

NEST DEPARTURE CALLS IN FEMALE SONGBIRDS¹

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Abstract. Females of at least 15 species of North American passerines give distinctive nest departure calls. These calls consist of a series of notes uttered while flying away from the nest. Less often, the call is given while flying to the nest. It is heard during nest-building, incubation, brooding, and nestling care. The behavior is found in emberizid finches and icterines in North America, and possibly muscicapids (Sylviinae) in Europe. It occurs almost exclusively in birds nesting in marshes or grasslands. Birds giving this call could incur a great cost if predators locate nests using these calls. Proposed benefits of calling include reduction of harassment by males, discouragement of settlement by females, promotion of anti-predatory vigilance by mates, advertisement of receptivity for copulation, and distraction of potential predators away from the nest. The reduction of harassment and increased vigilance hypotheses have the strongest support. The behavior is more common in species in which visibility of birds close to the ground is poor and in which the intra-sexual competition among males is intense which thus increases the risk that an already mated female will be mistaken for an intruding male.

Key words: Nest departure calls; female vocalization; nest behavior; mate harassment; songbirds.

INTRODUCTION

Songbirds are characterized by a diversity of vocalizations that serve specialized functions associated with breeding. Although most female vocalizations function similarly to those of males, some are unique to the female sex role (Dufty 1982, Hurly and Robertson 1984, Dickinson and Falls 1989, Yasukawa and Searcy 1982). This review describes one such call, the "nest departure call." Although its context and structure vary among species, in all cases the call makes the trip from the nest easily identified and the nest location easily determined, at least to human observers.

We restrict the definition of the nest departure call to a vocalization initiated the moment the bird leaves the nest in flight. The definition excludes some otherwise similar vocalizations, such as those both males and females of some species give when they are on the nest. This definition also excludes calls that females give after having left the nest, including alarm calls and contact notes given between pair members as they approach and depart the nest area.

In preparing this review, we surveyed the literature and corresponded with nearly fifty field workers to determine the taxonomic distribution of nest departure calls among passerines. Herein we report our findings, evaluate several possible adaptive explanations, and suggest further observations and experiments.

TAXONOMIC AND ECOLOGICAL CORRELATES OF SPECIES GIVING NEST DEPARTURE CALLS

Birds known to give the call at some stage in their nesting cycle are listed in Table 1. In North America, nest departure calls have been reported in icterines (*Agelaius*, *Xanthocephalus*, *Sturnella*, and *Quiscalus*), and emberizid finches (*Aimophila*, *Melospiza*, *Spizella*, *Ammodramus*, and *Passerulus*). The call also has been reported in two marsh-nesting species of old world warblers, the Great Reed Warbler (*Acrocephalus arundinaceus*), and the Sedge Warbler (*A. schoenobaenus*) (B. Leisler, pers. comm.). It appears, therefore, that nest departure calls may have evolved at least three times, and possibly as many as seven times in songbirds.

Although the number of taxonomic groups involved are small, their habitats are similar: Thirteen of the 15 species place nests in dense marshy (6), grassy (5), or shrubby (2) habitats. The two remaining species, both grackles, usually place

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their nests in trees adjacent to marshes, fields, or shrubs and spend considerable time foraging in such habitats.

Based on our review of the literature, correspondence with other workers, and field experience, we were unable to find examples of nest departure calls in other major taxonomic groups outside of Emberizinae and Icterines. We also failed to find examples among forest species. Our survey also revealed that the following related species apparently do not to give such a call: Bobolink (*Dolichonyx oryzivorus*), Dickcissel (*Spiza americana*), Northern Oriole (*Icterus galbula*), Brewer's Blackbird (*Euphagus cyanocephalus*), Clay-colored Sparrow (*Spizella pallida*), Lapland Longspur (*Calcarius lapponicus*), and Chestnut-collared Longspur (*C. ornatus*).

SOCIAL ORGANIZATION OF SPECIES GIVING NEST DEPARTURE CALLS

We categorized the social organization of species giving the call in two ways: mating system and characteristic nesting density. Mating systems were assigned as predominantly monogamous or polygynous based on whether more than approximately 20% of the males in a population are polygynous (Ford 1983). Species were classified as colonial (pairs have small nest territories); high density (non-colonial, all-purpose territories regularly less than 0.10 ha); and low density (all-purpose) territories. If high density occurs in only a portion of a breeding population (as in Red-winged Blackbird [*Agelaius phoeniceus*], Swamp Sparrow [*Melospiza georgiana*], Seaside Sparrow [*Ammodramus maritimus*], and Eastern Meadowlark [*Sturnella magna*]), we designate this as patchy.

Approximately half of the species giving nest departure calls are regularly polygynous (Table 1). This value is high when compared with the frequency of polygyny among all songbirds, but close to the expected proportion of polygyny in marsh and grassland nesting species (Verner and Willson 1966). Relatively high density and patchy dispersion characterizes species giving the nest departure call (Table 1): truly colonial (3 species), high-even (1), and high-patchy (8).

GEOGRAPHIC VARIATION IN CALL FREQUENCY

Geographic variation in frequency of call use is known for at least two species. Female Red-winged Blackbirds in an eastern Washington

population were found to give the call more frequently at all stages of the nesting cycle than in a western Washington population (Small and Boersma 1990). This difference was attributed primarily to population density differences, the eastern site having more compact territories and larger harem sizes.

Song sparrows (*Melospiza melodia*) typically do not give distinct nest departure calls (Nice 1943; Greenberg, pers. obs.). However, females on Mandarte Island and other localities around Puget Sound, British Columbia, do regularly give these calls. Again, population density may be a factor. The islands of Puget Sound are known for their extraordinarily high numbers of Song Sparrows, with territories on Mandarte Island averaging 0.03 ha (Tompa 1962) compared with 0.2–0.5 ha typical of other populations of Song Sparrow (Nice 1943).

CONTEXT OF THE NEST DEPARTURE CALL

Nest departure calls have been reported at all stages of the nesting cycle for different species (Table 1). Where information on nesting cycle stage was available (11 species), 91% of the species apparently use the call during nest building, incubation, and brooding. Females alone perform these duties in all but one species, the Brewer's Sparrow. It is unknown whether only one or both sexes give nest departure and arrival calls that have been heard (K. L. Peterson, pers. comm.).

The call's use during nestling feeding has been observed in 44% of nine species with reliable information about this stage. In contrast to other species, nest-departure calling has been reported for the later stages exclusively (brooding and feeding nestlings) in the Sharp-tailed Sparrow (*Ammodramus caudacutus*) (W. DeRagon, pers. comm.). Quantitative data on the call's frequency of use throughout different nesting stages are available for only the Red-winged Blackbird (Beletsky and Orians 1985, Small and Boersma 1990). Both studies found a sharp decrease from the early stages to the nestling stage. Neither study, however, distinguished between nestling stage trips that resulted in brooding versus feeding young. This distinction may be critical because departure calls given during the nestling stage are reported in only four species.

Nest "departure" calls are given uncommonly during flights to the nest. McDonald (1986) reported calling in 79% of 258 observed departures

TABLE 1. Species, habitat, predominant mating system, density, and breeding context of female North American songbirds giving nest departure calls.

Species	Habitat	Mating system ^a /density ^b	Breeding stage ^c			Reference
			Nb	Inc	Brd	
Botteri's Sparrow (<i>Aimophila botterii</i>)	Grassland	M/	+	+	+	E. A. Webb, pers. comm.
Brewer's Sparrow (<i>Spizella breweri</i>)	Shrub	M/				K. L. Peterson, pers. comm.
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	Grassland/marsh	M?/high patchy				J. B. Williams, pers. comm. N. T. Wheelwright, pers. comm. R. L. Smith 1959
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	Grassland	M/				
Sharp-tailed Sparrow (<i>Ammodramus caudacutus</i>)	Marsh	P/high patchy	-	-	+	J. S. Greenlaw, pers. comm. W. DeRagon, pers. comm. McDonald 1986
Seaside Sparrow (<i>Ammodramus maritimus</i>)	Marsh	M/high patchy	+	+	+	
Song Sparrow, Mandarte Isl. (<i>Melospiza melodia</i>)	Shrub	M/high patchy	+	+	+	J. N. M. Smith, pers. comm. A. L. E. Cassidy, pers. comm. Greenberg, pers. obs.
Swamp Sparrow (<i>Melospiza georgiana</i>)	Marsh	M/high patchy	+	+	+	
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	Grassland/marsh	P/high patchy	+	+	+	Orians and Christman 1968 Birks and Beletsky 1987 Small and Boersma 1990 Orians and Christman 1968
Tricolored Blackbird (<i>Agelaius tricolor</i>)	Marsh	M/colonial	+	+	+	T. E. Dickinson, pers. comm.
Eastern Meadowlark (<i>Sturnella magna</i>)	Grassland	P/high patchy	+	+	+	T. E. Dickinson, pers. comm.
Western Meadowlark (<i>Sturnella neglecta</i>)	Grassland	M/high even	+	+	-	
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)	Marsh	P/high patchy	+	+	+	Beletsky and Orians 1985
Great-tailed Grackle (<i>Quiscalus mexicanus</i>)	Small group	P/colonial	+	+	+	Kok 1971
Common Grackle (<i>Quiscalus quiscula</i>)	Small group	M/colonial	+	+	+	Wiley 1976c

^a M = predominantly monogamous; P = predominantly polygynous, as defined by Ford (1983).

^b High = high density; colonial, patchy, or even dispersal (see also text).

^c Nb = nest building; inc = incubating; Brd = brooding; Fdg = feeding nestlings.

and only 14% of 114 approaches ($\chi^2 = 243$, $P < 0.001$). Greenberg (pers. obs.) found that Swamp Sparrows call upon all departures, but that calling is extremely rare for arrivals. This is at least partly due to the differences in typical locomotory patterns. Departing female Swamp Sparrows fly from the nest and call in one, two, or three brief series, depending upon how many short flights are taken before diving into the marsh vegetation. Females return to the nest by sneaking silently through the vegetation. A similar difference in departures and arrivals was observed in meadowlarks by Dickinson (pers. comm.). Females from different populations of Red-winged Blackbirds vary considerably in their tendency to give arrival calls (Beletsky and Orians 1985, Dickinson 1987, Yasukawa 1989, Small and Boersma 1990).

Although not strictly fitting our definition, female calls similar or identical to the nest departure call are given during flights between successive foraging sites in at least two species (Sharp-tailed Sparrows [J. S. Greenlaw, pers. comm.] and Seaside Sparrows [McDonald, pers. obs.]). The degree to which the nest departure call is used in contexts other than nest-tending trips appears to differ among species. In female Red-winged Blackbirds the *chit* or Type I song is used most commonly during nest departures, but is also given when the female is on or near the nest, usually in response to her mate singing upon re-entry into the territory (Yasukawa 1989, Small and Boersma 1990). Female Red-winged Blackbirds have an alternative vocalization (*teer*) for aggressive interactions with other females. This note is occasionally incorporated into the ending of the nest departure call. The nest departure chatter of Great-tailed Grackles (*Quiscalus mexicanus*) is also likely to be used in female-female encounters (Kok 1971). Swamp Sparrows give individual chips during aggressive encounters or predator mobbing, but never in a rapid series as is heard in the nest departure call (Greenberg, pers. obs.). Seaside Sparrows, however, commonly use a call (*tchi*) similar to the nest departure call in both aggressive and intra-pair interactions (McDonald, pers. obs.). The nest departure calls of meadowlarks (Lanyon 1957, Dickinson, pers. comm.) are also used in intra-pair interactions. Thus, the call, or portions of this composite vocalization, may be used in different contexts. Its apparent variation may be artifactual, because for many species in Table 1, the call repertoire has not been studied in detail.

What we have designated as the nest departure call may very well be a mixture of calls with different functions.

RESPONSE TO CALLS BY CONSPECIFICS

Female Seaside Sparrows silently departing their nests are frequently chased by males. If chased females utter the *tchi* nest departure call in flight, however, the males usually swerve away and land (Greenlaw, pers. comm.). Similarly, McDonald (1986) found 70% of the 61 silent female Seaside Sparrow departures were chased by mates, but only 24% of the 289 vocal departures were challenged ($\chi^2 = 50.3$, $df = 1$, $P < 0.0001$, McDonald 1986). In a comparable study, female Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) were chased more frequently by their mates when they were silent (Gori, in Beletsky and Orians 1985). Similar results were noted for Red-winged Blackbirds (Birks and Beletsky 1987, Small and Boersma 1990). However, Small and Boersma detected a significant difference between silent and noisy females being chased by males in only their denser eastern Washington population. Neither they nor Yasukawa (1989) were able to observe many inter-mate interactions in study populations of lower density. In contrast, Eastern and Western (*Sturnella neglecta*) Meadowlark males were often observed to join and consort closely with vocal females after they left the nest (Dickinson pers. comm.).

Responses by other females to the nest departure call were examined by Beletsky and Orians (1985). They found that females did not tend to synchronize their departure from the nest, nor did they leave their nest when stimulated by a playback of the nest departure *chit*.

ACOUSTIC STRUCTURE OF NEST DEPARTURE CALLS

Nest departure calls of different species show structural similarities (Fig. 1). The calls also have acoustical features known to facilitate locating vocalizing birds, including broad-band frequency spectrums, high sound energy represented at the low- to mid-frequencies, short note duration with distinct onset and offset, and repetitiveness (Dooling 1982, Marler 1957). Nest departure calls are given in a series that not only further assists in locating the calling bird but also helps define the trajectory of the bird's flight path.

Although temporal patterns of most nest departure calls are simple and regular, some are more complicated. The Red-winged Blackbird

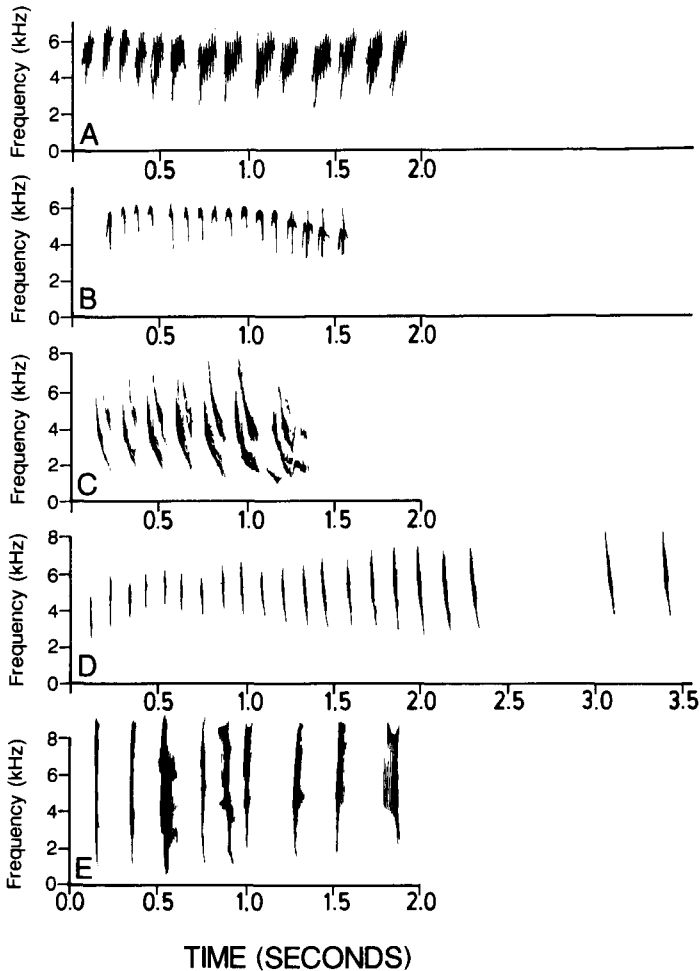


FIGURE 1. Audiospectrograms of representative female nest departure calls. A. Eastern Meadowlark; B. Red-winged Blackbird; C. Scott's Seaside Sparrow; D. Swamp Sparrow; E. Song Sparrow (Mandarte Island).

series of *chit* notes occasionally terminates with *teer* notes. Song Sparrow nest departure calls may consist of heterogeneous elements, beginning at a low intensity and increasing to a crescendo of chattering and wailing notes (Nice 1943). The Swamp Sparrow rhythm is often syncopated, ending with one or two accented chips (Greenberg, pers. obs.). This irregular rhythm may render the call more discernable over the highly regular song of sympatric Swamp Sparrows and Long-billed Marsh Wrens (*Cistothorus palustris*) songs.

POSSIBLE COSTS OF NEST DEPARTURE CALLS

Females giving nest departure calls may incur the cost of attracting the attention of predators

to themselves and to their nests. An experiment on Red-winged Blackbirds by Yasukawa (1989) tested this apparent cost. He placed mock nests in a marsh and found that predation at nests accompanied with playback of nest departure *chit* calls was five times greater than at mock nests with no playback. Curiously, the nests were actually depredated at night by mink (*Mustela vison*). Yasukawa observed mink active during the day, and he suggested that these mammals locate the nest using the nest departure call and then return at night to avoid mobbing.

Some of the details of methods used in Yasukawa's study make it difficult to evaluate how the experimental effect relates to that of the actual nest departure calling. For example, the *chit* calls were broadcast at an artificially regular rate

which could be more easily traced than the irregular bursts of chits given by departing females under non-experimental conditions. On the other hand, the actual presence of a bird flying from the nest might further increase nest conspicuousness to visually oriented predators.

ADAPTIVE HYPOTHESES FOR NEST DEPARTURE CALLS

The following five hypotheses have been proposed as benefits of nest departure calling: 1) prevention of harassment by mates and other males; 2) advertisement of female receptivity for copulation; 3) discouragement of additional female settlement on territory; 4) encouragement of male vigilance against predators; 5) distraction of predators away from nest. We discuss these hypotheses, both in terms of supporting experimental and observational data, and their ecological and behavioral contexts.

Prevention of harassment by mates and other males. Several workers (Beletsky and Orians 1985; McDonald 1986; Dickinson 1987; J. S. Greenlaw, pers. comm.) have argued that female nest departure calls may function to reduce the possibility of attack by mates or, secondarily, other males. The harassment need not be sexually-oriented, as suggested by Beletsky and Orians (1985). It could also result from the male's low threshold for an aggressive response toward any potential conspecific, thus becoming a non-adaptive by-product of an otherwise adaptive behavior (McDonald 1986, Small and Boersma 1990). This response can be triggered, even in moderately dimorphic species, when a female suddenly leaves grass or shrubs and enters the view of her vigilant mate. The "wing flutter display" of male Wilson's Phalaropes (*Phalaropus tricolor*) may be an analogous non-vocal behavior that appears to deter mate harassment (Colwell and Oring 1988).

A specific prediction of this harassment prevention hypothesis is that females uttering the call are less likely to be challenged than non-vocal females. The prediction is supported by observations that males tend to chase silent females in Seaside Sparrows (Greenlaw, pers. comm.; McDonald 1986) and blackbirds (Gori, unpubl.; Birks and Beletsky 1987; Small and Boersma 1990). The hypothesis is also consistent with the decline in use of the call during nestling feeding—a time when males and females are often in more continuous acoustic or visual con-

tact. The harassment hypothesis is compatible with the habitat distributions and characteristic social systems of species known to give the call. These species nest in dense vegetation and tend to have compact, patchy territories where male-male interactions are relatively frequent. The combination of a high level of aggressive interactions and poor visibility around the nest would favor females developing acoustic signals that discourage harassment arising from mistaken identification by mates.

A potential problem with the harassment prevention hypothesis is that not only would the resident female avoid harassment, but, unless calls are individually distinguishable, an interloping male could imitate the female and thus reduce the probability of his being attacked. If such interloping did occur, this should rapidly select for imitative calls in males which would, in turn, reduce the value of nest departure calls for females. The possibility of such deception may explain why some males join departing females—to check that she really is his mate. It may also explain the acoustic and visual conspicuousness of the call coupled with flight from the nest: because the trajectory of the performance is easy to follow, the male may learn to associate the call with a particular part of his territory, and he could be entrained not to attack at that location. A prediction that can be tested experimentally is that resident males should respond more aggressively to nest departure calls broadcast from an inappropriate part of the territory.

Fertility signaling and mate coordination hypotheses. Two hypotheses have been proposed suggesting that the nest departure call functions primarily in mate choice. One of these, the fertility advertisement hypothesis (Montgomery and Thornhill 1989), proposes that females give loud calls to attract potential mates, incite male-male competition, and hence allow females to choose a dominant mate. Since a major prediction would be that calls should be used mostly when pairing commences, a serious problem with this hypothesis is that nest departure calling is not restricted to solely the early parts of the nesting cycle when females are receptive to copulations.

The other hypothesis suggests that nest departure calls could be used to coordinate activities and strengthen pair bonds (Wiley 1976a, 1976b, 1976c). Again, the prediction is that the

call should be most often used during pair formation and copulation when "mate coordination" activities are especially prevalent. This hypothesis seems to generate few other predictions regarding the behavioral and ecological contexts of the call. For example, it is not clear why such coordinating calls should occur upon nest departure, versus any flight. Nor does it follow that calling should occur primarily in grassland or marsh nesting species that nest at high densities, unless pair bonds in these habitats require repeated confirmation.

Discouragement of settling of additional females. Small and Boersma (1990) argued that the nest departure call functions, in part, to advertise the presence of a settled female to other females. Their primary evidence is that calling decreases through the nesting cycle, as fewer females attempt to settle on territories. However, other factors change as well, such as the amount of time a female spends on the nest and out of contact with her mate. It would be difficult to use the female discouragement hypothesis to explain the rapid shift from calling to non-calling when females stop brooding nestlings. Furthermore, the female discouragement hypothesis would be more appropriately tested if the calling were compared for nests at similar stages of the cycle but at different calendar dates. Another argument against this hypothesis is that in polygynous Yellow-headed Blackbird females, settling patterns are independent of each other, and females do not influence one another's reproductive success (Lightbody and Weatherhead 1987). Furthermore, although there is some evidence that females within a Red-winged Blackbird harem space out their nesting activity (Small and Boersma 1990), the primary aggressive call used is the Type II song or *teer* note, and not the nest departure *chit* note. Finally, this hypothesis seems less appropriate for the numerous predominantly monogamous species that give nest departure calls.

Promotion of vigilance against predators. Males may help protect nests and foraging females from predators through vigilance, alarm calling and mobbing. The female's nest departure call could play a dual role of alerting her mate to an unprotected nest, as well as to her own exposure while off the nest. Yasukawa (1989) found that male Red-winged Blackbirds more actively defended artificial and real nests accompanied with *chit* call playback than those without *chit* call

playback. He also found that females with successful nests had responded to their mate's song with *chit* calls more often than females with failed nests.

However, neither Beletsky and Orians (1985) nor Small and Boersma (1990) were able to show that female Red-winged Blackbirds give nest departure calls more often when males were nearby or prior to trips out of the territory. Furthermore, there is no direct evidence that males play a role in protecting females or preventing nest predation. The tendency for male meadowlarks and other species to consort closely with foraging females during incubation, however, suggests a role for male vigilance (Dickinson, pers. comm.).

Predator distraction hypothesis. Females that call while leaving the nest may immediately attract attention to themselves and thus away from the nest. However, the details of the nest departure call do not support this explanation. If the call functions to distract predators, then one would expect it to be given during all stages of the nesting cycle, and perhaps most frequently and vigorously when there are more valuable nestlings. Yet females of most species either quit calling or decrease call frequency during the nestling stage. Secondly, one would expect the utterance of the call to be highly associated with the female's perception of a predator in the vicinity. However, females usually fail to give a nest departure call when flushed from the nest. Finally, some of these species (e.g., meadowlarks, Dickinson, pers. comm.) have other well developed distraction displays.

CONCLUSIONS AND FUTURE STUDY

Nest departure calls have been described for at least 17 species of songbirds in the families Icteridae, Emberizidae, and Muscicapidae. Despite its limited distribution across major taxa, the call may have evolved independently at least several times. Alternatively, nest departure calling may represent a previously available call within the females' repertoires that is elicited in a nest-related context.

In any event, the species known to give this call are clearly associated with dense grassy or shrubby habitats. Nearly all (15 of the 17 species) breed in such habitat, which tends to be dominated by sparrows and blackbirds in the new world, and warblers in the old world. These open habitats have attributes that, along with the ecological and social contexts cited above, suggest a

primary function of nest departure calls is to reduce the probability of males harassing females when they are off the nest. An additional hypothesis, that females are alerting males of their continued attendance at the nest and thereby insuring his vigilance, has also received experimental support. The possibility that female nest departure calls function primarily to incite male competition during periods of sexual receptivity does not seem to be appropriate for calls uttered mainly following clutch completion. The hypothesis that calls coordinate pair activity by strengthening the pair bond is too general to explain the specific contextual correlations associated with the nest call. Two additional hypotheses, distraction of predators and discouragement of additional female settlements, also seem inconsistent with the contextual and temporal correlations reported for most species giving the call.

It is clear, however, that there are variable circumstances associated with the call's utterance and the frequency with which it is given. It is possible that nest departure calls may have several functions, and that the relative importance of these functions may differ geographically and among taxa.

Considerably more observations are needed on the details of the nest calling behavior, as related to the natural history of species giving this call. Much of the comparative analysis presented in this paper is tentative, awaiting a more complete survey in other taxa. The geographic variation suggested in Red-winged Blackbirds and Song Sparrows can be explored to test adaptive hypotheses. Although the occurrence of the nest departure call has been reported for old world warblers, it is poorly documented outside of North America. Surveys in other biogeographic realms could test the ability to generalize ecological correlates seen in new world birds.

Since details on the frequency and context of the calling have been quantified for only a few species, distinguishing between functional hypotheses will depend on more rigorously collecting data on the call's characteristic contexts. Additional experiments could test the influence of location within the territory, individual mate recognition, male response to released non-calling females, and the reaction of males to departure call playback during different stages of the breeding cycle.

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LITERATURE CITED

- BELETSKY, L. D. 1983. Aggressive and pair-bond maintenance songs of female Red-winged Blackbirds (*Agelaius phoeniceus*). *Z. Tierpsychol.* 62: 47-54.
- BELETSKY, L. D., AND G. H. ORIAN. 1985. Nest-associated vocalizations of female Red-winged Blackbirds, *Agelaius phoeniceus*. *Z. Tierpsychol.* 69:329-339.
- BIRKS, S. M., AND L. D. BELETSKY. 1987. Vocalizations of female Red-winged Blackbirds inhibit sexual harassment. *Wilson Bull.* 99:706-707.
- COLWELL, M. A., AND L. W. ORING. 1988. Wing fluttering display by incubating male Wilson's Phalaropes. *Can. J. Zool.* 66:2315-2317.
- DICKINSON, T. E. 1987. The vocal behavior of female Red-winged Blackbirds *Agelaius phoeniceus*. Ph.D. diss., Univ. Pennsylvania, Philadelphia, PA.
- DICKINSON, T. E., AND J. B. FALLS. 1989. How Western Meadowlarks respond to simulated intrusions by unmated females. *Behav. Ecol. Sociobiol.* 25: 217-225.
- DOOLING, R. J. 1982. Auditory perception in birds, p. 95-130. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, Vol. 1. Academic Press, New York.
- DUFTY, A. M. 1982. Response of Brown-headed Cowbirds to simulated conspecific intruders. *Anim. Behav.* 30:1043-1052.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds, p. 329-356 *In* R. F. Johnston [ed.], *Current Ornithology*, Vol. 1. Plenum Press, New York.
- HURLY, T. A., AND R. J. ROBERTSON. 1984. Aggressive and territorial behaviour in female Red-winged Blackbirds. *Can. J. Zool.* 62:148-153.
- KOK, O. B. 1971. Vocal behavior of the Great-tailed Grackle (*Quiscalus mexicanus prosopidicola*). *Condor* 73:348-363.
- LANYON, W. E. 1957. The comparative biology of meadowlarks (*Sturnella*) in Wisconsin. *Publ. Nuttall Ornithol. Club* 1:1-67.
- LIGHTBODY, J. P., AND P. J. WEATHERHEAD. 1987. Interactions among females in polygynous Yel-

- low-headed Blackbirds. *Behav. Ecol. Sociobiol.* 21: 23-30.
- MARLER, P. 1957. Specific distinctiveness in male communication signals of birds. *Behaviour* 11:13-39.
- McDONALD, M. V. 1986. The ecology and behavior of Scott's Seaside Sparrow. Ph.D.diss., Univ. Florida, Gainesville, FL.
- MONTGOMERIE, R., AND R. THORNHILL. 1989. Fertility advertisement in birds: A means of inciting male-male competition? *Ethology* 81:209-220.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow II. *Tran. Linn. Soc. of New York. American Museum Natural History*, NY.
- ORIAN, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed blackbirds. *Univ. Calif. Pub. Zool.* 84:1-81.
- SMALL, M. P., AND P. D. BOERSMA. 1990. Why female Red-winged Blackbirds call at the nest. *Wilson Bull.* 102:154-160.
- SMITH, R. L. 1968. *Ammodramus savannarum* (Gmelin) Grasshopper Sparrow, p. 725-745. In O. L. Austin, Jr. [ed.], *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies*. Smithsonian Institution Press, Washington, DC.
- TOMPA, F. S. 1962. Territorial behavior: The main controlling factor of a local Song Sparrow population. *Auk* 79:687-697.
- VERNER, J., AND M. F. WILLSON. 1966. The influence of habitat on the mating systems of North American passerine birds. *Ecology* 47:143-147.
- WILEY, R. H. 1976a. Communication and spatial relationships in a colony of Common Grackles. *Anim. Behav.* 24:570-584.
- WILEY, R. H. 1976b. Affiliation between the sexes in Common Grackles. I. Specificity and seasonal progression. *Z. Tierpsychol.* 40:59-79.
- WILEY, R. H. 1976c. Affiliation between the sexes in Common Grackles. II. Spatial and vocal coordination. *Z. Tierpsychol.* 40:244-264.
- 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.
- YASUKAWA, K., AND W. A. SEARCY. 1982. Aggression in female Red-winged Blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* 11:13-17.