldered Blackbirds this occurs prior to territory settlement. Experiments in Red-winged Blackbirds illustrate that male song has an important function in territory defense (reviewed by Searcy and Yasukawa 1995). In contrast, song in Red-shouldered Blackbirds, by either sex, was infrequent following territory settlement, suggesting that territorial defense may not by a primary function of their songs. The song of female Red-winged Blackbirds is unlike the song of female Red-shouldered Blackbirds (Whittingham et al. 1992); however, in both species song seems to be important in intrasexual interactions. For female Red-winged Blackbirds this occurs primarily on the breeding territories (Beletsky 1983), while for female Red-shouldered Blackbirds it is associated with interactions prior to the nesting period.

The similarities between male and female Red-shouldered Blackbird duet and solo songs suggests similarities in function (Baptista 1978). Our data suggest that duet and solo songs of both sexes are important in intersexual and intrasexual interactions prior to the nesting period. Additional information on the vocal and social behavior of Red-shouldered Blackbirds throughout the year will be necessary to understand fully the function of duet and solo songs. Our observations suggest that the processes of mate attraction and territory establishment will be an important focus.

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LITERATURE CITED

ARCESE, P., S. K. STODDARD, AND S. M. HIERBERT. 1988. The form and function of song in female Song Sparrows. Condor 90:44–50.

ARROWOOD, P. C. 1988. Duetting, pair bonding and agonistic display in parakeet pairs. Behaviour 106:129–157.

BAPTISTA, L. F. 1978. Territorial, courtship and duet songs of the Cuban Grassquit (*Tiaris canora*). J. Ornithol. 119:91–101.

———, P. W. TRAIL, B. B. DEWOLFE, AND M. L. MORTON. 1993. Singing and its functions in female White-crowned Sparrows. Anim. Behav. 46:511–524.

BELETSKY, L. D. 1982. Vocalization of female Northern Orioles. Condor 84:445–447.

———. 1983. Aggressive and pair-bond maintenance songs of female Red-winged Blackbirds (*Agelaius phoeniceus*). Zeit. Tierps. 62:47–54.

CATCHPOLE, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). Behaviour 46: 300–320.

CHENG, M-F. 1992. For whom does the female dove coo? A case for the role of vocal self stimulation. Anim. Behav. 43:1035–1044.

FARABAUGH, S. 1982. The ecological and social significance of duetting. Pp. 85–124 *in* D. Kroodsma, E. Miller, and H. Ouellet (eds.). Acoustic communication in birds. Academic Press, New York.

GARRIDO, O. AND A. KIRKCONNELL. 1996. Taxonomic status of the Cuban form of the Red-winged Blackbird. Wilson Bull. 108:372–374.

HANSKI, I. AND A. LAURILA. 1993. Variation in song rate during the breeding cycle of the Chaffinch, *Fringella coelebs*. Ethology 93:161–169.

HOELZEL, A. R. 1986. Song characteristics and response to playback of male and female robins *Erithacus rubecula*. Ibis 128:115–127.

HOOKER, T. AND B. I. HOOKER. 1969. Duetting. Pp. 185–205 *in* R. A. Hinde (ed.). Bird vocalizations. Cambridge Univ. Press, Cambridge.

KELLNER, C. J. AND G. RITCHISON. 1988. Possible functions of singing by female Acadian Flycatchers (*Empidonax virescens*). J. Field Ornithol. 59:55–59.

KRINER, E. AND H. SCHWABL. 1991. Control of winter song and territorial aggression of female robins (*Erithacus rubecula*) by testosterone. Ethology 87:37–44.

KROODSMA, D. E. 1976. Reproductive development in a female songbird: differential stimulation by quality of male song. Science 192:574–575.

MARSHALL, J. T. 1964. Voice in communication and relationships among Brown Towhees. Condor 66:345–356.

MØLLER, A. P. 1991. Why mated birds sing so much: mate guarding and male announcement of mate fertility status. Am. Nat. 138:994–1014.

MONTGOMERIE, R. AND R. THORNHILL. 1989. Fertility advertisement in birds: a means of inciting male-male competition? Ethology 81:209–220.

MORTON, M. L., M. E. PERYRA, AND L. F. BAPISTA. 1985. Photoperiodically induced ovarian growth in the White-crowned Sparrow (*Zonotrichia leucophrys gambelli*) and its augmentation by song. Comp. Biochem. Physiol. 80A:93–97.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. I. Mating and nesting activities. Wilson Bull. 68:4–37.

PAYNE, R. B., AND N. J. SKINNER. 1970. Temporal patterns of duetting in African barbets. Ibis 112:173–183.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American Passerines. Slate Creek Press, Bolinas, California.

QUAINTANCE, C. W. 1938. Content, meaning and possible origin of male song in the Brown Towhee. Condor 40:97–101.

RADESATER, T. AND S. JAKOBSSON. 1988. Intra- and intersexual functions of song in the Willow Warbler (*Phylloscopus trochilus*). Proc. Inter. Ornithol. Congr. 19:1382–1390.

RITCHISON, G. 1986. The singing behavior of female Northern Cardinals. Condor 88:156–159.

SEARCY, W. A. 1988. Do female Red-winged Blackbirds limit their own breeding densities? Ecology 69:85–95.

——— AND K. YASUKAWA. 1990. Use of song repertoire in intersexual and intrasexual contexts by male Red-winged Blackbirds. Behav. Ecol. Sociobiol. 27:123–128.

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

SMITH, W. J. 1994. Animal duets: forcing a mate to be attentive. J. Theor. Biol. 166:221–223.

SONNENSCHEIN, E. AND H-U. REYER. 1983. Mate-guarding and other functions of antiphonal duets in the Slate-coloured Boubou (*Laniarius funebris*). Zeit. Tierps. 63:112–140.

THORPE, W. H. 1972. Duetting and antiphonal singing in birds: its extent and significance. Behaviour, supplement 18:1–197.

WHITTINGHAM, L. A. AND R. J. ROBERTSON. 1994. Food availability, parental care and male mating success in Red-winged Blackbirds (*Agelaius phoeniceus*). J. Anim. Ecol. 63: 139–150.

———, A. KIRKCONNELL, AND L. M. RATCLIFFE. 1992. Differences in song and sexual dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoeniceus*). Auk 109:928–933.

———,———, AND ———. 1996. Breeding behavior, social organization and morphology of Red-shouldered (*Agelaius assimilis*) and Tawny-shouldered (*A. humeralis*) blackbirds. Condor 98:832–836.

WICKLER, W. 1980. Vocal duetting and the pair bond: I. Coyness and partner commitment. A hypothesis. Zeit. Tierps. 52:201–209.