

## A CONTEXTUAL ANALYSIS OF TWO SONG VARIANTS IN THE BOBOLINK

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**ABSTRACT.**—Male Bobolinks (*Dolichonyx oryzivorus*) sing two variants of primary song, with the shorter beta variant being a derivative of the longer alpha variant. The beta song is sung most frequently during territory boundary disputes and at times of day and season when territory conflicts are most intense. The alpha song is sung most frequently during preterritorial displays, when unmated females are in the area, and during courtship. The proportion of song types given during courtship progressively shifts toward more alpha songs from day 1 to day 4 of the mating process. During circle flights, which are directed specifically toward females, alpha songs are given almost exclusively. Hence, the beta song apparently conveys a more aggressive message than the alpha song.

Further analysis shows that length of song sequences (i.e., degree of fragmentation or compounding of songs) is associated with intensity of the signal.

Analyses of the structural differences between the two song variants and the patterns of song fragmentation lead to several predictions regarding the meaning of particular song syllables. Present evidence indicates that the introductory notes convey information about individual identity, possibly species identity, and song type identity. The next whistled segment apparently conveys information that serves to attract the attention of females, while the long warbled syllables that comprise much of both song types convey primarily an aggressive signal.

Several hypotheses regarding the evolution of multiple song types are discussed in light of the data for Bobolinks. The Beau Geste and status signalling hypotheses do not seem applicable to this species. The significance of aggressive behavior during courtship is also discussed.

The importance of primary song as a means of defending territories and attracting mates has been apparent since Moffat (1903) and Howard (1920) first documented territoriality in birds (see Thorpe 1961, Armstrong 1963). Primary song can be interpreted as a persuasion signal (after Hamilton 1973), designed either to repel competing males or to attract prospective mates, but the manner by which song behavior fulfills those functions is only poorly understood.

Most functional analyses of territorial song have been interpreted within the framework of motivation theory or in terms of information transfer (e.g., Andrew 1961, Marler 1961, Smith 1969a, Thorpe 1972). Few attempts have been made to understand how the design features of song behavior enhance reproductive success. Although many evolutionary analyses of song behavior have been concerned with how songs maintain reproductive isolation (e.g., Dilger 1956, Marler 1957, 1960, Borror 1961, Falls 1963, 1969, Gill and Lanyon 1964, Konishi 1970, Emlen 1972, Shiovitz 1975, Boughey and Thompson 1976), few have considered how songs achieve their functions of territory defense and mate attraction. Perhaps that is because the direct reproductive conse-

quences of song behavior are difficult to measure. Nevertheless, the problem can be approached by comparing the design features of songs with predictions derived from a priori theory (see, for example, Krebs 1977a, b, Krebs et al. 1978, Smith and Reid 1979, Yasukawa 1981, Yasukawa et al. 1981).

Many passerine birds sing more than one type of primary song, but the function of multiple song types is not yet clear and probably differs among species. One hypothesis (the Beau Geste hypothesis) is that multiple song types allow territorial males to increase the apparent density of territory residents, thereby discouraging nonterritorial males from seeking entry to the local area (Krebs 1977a, 1978). Several predictions drawn from this hypothesis are supported by data from Great Tits (*Parus major*) and Red-winged Blackbirds (*Agelaius phoeniceus*; Krebs 1977b, Krebs et al. 1978, Yasukawa 1981). A second hypothesis is that larger song repertoires indicate higher competitive ability or greater reproductive experience, thereby making males with larger repertoires less likely to be challenged by competing males or more successful in attracting females (Yasukawa 1981). Repertoire size is correlated with the pairing success of male

Red-winged Blackbirds, but the correlation seems to result indirectly from the ability of males with larger repertoires to control better territories (Smith 1976, 1979, Yasukawa et al. 1981). Similarly, larger repertoire size in Northern Mockingbirds (*Mimus polyglottos*) is correlated with larger territory size and not directly with earlier pair formation (Howard 1974).

Both the Beau Geste hypothesis and the status signalling hypothesis imply that each of several song types in a repertoire conveys identical information, with repertoire size rather than functional differentiation of song types being the important consideration. However, in many species different song types do convey different information or at least are associated with different functional contexts. Distinctively different song types either may be associated with territory defense and mate attraction, as in wood warblers and certain other birds (Smith 1959, Morse 1967, 1970, Beason and Franks 1974, Lein 1978, Nolan 1978, Kroodsma 1981), or they may involve more subtle functional differences (e.g., Ficken and Ficken 1967, Smith 1969b, 1970). A first step in understanding the evolution of multiple song types, therefore, is to determine what functional differentiation, if any, is associated with the various song types in a species' repertoire.

My purpose here is to present a contextual analysis of the two distinctive song types sung by male Bobolinks (*Dolichonyx oryzivorus*). The two song types are used in both territorial and courtship contexts. They are given variously as partial songs (i.e., fragments of full songs), as complete songs, or as compound songs (i.e., full songs with additional songs or song fragments appended to the end in a continuous stream). My research on Bobolink song was carried out as an adjunct to my studies of Bobolink polygyny, but the complexity of Bobolink song makes it interesting in itself. I conducted the study mainly with the intent of identifying possible differences in the meaning (as defined by Smith 1965) of the two song types, along with the communicatory significance of song fragmentation and compounding. Nevertheless, although my data were collected before the above-mentioned hypotheses about multiple song types had been published, they have useful implications for future analyses.

#### DESCRIPTION AND SYMBOLIC REPRESENTATION OF BOBOLINK SONG

The primary song of Bobolinks has been described by Bent (1958) as "a bubbling delirium of ecstatic music" and by Mathews (1921) as

"a mad, reckless song-fantasia, an outbreak of pent-up, irrepressible glee." Understandably, it is therefore difficult to capture all details of Bobolink song in a simple coding system. Nevertheless, the particular attributes of the local song dialect of Bobolinks breeding in southeastern Oregon, where I worked, proved more amenable to symbolic coding than any Bobolink songs that I have heard elsewhere. This circumstance allowed me to analyze the contexts associated with a very large number of songs without having to resort to sophisticated electronic equipment (which was largely unavailable to me).

The two song types rendered by male Bobolinks are variants of a single song. The alpha ( $\alpha$ ) song sounds something like "Puck puck pi, deedla eh ah, eeee-ew, d-t-d-t dee," rapidly warbled gurgling notes (of variable duration), "ew." The beta ( $\beta$ ) song sounds something like "Pete-n pete-n d-t-d-t dee," rapidly warbled gurgling notes (of variable duration), "ew." In some individuals, an additional note "Der" is included at the beginning of the song. The  $\alpha$  and  $\beta$  songs are typically characterized by differing introductory notes, although some males use the same notes ( $\alpha$  type or a "hybrid" combination of  $\alpha$  and  $\beta$  types) for both song variants. The  $\beta$  song also lacks the interior syllables (i.e., "deedla eh ah eeee-ew") of the  $\alpha$  song. Otherwise the two song types are quite similar, with the  $\beta$  song evidently being a shortened derivative of the  $\alpha$  song (Fig. 1).

To analyze Bobolink song behavior, I devised a coding system to keep records of the songs given in each behavioral context. In this system the song type is indicated by an  $\alpha$  or  $\beta$  symbol. For incomplete renditions of a song type or for compound songs, that portion sung by the bird is indicated by a second symbol that represents the last song syllable given. (The term "syllable" refers here to a discrete, identifiable portion of the full song and marks a clear change of cadence or tempo as heard by a human observer.) These symbols and their meanings are given in Table 1.

The introductory notes of both song types vary considerably among males but sound stereotyped for each individual. Although the degree of stereotypy was not confirmed with sonographic analysis, I was able to recognize many individual males on that basis alone. The identity of such males could be confirmed independently by unique color band combinations and unique plumage characteristics (see Wittenberger 1978). Other parts of the songs also vary, but not as frequently or as noticeably. A few males left out the "eh ah" syllables of the  $\alpha$  song. One male gave two nasal-sounding descending whistles that sounded like harsh "ew"

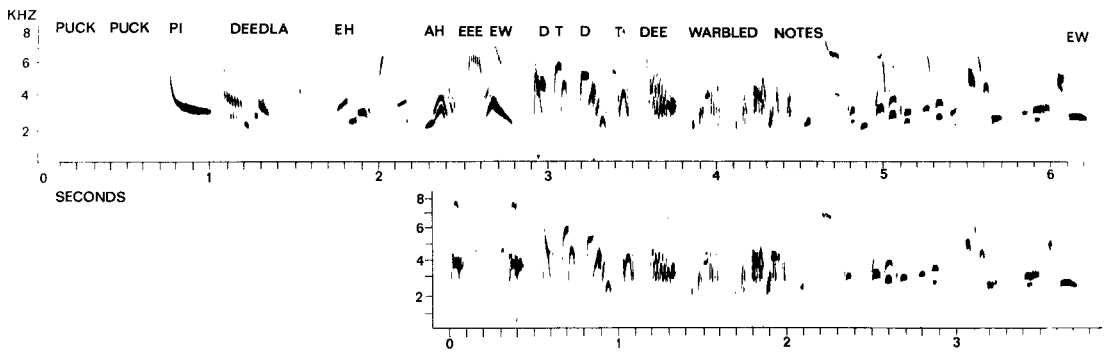


FIGURE 1. Sound spectrograms of the alpha (top) and beta (bottom) song types given by male Bobolinks in Oregon. A phonetic transcription of the alpha song is included. The beta song type begins with different introductory notes and lacks the interior syllables of the alpha song type but is otherwise identical (see text).

notes in place of the “eeee-ew” syllables of his  $\alpha$  song. Some males gave high-pitched, distorted, or garbled songs that differed markedly from those of typical males. The  $\alpha$  and  $\beta$  song types of these males were barely recognizable as such because they resembled the “subsongs” given occasionally by caged juvenile males during late summer and early autumn. Among banded males, only yearlings had such songs during the breeding season, but six of eight banded yearlings in 1975 sang normal songs (Wittenberger 1978).

Most partial songs or song fragments began

with the introductory notes and were given in the normal sequence of syllables. However, on rare occasions very excited males skipped syllables or switched from one song type to the other in mid-song. Also, fragments were sometimes begun in the middle and then terminated after several syllables had been given, after the song had been completed, or in the middle of a continuation song appended to the end of the initial song fragment. I refer to such fragments, which are characterized by the omission of introductory notes, as “interior fragments.”

Compound songs consisted of a complete  $\alpha$  or  $\beta$  song with additional complete songs or song fragments appended to them in a continuous stream. They began with either the  $\alpha$  or  $\beta$  sequence, but continuation beyond the initial song almost invariably consisted of  $\alpha$  songs or song fragments. Only 2 of 1,187 compound  $\beta$  songs consisted of two  $\beta$  songs in succession, and none of 341 compound  $\alpha$  songs consisted of an  $\alpha$  song followed by a  $\beta$  song. The introductory notes and “eh ah” syllables are usually, but not always, omitted from songs and song fragments appended to the initial songs of compound song sequences given during flight. Flight songs aurally resemble those given from perches, and they are also indistinguishable from perched songs by sonographic analysis (Avery and Oring 1977).

Several song attributes were not quantified despite their probable importance. Songs varied markedly in loudness and, to a lesser degree, in tempo. Singing rates were also highly variable, depending upon time of day, context, and peculiarities of the individual male.

## STUDY AREA AND METHODS

The study was conducted during the 1975 and 1976 breeding seasons at the Malheur National Wildlife Refuge, south of Burns, Oregon.

TABLE 1. The symbols used to represent components of Bobolink primary song, along with some commonly coded song sequences, and a phonetic transcription of the song components or song sequences corresponding to them.

Symbol	Song component and phonetic transcription
$\eta$ (nu)	Introductory notes (“Puck puck pi” or “Pete-n pete-n”)
$\omega$ (omega)	Interior syllable of $\alpha$ song (“deedla”)
@	Interior syllable of $\alpha$ song (“eh ah”)
$\Delta$ (delta)	Interior syllable of $\alpha$ song (“eeee-ew”)
+	“d-t-d-t dee” syllable of either song
'	Song was abruptly terminated part way through warbled syllables
Commonly coded song sequences	
$\alpha\eta$	“Puck puck pi”
$\alpha\omega$	“Puck puck pi deedla”
$\alpha@$	“Puck puck pi deedla eh ah”
$\alpha\Delta$	“Puck puck pi deedla eh ah eeee-ew”
$\alpha\Delta+$	“Puck puck pi deedla eh ah eeee-ew d-t-d-t dee”
$\alpha'$	Alpha song terminated abruptly during warbled syllables
$\alpha$	Entire alpha song
$\beta\eta$	“Pete-n pete-n” or “Der pete-n pete-n”
$\beta\eta+$	“Pete-n pete-n d-t-d-t dee”
$\beta'$	Beta song terminated abruptly during warbled syllables
$\beta$	Entire beta song

The study area consisted of a wet grassy meadow on irrigated land (for details see Wittenberger 1978, 1980). All data were collected in the best available habitat on the refuge, as identified by the order in which habitats were occupied by both males and females, population density, and prevalence of polygyny (see Wittenberger 1978, 1980). Individual identities, locations of territory boundaries, number of mates, dates of pair formation, and breeding chronologies were known for all resident males studied.

Observations were made from an hour before dawn to mid-morning, beginning on the day when males first arrived on the study area and continuing until nearly all females in the population had mated. Most observations of territorial advertisement song were made without the aid of a blind, but most observations of courtship behavior were made from a blind. I dictated my coded observations into a portable tape recorder, a procedure that enabled me to watch singing males continuously and to record rapid behavioral events without interruption. For each observation session the date, male identities, and contexts as defined below were recorded. Times were recorded frequently, whenever pauses in male behavior permitted. The two sound spectrograms in Figure 1 were made with a Kay Electric Sonagraph 66A, using the wide band selector. They were made from tape recordings of some representative songs that were recorded with a Gibson parabola and Uher 4000 Report L tape recorder at a speed of 19 cm/s.

## RESULTS

### SONG BEHAVIOR IN PRETERRITORIAL AND TERRITORIAL CONTEXTS

I analyzed song behavior of males in the following preterritorial and territorial contexts:

*Flight.* A perched male taking flight in response to a male intruding onto his territory, approaching his territory boundary, or flying overhead.

*Preterritorial dispute.* Three or more perched males singing and displaying toward one another within a preterritorial flock.

*Solo song bout.* A territorial male singing toward no particular male or female from a prominent perch or from the ground within his territory.

*Countersinging.* Two neighboring males singing more or less alternately toward each other across a territory boundary from distances of 10–60 m.

*Boundary dispute.* Two neighboring territorial males or an intruding nonterritorial male and a territorial male singing in close proximity and exhibiting various postural displays

TABLE 2. Percent frequency that  $\alpha$  and  $\beta$  song variants were given by male Bobolinks in territorial contexts. Superscripts indicate significant differences across rows, with  $a > b > c$ ,  $\chi^2$ ,  $P < .05$ .

	Pre-territorial disputes	Counter-singing bouts	Solo bouts	Boundary disputes
No. of songs	469	528	8,011	1,615
$\alpha$ variant	60.3 <sup>a</sup>	54.0 <sup>b</sup>	47.0 <sup>c</sup>	44.5 <sup>c</sup>
$\beta$ variant	39.7 <sup>a</sup>	46.0 <sup>b</sup>	53.0 <sup>c</sup>	55.5 <sup>c</sup>

associated with "parallel walks" (as described by Martin 1967) along a territory boundary.

The entire song sequences given by males during flight were difficult to record because songs are given rapidly and often end out of earshot. However, the first songs given by males upon taking flight were usually  $\alpha$  songs. Of 288 songs recorded, 94.1% were of the  $\alpha$  type. I did not discern any variation in the prevalence of  $\alpha$  songs in relation to the stimulus provoking flight, but I did not test this possibility quantitatively. Males flying toward an intruder might be expected to signal a strong willingness to defend their space, but the evidence presented below does not indicate that  $\alpha$  songs are especially aggressive. Indeed, the evidence indicates just the opposite.

I did not include the conspicuous "song-flight" displays of male Bobolinks (see Martin 1967) in the above analysis, although these displays were usually also accompanied by long sequences of compound  $\alpha$  songs. Martin (1967) interpreted song-flights as territorial advertisement displays, but the high frequency of  $\alpha$  songs during these displays is in marked contrast to perched territorial songs (see below). Most song-flights that I observed were given when I was not concealed in a blind, as were those observed by Martin. When I observed Bobolinks from a blind, I rarely saw song-flights except when raptors or other avian predators were flying overhead. At such times all males in the vicinity took flight and displayed in concert, suggesting that song-flights are actually a response to potential predators. Song-flights do not represent true mobbing behavior, however, as they are not oriented toward the predator. Bobolinks rarely mobbed predators in the fashion of colonial blackbirds. In four summers of study, I saw only one instance of mobbing: an attack by two males on an American Kestrel (*Falco sparverius*) that had attempted to land on a male's territory during the incubation period of that male's only nest.

The proportion of  $\alpha$  and  $\beta$  songs given by perched males varied significantly with context (Table 2).  $\beta$  songs were given more frequently in contexts where territorial males were

more directly threatened by other males, suggesting that they signalled a higher level of aggressiveness (i.e., a stronger propensity to defend the space) than did  $\alpha$  songs. The frequency of  $\beta$  songs was lowest during preterritorial disputes, when males were not yet defending territories, and highest when an intruding male was directly challenging a territory owner during a boundary dispute. However,  $\beta$  songs were given as often in solo song bouts as they were in boundary disputes, even though males should not be as threatened while singing alone.

The higher frequency of  $\beta$  songs in solo bouts than in countersinging bouts suggests that territorial males are less threatened by neighbors than by unknown potential aggressors. Playback experiments with other species show that territorial males typically give weaker or less aggressive response to neighboring males than to strangers, which supports such an interpretation (see Weeden and Falls 1959, Falls 1969, Beer 1970, Emlen 1971, Goldman 1973, Falls and McNicholl 1979). However, in my study the difference may have stemmed instead from a temporal bias in sampling intensity. Data for countersinging males were collected after dawn and before males began acquiring mates, while data for solo bouts were collected at all times of morning throughout the season. When I compared only data collected after dawn, to eliminate temporal biases, the observed difference disappeared. During the period when data on countersinging were collected, 50.7% of 965 songs were of the  $\alpha$  type, compared to 54.0% of 528 songs for countersinging bouts.

#### TEMPORAL ANALYSIS OF SOLO SONG BOUTS

I further examined the hypothesis that  $\alpha$  and  $\beta$  song types reflect differing levels of aggressiveness by analyzing seasonal and diurnal changes in their frequencies within a particular context. Threats of intrusion and chances of attracting mates vary with both season and time of day. These variations should lead to predictable changes in the frequency that each song type is given if  $\beta$  songs really are more aggressive than  $\alpha$  songs. The frequency of  $\beta$  songs should increase when territories are most threatened, and decrease when females are most actively seeking mates. Only data for solo song bouts were sufficiently extensive to allow for a temporal analysis.

Seasonal variations in song behavior were studied by separating the breeding season into three stages: (1) the premating period, from the time when males first established territories to the time when they first began to acquire mates, (2) the early mating period, when males

were acquiring their first mates, and (3) the late mating period, when all males on the study area had obtained one mate and many had begun advertising for second mates. The premating period corresponded to 17–27 May 1975 and 18–22 May 1976. The early mating period corresponded to 28 May–2 June 1975 and 23–28 May 1976. The late mating period corresponded to 29 May–4 June 1976 (no data were collected for the late mating period in 1975).

Predicting the expected pattern of temporal change in song frequencies requires a description of male and female activity patterns during early morning hours. During the premating period, males began singing about 45 min before dawn, which occurred around 04:30. For about an hour, newly arriving males often encroached upon the territories of resident males, and disputes between males were frequent. Shortly after sunrise, males began feeding more, and the frequencies of both song behavior and territorial fighting diminished. Conflicts continued at this lower frequency until about 10:00, but few new males entered the local area after dawn. Females were absent, not yet visiting territories, or not yet eliciting male attention during this period.

During the early mating period, males began singing about an hour before dawn. For the first 15 min they preened themselves and sang only sporadically. There followed a period of continuous singing, chasing, and fighting until shortly before dawn. Females foraged in undefended areas and were not in evidence around male territories until almost dawn, when they began visiting territories. Sexual chases and courtship were then frequent for the next 1–2 h. Thereafter, courtship activity and male song became sporadic, and most time was devoted to foraging and other activities.

Activity patterns were similar during the late mating period, but they occurred at lower intensities. Most males possessed territories, and most females were mated. Song rates waned rapidly after dawn, and boundary disputes were infrequent. Males were preoccupied with advertising for, or courting, females rather than with territory defense.

Given the above activity patterns, I predicted that: (1) Males should sing  $\beta$  songs most frequently during the predawn hours of the early mating period because most songs at that time appeared to be directed toward other singing males and because females were not yet present on male territories. (2) During all periods of the season, except possibly the late mating period, males should sing more  $\beta$  songs during predawn hours than after dawn because territory disputes were most intense before

TABLE 3. Percent frequency that  $\beta$  songs were given by male Bobolinks in solo song bouts as a function of season and time of day. Frequency of  $\alpha$  songs equals one minus frequency of  $\beta$  songs. Superscripts indicate significant differences, with a > b across rows and x < y down columns,  $\chi^2_1$ ,  $P < .05$ . Number of songs is given in parentheses.

Stage of season	-60 min to dawn	Dawn to +45 min	After +45 min
Premating period	52.6 <sup>ay</sup> (601)	46.7 <sup>b</sup> (914)	49.4 (926)
Early mating period	58.3 <sup>ax</sup> (2,838)	49.3 <sup>b</sup> (831)	55.1 (316)
Late mating period	49.9 <sup>y</sup> (1,161)	53.1 (343)	54.0 (87)

dawn and most newly arriving males in an area arrived before dawn. Moreover, males diverted their attention toward females after dawn during the early and late mating periods.

The results support both predictions (Table 3).  $\beta$  songs were given most frequently during the predawn hours of the early mating period. Within both the premating and early mating periods they were also given significantly more often before dawn than after dawn. The observed differences were not large, however, indicating that any functional distinction between the two song types is subtle.

#### SONG FRAGMENTATION

The functional significance of partial songs is difficult to predict. Shiovitz (1975) concluded that the distinctive introductory notes of Indigo Bunting (*Passerina cyanea*) songs serve to attract the attention of opposing males. Introductory notes probably also serve as individual identity signals (Thorpe 1972). If these interpretations are appropriate for Bobolinks, song fragments should be most prevalent when songs serve primarily either to attract attention to postural displays or to emphasize a male's individual identity. They should be least prevalent when songs serve as long-distance threat or advertisement signals. Hence partial songs should be most frequent when individuals are displaying near one another. Males are closest together during preterritorial disputes and boundary disputes, farther apart during countersinging, and most dispersed during solo bouts.

An analysis of song fragmentation according to context confirms the importance of proximity (Table 4). Song fragments were much more frequent for both song types during preterritorial and boundary disputes and during solo song bouts or countersinging bouts. The higher frequency of  $\alpha$  fragments during solo bouts as compared to countersinging bouts probably resulted from temporal differences in sampling intensity rather than from contextual differences in proximity (see below).  $\beta$  songs were fragmented less often than  $\alpha$  songs in every context, a difference that cannot be attributed to differences in proximity (which were zero within each context).

Shorter songs may signal lower levels of aggressiveness, a hypothesis that is especially plausible if the warbled sequence represents the most aggressive component of each song type. If so, the higher fragmentation rate of  $\alpha$  songs could be explained as an attenuation of aggressive signals during periods when males are focusing their attention more on females. The hypothesis that fragmentation attenuates aggressiveness of the song can be tested by analyzing temporal variations in the frequency of fragmentation. The variations should parallel those established above for song type frequencies.

Temporal changes in song fragmentation were analyzed in the same way as for song types. The data were analyzed separately for each song type. The analysis revealed three distinct periods for each song type, with relatively marked shifts in frequency between the time intervals (Table 5). The frequency that  $\alpha$  and  $\beta$  song types were fragmented within 15-min intervals was significantly correlated ( $r = 0.55$ ,  $df = 25$ ,  $P < .005$ ), indicating that the two song types were fragmented in parallel, albeit at different frequencies.

TABLE 4. Percent frequency and length of  $\alpha$  and  $\beta$  song fragments given by male Bobolinks in territorial contexts. Superscripts on totals indicate significant differences, with a > b > c > d across rows and x > y down columns,  $\chi^2_1$ ,  $P < .05$ .

Song fragment	Pre-territorial disputes	Counter-singing bouts	Solo bouts	Boundary disputes
<b><math>\alpha</math> Songs</b>				
No. of songs	283	285	3,764	719
$\alpha\eta$	0.7	2.8	2.6	6.7
$\alpha\omega$	12.0	2.8	10.1	23.4
$\alpha@$ , $\alpha\Delta$ , $\alpha\Delta+$	50.9	36.1	37.0	52.6
$\alpha'$	16.6	9.8	12.0	9.7
Other	2.5	0.7	0.9	3.3
Totals	82.7 <sup>bx</sup>	49.4 <sup>dx</sup>	62.6 <sup>cx</sup>	95.7 <sup>ax</sup>
<b><math>\beta</math> Songs</b>				
No. of songs	186	243	4,248	896
$\beta\eta$	11.8	2.9	3.6	15.2
$\beta\eta+$	9.7	1.6	5.5	13.2
$\beta'$	38.7	24.9	18.5	39.2
Other	8.6	0.8	2.2	5.5
Totals	68.8 <sup>ay</sup>	30.2 <sup>by</sup>	29.8 <sup>by</sup>	73.1 <sup>ay</sup>

TABLE 5. Percent frequency that  $\alpha$  and  $\beta$  songs were fragmented by male Bobolinks in solo song bouts as a function of season and time of day. Time periods are given as minutes before or after dawn. Superscripts indicate significant differences, with  $a > b > c$  across rows and  $x > y > z$  down columns,  $\chi^2_1$ ,  $P < .05$ . Number of songs is given in parentheses.

Stage of season	-60 to -45 min	-45 to -15 min	-15 to >+60 min
$\alpha$ Songs			
Premating period	—	61.1 <sup>ax</sup> (162)	47.7 <sup>bz</sup> (1,079)
Early mating period	75.4 <sup>ay</sup> (122)	62.2 <sup>bx</sup> (812)	80.8 <sup>ax</sup> (812)
Late mating period	89.0 <sup>ax</sup> (137)	43.6 <sup>ay</sup> (351)	74.6 <sup>by</sup> (295)
$\beta$ Songs			
Premating period	—	32.9 <sup>ax</sup> (164)	23.8 <sup>bz</sup> (1,036)
Early mating period	30.6 <sup>y</sup> (160)	24.8 <sup>by</sup> (1,121)	37.2 <sup>ay</sup> (958)
Late mating period	47.6 <sup>ax</sup> (126)	24.7 <sup>by</sup> (380)	44.0 <sup>ax</sup> (302)

Songs were fragmented most frequently during the first 15 min of predawn song throughout the mating season (Table 5), while males were not threatened by outside intrusions. During the next 30 min of the early and late mating periods, while territorial conflicts were most intense and frequent, song fragments were significantly less frequent. Thereafter, song fragments became more numerous for the rest of the morning, during the time when females were most active in seeking mates. Significantly, this increase did not occur during the premating period, when males were not yet advertising for females. Thus, songs were fragmented least often when territorial males were most threatened by encroaching males and most often when they were not as threatened or when they were advertising for females.

#### COMPOUND SONGS

The frequency with which compound songs are given should vary inversely with the frequency of song fragmentation if song length is an important variable. Contextual analysis showed that compound songs were most frequent in solo bouts and countersinging bouts and least frequent in boundary disputes and preterritorial disputes, just opposite to the pattern for song fragmentation (Table 6). Also,  $\beta$  songs were compounded more often than  $\alpha$  songs, again the opposite of song fragmentation. Longer segments were given for both fragmented and compounded  $\beta$  songs compared to fragmented and compounded  $\alpha$  songs respectively, indicating a general shift toward more complete or longer renditions of the  $\beta$  songs as compared to  $\alpha$  songs.

Regression analysis confirmed the inverse relationship between compounding and fragmentation. The frequency with which  $\alpha$  songs were fragmented within 15-min intervals was negatively correlated with the frequency with which they were compounded during the early and late mating periods, though not during the premating period ( $r = .66$ ,  $df = 17$ ,  $P < .001$ ).

For  $\beta$  songs fragmentation frequency was negatively correlated with frequency of compounding for all stages of the breeding season ( $r = .55$ ,  $df = 25$ ,  $P < .005$ ). Moreover, the frequency that  $\alpha$  songs were compounded was strongly correlated with the frequency that  $\beta$  songs were compounded ( $r = .82$ ,  $df = 25$ ,  $P < .001$ ). Thus song fragmentation and song compounding did not occur independently of one another for either song type. Song length itself therefore represents an important component of the signal.

If indeed song length modifies the strength of aggressive signals, compound songs should become more frequent at times when males are most threatened by intruders, while being less frequent at times when males are actively seeking females. As predicted, compound songs were least frequent during the first 15 min of

TABLE 6. Percent frequency that  $\alpha$  and  $\beta$  songs were compounded by male Bobolinks in territorial contexts. Superscripts indicate significant differences, with  $a > b > c$  across rows and  $x > y$  down columns,  $\chi^2_1$ ,  $P < .05$ .

Song sequence	Preterritorial disputes	Duets	Solo bouts	Boundary disputes
$\alpha$ Songs:				
No. of songs	283	285	3,764	719
$\alpha\alpha\eta$	0.7	2.8	3.3	0.3
$\alpha\alpha\omega$	0.4	2.1	3.6	0.1
$\alpha\alpha@$ , $\alpha\alpha\Delta$ , $\alpha\alpha\Delta+$	0.4	0.0	0.9	0.0
$\alpha\alpha'$	0.0	0.0	0.0	0.0
$\alpha\alpha$	0.0	0.0	0.1	0.0
Other	0.0	0.0	0.4	0.0
Totals	1.5 <sup>b</sup>	4.9 <sup>y</sup>	8.3 <sup>ay</sup>	0.4 <sup>y</sup>
$\beta$ Songs:				
No. of songs	186	243	4,248	896
$\beta\alpha\eta$	0.5	4.1	6.0	1.7
$\beta\alpha\omega$	1.1	2.9	8.2	1.1
$\beta\alpha@$ , $\beta\alpha\Delta$ , $\beta\alpha\Delta+$	0.5	1.2	6.3	0.3
$\beta\alpha'$	0.0	0.0	0.5	0.0
$\beta\alpha$	0.0	0.4	0.2	0.1
$\beta@$ , $\beta\Delta$ , $\beta\Delta+$	1.7	6.2	4.1	0.9
Other	0.0	1.6	2.4	0.2
Totals	3.8 <sup>c</sup>	16.4 <sup>bx</sup>	27.7 <sup>ax</sup>	4.3 <sup>cx</sup>

TABLE 7. Percent frequency that  $\alpha$  and  $\beta$  songs were compounded by male Bobolinks in solo bouts as a function of season and time of day. Time of day is given as minutes before or after dawn. Superscripts indicate significant differences, with  $a > b$  across rows and  $x > y$  down columns,  $\chi^2_1$ ,  $P < .05$ .  $n$  = number of songs, given in parentheses.

Stage of season	-60 to -45 min	-45 to -15 min	-15 to +15 min	+15 to >+60 min
$\alpha$ Songs:				
Premating period	—	15.4 <sup>x</sup> (162)	11.8 <sup>x</sup> (305)	15.1 <sup>x</sup> (774)
Early mating period	0.8 <sup>b</sup> (122)	7.0 <sup>ay</sup> (812)	1.9 <sup>by</sup> (470)	2.4 <sup>by</sup> (342)
Late mating period	2.9 <sup>b</sup> (137)	12.0 <sup>ax</sup> (351)	9.7 <sup>x</sup> (144)	4.6 <sup>by</sup> (151)
$\beta$ Songs:				
Premating period	—	39.6 <sup>x</sup> (164)	37.0 <sup>bx</sup> (441)	46.4 <sup>ax</sup> (595)
Early mating period	17.5 (160)	27.5 <sup>ay</sup> (1,121)	10.4 <sup>by</sup> (742)	25.5 <sup>ay</sup> (216)
Late mating period	12.7 <sup>b</sup> (126)	37.9 <sup>ax</sup> (380)	20.4 <sup>by</sup> (191)	15.8 <sup>by</sup> (101)

predawn song in the early and late mating periods, when males spent more of their time preening, and during the period just after dawn, when males were most actively engaged in advertising for females (Table 7). Compound songs were most frequent before dawn when territorial conflicts were most common, except during the premating period when they were numerous throughout the morning.

#### SONG BEHAVIOR IN MATING CONTEXTS

I analyzed male song behavior for the following courtship and mating contexts:

*Courtship.* A perched male singing toward a female on his territory, accompanied by postural displays associated with courtship (see Martin 1967).

*Circle flight.* Songs given during short circular flights by males while courting females. Circle flights are distinguished from song flights by their lower altitude and shorter duration and by their restriction to courtship situations (Martin 1967). They are most prevalent during the first two days of courtship. Circle flights given by unmated males toward females flying overhead were excluded from my analyses.

*Mounting attempt.* Songs given in flight following unsuccessful copulation attempts, generally during the second or third day of courtship.

*Approach to female.* Songs given by a male when I deliberately walked toward his recently mated female. These data were collected within the first two days of pair formation.

$\beta$  songs became progressively less frequent on successive days of courtship (Fig. 2). Assuming that higher frequencies of the  $\beta$  song reflect higher levels of male aggressiveness, this decline conforms to the general observation that courting males are especially aggressive during early stages of courtship (Andrew 1961, Bastock 1967, Hinde 1970). Several associated changes also support this interpretation. On the first day of courtship, songs were given loudly and rapidly, and males behaved in a

very excited manner, constantly flying from perch to perch. They often provoked females to flight by landing next to them and singing intensely or pecking them. These behaviors were still evident on the second day of courtship, although male displays were less vigorous. By the third day of courtship and thereafter, courtship songs were sung very softly and were inaudible to me beyond about 10–15 m.

Songs were frequently fragmented during courtship (Table 8), possibly reflecting the importance of introductory notes in drawing attention to the male as well as emphasizing his identity. As in territorial contexts,  $\beta$  songs were fragmented less often than  $\alpha$  songs. Hence song length may signal the intensity of male aggressiveness in mating contexts as well as in territorial conflicts. The more frequent fragmentation of  $\beta$  songs as courtship progressed supports that interpretation. It also supports the hypothesis that male aggressiveness gradually declines as courtship proceeds. Very few songs reached the warbled sequence of notes once females began copulating on the third day of courtship.

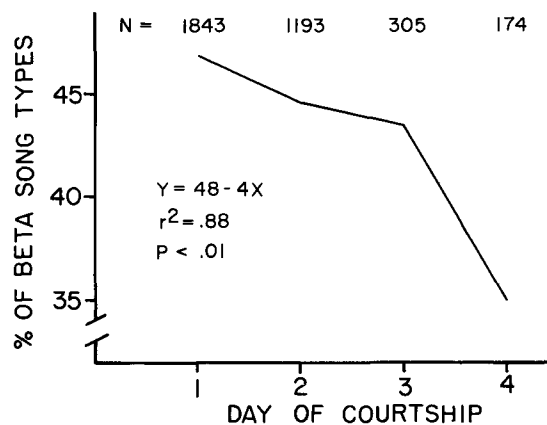


FIGURE 2. Percent frequency of beta songs given by courting male Bobolinks on successive days of courtship. Data were collected during early morning hours and comprise observations on 10 males.



TABLE 8. Percent frequency that  $\alpha$  and  $\beta$  songs were fragmented by courting male Bobolinks as a function of day of courtship. Superscripts indicate significant differences, with a > b across rows and x > y down columns,  $\chi^2$ ,  $P < .05$ .

Song type	Day 1	Day 2	Day 3	Day 4
<b><math>\alpha</math> Songs:</b>				
No. of songs	978	658	173	113
$\alpha\eta$	25.8	45.7	39.9	48.8
$\alpha\omega$	20.9	24.8	36.4	26.6
$\alpha@$ , $\alpha\Delta$ , $\alpha\Delta+$	22.9	22.8	20.2	16.8
$\alpha'$	2.4	0.6	0.6	0.0
Other	24.9	5.8	2.3	0.0
Totals	96.9 <sup>x</sup>	99.7 <sup>x</sup>	99.4	92.2
<b><math>\beta</math> Songs:</b>				
No. of songs	865	535	132	61
$\beta\eta$	23.2	36.1	47.0	62.3
$\beta\eta+$	19.4	23.0	23.5	29.5
$\beta'$	32.7	29.5	26.5	6.6
Other	1.0	0.0	0.0	0.0
Totals	76.3 <sup>xy</sup>	88.6 <sup>by</sup>	97.0 <sup>a</sup>	98.4 <sup>a</sup>

Songs given during circle flights and after unsuccessful mounting attempts were predominantly of the  $\alpha$  type: 93.8% of 193 songs given during circle flights and all 12 songs heard after mounting attempts were  $\alpha$  variants. This finding strengthens the hypothesis that the  $\alpha$  song is more important than the  $\beta$  song in mate attraction.

Virtually all songs given during circle flights and mounting attempts were fragments, many of which were interior fragments lacking introductory notes (Table 9). The prevalence of interior fragments in these contexts is especially interesting because  $\beta$  songs differ from  $\alpha$  songs principally by the absence of these syllables. The occurrence of interior fragments in several additional contexts clarifies their meaning.

The many "other"  $\alpha$  fragments given on the first day of courtship (see Table 8) were interior fragments (Table 9). These were given by highly excited males, usually loudly and in rapid succession. When I observed without a blind, interior fragments became markedly more frequent. Of 978  $\alpha$  songs that I heard from a blind on the first day of courtship, 21.4% were interior fragments, as compared with 66.3% of 469  $\alpha$  songs that I heard without a blind. Hence courting males uttered interior fragments three times as frequently when I was visibly present.

My conspicuousness likewise affected male song behavior in another context. Interior fragments were given very often whenever I walked slowly toward a recently mated male who was accompanied by his new mate (Table 9). Such behavior was so characteristic of recently mated males that I could use it as a reliable cri-

TABLE 9. Percent frequency of songs given by male Bobolinks in various mating contexts.

Song type	Circle flights	Mounting attempts	Day 1 of courtship (in blind)	Day 1 of courtship (no blind)	Approach to female
No. of songs	193	12	1,843	562	82
$\alpha\eta$	1.0	8.3	13.7	13.3	0.0
$\alpha\omega$ , $\alpha@$ , $\alpha\Delta$ , $\alpha\Delta+$	23.1	8.3	23.2	6.4	1.2
$\alpha'$	37.8	0.0	1.3	5.2	0.0
$\alpha$	4.7	0.0	1.3	1.1	0.0
Compound $\alpha$	2.1	0.0	0.1	0.0	0.0
$\delta\omega$	4.7	0.0	0.8	0.7	0.0
$\delta\omega@$ , $\delta\omega\Delta$ , $\delta\omega\Delta+$	2.6	8.3	0.0	2.5	1.2
$\delta\omega\alpha'$	2.6	0.0	0.0	2.5	1.2
$\delta\omega\alpha$	1.0	0.0	0.1	0.4	0.0
$\omega$	1.0	16.7	5.9	38.1	36.6
$\omega@$ , $\omega\Delta$ , $\omega\Delta+$	9.8	58.3	4.4	9.6	39.0
$\omega\alpha'$	1.6	0.0	0.2	2.0	2.4
$\omega\alpha$	1.6	0.0	0.4	0.7	6.1
Other $\alpha$ songs	2.6	0.0	0.4	0.7	3.7
All $\beta$ songs	6.2	0.0	46.9	18.0	9.8

terion of recent pair formation. Males always appeared highly excited in this context, flying from forb to forb, and singing loudly and rapidly. As I approached more closely, males would swoop down on the females and force them to fly if the females had not already retreated.

Finally, males often sang interior fragments when courtship was interrupted by Common Ravens (*Corvus corax*) or hawks flying overhead. One male gave 20 interior fragments in rapid succession while Red-winged Blackbirds were mobbing first a raven and then a Marsh Hawk (*Circus cyaneus*). Another male sang six interior fragments immediately after a Prairie Falcon (*Falco mexicanus*) stooped on and narrowly missed an adult male Red-winged Blackbird near where he was courting a female. On another occasion a third male looked up and sang an  $\omega@ \omega\Delta@$  sequence toward a Prairie Falcon as it flew over him. Finally, a male once sang continuous loud  $\omega$  syllables in rapid succession for 5 min while a yearling male Red-winged Blackbird was perched on a stake near his mate. As soon as the Red-winged Blackbird left, he stopped singing those notes and resumed courting the female.

## DISCUSSION

### SIGNIFICANCE OF BOBOLINK SONG VARIANTS

Interpretations of Bobolink song hinge on the communicatory role of the two song variants. The proportion of song types given during behavioral interactions varied according to context,  $\beta$  songs becoming more frequent as the conflict became more aggressive. This result suggests that the proportion of song types given during a bout somehow reflects the level of

aggressiveness communicated by the male. Smith (1969b, 1970) interpreted the two song types of *Sayornis phoebes* similarly. In phoebes, however, one song type was more common than the other and was associated mostly with nonaggressive behaviors of males while they were near their mates or nests. The other song type was most prevalent immediately following fights and appeared to signal strong aggressive tendencies. The level of aggressiveness communicated by male phoebes during a song bout appeared to be modulated by mixing aggressive and nonaggressive vocalizations.

In Bobolinks that is not the case. Both song types are associated with aggressive contexts. They are given with approximately equal frequencies, they occur in all territorial and courtship contexts where primary songs are used, and both are given at every intensity of song-spread, a graded postural threat display (see Martin 1967). Variations in the frequency of each song type across contexts are simply not large enough for the proportion of song types itself to reliably convey the intensity of a male's aggressiveness. The communicatory significance underlying the observed variation in song type frequencies is more subtle and probably has to do with the meanings conveyed by specific components of each song, as will be explained below.

Several explanations that have been proposed for the multiple songs given by other species of birds are inappropriate for Bobolinks. One explanation is that each song type conveys different information and is associated with entirely different social contexts, as occurs among New World warblers (Morse 1967, 1970, Lein 1972, 1978, Kroodsma 1981), Grasshopper Sparrows (*Ammodramus sava-narum*; Smith 1959), and possibly Horned Larks (*Eremophila alpestris*; Beason and Franks 1974). In Bobolinks, however, song types do not occur in separate contexts, hence the functional differentiation of the two songs must be more subtle.

A second explanation of multiple song types, referred to as the "antimonotony hypothesis," is that multiple types of song are given in order to avoid monotony or boredom (Hartshorne 1956, Kroodsma 1978). Although the possibility that birds experience and react to boredom should not be discounted, evidence from a wide variety of passerine birds does not support the antimonotony hypothesis (Dobson and Lemon 1975; but see Kroodsma 1978). I have no direct evidence for evaluating this hypothesis with respect to Bobolinks.

The Beau Geste hypothesis proposed by Krebs (1977a, 1978) and the status signalling

hypothesis proposed by Yasukawa (1981) may conceivably apply to Bobolinks. However, these explanations are most appropriate for more versatile songsters in which every song type is equivalent in function and different males have different song repertoires. While I do not have data for testing these hypotheses, neither seems sufficient for explaining the two song types sung by male Bobolinks because neither predicts their functional differentiation.

#### MEANINGS OF SONG COMPONENTS

The meanings of particular song components cannot be determined with certainty without careful playback experiments. Nevertheless, some hypotheses can be deduced on theoretical grounds and on the basis of present evidence.

First, the introductory notes of Bobolink song probably convey information about the identity of individual males and in many (though not all) cases about the identity of the song type when only fragmented songs are given. Each male sings the introductory notes in a characteristic manner, as required of individual identity signals (Marler 1961), and the identifying elements of a song should theoretically be placed near the beginning of the song (Thorpe 1972). Moreover, short song fragments often consist of only the introductory notes and are most often given during preterritorial displays, territorial boundary disputes, and late stages of courtship, when emphasizing individual identity should be especially important.

Second, the interior notes of the  $\alpha$  song, especially the loudly whistled *eeee-ew* syllable, probably serve as long distance signals for attracting the attention of females. These syllables seem to carry farther than other song components, and their presence or absence in a song is the sole distinction, other than the introductory notes, between the two song types.  $\alpha$  songs and  $\alpha$  fragments are given more frequently during displays directed towards females, suggesting that the syllables distinguishing the  $\alpha$  song from the  $\beta$  song are especially directed toward females. Moreover,  $\alpha$  fragments are most commonly ended with these interior syllables during courtship and whenever recently mated pairs are approached by a human observer.

Third, the warbled syllables of both song types probably signal aggressive tendencies. Both songs certainly convey an aggressive message, and the warbled syllables are essentially the only syllables common to both song types. In addition, this interpretation of the warbled syllables explains why the  $\beta$  song occurs more

commonly in more aggressive contexts. Assuming that aggressiveness is conveyed particularly by the warbled syllables, a male can sing a more aggressive song by omitting syllables involved in mate attraction, thereby allowing him to sing the aggressive elements earlier in the song. That is exactly how the  $\beta$  song differs from the  $\alpha$  song (except for the differing introductory notes). Further, this interpretation helps explain why  $\beta$  songs are fragmented less frequently than  $\alpha$  songs. An  $\alpha$  song intended primarily for mate attraction should be terminated after the female-oriented syllables are given. Both song types should be fragmented during the warbled sequence either when attenuation of aggressiveness is intended or when a song is prematurely ended to allow earlier singing of the next song. Only  $\alpha$  songs, however, should be fragmented specifically to eliminate the aggressive component entirely. My data show that the more frequent fragmentation of  $\alpha$  songs results entirely from the large number of  $\alpha$  songs that are ended after some or all of the interior syllables are given. Finally, this interpretation supports Morton's (1977) hypothesis that pure frequency song components tend to convey appeasement messages while broad frequency band signals (such as the warbled sequence) tend to convey more aggressive messages.

#### SIGNIFICANCE OF SONG FRAGMENTATION

In addition to the reasons for song fragmentation already mentioned, I can offer several other explanations as to why males often sing partial songs. In territorial boundary disputes a male may be able either to remind his opponent of previous adverse encounters or discourage him from initiating future encounters by repeatedly singing identifying elements of his song. In courtship contexts a male may expedite pair formation by emphasizing his identity, since pair bonding is predicated upon females' learning to recognize and become familiar with individual males.

Song fragments may also draw the attention of recipients to postural displays (Shiovitz 1975). Postural displays are more common and possibly more effective than vocal signals when given over short distances. Short vocal signals may be better than longer ones for drawing attention to postural displays if the latter distract the recipient after its attention has been gained.

Finally, introductory elements may be less likely than full songs to evoke either strongly aggressive responses from rival males (Dawkins and Krebs 1978) or withdrawal responses from females. For example, Emlen (1972)

found that male Indigo Buntings respond more weakly to playback of introductory elements of their primary song than to other elements. Signals that elicit weaker responses should be especially advantageous when males are near their opponents or prospective mates because they minimize the chances for eliciting adverse responses—exactly when partial songs are most often given by male Bobolinks.

#### SIGNIFICANCE OF MALE AGGRESSION IN MATING CONTEXTS

The prevalence of male aggression in courtship behavior is widely recognized (see Tinbergen 1951, Andrew 1961, Marler and Hamilton 1966, Bastock 1967) and is usually interpreted as resulting from a generalized motivation that "spills over" from territorial contexts. This interpretation is evolutionarily unsound, however, since aggressiveness has the effect of making pair bonding take more time to accomplish. Without positive advantages to individual males, selection should quickly favor males who avoid aggressive behaviors while courting females.

Some positive advantages of aggression during courtship can be suggested for Bobolinks. Females do not begin copulating until the third day of courtship. If they remain for two days and then leave, males have wasted much time and hence are placed at a mating disadvantage. Mating is highly synchronous in Bobolinks, with attraction of second and third mates occurring in succession at three to eight-day intervals (Martin 1971, Wittenberger 1978, 1980). The earliest males to gain mates are therefore better able to seek second mates than males who are still busy seeking or courting their first mates. By behaving aggressively during early stages of courtship, males elevate the costs that females must pay to remain on a territory. These costs are presumably less than the benefits that females derive by remaining to breed, but they may well exceed the benefits that a female could derive by staying for a few hours or a day to forage. The pattern of aggressiveness in Bobolink courtship corresponds closely to that predicted by the hypothesis that males test female intentions. Males are highly aggressive for the first two days, while females are not yet committed to remaining; they become much less aggressive on following days, after the female begins copulating. Other hypotheses have also been advanced, such as reducing chances that earlier matings by other males reduce the courting male's probability of paternity (reviewed in Wittenberger 1981), but these hypotheses do not seem applicable to Bobolinks. For instance, no female was ever seen to copulate

before the third day of courtship, and no female who had been with a male for that length of time was ever seen to leave and re-mate. Nevertheless, additional evidence will be required before the significance of male aggression during courtship can be adequately understood.

## SUMMARY

The beta variant of the primary song sung by male Bobolinks appears to be a shortened derivative of the alpha song. It apparently conveys a more aggressive message than the alpha song, as it is given in song bouts more often in territorial boundary disputes and at times of day and season when territorial conflicts are most intense. The beta song is given less frequently during preterritorial displays and at times when many unmated females are visiting male territories. During courtship the beta song is nearly as frequent as the alpha song for the first day but declines in frequency thereafter. During circle flight displays directed toward females by courting males, the alpha song type is given almost exclusively.

Both song variants are regularly given as partial (i.e., fragmented) songs and as compound songs consisting of additional songs or song fragments appended to an initial complete song. Song fragments are most frequent during preterritorial and territorial boundary displays, when two or more males are in close proximity. They are least frequent during solo song bouts and when neighboring males sing alternately toward one another from a greater distance. Song fragments are common during courtship and increase in frequency as courtship progresses. Alpha songs are fragmented more often than beta songs. Compound songs show exactly opposite patterns from those of song fragments, and their frequency is negatively correlated with the frequency that song fragments occur both by context and as a function of time of day and season.

These findings suggest the following interpretation: The introductory notes of both song types probably identify the individual male and the song type. Interior syllables of the alpha song are probably involved specifically with mate attraction. The warbled sequence of syllables common to both song types probably conveys aggression. The beta song is probably more aggressive than the alpha because these warbled syllables are given earlier in the song and the female-oriented syllables are omitted. The beta song may have evolved in consequence of this functional differentiation.

Males probably sing fragmented songs for several reasons. Song fragmentation allows males to emphasize individual identity, atten-

uate the aggressiveness of the signal, and eliminate aggressive components of the song while attracting and courting mates. Song fragments consisting solely of the interior syllables of alpha song are associated with contexts in which males are highly excited or disturbed. The meaning of interior syllables is especially interesting because beta songs differ from alpha songs mainly by lacking those syllables.

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