

Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality

Stéphanie M. Doucet and Robert Montgomerie

Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

Much attention has been devoted to understanding the evolution of elaborate male ornaments and how they may signal male quality. However, the evolution of multicomponent sexual signals remains poorly understood, and past research on this type of signaling has been largely theoretical. Satin bowerbirds, *Ptilonorhynchus violaceus*, are polygynous, are sexually dichromatic, and construct sexually selected display structures (bowers): a model system for investigating the evolution and signal function of multiple sexual signals. We studied the interrelationship between bower features, plumage coloration, and indicators of male quality in this species. To do this, we located the bowers of male satin bowerbirds in rainforest in Queensland, Australia, and quantified bower quality. We captured the male bower owners and used reflectance spectrometry to objectively measure the plumage coloration of several body regions. We measured various indicators of male health and condition, including the intensity of infection from ectoparasites and blood parasites. Bower quality and male ultraviolet plumage coloration were significantly correlated. By using multiple regression analyses, we show that bower quality predicts ectoparasite load and body size, whereas ultraviolet plumage coloration predicts the intensity of infection from blood parasites, feather growth rate, and body size. Our findings support the multiple messages hypothesis of multicomponent signals: Female satin bowerbirds should assess both male and bower features to choose the highest quality mates. *Key words*: bowerbirds, bowers, honest advertisement, multiple ornaments, parasites, plumage color, sexual selection, structural colors. [*Behav Ecol* 14:503–509 (2003)]

Elaborate, secondary sex traits are often presumed to communicate aspects of male quality to discriminating females (Andersson, 1994). In many species, elaborate sexual displays involve several distinct signals such as plumage ornamentation, song, and display behavior. Some theoretical models have shown that, under certain circumstances, species could evolve multiple quality-revealing sexual ornaments (Johnstone, 1995a), but other models propose that honest advertising should favor a single most-revealing signal at the expense of others (Johnstone, 1996; Schluter and Price, 1993). Despite some theoretical consideration (Johnstone 1995a, 1996; Schluter and Price, 1993), the evolution of multiple quality-indicating sexual ornaments has received little empirical support (for exceptions, see Johnstone, 1995b). In many species, the evolution of more than one sexual signal can be more accurately attributed to Fisherian arbitrary selection (Fisher, 1958; Møller and Pomiankowski, 1993; Pomiankowski and Iwasa, 1993), signal amplification (Hasson, 1989), enhanced signal detection (Rowe, 1999), or to distinct signals intended for different receivers (Pryke et al., 2001a,b).

In satin bowerbirds, *Ptilonorhynchus violaceus*, males clear display courts, build bowers (elaborate structures constructed from twigs), and decorate the bower platform with a variety of colorful natural and human-manufactured objects (see Marshall, 1954). Females of this species observe male courtship from within the bower avenue, and the sexual display of courting males incorporates song mimicry, ritualized prancing, and brilliant plumage coloration. Because different components of the male satin bowerbird's display will vary

on different time scales (daily for bowers and yearly for plumage color), these multicomponent sexual signals may reveal different aspects of male quality (Johnstone, 1995b; Møller and Pomiankowski, 1993), and females may thus obtain useful information from evaluating all components of male display.

In satin bowerbirds, individual variation in the quality of bower construction, the numbers and types of decorations adorning the bower platform, and age-correlated features of courtship song are known to influence female choice of copulation partners, as measured by male mating success (Borgia, 1985b; Lofredo and Borgia, 1986). In contrast to other features of the sexual display of male satin bowerbirds, the structurally based iridescent plumage of males has received less attention, even though this species is highly sexually dichromatic and plumage ornamentation is a prominent feature of male courtship display. Recent studies of other bird species have shown that structural plumage coloration can honestly signal condition (Doucet, 2002; Keyser and Hill, 1999), male quality (Keyser and Hill, 2000), and viability (Sheldon et al., 1999). Thus plumage coloration may be a quality-indicating mechanism in male satin bowerbirds and may function as a key component of a complex, multimodal sexual signal of male quality. In the present study, we investigated how multicomponent sexual signals can potentially reveal male quality in this species by studying the relationship between male plumage coloration, bower features, and various indicators of male health and condition.

METHODS

This study was conducted from September–December 2000 in a 700-ha study area in Mount Baldy State Forest, Queensland, Australia (17°30' S, 145°30' E). The dominant habitat was rainforest with a sharp transition to wet sclerophyll forest at the northeastern edge of our study area. We located 12 satin bowerbird bowers in our study area by listening for male

Address correspondence to S.M. Doucet, who is now at the Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849, USA. E-mail: doucets@auburn.edu.

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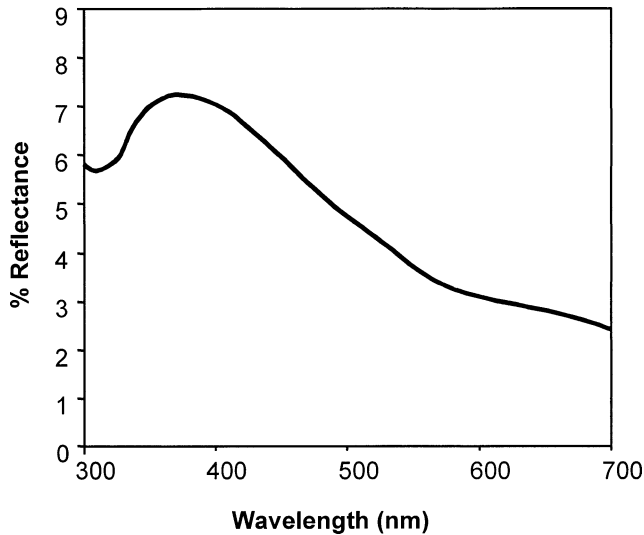


Figure 1
Representative reflectance spectrum (average of rump, mantle, breast, and wing coverts) for one adult male satin bowerbird. This individual was chosen because its plumage color was closest to the mean for the color variables we calculated across all individuals sampled.

advertisement calls, usually given near bowers, and systematically searching for active display sites. We assessed bower quality by evaluating bower construction and quantifying the number of decorations used. Two observers independently evaluated four features of bower construction—overall symmetry of the structure, stick size, stick density, and overall quality of construction—each on a scale from one (poor) to four (excellent). We calculated a bower quality score for each bower as the sum of these measures averaged between the two observers. Similar indices of bower quality have been shown to correlate with mating success in several species of bowerbird (Borgia, 1985b; Borgia and Mueller, 1992; Lenz, 1994; Uy and Borgia, 2000). To assess the extent of bower decoration, we regularly visited bowers from mid October to late November ($n = 3\text{--}7$ visits per bower) and recorded the number of each type of decoration present on the bower. For our analyses, we used the mean number of decorations recorded at each bower.

We caught 11 adult males (10 of which held bowers) near their display sites by using mist nets baited with blue objects, and fitted them with a unique combination of color bands. We measured tarsus length (to nearest 0.1 mm) as an index of body size that is independent of age and condition. We also measured the mass (to the nearest gram) of each bird and used the residuals of a regression of body mass on tarsus length as an index of body condition. We noted whether feathers were predominantly old, new, or molting, and we removed the right outer rectrix to assess daily feather growth rate.

Plumage color

We quantified plumage reflectance by using an Ocean Optics S2000 spectrometer and a pulsed xenon lamp (PX-2; Ocean Optics, Dunedin, Florida, USA). Measurements were taken with a single fiber-optic probe that provided illumination from the light source and transferred the reflected light to the spectrometer. The probe was mounted in a hard rubber cover that excluded external light from the measurement area (approximately 3 mm^2) and maintained the probe perpen-

dicular to the feather surface. All spectral measurements are expressed as the proportion of light reflected relative to that reflected from a Spectralon white standard, an almost perfect reflector. We measured plumage reflectance on four body regions for each individual: wing coverts, breast, mantle, and rump, taking five readings from each region and moving the probe by at least 5 mm between readings. We restricted spectral analyses to wavelengths from 300–700 nm, as most birds are sensitive to ultraviolet (UV) wavelengths (300–400 nm; Cuthill et al., 2000), and 700 nm is likely the upper limit of the vertebrate visual spectrum (Jacobs, 1981).

We summarized reflectance data by calculating five color variables: total brightness, UVV-brightness, UVV-chroma, contrast, and hue. We calculated total brightness as the mean of reflectance values, in 1-nm intervals, from 300–700 nm (Andersson, 1999; Endler, 1990); this measurement thus gives the mean proportion of incident light that is reflected from the feather surface in the bird-visible range of wavelengths. Similarly, we calculated UVV-brightness as the mean of reflectance values in the UV-violet region of the spectrum (300–420 nm; Andersson et al., 1998), in which peak reflectance occurred in all males. As a measure of spectral saturation, we calculated UVV-chroma as the proportion of total reflectance occurring in the UV-violet region of the spectrum. We calculated contrast as the difference between the maximum and minimum reflectance across the 300–700-nm range, such that higher contrast indicates a more intense color (Keyser and Hill, 1999, 2000). Given the simple, unimodal shape of adult male satin bowerbird reflectance spectra (Figure 1), contrast is likely a reliable estimate of color intensity in this species. Finally, to approximate hue, we used the wavelength at which maximum reflectance was reached, a commonly used index of spectral location (see Keyser and Hill, 1999, 2000; Sheldon et al., 1999).

We also calculated an overall ornamental color score using principal components analysis (PCA). We first calculated the mean of each color variable for each body region on each male. We then performed a PCA by using the mean total brightness, UVV-chroma, contrast, and hue averaged over the four regions of each male studied. The first principal component (PC1) from this analysis explained 46% of the variation in color among males, with total brightness, contrast, and UVV-chroma having the highest positive loadings on the PC1 axis (eigenvectors = 0.70, 0.59, and 0.39, respectively). Therefore, males with a high “PC1 color score” displayed an overall bright and highly saturated ornamental plumage coloration. We did not include UVV-brightness in the PCA because of all the color variables calculated, this was the most variable both within and among males (see below); thus, we wanted to investigate the influence of UVV-brightness for each body region separately.

Parasites

We assessed ectoparasite load by counting the number of *Myrsidea ptilonorhynchi* lice on the head (especially near the eyes) of each male. This louse belongs to a suborder in which species are known to consume feathers and to feed on the blood and skin of their hosts; thus, these lice probably elicit specific immune responses in their hosts and can have a considerable effect on host fitness (Clayton, 1991a,b). This louse is the only common ectoparasite on satin bowerbirds, and it is found mainly around the head and eyes where birds cannot easily preen (Borgia, 1986a; Borgia and Collis, 1989, 1990).

To assess the intensity of infection from blood parasites, we collected a small sample of blood from the brachial vein of each male, drawing blood into a capillary tube and thinly

Table 1
Correlation matrix of measures of male satin bowerbird plumage color and bower structure used in multiple regression analyses

	UVV-brightness				No. of decorations	Bower quality	PCI color score
	Coverts	Rump	Mantle	Breast			
UVV-brightness							
Wing coverts		−0.26	−0.36	0.37	0.35	0.30	0.37
Rump	0.46		0.14	0.29	0.39	0.51	0.58
Mantle	0.30	0.70		−0.19	0.45	0.41	0.26
Breast	0.29	0.42	0.59		0.49	0.40	0.66 ^a
No. of decorations	0.32	0.27	0.19	0.16		0.73 ^a	0.83 ^a
Bower quality score	0.40	0.13	0.24	0.25	0.02		0.77 ^a
PCI color score	0.29	0.08	0.47	0.04	0.003	0.009	

Values above diagonal are correlation coefficients (r); below diagonal are p values.

^a Correlation coefficients with $p < .05$ before Bonferroni correction.

smearing it onto a glass slide. We prepared the slides by using the Hema 3 staining procedure (Fisher Scientific). We then observed each slide at $\times 1250$ magnification under oil immersion, scanning for haemosporidian parasites until 10,000 red blood cells had been surveyed, and identifying each parasite to genus (Campbell, 1988). All but one of the blood parasites scored were *Haemoproteus*; thus, only mature (intra-erythrocytic) *Haemoproteus* parasites are considered in the following analyses. All slides were scored by the same observer, blind to the identity of the individual bird being scored.

We assessed feather growth rates by measuring the width of alternating dark and light bars on the right outer rectrix of each male. Each pair of bars represents 1 day's growth (Michener and Michener, 1938), and the width of these bars has been associated with nutritional condition in several species (Grubb, 1989, 1991; Jenkins et al., 2001). We measured the width of six pairs of bars on either side of the midpoint of the feather, from which we calculated a 12-day average daily feather growth rate for each male (see Hill and Montgomerie, 1994).

Statistical analysis

None of the variables described in this study deviated significantly from normality (all, $p > .10$); thus, no transformations were required for parametric analyses. Values are reported as mean \pm SE, and all probabilities are two-tailed. To determine which plumage and bower variables would best predict four male traits that may reveal male quality (ectoparasite load, intensity of infection from blood parasites, feather growth rate, body size), we constructed four backward stepwise multiple regression models. In each of the four models, we used PCI color score, UVV-brightness (of rump, wing coverts, mantle, and breast, separately), bower quality score, and number of bower decorations as potential predictor variables. We performed a backward selection procedure so that variables that could significantly predict male traits in combination would be included in the models even if they were not significant predictors individually (see Zar, 1999). The models reported here include only variables that were significant predictors ($p \leq .05$) of each quality trait under investigation. We also constructed correlation matrices and examined leverage plots for indications of collinearity in predictor variables that might make these regression models difficult to interpret; none of the regression models showed evidence of serious problems with collinearity. Because of our small sample size, we make no attempt to assess the relative

importance of these different signals in predicting aspects of male quality, although the standardized regression coefficients may serve as a rough guide. Analyses that could reliably reveal the relative importance of different predictor variables (e.g., path analysis) would require much larger sample sizes.

RESULTS

Plumage coloration

The rump, mantle, breast, and wing coverts of male satin bowerbirds reflect most strongly in the UV and violet regions of the bird-visible spectrum (Figure 1). Indeed, the average male hue across the four body regions measured was 362 ± 6.8 nm, well within the UV range (300–400 nm). There was considerable variation in male plumage characteristics, both among males and among body regions within males. UVV-brightness was the most variable of the plumage characteristics we calculated, with coefficients of variation (CV) among males ranging from 0.25–0.38 for the wing coverts, mantle, breast, and rump. In comparison, mean CVs for total brightness, UVV-chroma, contrast, and hue were 0.29, 0.08, 0.17, and 0.07, respectively. Mean UVV-brightness was also significantly different across the four body regions measured (ANOVA: $F_{3,40} = 5.86$, $p = .002$; mean UVV-brightness of the rump, 7.8 ± 0.90 ; mantle, 10.5 ± 0.79 ; breast, 6.3 ± 0.66 ; wing coverts, 7.0 ± 0.64) despite looking identical to us. Interestingly, correlations of UVV-brightness between regions (within males) were weak and both positive and negative (Table 1).

Plumage coloration and bower characteristics

Measures of bower structure and male plumage coloration were intricately associated in satin bowerbirds. Male ornamental plumage color (PCI color score) was significantly positively related to both bower quality (Figure 2a) and the average number of decorations adorning bowers (Figure 2b). Thus, the satin bowerbird's bower provides females with a useful index of a male's appearance, even in his absence, with bower quality score and number of decorations together explaining about 75% of the variation in this PCI color score (multiple regression: $F_{2,7} = 10.3$, $p = .008$).

Parasites

To determine whether plumage coloration and bower features revealed aspects of male quality, we compared these attributes to the degree of infection from ectoparasites and

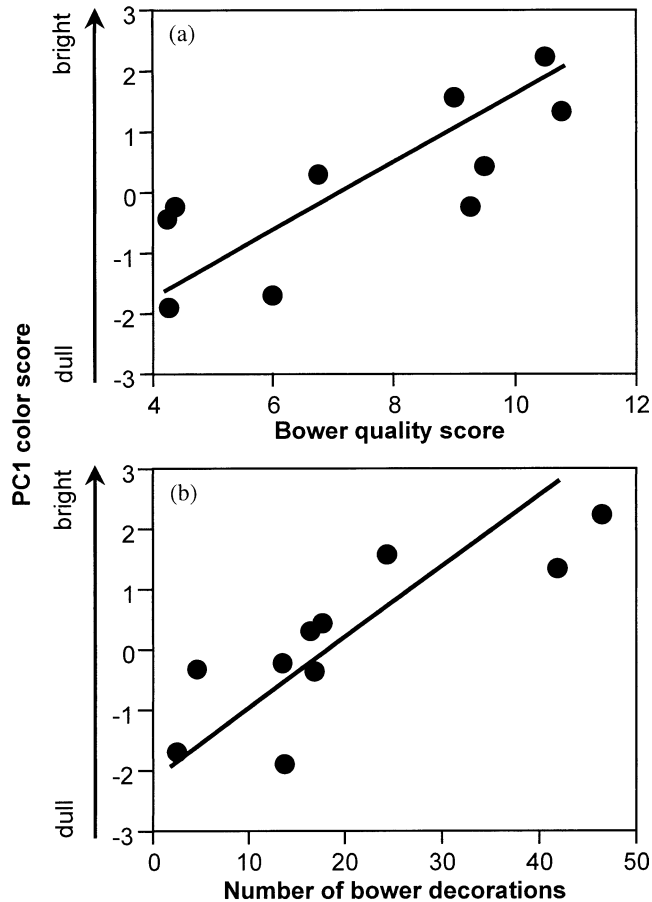


Figure 2
Relations between overall male plumage color (PC1 color score) and bower quality score (a; $y = -3.8 + 0.5x$; $r^2 = .60$, $n = 10$, $p = .009$) and average number of decorations (b; $y = -2.1 + 0.1x$; $r^2 = .69$, $n = 10$, $p = .003$) in male satin bowerbird bowers. Males with high PC1 color scores displayed high total brightness, contrast, and UVV-chroma in their structural plumage coloration. Trend lines are model II regressions.

endoparasites. In a stepwise multiple regression analysis, the quality of bower construction emerged as the only significant predictor of ectoparasite load among the variables tested (Table 2, Figure 3). That is, males with high quality bowers had fewer ectoparasites, and bower quality explained more than 50% of the variation in ectoparasite load. On the other hand, variation in the intensity of endoparasite infection was best explained by the UVV-brightness of the male's rump plumage (Table 2, Figure 3); males with the brightest rumps had the lowest intensity of infection by *Haemoproteus* blood parasites, with rump UVV-brightness explaining 50% of the variation in the intensity of infection.

Feather growth rate

Overall plumage color (PC1 color score), rump UVV-brightness, and wing covert UVV-brightness were all significant predictors of feather growth rate (Table 2, Figure 3), together explaining 74% of the variation in growth rate. PC1 color score was the best predictor of feather growth rate, explaining 46% of the variation. Note, however, that PC1 color score varied negatively with feather growth rate, in the opposite direction to that predicted. Rump and wing covert UVV-brightness, on the other hand, were positive predictors

of feather growth rate and together explained an additional 28% of the variation. UVV-brightness of rump and wing coverts were not correlated within males nor was either of these significantly correlated with PC1 color score (Table 1).

Body size

Rump UVV-brightness, bower quality score, and number of bower decorations were all significant predictors of body size (Table 2, Figure 3), together explaining more than 80% of the variation in tarsus length. Rump UVV-brightness was the best predictor of tarsus length (Table 2), explaining 46% of the variation, with bower quality score and number of decorations together explaining an additional 36% of the variation. Bower quality score and number of decorations were significantly correlated within males, but neither of these bower variables was correlated with rump UVV-brightness (Table 1). Rump UVV-brightness and average number of bower decorations were positive predictors of tarsus length, whereas bower quality score was a negative predictor. Note, however, that bower quality was a negative predictor of tarsus length only in this multiple regression analysis, in which the number of bower decorations is statistically controlled. By itself, bower quality score was positively, although not significantly, related to tarsus length ($r = .10$, $n = 10$, $p = .79$).

DISCUSSION

Our analyses show that male plumage coloration and bower quality features are intricately related in satin bowerbirds and that, together, these elaborate sexual ornaments reveal important aspects of male quality. This is the first study to identify an association between bower features and male plumage ornamentation in bowerbirds, suggesting that bowers are an extension of the male phenotype that females can use to assess male quality. It is possible that the observed positive relations between bower quality score, number of decorations, and overall plumage color (PC1 color score) (Figure 2) may result from a general increase in the quality of bower construction (Borgia, 1986b) and structural plumage color with male age. However, females seem to consistently prefer specific individuals in a population (Uy et al., 2000, 2001), thereby suggesting that some aspects of male quality may be independent of age. More work will be needed to determine the effects of male age on their plumage coloration and quality of bower construction to determine whether these signals also provide females with useful fitness-related information about male longevity.

As we have shown, the signal function of decorated bowers and bright plumage in satin bowerbirds may be explained in part by their significant correlation with parasite load, an important indicator of male quality (see also Doucet and Montgomerie, in press). According to the Hamilton-Zuk hypothesis of parasite-mediated sexual selection, females should prefer males with the most elaborate sexual ornaments because the degree of ornament elaboration may be limited by a male's ability to resist disease infection (Hamilton and Zuk, 1982). Hence, by mating with highly ornamented males, females stand to acquire heritable parasite resistance for their offspring (Hamilton and Zuk, 1982). Here, we provide support for the Hamilton-Zuk hypothesis by two means. First, we show that quality of bower construction is a significant predictor of ectoparasite load in this population. Thus, females could potentially assess male ectoparasite load by evaluating bower quality, even in the absence of the bower owner. In another population of satin bowerbirds, male ectoparasite load was negatively related to mating success but was unrelated to bower quality (Borgia and Collis, 1989,

Table 2
Significant predictors of male quality in satin bowerbirds

Dependent variables	Significant predictors	β'	<i>F</i>	<i>p</i>	df
I. Ectoparasites	Bower quality score ($R^2 = .51$)	-0.72	8.4	.02	1,8
II. Endoparasites	Rump UVV-brightness ($R^2 = .50$)	-0.70	8.9	.02	1,8
III. Feather growth rate	Whole model ($R^2 = .74$)		6.7	.02	3,9
	PC1 plumage color score	-1.39	17.8	.004	1,9
	Wing coverts UVV-brightness	0.66	5.9	.04	1,9
	Rump UVV-brightness	0.63	5.0	.05	1,9
IV. Body size	Whole model ($R^2 = .82$)		8.9	.01	3,8
	Rump UVV-brightness	0.83	16.7	.006	1,8
	Bower quality score	-0.89	10.4	.02	1,8
	Number of decorations	0.77	8.9	.02	1,8

Each model was constructed using backward stepwise multiple regression analysis with both bower features (bower quality score, number of decorations) and plumage features (PC1 plumage color score, UVV-brightness of the wing coverts, mantle, rump, and breast) as independent variables. Standardized regression coefficients (β') and significance tests are shown for each significant predictor variable.

1990). Second, we show that a male's rump UVV-brightness can reveal the intensity of his infection from blood parasites. Thus, female satin bowerbirds can assess haemosporidian parasite intensities by evaluating male plumage brightness during courtship display (Figure 3).

We also found that rump plumage coloration, average number of bower decorations, and quality of bower construction were significant predictors of male body size (Figure 3). The association between the number of decorations and body size is perhaps best explained in the context of male choice of bower decorations. Male satin bowerbirds preferentially decorate their bowers with blue feathers, flowers, and berries, as well as small mammal skulls and other bones, all of which are relatively rare in the surrounding environment (Borgia and Gore, 1986; Doucet SD and Montgomerie R, unpublished data). As a consequence, theft from other males appears to be the primary means of obtaining these decorations (Borgia and Gore, 1986). Larger males may have a competitive advantage during theft-related confrontations, allowing them to steal more decorations from other males and to defend their own decorations from thieving neighbors.

The fact that overall plumage color (PC1 color score) was negatively associated with tail feather growth rate is surprising. Growth rates have traditionally been used as indicators of condition at the time of molt (Grubb, 1989, 1991; Jenkins et al., 2001), and positive associations between feather growth rate and quality-indicating plumage coloration have been found in several species (Doucet, 2002; Hill and Montgomerie, 1994; Keyser and Hill, 1999). We can only suggest that feather growth rate may not be a useful index of male plumage quality in satin bowerbirds, for two reasons. First, males who built better quality bowers also had a higher PC1 color score (Figure 2), suggesting that this overall plumage color score is a good measure of male quality despite its negative association with feather growth rate. Second, males spend considerable time and effort building, maintaining, and defending their bowers during the breeding season (Borgia, 1985a; Borgia and Gore, 1986), and this may explain the negative relationship between bower quality and residual body mass in our study ($r = -.79$, $n = 10$, $p = .009$). Our findings suggest that males had to work hard to maintain their high-quality bowers, perhaps at the expense of other maintenance activities such as foraging. Thus, by the end of the breeding season when molt begins (Vellenga, 1980), high-

quality, nutritionally stressed males might be expected to grow their new feathers more slowly.

In summary, our study shows that bower features and male plumage coloration together explained considerable variation in four potential quality indicators: ectoparasite load, intensity of infection from blood parasites, feather growth rate, and body size. Consequently, female satin bowerbirds could assess males using both bower features and male plumage coloration (Figure 3) to obtain better information about male quality than is available from either trait alone. It is already known that male mating success is related to bower quality in this species (Borgia, 1985b), and our study associates bower quality with ectoparasite load and body size. Despite this, only the UVV-brightness of the rump was a significant predictor of the intensity of infection from blood parasites. Our findings support recent work on mate searching strategies of the female satin bowerbird; Uy et al. (2000, 2001) found that females make courtship visits to only a subset of males in a population, and eventually mate with only a subset of the males they visit. This sequential elimination process is complemented by our findings: Bower features can signal aspects of male quality; however, both bower features and plumage traits must be evaluated if females are to gain an overall appreciation of male quality.

Given that bowers and plumage can vary on different time scales, and that these various components of the male's phenotype reveal different aspects of male quality, our study supports the multiple messages hypothesis of multicomponent signaling (Johnstone, 1995a; Møller and Pomiankowski, 1993). Thus, the evolution of multiple sexual ornaments in satin bowerbirds may be driven by selection pressure to signal multiple aspects of male quality. However, our findings also suggest that sexual signals and the quality information they reveal follow a complex mosaic in which both signal redundancy and exclusivity may coexist (Figure 3). It seems likely that further study of multicomponent sexual signaling will reveal similar patterns in other species. Because our sample of males and bowers was relatively small, our statistical analyses may have lacked the power to detect other potentially revealing relationships. Thus, our main findings (Table 2, Figure 3) are likely a conservative estimate of the extent of multicomponent signaling in satin bowerbirds.

Interestingly, female satin bowerbirds appear to have relatively large brains compared with those of their male counterparts (Madden, 2001). Although male brain capacity

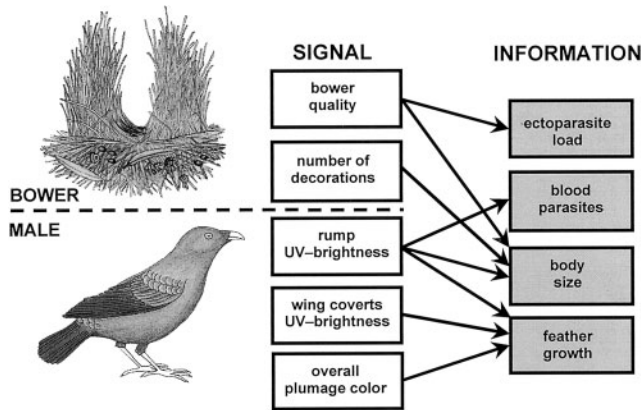


Figure 3
Associations between five male attributes (signals) potentially used by females in mate choice and four indicators of male quality (information) in the satin bowerbird. Arrows show variables that significantly ($p \leq .05$ in multiple regression models) predicted each target quality indicator.

is probably essential to building complex bowers, searching for bower decorations, and decorating bowers appropriately, female brain size may be as important in searching for potential mates (Uy et al., 2000, 2001) and assessing complex bowers, male plumage, and elaborate male displays. Thus, female satin bowerbirds may be particularly well suited to evaluate the impressive array of signals of quality discovered so far in this species, from bower features and male plumage coloration to song and perhaps even display complexity.

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