Original Article (原著論文)

How Interacting Multiple Male Sexual Signals Influence Female Choice in the Great Bowerbird

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Abstract. Male courtship displays commonly involve multiple sexual signals. While there has been considerable interest in female choice for male multiple signals, few studies have investigated how these signals interact. We analyzed courtship behaviours of male Great Bowerbirds *Chlamydera nuchalis*, which include both acoustical elements, including ticking sounds of three types (SS, MS and LS), and locomotive elements, including dancing around the bower. Our results show that the ticking sounds played an important role in female choice. Males that uttered more LS sounds (louder and longer than the other two types) attracted more females, which suggests that intense display enhances mating success. In addition, males uttering more LS type calls had a larger bower, which suggests that a large bower provides females a safe protection against male's vigorous display and that the male can perform display more intensely. These results show that the multiple signals interacted with each other.

Key words: Bower, Courtship display, Female choice, Great Bowerbird *Chlamydera nuchalis*, Multiple sexual signals.

キーワード: あずまや, 求愛ディスプレイ, メスの選り好み, オオニワシドリ *Chlamydera nuchalis*, 多重的性的シグナル.

Introduction

Males of many species have multiple sexual display traits (Andersson 1994). There has been a great deal of interest in how multiple male display traits evolve and how they are maintained (e.g. Møller & Pomiankowski 1993, Johnstone 1996). To understand the evolution of multiple traits, it is critical to understand how each trait influences female choice (e.g. Borgia 1995a, Gibson 1996, Rowe 1999, Kodric-Brown & Nicoletto 2001). Yet there have been few studies of signal interaction.

The bowerbirds form a distinctive passerine family (Ptilonorhynchidae) that is endemic to Australia and New Guinea, comprising twenty species in eight genera (Frith & Frith 2004). Bowerbirds have the most complex set of displays among all organisms. Except in the case of the catbirds *Ailuroedus*, male birds of all species build specialized structures called bowers. The bower is a structure, typically comprised of sticks, placed beside a display court on the ground (Gilliard 1963, Frith & Frith 2004). Two types of bowers can be distinguished, based on their form; maypoles and avenues. A maypole

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bower is a large accumulation of epiphytic orchid stems, sticks, or other vegetation whereas an avenue bower is composed of two parallel walls creating a central avenue, which the female enters for courtship and copulation (Frith & Frith 2004). Females raise their young unassisted by males, and males do not associate with females after mating.

The collection of building materials for the bower, and of the decorations that are piled up around them, probably imposes high time and energetic costs on the male. For example, the Golden Bowerbird *Prionodura newtoniana*, a maypole-type bower builder, builds two towers about 2m in height (Frith & Frith 2004). Even among the avenue building species, one male bowerbird carried about 2,000–5,000 sticks to a bower (Frith & Frith 2004). To date most behavioural studies of bowerbirds have investigated the relationship between mating success and the characteristics of bowers and decorations (Vellenga 1970, 1980, Borgia 1985, 1995a, 1995b, Borgia & Mueller 1992, Doucet & Montgomerie 2003, Madden 2003). However, bowers and display courts provide a stage for male behavioural displays that include plumage, acoustical and locomotive elements, directed at a female during courtship. Nevertheless, the role of behavioural displays in female mating decisions has attracted attention only relatively recently.

Bowers are attractive to females, and males with well-built bowers mate proportionately more often than those with bowers of lower quality, which indicates that bowers play an important role in mate attraction (Borgia 1985, 1995b, Borgia & Mueller 1992). The indicator hypothesis suggests that females may be able to assess the quality of the bower (Borgia *et al.* 1985). In Satin Bowerbirds, *Ptilonorhynchus violaceus*, however, females also prefer the most intensely displaying males as mates (Borgia & Presgraves 1998, Patricelli *et al.* 2002). These displays may serve as indicators of genetic or proximate benefits (Andersson 1994), but they can also threaten females, because they involve sudden movements and are similar to male-male aggression displays (Borgia & Presgraves 1998), and because females are at risk of forced copulation by courting males (Borgia 1995b). Female Spotted Bowerbirds, *Chlamydera maculata*, prefer to mate with males that give highly aggressive courtship displays, and bowers have coevolved to reduce the threat of these displays to females (Borgia 1995a, Borgia & Presgraves 1998). When the wall between the male and female was experimentally removed, courting males reduced the intensity of their displays (Borgia & Presgraves 1998). These studies suggest that the function of bowers is threat reduction from male courtship displays.

The Great Bowerbird (*Chlamydera nuchalis*) is distributed across northern Australia, with one subspecies (*C. n. nuchalis*) in the northwest and the other (*C. n. orientalis*) in the northeast (Frith & Frith 2004), but relatively little is known about either subspecies. This species builds an avenue-type bower with sticks and piles of various materials like land snail shells, bones of mammals, green fruits, and human-made materials (glasses, metals and plastics) in and around the bower. The sexual display of the male Great Bowerbird also involves unique behavioural display traits. In this study, we tested the prediction that intense displays are attractive to females by collating the male mating success with variables that might indicate the level of intensity in male courtship. Energetic display is costly for a male and is likely to be an honest signal conveying his quality to a female. The Great Bowerbird is sexually dimorphic in body size, a male being

larger than a female (Frith & Frith 2004; personal observation). Robson *et al.* (2005) demonstrated that the mating success of male Satin Bowerbirds was related not only with behavioural and bower displays but also with their body size. We, therefore tested whether the level of display intensity is correlated with the body size.

Bowers of Great Bowerbirds vary substantially in size among owners (Y. Katsuno & T. Okida, personal observation). In this study, we also tested whether larger bowers attracted females, and whether bowers served to reduce the threat to females. If a bower has a threat reduction function, well-build (large) bowers allow owners to display more intensely than small bowers. Therefore, we examined the relationships between bower size and display intensity.

Methods

Study area

The study area, about 20 km², was located at Coomalie Farm (13°00' S, 131°08' E), 85 km south of Darwin, Northern Territory, Australia. The dominant vegetation type is tall savanna woodland comprising various *Eucalyptus* and *Corymbia* species, with a grassy understorey, dominated by tall annual spear grass *Sarga* spp. and perennials such as *Heteropogon contortus*. Fires occur annually during the dry season (May–October), burning off the grasses, although late fires also scorch the canopy.

Banding and monitoring at bowers

Sixteen Great Bowerbird bowers were found at the study site in 2005. Individual birds were captured using mist nets both at feeding and bower sites in 2005. Individual birds were banded with unique, three-color plastic band combinations on each leg. We measured wing length, tail length, tarsus length and weight of captured birds. In total, twelve owners were captured. From 27 August to 9 December 2005, we recorded behaviours of owners with digital video cameras at twelve bowers. We monitored bowers for two hours per day during the morning (06 : 00–12 : 00). Total monitoring time was 27 days (=54 hours) at each bower. All individuals with the lavender-pink nuchal crest are males (Y. Katsuno, unpublished data), so visitors without such a crest were treated as females. Not all visitors that were courted at bowers were females. We also observed banded males courting other marked males.

Male behavioural displays analysis

All of the 116 courtships recorded on videos were scored for duration and outcome (copulation or no copulation). At some bowers, we could not collect sufficient recordings because males courted at the opposite side of the bower or voice data were disturbed by noise. We omitted such males from the analysis. Forty-five courtships of seven owners were analyzed in detail.

Warham (1962) separated courtship displays into central and peripheral ones. The male typically starts his display from the corner of the bower near the bower entrance. Here he performs a stationary display by leaning forward and turning his head to expose

Table 1. The duration of courtship displays (n=45).

	Mean	SD	Range
Total display time (s)	88.5	37.3	35–207
Central display time (s)	67.4	31.8	23–161
Central display time / Total display time (%)	78.6	12.6	31.65–97.92

Fig. 1. Spectrogram of typical ticking calls of the Great Bowerbird, showing the acoustic parameters considered in this study: (a) length of each ticking sound type (SS, MS, LS). (b) time interval between two successive sounds (showing SS interval as an example).

his nuchal crest to the female (Frith & Frith 2004). He repeats to bob his head, and picks up a decoration with his beak, then drops it. In this study, a “Central display” was defined as a series of these stationary displays performed around the entrance of the bower. During the display he utters ticking sounds continuously. “Peripheral displays” were defined as a series of hopping and walking displays performed along the outside of the bower wall towards the far end of the bower. During the Peripheral display, the male

Table 2. Characteristics of ticking calls in Central display (n=7).

	Mean	SD	CV
SS length (ms)	79.08	1.32	0.02
MS length (ms)	124.37	1.32	0.01
LS length (ms)	172.47	2.64	0.02
SS interval (s)	0.42	0.11	0.27
MS interval (s)	3.04	0.34	0.11
LS interval (s)	3.30	0.28	0.09
SS rate	0.19	0.09	0.47
MS rate	0.17	0.03	0.17
LS rate	0.09	0.02	0.24

often walks in a forward-bent posture, with the crest opened and wings stretched horizontally. Central displays are often interrupted by Peripheral displays, after which the male returns to where he began the Central display and resumes it. As Central displays represented most of the courtship display ($78.6 \pm 12.6\%$; Table 1), we analyzed their characteristics, excluding the final part of the display that ended in copulation activity as the latter is obviously repressed during courtship. As noted above, the male's Central display is mainly composed of two behaviours, picking up decorations and uttering ticking calls, often closely watched by females (T. Okida, personal observation). Therefore, we measured the rate at which decorations were picked up and, performed spectrographic analysis of ticking calls with Avisoft-SASLab Light for Windows (Avisoft Bioacoustics). Ticking calls were divided into three types (SS, MS and LS) based on the spectrographic pattern of the note (Fig. 1). The SS type was a brief, soft note that was repeated at short intervals. At the other extreme, the LS type was a loud and relatively long note, repeated at long intervals of about three seconds. The MS type was similar to the LS type except for its shorter length. For each call, we selected and measured the following structural features: the call rate (the number of notes divided by the duration of the Central display, in seconds), length of a note (Fig. 1a), and the time interval between two successive notes (e.g. SS–SS interval: Fig. 1b). The length of each call type varied little among owner males, whereas variations in SS–SS interval, SS rate and LS rate were large (Table 2).

Size of bower

The characteristics of twelve bowers were measured on three occasions in 2005 (5 August–26 August, 9 October–20 October, 26 November–2 December) to obtain averaged values for each bower. For each bower we measured the height, width, and length of bowers (Fig. 2), then calculated its size (= width x length) and volume (= width x length x height) for use in the following analysis.

Male body size and mating success

Each male's attractiveness to females was gauged by his mating success, which was measured as the number of females that mated with him during each over all observations (Fig. 3). We used wing length, tarsus length and body mass as a measure of the male's

Fig. 2. Measurements taken on bowers.

Fig. 3. The distribution of copulations among males of the study population in 2005. Males are ranked by decreasing numbers of copulations observed.

body size.

Statistical analyses

We used a multiple regression analysis to relate the characteristics of male courtship displays with mating success. Because some traits of ticking calls correlated with each other, we performed principal component analysis in order to reduce the number of variable and used the first two principal components of these traits (intervals and rates of three sound types; Table 2) as independent variables. One trait of locomotion (the rate at which decorations were picked up) was also included in the analysis. Because variances were very small, lengths of notes were not included in the model (Table 2). Next, we

conducted a multiple regression analysis to identify parameters influencing male mating success, considering only the first-order interactions. By the stepwise method, we selected two best-fit models based on the Akaike Information Criterion (AIC). For all data analyses we used the R statistical package (<http://cran.r-project.org/>). Means are expressed with SD.

Results

Male behavioural display traits and mating success

PC1 and PC2 accounted for about 77% of the variance among the six call variables. PC1 appears to capture most of the variation caused by LS interval, MS rate, and LS rate (Table 3). While the signs of eigenvectors for both LS interval and MS rate were positive, those for LS rate was negative. Therefore, PC1 is a factor decreasing LS rate and, simultaneously, increasing MS rate. PC2, on the other hand, decreased SS rate while increasing SS interval (Table 3).

In the multiple regression analysis Model 1 including only PC1 had the smallest AIC, while the second best fitted model (Model 2) included both PC1 and Pick-up rate (Table 4). In both models, only PC1 had a significant influence on mating success, which indicated that males with a higher LS rate, and lower MS rate, enjoyed higher mating success. There was a significant positive correlation between LS rate and male mating success ($r=0.96$, $n=7$, $P<0.001$, Fig. 4).

In individual display events, there was a positive correlation between LS rate and Pick-up rate ($r=0.61$, $n=45$, $P<0.0001$, Fig. 5). Such a positive correlation was also seen among males ($r=0.69$, $n=7$, $P=0.084$).

Table 3. Details of the first two principal components of ticking calls uttered by bower-owning males during the Central display.

	Eigenvalues	Cumulative percent	Eigenvectors					
			Interval			Rate		
			SS	MS	LS	SS	MS	LS
PC1	3.48	58.02	-0.23	-0.38	0.50	0.32	0.49	-0.45
PC2	1.13	76.79	0.74	0.03	0.22	-0.52	0.18	-0.32

Table 4. Parameter estimates for multiple regression of mating success.

	R ²	R ² *	P	AIC	Intercept	PC1	Pick-up rate
Model 1	0.82	0.79	0.005	1.48	2.57	-1.05**	
Model 2	0.85	0.77	0.023	2.40	-0.93	-0.97*	16.33

R²*: adjusted R².

* $P<0.05$, ** $P<0.01$.

PC2 and all interactions were excluded from models as a result of the stepwise treatment.

Fig. 4. The relationship between mating success and mean LS rate among bower-owning male bowerbirds. Mating success indicates the number of copulations during the 27-days observation period.

Fig. 5. The relationship between LS rate and Pick-up rate.

Fig. 6. The relationship between mean LS rate and wing length of bower-owning male bowerbirds.

Male behavioural display traits and body size

The mean LS rate was significantly correlated with the wing length of owner males ($r=0.78$, $n=7$, $P=0.038$, Fig. 6), but not significant with the tarsus length ($n=7$, $P>0.50$). The mean LS rate was not significantly correlated with body mass either ($n=7$, $P>0.70$). However, body mass data of one male was extraordinarily larger, 258 g, nearly at a maximum of body mass data reported so far (Frith & Frith 2004). If this data was

Fig. 7. The relationship between bower size and mean LS rate of male bowerbirds.

excluded from the dataset as an outlier, the correlation was positive, although still marginal ($r=0.75$, $n=6$, $P=0.086$).

Bower size and mating success

We tested the hypothesis that females use bower size as a cue in mate choice. The related prediction is that bower size correlates with the male body size and/or male mating success. Both size and volume of a bower were positively correlated with mating success, but not significant (size: $r=0.437$, $n=12$, $P=0.155$; volume: $r=0.425$, $n=12$, $P=0.168$). The size and volume of a bower were not significantly correlated with either of three body size parameters, $P>0.50$ ($n=12$) for wing length, tarsus length and body mass, respectively.

Relationship between bower size and courtship traits

Finally we tested the prediction that larger bowers enable males to display more intensely. Bower size was significantly correlated with mean LS rate ($r=0.80$, $n=7$, $P=0.031$, Fig. 7). There was a positive, but not significant, correlation between bower volume and LS ticking call rate ($r=0.62$, $n=7$, $P=0.140$).

Discussion

The function of behavioural display

Our study focused on the Central displays of great bowerbirds, which include both visual (picking up decorations) and acoustical (ticking call) elements. Ticking calls were divided into three types (SS, MS and LS) based on the spectrographic characters. SS calls were a soft and short, and repeated at brief intervals. On the other hand, MS and LS calls were loud and relatively long. The LS rate was correlated with male mating success, suggesting that LS calls are closely related in courtship displays, and that the acoustic display has an important role in female mate choice. Males uttering longer ticking notes, more frequently, attract more females.

The rate at which males gave LS calls was positively, but marginal, correlated with their rates of picking up decorations. Therefore, the LS rate may be the primary indicator of display intensity in male courtship displays. Intense male displays may be attractive to

females as seen in the Satin Bowerbird and Spotted Bowerbird (Borgia 1995a, Borgia & Presgraves 1998, Patricelli *et al.* 2002). Because larger males are able to perform display more vigorously, intense display could be an honest sexual signal conveying male's quality.

Males typically display from the corner of the bower near the bower entrance, where they are partially hidden behind the bower wall from the female (T. Okida, personal observation). Acoustic displays may therefore be the most efficient way to provide information to a female about his quality.

Female Satin Bowerbirds visit multiple males to compare their displays, then return and finally copulate with a single male (Uy *et al.* 2001). In the Great Bowerbird, it is unknown how females choose a male. In this study, however, we analyzed male Great Bowerbirds' courtships without copulation, and show that ticking calls play an important role in female mate choice. This result suggests that female Great Bowerbirds also use signal information of males before copulation.

The function of the bower

The bower is another component of the male's sexual display. Female Satin Bowerbirds prefer males with well-built and well-decorated bowers (Borgia 1985, Borgia & Mueller 1992), indicating that bowers and their decorations play an important role in mate attraction. In this study, we represented bower size by the area occupied with walls and avenue. Bower size was positively, but not significantly, correlated with mating success in the Great Bowerbird. On the other hand, bower size was not correlated with any parameters of male's body size at all. These facts suggest that a bower has some functions other than a sexual signal conveying male's quality to females.

In the Spotted Bowerbird, when the wall between the male and female was experimentally removed, courting males reduced the intensity of their displays (Borgia & Presgraves 1998). This result suggests that the bower wall allows the male to perform his display more intensely. In this study showed that bower size (but not volume) was marginally correlated with the rate of ticking calls, indicating that larger bowers enable males to display more intensely. We have often observed that when females were startled from the bower, males ceased movement and vocalizations, and resumed only when the female returned to the bower (T. Okida, personal observation), indicating that bowers still play an important role in male courtship displays in this species. Bowes may influence female mate choice indirectly, rather than directly, by enhancing the intensity of the male display.

Several elements of the male great bowerbird's courtship display appear to collectively contribute to their overall mating success. Robson *et al.* (2005) showed that different displays had different function to enhance the mating success in the Satin Bowerbird: 'solitary display' (= display performed when no other birds were in or near a bower) for enhancing female visiting rates and painting behaviour for enhancing copulation rates. In this study, we analyzed the behavioural display performed by the bower owner to females. The male Great Bowerbird utters a large harsh call at his bower (personal observation), which may attract females to his bower. Such an advertisement call, singing and dancing display to visiting females and bower structure may constitute a

set of multiple signals. However further experimental studies are required to clarify how individual signals interact and whether the intensity of a male's behavioural display is constrained by his quality, i.e. ability can refer to vocal, or the size of his bower.

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オオニワシドリにおけるオスの性的シグナル間の相互作用とメスの 選り好みへの影響

多くの動物では、オスは複数の手段で求愛ディスプレイを行うことが知られている。このような多重の性的シグナルに対するメスの選り好みについては多くの研究がなされているが、シグナル間の相互作用についてはほとんど研究がない。著者らは、オオニワシドリ *Chlamydera nuchalis* の求愛ディスプレイを分析し、性的シグナル間の相互作用と、交尾成功との関連を明らかにした。本種ではオスがあずまやを作りメスを誘引するが、あずまやを訪れた雌に対して盛んにディスプレイ行動を行う。あずまやと行動ディスプレイは異なる性格の性的シグナルである。行動ディスプレイには、音声的要素としての「チッチッ」音と、運動的要素としてのあずまやの周辺でのダンスが見られた。「チッチッ」音には3つの異なるスペクトル型 (**SS**, **MS**, **LS**) があり、メスの選り好みに重要な役を果たし、大きく長い **LS** 型の音声をよく発するオスはより多くのメスと交尾できた。この事実は激しいディスプレイは交尾成功を高めることを示唆している。さらに、**LS** 型音声をよく発するオスのあずまやはより大きかった。この事実は、あずまやはメスにオスの激しいディスプレイからの安全な場所を提供し、これによりオスはディスプレイの激しさをさらに高めることができることを示唆している。これらの結果は、異なる種類の性的シグナルが相互に作用し合っていることを示している。

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