

TESTS OF THE FUNCTION OF THE SONG REPERTOIRE IN BOBOLINKS¹

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Abstract. Bobolinks (*Dolichonyx oryzivorus*) have a two song repertoire consisting of an alpha song and a beta song. The alpha song consists of distinct introductory notes, followed by a series of interior notes, and ending with a sequence of warbled notes. The beta song has a unique set of introductory notes followed immediately by a series of warbled notes. In this study, observations and experiments were conducted to test the following hypotheses on the functional significance of the Bobolink repertoire: (1) different song types convey different messages; (2) the size of the repertoire is a signal, e.g., of male quality; (3) song switching is a signal of aggressive or sexual motivation; and (4) song matching is a signal to conspecific intruders. Hypothesis 2 was ruled out *a priori* for Bobolinks because there is no variation in repertoire size in this species. Males did not change their relative use of the two song types with time of the season, or with location in the territory, as might be expected if the different song types and note types convey different messages. Aggressive response by territorial males was equally strong to the two song types, providing further evidence against the separate messages hypothesis. Males did not alter the frequency of switching between song types when presented with caged males or caged females; therefore neither an intrasexual nor an intersexual function of song switching was supported. There was no tendency for males to match the song type of the playback. However, males tended to respond with the opposite song type to that of the playback. This suggests that territorial male Bobolinks may be responding to the song of intruders by singing the alternate song type, a strategy that, in species with a two song repertoire, is functionally identical to song matching.

Key words: Song; song repertoires; bobolink; *Dolichonyx oryzivorus*.

INTRODUCTION

Many passerine birds possess multiple forms of the species-typical song, and various hypotheses have been proposed for the function of these song repertoires. One idea is that different song types convey different messages: one song type may be used for attracting mates and another for territory defense (Ficken and Ficken 1965; Morse 1966, 1970; Baptista 1978; Kroodsmas et al. 1989), or each of several song types may signal different levels of aggressive motivation (Lein 1972, 1978; Schroeder and Wiley 1983; Nelson and Croner 1991). A second hypothesis is that the various song types are interchangeable, while the message is carried by the number of song types. For example, Baker (1986) suggests that repertoire size functions as an "honest advertisement" of male quality. A third hypothesis is that the rate of switching between song types is used for signaling (Falls and Krebs 1975, Falls

and D'Agincourt 1982, Kramer et al. 1985, Searcy and Yasukawa 1990). A fourth hypothesis is that the function of repertoires is to allow song matching between males. Song matching may function in territory defense as a signal of deterrence directed at a particular intruder (Krebs 1977, Krebs et al. 1981). These hypotheses are not necessarily mutually exclusive.

In this study, I investigated the function of the Bobolink (*Dolichonyx oryzivorus*) song repertoire. Each male Bobolink in a local population sings the same two highly stereotyped song types, which are termed the alpha and beta songs (Avery and Oring 1977, Wittenberger 1983, Capp and Searcy 1991a). Examples of the two song types from my study population have been presented elsewhere (Capp and Searcy 1991a). The alpha song is about 7 sec long and consists of alpha introductory notes, followed by a series of interior notes, and ending with a sequence of warbled notes. The beta song is about 4.5 sec long and consists of distinctive beta introductory notes followed by a series of the same warbled notes as in the alpha song.

¹ Received 11 September 1991. Accepted 30 January 1992.

Since the Bobolink repertoire consists of only two song types and all males sing a version of each, song repertoire size cannot be used as a signal. Therefore, the second hypothesis (above) can be eliminated.

Based on a contextual analysis of song, Wittenberger (1983) suggested that the two song types of the Bobolink conveyed different messages, with the alpha song functioning in mate attraction and the beta song used primarily intrasexually. Additionally, he suggested that the interior notes of the alpha song and the warbled notes of both songs had intersexual and intrasexual functions, respectively. Capp and Searcy (1991a) tested this hypothesis by presenting, separately, a caged male, a caged female, and an empty control cage to territorial males. The subjects did not alter their use of the two song types between contexts. Furthermore, use of the two song types did not predict aggressiveness towards the caged male (Capp and Searcy 1991b). These results weigh against the separate messages hypothesis. Below I present further tests of the separate messages hypothesis, and of the switching and matching hypotheses.

Seasonal changes in song type frequency have been used to support the separate messages hypothesis. For example, Wittenberger (1983) presented evidence that the beta song of Bobolinks predominated prior to the presence of females on male territories. This was used as evidence for an aggressive function for the beta song since it appeared that much male activity at that time was devoted to territory defense. Similarly, Lemon et al. (1987) found that American Redstarts (*Setophaga ruticilla*) exhibit an early peak in the repeat mode of singing followed by an increase in the serial mode. The shift in singing patterns occurs at the time of female arrival and the beginning of courtship which suggests a mate attraction function for the repeat mode of singing. Additionally, many studies have found that repertoire use changes as the breeding season progresses (Ficken and Ficken 1965; Morse 1966, 1970; Lein 1978, 1981; Lemon et al. 1987; Staicer 1989).

I looked at the effects of season on Bobolink singing behavior in two ways. First, I analyzed the use of song types, note types, and switching frequency in relation to the song recording date to determine whether any seasonal biases in these parameters occurred. Secondly, I compared the singing behavior of territorial males before and

after the arrival of females on the breeding grounds. The original rationale for this second analysis was that song would be male directed before female arrival while female directed song would be evident after female arrival, as Wittenberger (1983) assumed. However, in other species it has been observed that the song that apparently functions intersexually predominates prior to the arrival of females on the breeding ground (Ficken and Ficken 1965, Morse 1966, Lemon et al. 1987). Thus it is possible that my original assumption, that intrasexual song predominates over intersexual song prior to female arrival, ought to be reversed. Nevertheless, under either assumption, a change in use of song types when females arrive is evidence for different messages.

Differential use of song types between the center and edge of the territory has also been used to support the separate message hypothesis. It is usually argued that individuals are more aggressive at the center of their territory than at the periphery (Huxley 1934, Tinbergen 1960) and differential response to playbacks has borne this out in some species (Ickes and Ficken 1970, Falls and Brooks 1975, Melemis and Falls 1982). Several studies have shown that use of song types varies with male location on the territory (Morse 1966, Smith et al. 1978, Staicer 1989). Typically, one song type or singing pattern is found to predominate at the territory center and another at the edge, as in Chestnut-sided Warblers (*Dendroica pensylvanica*) (Lein 1978) and Tufted Titmice (*Parus bicolor*) (Schroeder and Wiley 1983). Such findings, then, support the idea that song types are used to signal varying levels of aggressiveness. Below I compare the use of song types and note types between territory center and edge for Bobolinks.

Response to playback of different song types can also be used as a test of the separate messages hypothesis. MacNally and Lemon (1985) predicted a stronger response to playbacks of the more aggressive serial songs than repeat songs in the American Redstart. Similarly, Nelson and Croner (1991) predicted stronger responses to playbacks of the more aggressive complex song in Field Sparrows (*Spizella pusilla*). Presumably, the assumption for these *a priori* predictions is that territorial males are more responsive to intrasexual signals than to epigamic signals. However, it could be just as convincingly argued that males should be more responsive to less aggres-

sive signals because there is less chance of retaliation from the signaller. In fact, Willow Warblers (*Phylloscopus trochilus*) (Jarvi et al. 1980) and Great Reed-Warblers (*Acrocephalus arundinaceus*) (Catchpole 1983) give weaker responses to more aggressive vocal signals. Thus, discrimination between distinct song types is strong evidence for differential functions, but cannot adequately define those functions. Here, I tested male response to playback of the two Bobolink song types. Stronger response to one song type would support separate messages but would be ambiguous as to which was more aggressive.

The hypothesis that the rate of switching between song types is used as a signal was tested in two ways. First, switching rates were compared for periods in which caged males and caged females were presented relative to controls. Similar experiments have been used to show that rapid switching between song types may be either an aggressive, intrasexual signal (Kramer et al. 1985) or an intersexual, courtship signal (Searcy and Yasukawa 1990). Second, switching rates were compared for the periods before and after female arrival.

In most passerine species studied, males respond vocally to conspecific playbacks in a non-random manner. A common response to playbacks is song matching (Ficken and Ficken 1970, Kroodsma 1979, Krebs and Kroodsma 1980, Krebs et al. 1981, Falls et al. 1982, Schroeder and Wiley 1983, Weary et al. 1990, many others). Several ideas have emerged to explain the function of song matching by territorial males. If song functions in territory defense, matching the song of an intruder may act as an aggressive signal directed at a particular individual (Bremond, in Armstrong 1973). Krebs et al. (1981) proposed that song matching in Great Tits (*Parus major*) functions as a graded signal in territory disputes since the probability of matching is closely correlated with the strength of response to playbacks. Here I looked for song matching by recording male singing during playback of the two song types.

METHODS

STUDY SITES AND GENERAL METHODS

The study was conducted in the vicinity of the University of Pittsburgh's Pymatuning Laboratory of Ecology located near Linesville, Crawford

County, Pennsylvania. The preferred breeding habitat of Bobolinks is large expanses of grassland. My study sites were on several large hayfields owned by the Pennsylvania Game Commission and private farmers in the area. Males were captured with mist nets and playback of conspecific song. It is unlikely that this experience would bias later responses of test males. The playback was not a complete song but rather, consisted of the first part of the alpha song, and at least one week elapsed between the capture time and subsequent testing of a particular male. Captured males were color banded for identification. Some males could be identified by their unique plumage patterns and so were not captured and banded.

Each of the experiments in this study involved the recording of song and spectrographic analysis. In 1987, song was recorded using a Sony TCM-500 cassette tape recorder, a Sony ECM-170 electret condenser microphone, and a Sony PBR-330 parabolic reflector. A headset with attached microphone was connected to the recorder to facilitate commentary on the tape. In 1988 through 1990, recordings were made using a Marantz PMD221 cassette tape recorder with a Marantz EC-3S cardioid condenser microphone and a Sony PBR-330 parabolic reflector. A headset was connected to the tape recorder and comments were made directly into the single microphone. In all years recording sessions were performed between 05:30 and 09:30 hr.

Sound spectrograms of recordings from 1987 and 1988 were made using a Model 4512 Princeton Applied Research FFT Real Time Spectrum Analyzer at the Rockefeller University Field Research Center. Spectrograms of Bobolink song recorded in 1989 and 1990 were made using MacSpeech Lab II and a Macintosh IIcx computer at the University of Pittsburgh.

Not all songs sung by Bobolinks are complete alpha or beta songs. Rather, many are partial songs of varying length, while others are long sequences composed of several songs strung together without a noticeable break and ending at various places in the song. This pattern complicates classification of songs to song type. I classified each vocalization as a song type based on the type of introductory notes sung. Capp and Searcy (1991a) found that greater than 99% of Bobolink songs can be correctly classified by the introductory notes. The song variables analyzed were the proportions of alpha song, beta song,

interior notes, warbled notes, and song switches, as well as total song rate, alpha song rate, and beta song rate. Rates are presented as songs per minute. The proportions of alpha and beta songs are complementary, as are the proportions of interior and warbled notes. Therefore, only the values and statistical results for the proportion of alpha songs and interior notes will be presented as it would be redundant to also present the results for the proportions of beta songs and warbled notes. All data sets were tested for skewness, kurtosis, and homoscedasticity. The angular transformation was applied to proportions prior to parametric statistical analyses. Where the assumptions of parametric statistics were violated, a non-parametric equivalent was used to analyze the data (Sokal and Rohlf 1981, Rohlf and Sokal 1981).

SONG SWITCHING IN INTER- AND INTRASEXUAL CONTEXTS

In this experiment, contexts were manipulated on the territories of male bobolinks. The methodology is presented here in abbreviated form as the details of the procedure have been presented elsewhere (Capp and Searcy 1991a). Each territorial male was presented, on separate days and in random order, with a caged male, a caged female, and an empty control cage. The cage measured 30 cm on a side and was mounted to a 1 m long metal pole. The pole was stuck in the ground well inside a test male's territory boundary, and the 15 min recording period commenced when the focal male was detected on his territory. The caged male represented a conspecific intruder, and since Bobolinks are polygynous (Martin 1967, 1974; Wittenberger 1978) the caged female represented a potential addition to the territorial male's harem. Presentations of caged males and caged females have been found to elicit vocal and behavioral changes in territorial males that are similar to natural intersexual and intrasexual contexts (Capp and Searcy 1991a). Experiments were conducted between 19 May–25 June in 1987 and from 14 May–25 May in 1988. Statistical analysis compared the frequency of song switches between treatment and control periods using a *t*-test for paired comparisons.

SEASONAL EFFECTS ON SINGING BEHAVIOR

To evaluate the effects of season on singing behavior, I utilized the data from the control pe-

riods of the context manipulation experiment. Only an empty cage was presented during these periods, so the subjects were singing without disturbance. The singing behavior of the territorial male was recorded for a period of 15 min. Recording sessions ran from 22 May–23 June in 1987 and from 17 May–28 May in 1988. Seasonal effects on song were analyzed using the Spearman coefficient of rank correlation.

In northwestern Pennsylvania male Bobolinks arrive on their breeding grounds in late April or early May. Several days after their arrival, and before the females arrive, male Bobolinks begin to establish territories. Females arrive approximately seven to 10 days after the males. For the pre-female arrival data, I made 15 min recordings of the singing behavior of males actively setting up territories. These data were collected up to the day that the first female Bobolink of the season was observed on the study sites. At that time data collection was discontinued and any recordings made that day were excluded from the analysis. Males were recorded from 6 May–9 May in 1989 and from 3 May–7 May in 1990. Post-female arrival data were taken from the control periods of the context manipulation experiments in 1987 and 1988.

The singing behavior of territorial males before the arrival of females was compared to their singing behavior after females had arrived on the breeding grounds. *T*-tests for independent samples were performed where the assumptions of parametric statistics were met. Data sets not meeting those assumptions were analyzed using the Mann-Whitney *U*-test.

TERRITORY LOCATION EFFECTS ON SONG

In this part of the study, I compared the singing behavior of male Bobolinks in the center of their territories with their singing behavior at the edge of their territories. Territory size in the Bobolink is quite variable, ranging from 0.50–1.25 ha (Martin 1967). Many of the territories in my study population are bordered on at least one side by plowed fields, roads or woodlots. The boundaries of adjacent territories are not as neatly defined but are generally distinct. I defined a belt extending 20 m from the territory boundary toward the center as territory edge; the area inside this belt was considered the territory center. Males were recorded during spontaneous singing for a period of 15 min from 22 May–12 June in 1989

and from 26 May–14 June in 1990. Commentary on the positions of males on their territories was made directly onto the recording. Statistical analysis was performed using a *t*-test for paired comparisons.

PLAYBACK EXPERIMENT

A playback experiment was conducted from 26 May–15 June in 1990. Five min playbacks of the alpha song and beta song were presented to territorial males. Six playback tapes were constructed from three alpha song exemplars and three beta song exemplars recorded in previous years from five different males. Each 5 min playback consisted of one exemplar of either the alpha song or the beta song. The alpha song was presented at a rate of 4 songs/min and the beta song was presented at a rate of 6 songs/min. The alpha song is on average 2.5 sec longer than the beta song, and these rates of presentation reflect the difference in length of the two song types. Due to the considerable difference in length of the two song types, song rate and total time with song could not both be controlled. I chose to control the latter. These rates of presentation are within the range of singing rates of Bobolinks during spontaneous singing.

Each territorial male was presented with a randomly chosen alpha and beta song on separate days with at least one day between test days. The order of presentation of the song types was determined by a coin toss. Each 5 min playback period was preceded by 5 min of control during which time the tape player and speaker were on but the tape was not played. Playbacks were presented over a Nagra Kudelski DSM speaker placed near the center of the territory. The speaker was connected by a 20-m cable to a Uher 4400 Report reel-to-reel tape recorder. Marking poles were set at 2, 8, and 16-m from the speaker to aid in distance estimates. Estimates were made in 2-m intervals between 2 and 5 min and at 1-m intervals between 0 and 2-m. Beyond 20-m a distance of 30-m was recorded. This is a reasonable estimate of the mean distance between 20-m and the territory edge given the size of Bobolink territories.

The singing behavior of the focal male was recorded during control and playback periods. Estimates of the focal male's distance from the speaker were made directly into the microphone. Distances were extracted from these recordings and entered on a flow chart at 5 sec intervals.

The Wilcoxon Matched Pairs Signed-Ranks Test was used to compare the average distance of approach and distance of closest approach for alpha playback versus control, beta playback versus control, and alpha playback versus beta playback.

The singing behavior of test males during the playback periods was analyzed two ways. A chi-square test was used to determine whether the first song performed by the focal male in response to the playback was dependent on the playback song type. In the second analysis the proportion of alpha songs performed during the alpha playback and the proportion of beta songs performed during the beta playback were compared with respective control periods using a *t*-test for paired comparisons.

RESULTS

SONG SWITCHING IN INTER- AND INTRASEXUAL CONTEXTS

The frequency with which male Bobolinks switched between song types did not differ between treatment and control periods for presentations of either the caged male or caged female. The mean frequency of song switches during the caged male presentations was 0.47 (Confidence Limits [CL]: 0.40–0.53) and was 0.46 (CL: 0.40–0.52) during the paired control periods ($n = 20$, $t = 0.17$, $P > 0.80$). During the caged female presentations, males switched between song types at a frequency of 0.47 (CL: 0.36–0.59) as compared to 0.42 (CL: 0.32–0.52) for the corresponding controls ($n = 20$, $t = 0.91$, $P > 0.35$).

SEASONAL EFFECTS ON SINGING BEHAVIOR

Correlations between recording date and song variables indicated there were no significant seasonal changes in song (Table 1). There was a trend toward a decreasing singing rate with the advance of the breeding season. Weak negative correlations of both the alpha song rate and the beta song rate with time show the same tendency. However, none of these relationships was statistically significant. In addition, the proportions of alpha songs, interior notes, and song switches were not significantly correlated with the time of the breeding season (Table 1).

The singing behavior of territorial males before females arrived on the breeding ground did not differ significantly from their singing behav-

TABLE 1. Correlations between test date and song variables. The values of r_s and z are corrected for ties. Sample size is 21 for all correlations.

Song variable	r_s	z	P
Proportion of alpha songs	0.22	1.00	>0.30
Total song rate	-0.30	-1.36	>0.15
Alpha song rate	-0.31	-1.38	>0.15
Beta song rate	-0.36	-1.61	>0.10
Proportion of interior notes	0.14	0.63	>0.50
Proportion of song switches	-0.15	-0.67	>0.50

ior after female arrival for any of the song variables analyzed (Table 2).

TERRITORY LOCATION EFFECTS ON SONG

A total of 18 territorial males were recorded. One male stayed on the edge of his territory for the entire 15-min period and was therefore of no value in a pairwise analysis of the effects of territory location on singing behavior. Additionally, four other males spent most of a recording period either on the edge or in the center of their territories. For these males, in order to get better samples of song, I waited until the focal male moved to the opposite location and then I resumed recording. Thus, the recording periods for these four males were discontinuous and I felt it was inappropriate to calculate singing rates for these males.

Of each 15 min recording period, males spent on average 6.27 min in the center of their territory and 8.36 min at the territory edge. Several males left their territory during the recording period for an overall average of 0.37 min. The proportion of all songs recorded in the center of the territory was 0.42 and 0.58 on the edge. However, this difference simply reflects the amount of time spent in the two territory locations. There was a strong correlation between the amount of

time in a location and the proportion of all songs recorded during the 15 min sampling period ($n = 13$, $r_s = 0.91$, $z = 3.16$, $P = 0.002$). The equality of singing rates found in the center and edge of territories provides further evidence that song output is independent of location (Table 3). Additionally, no significant differences between locations were found for the proportion of alpha songs, the proportion of interior notes, total song rate, alpha song rate, or beta song rate (Table 3).

PHYSICAL RESPONSE TO PLAYBACKS OF ALPHA AND BETA SONGS

Males responded to playback of both alpha and beta songs by approaching closer to the speaker. The mean distance to the speaker for 12 of the 14 territorial males tested was less during the alpha song and beta song playbacks than during the respective control periods. Overall, the mean distance to the speaker was 13.9 m (± 6.7 SD) during the alpha playback versus 25.8 m (± 5.4 SD) during the control ($z = 3.11$, $t = 3$, $P < 0.01$) and 13.7 m (± 5.4 SD) during the beta playback versus 23.2 m (± 7.4 SD) during the control ($z = 3.04$, $t = 4$, $P < 0.01$). Response to playback of the two song types was similar. The mean distance to the speaker was less during the beta playback than during the alpha playback for eight males, was less during alpha playback for five males, and there was one tie. The mean distances overall were not significantly different between playback types ($z = 0.17$, $t = 43$, $P > 0.80$).

For 12 of 14 males, distance of closest approach to the speaker was lower during the playback periods than during the respective control periods. There were two ties during the alpha song playback comparison. Overall, the mean distance of closest approach was 7.4 m (± 5.8 SD) during the alpha playback versus 22.6 m (± 8.3 SD) during the control ($z = 3.06$, $t = 0$, $P < 0.01$) and 7.4 m (± 6.3 SD) during the beta

TABLE 2. Comparisons of territorial male singing behavior pre- and post-female arrival on the breeding grounds. The sample size for pre-female arrival is 11 and for post-female arrival is 21.

Song variable	Mean (SE)		Test statistic	P
	Pre	Post		
Proportion of alpha songs	0.55 (0.03)	0.52 (0.03)	$U = 79.5$	>0.15
Total song rate	3.35 (0.44)	3.33 (0.37)	$t = 0.04$	>0.90
Alpha song rate	1.87 (0.29)	1.64 (0.19)	$t = 0.69$	>0.45
Beta song rate	1.48 (0.19)	1.69 (0.21)	$t = 0.63$	>0.50
Proportion of interior notes	0.43 (0.01)	0.49 (0.03)	$U = 97.5$	>0.40
Proportion of song switches	0.38 (0.04)	0.43 (0.03)	$U = 88.5$	>0.25

TABLE 3. Comparisons of Bobolink singing behavior between the center and edge of the territory.

Song variable	Mean* center	Mean edge	<i>t</i>	<i>P</i>
Proportion of alpha songs (<i>n</i> = 17)	0.49 (0.40–0.57)	0.54 (0.45–0.63)	1.29	>0.20
Total song rate (<i>n</i> = 13)	4.19 (0.45)	4.18 (0.38)	0.02	>0.90
Alpha song rate (<i>n</i> = 13)	1.87 (0.28)	1.95 (0.16)	0.31	>0.70
Beta song rate (<i>n</i> = 13)	2.53 (0.32)	2.40 (0.34)	0.44	>0.60
Proportion of interior notes (<i>n</i> = 17)	0.42 (0.36–0.48)	0.43 (0.38–0.48)	0.42	>0.60

* 95% confidence limits are given for proportion data and standard errors are given for rates.

playback versus 19.3 m (± 9.4 SD) during the control ($z = 2.86, t = 7, P < 0.01$). Comparing the playback periods, 5 of 14 territorial males approached closer to the speaker during the alpha playback, 8 approached closer during beta playback, and there were 5 ties. Overall, there was no significant difference in the distance of closest approach between the playback periods ($z = 0.06, t = 22, P > 0.90$).

VOCAL RESPONSE TO PLAYBACKS OF ALPHA AND BETA SONGS

The first vocal response of territorial males to the playback was independent of playback type (i.e., alpha song and beta song) ($n = 28, \chi^2 = 0.15, df = 1, P > 0.60$). In response to the alpha playback, eight males first sang an alpha song and six males sang a beta song. In response to the beta playback, nine males first sang an alpha song and five males sang a beta song.

Although I tested 14 males, comparisons of song between playback and control periods could be made for only 13 males because two birds did not sing during their control period and I utilized a paired statistical design. Eight of 13 males sang a higher proportion of beta songs during the control periods than during beta playback periods, and the overall difference was significant (Fig. 1a, $t = 4.17, P < 0.02$). Similarly, 9 of 13 male Bobolinks sang a higher proportion of alpha songs during the control periods than during the alpha song playback periods. However, the overall difference in means was not significant (Fig. 1b, $t = 0.93, P > 0.30$). In addition, the vocal responses of males were independent of the order of song type presentation. A comparison of the proportion of alpha songs performed during the alpha and beta playback periods showed that territorial males tended to respond with the op-

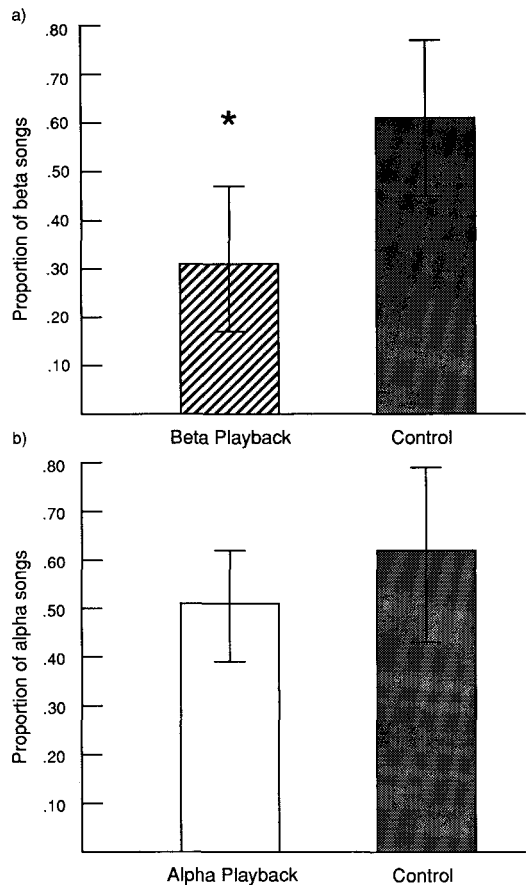


FIGURE 1. Mean proportion of song types by territorial males in response to playbacks of the alpha and the beta song: (a) the proportion of beta songs comparing beta playback with control periods, (b) the proportion of alpha songs comparing alpha playback and control periods. Vertical lines are 95% confidence limits. Sample size is 13. * indicates $P < 0.02$.

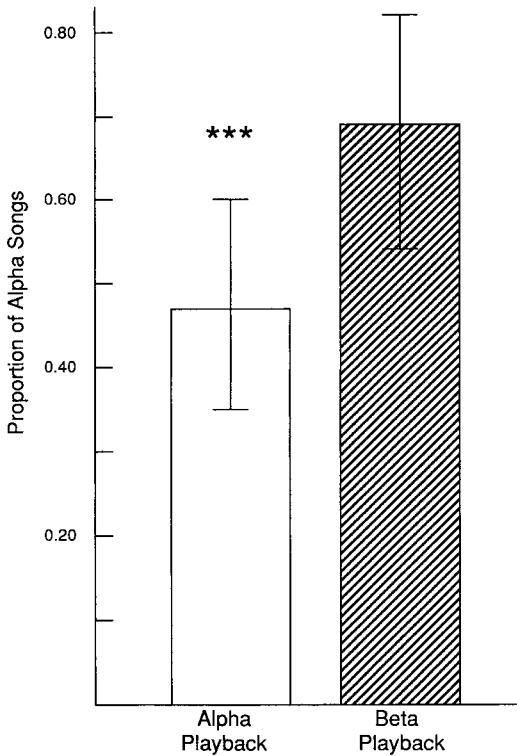


FIGURE 2. Mean proportion of alpha songs by territorial males in response to playbacks of the alpha song and the beta song. Vertical lines are 95% confidence limits. Sample size is 14. *** indicates $P = 0.001$.

posite song type from the playback. Twelve of 14 males sang a higher proportion of alpha songs during the beta playback than during the alpha playback. The mean proportion of alpha songs during the alpha and beta playback periods was 0.48 and 0.69 respectively, a highly significant difference (Fig. 2, $t = 4.17$, $P = 0.001$).

DISCUSSION

SONG SWITCHING IN INTER- AND INTRASEXUAL CONTEXTS

Several studies have shown that an increased rate of switching between song types functions as a signal of heightened aggressiveness in male-male contexts (Falls and Krebs 1975, Kramer et al. 1985). In contrast, Searcy and Yasukawa (1990) found that male Red-winged Blackbirds increased switching rates in response to female mounts and decreased switching in response to male mounts. Furthermore, it has been shown that in Meadowlarks (*Sturnella* spp.), switching between song types increases during both male-

male and male-female contexts (Falls and D'Agincourt 1982, D'Agincourt and Falls 1983). Thus, rapid switching can signal either aggression or courtship. However, territorial male Bobolinks showed no tendency to alter the frequency of song switches during either male presentations or female presentations as compared to controls. Therefore, in Bobolinks it appears that neither aggressive nor sexual motivation is signalled by variations in song switching.

SEASONAL EFFECTS ON SINGING BEHAVIOR

Results of this study suggest that differences in the seasonal context do not affect the use of the Bobolink song repertoire. Correlation analyses of song types and note types with testing date did not reveal a seasonal shift in Bobolink singing behavior and therefore provided no evidence for separate messages of the alpha and beta songs, or interior and warbled notes. The pattern of singing as the breeding season progresses may be more complicated than my correlation analyses assume, however. That is, the singing behavior of territorial males may be adjusted to specific stages of the breeding cycle—mating, nesting, incubation, and fledging. All of the males I tested were mated, but I did not know the exact stage of the breeding cycle for any of the males. A visual examination of the scattergrams for each of the song variables versus date of recording did not reveal any obvious patterns that would indicate such a relationship. However, this possibility cannot be ruled out.

The analysis I performed of Bobolink song before and after female arrival on the breeding grounds utilized the same logic inherent in Wittenberger's (1983) conclusion that the beta song functions intrasexually and the alpha song functions in mate attraction. Prior to the arrival of females and during territory establishment, it was expected that male song would be directed toward other males, reflecting their territorial activities in addition to the lack of a female audience. Upon the arrival of females, it was predicted that male song would reflect their mate attraction activities. In terms of the proposed functions of Bobolink song, the beta song and warbled notes should predominate before the arrival of females, and an increase in alpha song and interior notes should be evident after female arrival. Using this logic, I found no evidence that different messages are conveyed in Bobolink song.

There were no differences in singing rates, the use of song types, or the use of note types before and after female arrival on the breeding grounds. Thus, neither measure of seasonal effects on Bobolink singing behavior supports the separate messages hypothesis. The reason for the disparity between my results and Wittenberger's results is not immediately clear. A possibility is that singing behaviors simply differ between the two populations. My results, however, are consistent with the findings of Capp and Searcy (1991a) which provided no evidence for separate functions of song types or note types. In addition, there was no difference in the frequency of song switches before and after female arrival. This result corroborates the results of the context manipulation experiment and strengthens the argument that song switching does not signal aggressive or sexual motivation in Bobolinks.

TERRITORY LOCATION EFFECTS ON SONG

The prevailing argument is that territorial males are more aggressive near the center of their territories and that aggressiveness decreases toward the territory boundaries. If the beta song of Bobolinks functions intrasexually as proposed, and assuming that the level of aggressiveness is reflected in territory location in the predicted direction, then a higher frequency of beta song would be predicted at the territory center as compared to the territory edges. In this study there was no indication that either song types or note types were used preferentially between territory locations, and thus there was no evidence that these song variables signal different levels of aggressive motivation. However, it remains a possibility that the level of male aggression is related to particular areas of the territory such as preferred perch sites (Staicer 1989), location of nest sites (Lemon et al. 1987), or familiarity with certain portions of the territory (Waser and Wiley 1980), rather than the geographic center. Moreover, location biases in male aggressiveness may be more dependent on the proximity of conspecific intruders than on territory location per se (Simpson 1985).

PHYSICAL RESPONSE TO PLAYBACKS OF ALPHA AND BETA SONGS

Differential response of territorial males to playbacks of conspecific song variants is strong evidence that different messages are conveyed even

though meaning cannot be directly determined. Although there has been no evidence to support an intersexual function for the alpha song and an intrasexual function for the beta song in my study population of Bobolinks (Capp and Searcy 1991a, 1991b; this study), other separate messages may be conveyed by the two Bobolink song types. The importance of the playback experiment in this study was in the potential of revealing separate messages for the alpha and beta song through differential response without regard to their precise meanings. Comparisons between playback periods and controls clearly showed that the male Bobolinks of this study recognized both song types as conspecific song. It was also clear, in comparisons between playbacks of the alpha and beta songs, that territorial males do not respond differently to the two song types. Therefore, the results of this experiment provide strong evidence that the two song types do not convey different messages.

VOCAL RESPONSE TO PLAYBACKS OF ALPHA AND BETA SONGS

The male Bobolinks of this study showed no tendency to match song types. This was demonstrated by two results: (1) the first song given by males during song playback periods did not match the playback song type, and (2) the proportion of alpha and beta song types performed by territorial males was not higher during the respective playback periods as compared to controls. In the first analysis, it was assumed that the first song performed during the playback period was elicited by the playback. This may or may not be true. A future study using a relevant operational measure of response to the onset of the playback may provide a clearer analysis. The second analysis showed that territorial males tended to respond to conspecific playbacks by singing the alternate song type. This was evident in the high proportion of alpha songs performed during the beta playback as compared to controls. Whether males consistently perform beta songs in response to the alpha song is not as clear although comparisons between alpha and beta playbacks suggest this.

Several other "non-matching" patterns of countersinging have been presented in the literature. A common pattern of vocal dueling in the Marsh Wren (*Cistothorus palustris*) is for one of the birds to sing the next song in a favored and predictable sequence of song types of the

other bird (Kroodsma 1979). If such a system of countersinging were consistent, then a non-matching pattern would result. This explanation does not seem applicable to Bobolinks, however. The anticipation and matching of the next song in a sequence relies largely on the way a species presents its repertoire. Marsh Wrens sing with immediate variety and individuals have favored orders of song presentation. I have found no obvious pattern of repertoire presentation in Bobolinks. During spontaneous singing, Bobolinks may sing one song type in bouts of varying length before switching to the other song. However, immediate switching between song types is also common. Thus, the order of song types during a singing performance by Bobolinks does not have the predictability needed for anticipating the next song.

Could male Bobolinks simply be avoiding the use of songs heard on the playback? Whitney and Miller (1983) have shown that Wood Thrushes (*Hylocichla mustelina*) avoid matching playbacks of their own songs or song types of other individuals that are very similar to ones in their own repertoire. Such a program of avoidance would also produce a non-matching pattern of countersinging. The explanation given for this observation is directly related to song sequencing in that species. Wood Thrushes sing with immediate variety and it is suggested that singing (or hearing) a certain song type inhibits the immediate repetition of that song type. A similar explanation, invoking song avoidance, has been proposed for the song sequencing pattern in the Eurasian Blackbird (*Turdus merula*) (Toedt 1975). Again, this explanation doesn't appear to be applicable to Bobolinks because presenting songs in bouts is common in this species during spontaneous singing performances and, therefore, there is no apparent inhibitory effect of singing or hearing either song type.

The simplest hypothesis for explaining the pattern of singing in response to conspecific song in Bobolinks is that it is analogous to song matching. In species that have a two song repertoire, a system of singing the alternate song type in response to the song of a conspecific intruder is functionally identical to song matching. This is because the respondent has but two choices with which it can counter an intruder's song. Countering a particular conspecific song type with either song type in a systematic way suffices to signal the singer's awareness of a particular in-

truder. On the other hand, a system of "counter-matching" could not work in species that have more than two song types in their repertoire because of the ambiguity in choosing between alternative songs within and among respondents.

In summary, the results of seasonal effects, location effects, and the playback experiment are consistent in that they provide no evidence that the two different song types and note types possessed by each territorial male Bobolink convey different messages. The hypothesis that song repertoire size advertises male quality was discarded on the grounds that repertoire size is not variable between male Bobolinks. The analysis of Bobolink song in response to conspecific intruders and conspecific females did not support the hypothesis that song switching signals either aggressive or sexual motivation. The only hypothesis supported to some extent was that the Bobolink song repertoire functions in an unusual system of matched countersinging. The arguments proposed for the function of song matching in agonistic contexts are applicable to the "counter-matching" of male Bobolinks. Whether males are countering each song of an intruder with the alternate song type requires further study.

ACKNOWLEDGMENTS

I would like to thank the Livingston family, Weygant family, the Flough family, and the Pennsylvania Game Commission for allowing me to use their hayfields as my study sites. I am grateful to Susan Peters and Peter Marler for their assistance in the spectrographic analysis and to Steve Gaulin for his comments on an earlier draft of this manuscript. I am especially grateful to Bill Searcy for the invaluable discussions and many helpful suggestions throughout all phases of this study. This study was supported by NSF grants BNS-8513656 and BNS-890844 awarded to William A. Searcy.

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