MALE COURTSHIP VOCALIZATIONS AS CUES FOR MATE CHOICE IN THE SATIN BOWERBIRD (*PTILONORHYNCHUS VIOLACEUS*)

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ABSTRACT.—Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) court females at specialized structures called bowers. Courtship includes a complex pattern of vocalizations in which a broad-band, mechanical-sounding song is followed by interspecific mimicry. We studied the effect of male courtship displays on male mating success in Satin Bowerbirds. Data from 2 years of field research showed low between-male differences in mechanical components of courtship song and high variability between males in mimetic singing. Older males sang longer and higher-quality bouts of mimicry than did younger males. In one year, courtship song features were correlated with male mating success. The results suggest that female Satin Bowerbirds use male courtship vocalizations in their mate-choice decisions. We discuss hypotheses about assessment of male age and dominance from courtship vocalizations and suggest that these songs have evolved as a result of selection for male display characteristics that provide females with information about the relative quality of prospective mates. *Received 27 June 1985, accepted 20 September 1985.*

MALE Satin Bowerbirds (*Ptilonorhynchus violaceus*) build specialized structures called bowers that are used as sites for courting females and for mating (Vellenga 1970, Donaghey 1981, Borgia 1985). Females raise their young unassisted by males, and males do not associate with females after mating. Males decorate their bowers with a variety of natural objects and attempt to steal decorations and destroy the bowers of other males.

Much effort has been focused on understanding the role of the bower and its decorations in female mating decisions. Borgia (1985) demonstrated a skewed distribution of matings among male Satin Bowerbirds, differences among males in bower decoration and construction, and a consistent pattern of female preference for males with well-constructed and well-decorated bowers. In addition, male mating success is influenced negatively by bower destruction and decoration-stealing (Borgia 1986a, Borgia and Gore 1986).

Male courtship vocalizations are another component of male sexual display that may have important effects on female mating decisions. Male courtship is intense, involving dance movements and postures that are coordinated with the simultaneous production of complex vocalizations. The female crouches within the bower, closely observing the male during the display, and controls the outcome of the courtship either by signaling her willingness to copulate or by flying away. Given the complexity of male display and the attention females pay to displaying males, it is likely that male displays have an important effect on female mating decisions, yet there have been no detailed studies of display in any bowerbird species.

The relationship between male display and female choice in polygynous species, such as bowerbirds, in which males do not provide material benefits to females or their offspring, has been the subject of considerable speculation (Fisher 1930, Zahavi 1975, Davis and O'Donald 1976, Emlen and Oring 1977, Halliday 1978, Borgia 1979, West-Eberhard 1979, Bradbury 1981, Hamilton and Zuk 1982, Bradbury and Gibson 1983, Kodric-Brown and Brown 1984, Borgia et al. 1985). One view of the sexual selection process is that females choose mates based on characters that indicate the relative ability of males to sire fit (e.g. viable) offspring (Zahavi 1975, Halliday 1978, Borgia 1979, Hamilton and Zuk 1982, Thornhill 1980, Borgia et al. 1985). An alternative model suggests that male sexual displays are arbitrary results of the runaway process of sexual selection (Fisher 1930). This implies that female preferences have evolved that have no effect on enhancing the viability of the offspring (Lande 1981, Kirkpatrick 1982, Arnold 1983).

Developing hypotheses that separate these models has proven very difficult. One method

is to consider the evolution of male display (Borgia 1986a). Models that predict gains in off-spring viability require that male displays provide cues that allow females to assess characters important to demonstrating the quality of males as sires. For example, female preference for older males may produce offspring with high survivorship because these males have demonstrated high viability through their own survival (Trivers 1972, Howard 1974, Halliday 1978, Wilbur et al. 1978). If such a model is operating, then we expect that cues exist in males that indicate male age and that these are correlated with male mating success. Alternatively, females may prefer dominant (Borgia 1979) or disease-resistant males (Hamilton and Zuk 1982). By contrast, runaway models make no predictions about the nature of male displays and are untestable on that basis.

Our objectives here are to describe intrapopulational variation in the courtship-display vocalizations of Satin Bowerbirds, to look for correlates between male vocal patterns and other male characteristics such as age and bower quality, and to use these results to determine if the minimum conditions for male assessment models have been met.

METHODS

Field research was carried out at Wallaby Creek, Beaury State Forest, New South Wales, Australia, from August through December in 1982 and 1983. The study site is characterized by open-canopy, subtropical eucalyptus scrub forest and patches of rain forest.

Recordings of male Satin Bowerbird courtship songs were obtained with Uher 4000L and Marantz PMD 220 tape recorders, using small condenser microphones suspended in the foliage 1 m from the bower platform. Only sexual display songs at or near the bower were recorded, although male Satin Bowerbirds use a variety of calls in other behavioral settings and at places away from the bower. Observations of focal displaying males were made by field observers from blinds stationed within 10 m of the bower. In addition, a camera system was used to monitor activities continuously at bowers and to obtain records of male mating success (see Borgia 1985).

We recorded vocalizations in 1983 for 22 individual males (20 adults and 2 juveniles). Recordings from 1982 for 2 additional juveniles and 11 of the same adults were included in the analysis, for a total of 24 individuals. A mean of 12.0 vocal samples were analyzed for each male, with a total of 288 samples. Spectrographic sound analysis was performed using a Princeton Applied Research FFT Real Time Spectrum Analyzer (Model 4512). A Kay Elemetrics Digital Sono-Graph was used to prepare spectrograms.

Analysis-of-variance tests (one-way ANOVA), Spearman rank correlations (r_s), and the Student-Newman-Keuls (SNK) procedure for multiple comparisons of means were used for statistical comparisons (Helwig and Council 1982). Means are expressed as $\bar{x} \pm 1$ SD.

Because of the low amplitude of mimetic sounds (see below), it was not possible to accurately measure frequencies. However, it was apparent that quality of mimetic songs differed between males, and so a subjective method was used to produce an index of qualitative differences among mimetic songs of different males. All mimetic songs were given a score (1, 2, or 3) for "structural integrity": high-scored mimetic songs were of relatively pure tonal structure, free from broad-band and other atonal sounds produced by the singer, and were free from acoustical distortions resulting from production by the singer of other sounds during mimetic singing. Figures 2 and 3 represent several high- and low-scored mimetic songs.

To validate subjective scoring of mimetic songs, two volunteers were each given the same random sample of spectrograms taken from the analyzed data and were asked to sort the spectrograms on the basis of this three-level subjective scoring system. There was complete agreement between the results of the two independent trials and the results obtained by the author for the same sample ($r_s = 1.00$, $P < 0.001$).

RESULTS

Description of the male courtship song.—The song used by male Satin Bowerbirds during courtship (and in other specific behavioral settings; see below) consists of a long series of harsh-sounding buzzes and pulses followed immediately by a bout of interspecific mimicry. The two major portions of the courtship song henceforth will be termed the "mechanical" and "mimetic" portions.

The courtship song lasts 24.0 ± 8.2 s. Within the mechanical portion there are 2–6 ($\bar{x} = 4.2$) wide-band "long buzzes" (Fig. 1), each of which is 0.35–1.50 s long with a frequency range of 0.06 ± 0.01 to 7.39 ± 0.02 kHz. Each long buzz is separated from the next by one or more "short buzzes" (harsh sounds with a frequency range of 4.00 ± 0.03 to 7.20 ± 0.05 kHz, each of which lasts for less than 0.20 s) and several short (<0.10 s) pulselike sounds (Fig. 1). The mechanical portion of the song lasts 17.0 ± 3.2 s. For each mechanical song analyzed, the following variables were measured: the duration of
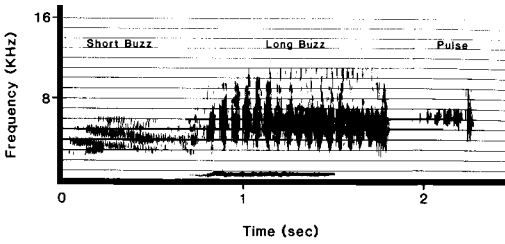
Fig. 1. Components of the mechanical portion of male Satin Bowerbird courtship song.

Fig. 3. Lewin's Honeyeater mimetic song: (A) high and (B) low scores for structural integrity. The sounds between 4.0 and 6.0 kHz are cicada calls.

the mechanical song; the numbers of long buzzes, short buzzes, and pulses; and the peak frequency (kHz), low frequency (kHz), and duration of each long buzz.

The mimetic portion of the courtship song consists of mimetic songs of either or both of two avian species: the Laughing Kookaburra (*Dacelo novaeguineae*) and the Lewin's Honeyeater (*Meliphaga lewinii*). No other bird species are regularly imitated by Satin Bowerbirds at Wallaby Creek, although individuals in other populations are known to mimic other bird species (Chaffer 1984). For the individuals in this study, when both kookaburra and honeyeater mimet-
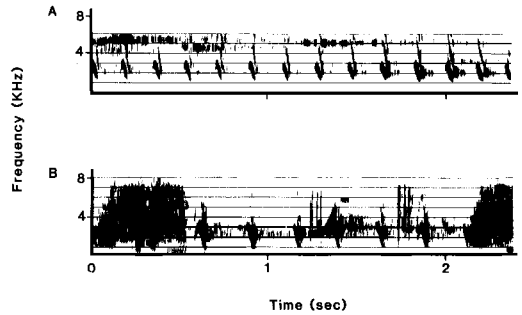
ic calls are given, the kookaburra call always precedes the honeyeater.

The kookaburra mimetic song is a structurally complex series of notes of gradually rising frequency and intensity (see Fig. 2A) and is given for 2.9 ± 1.6 s. The honeyeater call consists of a long train of simple, highly discrete notes of constant frequency (2.80–3.36 kHz). The notes are repeated rapidly for 4.0 ± 2.7 s (see Fig. 3A). For each mimetic song analyzed, the total mimetic, kookaburra, and honeyeater durations were measured.

Male courtship songs, age, and mating success.— For all 12 song variables measured, ANOVA tests indicated that a significant proportion of variability in these measurements was a result of between-male differences. For these variables, the average F-value was 4.24 (range: 2.26–6.51; each F significant at $P < 0.05$), and the average proportion of variability explained by differences among individuals (r^2) was 0.312 (range: 0.224–0.459).

We tested to determine if differences in the time of year at which the songs were recorded or if differences in behavioral settings affected song characteristics. Means for one- and two-week intervals were calculated for song variables in both years. Multiple comparisons of means (SNK) revealed no significant differences. Behavioral contexts in which recordings were obtained included male courtship songs given to females at the bower site, to juvenile and adult males at the bower, at empty bowers (i.e. no other conspecifics present), and from tree perches. Multiple comparison tests (SNK) of mean song characteristics by behavioral setting indicated that only songs given from tree perches differed significantly from other songs.
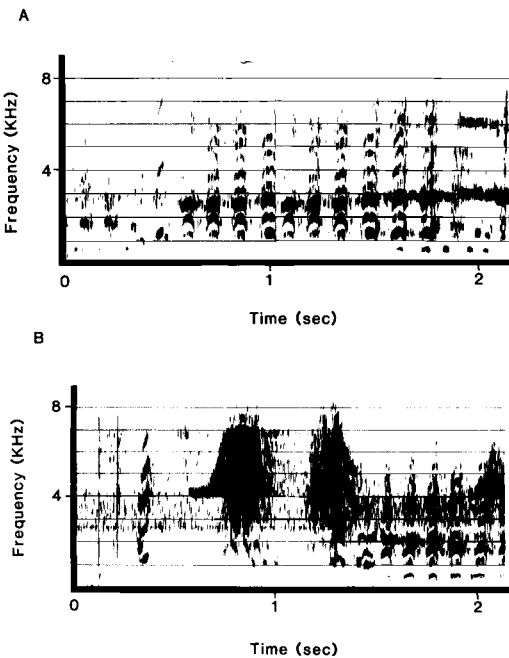

Fig. 2. Laughing Kookaburra mimetic song: (A) high and (B) low score for structural integrity. Note band of cicada calls between 3.5 and 4.0 kHz.

TABLE 1.   Comparisons of male age with mechanical and with mimetic song variables. SI = structural integrity.

	1982		1983	
	r_s	P	r_s	P
Mechanical song	$(n = 13)$		$(n = 22)$	
Mechanical duration	0.022	NS	−0.062	NS
Peak frequency	0.167	NS	0.046	NS
Low frequency	0.124	NS	0.065	NS
Frequency range	0.072	NS	−0.166	NS
No. of long buzzes	−0.073	NS	−0.073	NS
No. of short buzzes	0.071	NS	0.011	NS
Mimetic song	$(n = 13)$		$(n = 22)$	
Mimetic duration	0.217	0.001	0.621	0.001
Kookaburra duration	0.813	0.002	0.459	0.023
Kookaburra SI	−0.457	0.001	−0.743	0.001
Honeyeater duration	0.225	0.034	0.381	NS
Honeyeater SI	−0.334	0.001	−0.621	0.002

Data on tree songs constituted a very small part of the sample, and these data were excluded from further analysis.

Having demonstrated intermale variability in male courtship singing, we then divided the individuals into seven age categories based on known histories of uniquely color-banded individuals (see Borgia 1985). Male age was correlated significantly with mimetic but not with mechanical song features (Table 1). Older males tended to give songs with significantly longer mimetic portions than did younger males. The mimetic songs also varied qualitatively with age: in both 1982 and 1983, older males gave kookaburra and honeyeater calls of higher structural integrity than did younger males.

Even when juvenile males were excluded from analysis, adult males showed significant age-correlated differences in mimetic singing.

In 1982, there was a significant correlation of male mating success and the number of short buzzes in the mechanical song (Table 2), but this correlation was not significant in 1983. None of the other mechanical song variables measured was significantly correlated with mating success in either year. Mimetic songs showed a similar pattern (Table 2): in 1982, male mating success was significantly correlated with total mimetic duration and with kookaburra structural integrity, while in 1983 there were no significant correlations of any mimetic song variables and male mating success.

TABLE 2.   Comparisons of male mating success with mechanical and with mimetic song variables. SI = structural integrity.

	1982		1983	
	r_s	P	r_s	P
Mechanical song	$(n = 11)$		$(n = 22)$	
Mechanical duration	−0.484	NS	−0.357	NS
Peak frequency	0.355	NS	0.067	NS
Low frequency	0.429	NS	0.232	NS
Frequency range	0.050	NS	0.126	NS
No. of long buzzes	0.104	NS	−0.069	NS
No. of short buzzes	−0.706	0.003	−0.363	NS
Mimetic song	$(n = 11)$		$(n = 22)$	
Mimetic duration	0.774	0.040	0.007	NS
Kookaburra duration	0.270	NS	0.073	NS
Kookaburra SI	−0.635	0.024	0.080	NS
Honeyeater duration	0.522	NS	0.226	NS
Honeyeater SI	−0.079	NS	−0.234	NS

TABLE 3.   Comparisons of mimetic song types with male age and mating success.

| Percentage of songs with: | Age | | Mating success | | | |
| | | | 1982 | | 1983 | |
	r_s	P	r_s	P	r_s	P
Both mimetic types	0.220	NS	−0.086	NS	−0.239	NS
Only kookaburra	0.282	NS	−0.272	NS	0.050	NS
Only honeyeater	−0.237	NS	0.387	NS	0.025	NS
No mimicry	−0.349	NS	0.275	NS	0.033	NS
	(n = 24)		(n = 11)		(n = 22)	

Male Satin Bowerbirds do not invariably mimic both kookaburra and honeyeater calls each time they sing a courtship song. To test whether this variability is related to either age or mating success, we compared male age and mating success with the proportion of songs containing only kookaburra calls, those with only honeyeater calls, those with both types, and those with no mimicry at all. No significant correlations were found for either year (Table 3). There were no birds in the study that "specialized" exclusively in either one of the mimetic types, and all birds sang mimetic songs.

Spearman rank correlations were used to test for relationships between song features and bower quality and between song features and bower decorations (Table 4). Of the song variables measured, only the mechanical song duration was significantly correlated with bower quality (but only in 1983). Mechanical song duration was also correlated significantly with the total number of bower decorations (both years), but no other song variables (except honeyeater structural integrity and the low frequency of

long buzzes in 1982) were correlated with decorations.

DISCUSSION

We have described the relationship between intrapopulational patterns of male Satin Bowerbird courtship songs and characteristics such as male age and bower quality. Male age and mating success were positively correlated in both years (Borgia 1986b), so it appears that female Satin Bowerbirds prefer older males as mates. The significant correlation of male mating success with age-correlated features of songs in 1982, but not in 1983, suggests that females may use songs to assess male age. Male age is also positively correlated with bower quality (Borgia 1986b), which could provide another mechanism by which females can assess male age. However, the low correlation of courtship song variables with measures of bower quality indicates an independent effect of each of these factors on male mating success. These results are consistent with the hypothesis that male

TABLE 4.   Comparisons of song variables with decorations and bower quality. SI = structural integrity.

| Song feature | Bower quality | | Total no. decorations | |
| | 1982 | 1983 | 1982 | 1983 |
	P	P	P	P
Mechanical duration	NS	0.033	0.030	0.038
Peak frequency	NS	NS	NS	NS
Low frequency	NS	NS	0.033	NS
Frequency range	NS	NS	NS	NS
Number long buzzes	NS	NS	NS	NS
Number short buzzes	NS	NS	NS	NS
Mimetic duration	NS	NS	NS	NS
Kookaburra duration	NS	NS	NS	NS
Kookaburra SI	NS	NS	NS	NS
Honeyeater duration	NS	NS	NS	NS
Honeyeater SI	NS	NS	0.001	NS
	(n = 11)	(n = 22)	(n = 11)	(n = 22)

courtship vocalizations function as age markers, independent from other aspects of male display, and as indicators of male genetic quality.

Several observations suggest that Satin Bowerbirds learn and practice mimetic singing. In other populations of Satin Bowerbirds mimetic songs exhibit much variation both within and between populations, while other song features are rather invariable (Loffredo and Borgia in prep.). Further, male bowerbirds, especially young males, spend a great deal of time both within and outside of the breeding season performing their displays (Vellenga 1970, Chaffer 1984, Borgia in prep.). Together with our observations of age-related increases in the quality of songs, these results suggest that learning and practice may be important in the use of mimetic songs, as appears to be the case in other avian species that use interspecific mimetic singing (Nottebohm 1972, Payne 1973, Howard 1974, Catchpole 1980). The use of mimetic songs by Satin Bowerbirds may have resulted from selection for reliable age cues (Zahavi 1977, Borgia 1979, Kodric-Brown and Brown 1984). These songs are reliable because they require learning and practice, and thus young males cannot easily "cheat" (if females prefer older males) by sounding like older individuals.

Another model concerning the role of male courtship songs in influencing female choice is the male dominance model. Dominant males may be preferred as mates because they are able to demonstrate their vigor relative to other males through aggressive interactions (Alexander 1975, Cox and LeBoeuf 1977, Borgia 1979, Borgia et al. 1985). This prediction is supported by observations that female Satin Bowerbird mating decisions are affected by indicators of male dominance such as bower destruction (Borgia 1986a) and feather stealing (Borgia and Gore 1986). Loud vocal displays may attract more attention from competing males than do low-amplitude displays; thus, a male's ability to give a loud courtship song without interruption from neighboring males could provide evidence to a female of a male's dominance status (Borgia 1979; but see Foster 1983, Bradbury and Gibson 1983). We could not quantify the vocal data adequately to test this hypothesis. However, after listening to many calls we heard no apparent amplitude differences among males.

Courtship songs are coordinated with male dancing at bowers. Intermale differences have not yet been quantified for these dances. It is likely that female choice of male characteristics depends on the assessment of interacting characters. The failure to explain a large proportion of variation in male mating success with vocal display data may be due to the absence of data on dancing. In addition, the lack of significant correlations of mating success with vocal display data in 1983 may be due to the early commencement of breeding that year, which resulted in a highly atypical breeding season.

The present study suggests that male courtship songs contribute to the process of female mate choice by allowing females to estimate male age. Differences among males in courtship vocalizations explain some of the variation between males in their mating success. These results are consistent, at least for one year of this study, with models that suggest that females assess male age and use this as an indicator of male quality as a sire. We cannot exclude the possibility that the songs have evolved through runaway sexual selection in which females have evolved preferences for certain features of male display vocalizations independent of male quality. This is an interesting possibility because it differs from the tightly genetically programmed features commonly discussed in runaway sexual-selection models. It suggests that female preference for exaggerated male display has led to selection in males for the ability to learn complicated songs.

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