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## SONG VERSATILITY AND SOCIAL CONTEXT IN THE BOBOLINK<sup>1</sup>

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**Abstract.** We contextually analyzed the song of the Bobolink (*Dolichonyx oryzivorus*) to examine the role of sexual selection on song versatility. Recordings were obtained as territorial males were randomly presented with a caged male (a conspecific intruder), a caged female (a potential breeding partner), and an empty control cage. Sound spectrograms created from the recordings were analyzed and an index of versatility was calculated for each male in each manipulation so that individual song variation could be compared among behavioral contexts. These analyses suggest that more complex or versatile song production is being selected intersexually, whereas short repetitive song is intrasexually selected.

**Key words:** *Bobolink, Dolichonyx oryzivorus, mate choice, repertoire, sexual selection, song versatility.*

Song repertoires function intersexually in stimulating females to court and copulate and intrasexually in territorial defense (Catchpole and Slater 1995). One way to test which of these functions is more important is to determine whether males emphasize their repertoires more when courting females or when acting aggressively with other males. Using this method, Searcy and Yasukawa (1990) showed that male Red-winged Blackbirds (*Agelaius phoeniceus*) increase their rate of song switching when courting females, and decrease switching rate when confronting conspecific intruders. In this paper, we take a similar approach to examine repertoire function in Bobolinks (*Dolichonyx oryzivorus*).

Bobolinks are usually regarded as having only two

song types per male (Avery and Oring 1977, Wittenberger 1983). These two song types, termed “alpha” and “beta,” are distinguishable within a given population by their unique sequences of introductory notes as well as by overall length. Because male Bobolinks often sing variations of their primary songs that include complete, fragmented, and compound configurations of varying length, we chose to classify each unique vocalization as a distinct song variant. Trainer and Peltz (1996) reassessed the repertoire of the Bobolink, originally proposed by Wittenberger (1983), and suggested that each variant can be considered as a separate song type. Defining song in this way, and using an index of versatility from information theory, Trainer and Peltz (1996) concluded that individual male Bobolinks differ in the versatility of their song.

In this study, we adopt the Trainer and Peltz (1996) approach of viewing each song variant as a song type in the Bobolink, and utilize a versatility index to examine the role of sexual selection on song versatility. We then compare song versatility of territorial male Bobolinks in both male-male and male-female contexts to test whether song pattern versatility functions in intersexual or intrasexual communication in this species.

### METHODS

The data analyzed in this study were collected from 20 May–25 June 1987 and from 14 May–28 May 1988 near the University of Pittsburgh’s Pymatuning Laboratory of Ecology in northwestern Pennsylvania. Playback of conspecific song and mist netting were employed to capture territorial males. These males were then color banded for future identification. Some test males were not captured because they displayed plumage features that made them easily recognizable. Several nonterritorial, unpaired males and a few females

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were captured early in the season for use as stimuli during testing.

Recordings were obtained as sample territorial males were randomly presented with a caged male, a caged female, or an empty control cage. The caged male, in breeding plumage, was meant to represent a conspecific intruder, whereas the caged female presumably represented a potential breeding partner. Capp and Searcy (1991a) found that the presentation of caged males and females to territorial males elicits vocal and behavioral changes similar to natural intersexual and intrasexual interactions. Each presentation was conducted on separate days and we recorded for 15-min any vocal response elicited by each stimulus. Recording sessions were performed between 05:30 and 09:30 both years. Vocal responses in 1987 were recorded using a Sony TCM-500 cassette recorder with a Sony ECM-170 electret condenser microphone and Sony PBR-330 parabolic reflector. In 1988, recordings were obtained using a Marantz PMD221 cassette recorder with a Marantz EC-3S cardioid condenser microphone and Sony PBR-330 parabolic reflector. Sound spectrograms were created using a Model 4512 Princeton Applied Research FFT Real Time Spectrum Analyzer. An index of versatility was calculated for each male in each manipulation following the methods of Trainer and Peltz (1996). The following terminology was used to define repertoire components: a note consisted of any articulation showing no gaps in a spectrograph; a song variant consisted of any unique assemblage of notes preceded and followed by at least 0.5 sec of silence.

We used the original data collected by Capp and Searcy (1991b) to determine the number and repetitions of song variants for each territorial male during each stimulus context and control period. Indices of song versatility were calculated using a function that is equivalent to the Shannon-Weiner function (H). The function used by Trainer and Peltz (1996):

$$-\sum_{i=1}^s p_i(\log_2 p_i) / \log_2 n$$

where  $n$  = number of songs recorded in the male's sample, is equivalent to the evenness index from the Shannon-Weiner formula for diversity. In their study, Trainer and Peltz recorded the spontaneous song from males to assess variability in song presentation between males without time or song limits and without concern for the natural contexts that elicited the songs. In their case, the use of the evenness function, which controls for differences in the number of songs recorded between males seems appropriate. In our study, recording periods were restricted to 15-min time limits, and territorial males were presented with caged conspecifics to assess behavioral differences between different contexts, not between different birds. An important component of singing behavior is the effort given to song by territorial males during the time frame of our manipulated contexts. In fact, Capp and Searcy (1991b) found that presentations of caged males and caged females elicited significantly higher singing rates by territorial male Bobolinks as compared to controls (i.e., empty cage). Therefore, in our study, the Shannon-Weiner diversity function:

$$-\sum_{i=1}^s p_i(\log_2 p_i)$$

which allows for a reflection of singing effort between contexts was the more appropriate index of song versatility. In this equation,  $s$  is the number of different song variants in a male's sample and  $p_i$  is the proportion of the sample belonging to the  $i$ th song variant. Indices of versatility were compared between behavioral contexts and controls. Data sets were examined for skewness, kurtosis, and homoscedasticity. Because the assumptions of parametric statistics were violated in one of our data sets, the two-tailed Wilcoxon matched-pairs signed-ranks test was utilized in all comparisons (Sokal and Rohlf 1981).

## RESULTS

Song versatility indices were calculated for each sample male so that song variation could be contextually analyzed. To evaluate the song versatility of male Bobolinks within an intrasexual context, versatility indices from caged-male presentations were compared to those of the corresponding control period. The mean ( $\pm$  SE) song versatility did not differ between male presentations ( $2.94 \pm 0.12$ ) and the control period ( $2.87 \pm 0.17$ ) ( $z = -0.26$ ,  $n = 21$ ,  $P > 0.40$ ). To assess the song versatility of male Bobolinks within an intersexual context, versatility indices from the female presentations were compared to those of the corresponding control period. Song versatility was significantly greater for the female presentations ( $3.21 \pm 0.16$ ) than the control period ( $2.88 \pm 0.18$ ) ( $z = -3.25$ ,  $n = 21$ ,  $P < 0.001$ ). To investigate song versatility of territorial male Bobolinks between behavioral contexts, versatility indices from the male presentations ( $2.96 \pm 0.12$ ) and the female presentations ( $3.22 \pm 0.16$ ) were compared. The means used in this comparison differ from the means above, as do the above control means, because we lacked a song sample in one of the contexts for two of the males. The results of this comparison indicate that song versatility was significantly greater in the intersexual (female) context ( $z = -2.39$ ,  $n = 20$ ,  $P < 0.01$ ).

## DISCUSSION

Male Bobolinks of our study sang multiple variations of the basic song patterns for this particular population. Differences in song presentation were observed between individual males, and were reflected in the range and variation of versatility indices. Singing behavior also varied between social contexts. This contrasts with the results of Capp and Searcy (1991a, 1991b) who found no direct evidence supporting a relationship between song type and intrasexual or intersexual function. They based their song classification on which of the two distinct introductory sequences initiated a song, regardless of the number of notes that were contained in one complete vocalization. However, Capp and Searcy (1991a, 1991b) did observe a trend in which territorial male Bobolinks sang longer, more complex songs during male-female contexts, and shorter songs during male-male contexts. Our results from the female presentation-control comparison suggest that male Bobolinks modify their singing behavior by including more song variants when presented

with a potential breeding partner. This is reflected in the higher versatility index and is consistent with the trend observed by Capp and Searcy (1991a, 1991b). Greater versatility in song performance may convey valuable information to females about individual male quality and/or experience. Females may indirectly benefit because larger diverse repertoires may indicate increased genetic fitness that would have an impact on offspring viability and fitness (Catchpole 1996). Although it has been shown that territorial males significantly increase their singing rate during presentations of conspecific males compared to controls (Capp and Searcy 1991b), this did not translate into differences in song versatility between these contexts. This may reflect that males allocate proportionately more song to territorial defense, which is supported by the low indices of versatility during control periods.

Comparisons between the male presentations and the female presentations clearly suggest that territorial male Bobolinks alter singing behavior between these behavioral contexts. Males responded to female presentations with more versatile singing behavior as compared to the male presentations. The lower indices during male presentations, when looked at in conjunction with Capp and Searcy's studies, suggest that males encode aggression in song through shorter, less complex songs that are highly repetitive. Searcy and Yasukawa (1990) observed similar repertoire presentation in Red-winged Blackbirds (*Agelaius phoeniceus*). However, Kramer et al. (1985) suggest that male Song Sparrows (*Melospiza melodia*) increase their song switching rates in agonistic intrasexual situations.

These analyses suggest that more complex or versatile production of song is selected intersexually and that short, repetitive song is intrasexually selected in Bobolinks. Support for these hypotheses could be gained from field studies comparing male responses to playbacks that vary in versatility. Additionally, laboratory playback experiments can be designed to test whether females are more responsive to more versatile song patterns.

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