

HORMONAL CORRELATES OF BOWER DECORATION AND SEXUAL DISPLAY IN THE SATIN BOWERBIRD (*PTILONORHYNCHUS VIOLACEUS*)¹

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Abstract. Male Satin Bowerbirds court females with complex displays that include stick structures built adjacent to a decorated display court. Here we report circulating levels of testosterone and corticosterone in a natural population of Satin Bowerbirds and their relation to the development of complex mating displays. We found that (1) males without bowers had lower levels of testosterone than bower holders, (2) testosterone, but not corticosterone, levels were significantly correlated with male mating success, and (3) levels of testosterone, but not corticosterone, were consistently correlated with the quality of several important display characters that have been shown to be important in affecting male mating success. These results suggest that testosterone level is an important component of male mating success. We consider reasons why variation in testosterone levels persists among mature male bowerbirds given its potential to affect male mating success.

Key words: Sexual display; Bowerbird; hormone; testosterone; mate choice; *Ptilonorhynchus violaceus*; corticosterone.

INTRODUCTION

Male Satin Bowerbirds (*Ptilonorhynchus violaceus*), like many species in the family Ptilonorhynchidae, have developed complicated courtship displays oriented around a bower, a stick structure that they build and decorate (Vellenga 1970; Donaghey 1981; Borgia 1985a, 1986). Courtship displays at the bower involve harsh calls, vocal mimicry, and jumping or "dancing" postures (Loffredo and Borgia 1986). Naturalists have long been curious about the peculiar nature of these displays, and recently bowerbirds have attracted the attention of evolutionary biologists because they provide a model system for understanding the evolution of complex symbolic sexual displays. Investigations of the development of male display behavior have revealed that there is age-related improvement in male displays (Loffredo and Borgia 1986; Borgia, in preparation) and that male dominance may be important in determining male ability to obtain and hold a display site (Borgia 1985b; Borgia and Gore 1986; Borgia and Loffredo, in preparation). Previous

work has shown that female Satin Bowerbirds prefer males with well-constructed and well-decorated bowers (Borgia 1985a), and that male competition by destruction of other male's bowers (Borgia 1985b) and theft of decorations (Borgia 1985b) affects display characters important in female choice. Young males associate with older males at bowers and may learn some elements of display behavior (Vellenga 1970, Borgia 1986, Loffredo and Borgia 1986).

There is considerable evidence for the role of the steroid hormone testosterone in regulation of male-aggressiveness and courting behavior in birds (Balthazart 1983, Harding 1981, Harding et al. 1988, Hegner and Wingfield 1987, Wingfield 1984), although this has not been true in all cases (e.g., Rohwer and Wingfield 1981; Wingfield et al. 1982a, 1987). These studies involved investigations of bird species with relatively simple courtship displays and resource-based mating systems in which male success in obtaining a mate is primarily dependent on territory quality. Bowerbirds have a non-resource-based mating system, and female choice appears almost entirely dependent on the quality of male display. Investigation of courtship behavior in male Satin Bowerbirds is of special interest because the

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unique mating system allows numerous elements of male display to be quantified, and the development of these display components can be measured in relation to hormone levels. Castration of *Ptilonorhynchus violaceus* impairs bower building and displays to females, whereas testosterone injections partially restore these behaviors (Marshall, 1950), suggesting a major role for testosterone in social behavior of this species. Furthermore, because male bowerbirds can mate with many different females in a season, there is an opportunity to score the relative quality of male display independently of other factors such as those found in species in which territory quality affects mating decisions.

Recent studies of juvenile plumage Satin Bowerbirds show that testosterone can have a critical role in determining male success in aggression around feeding sites and in adult male plumage development (Collis and Borgia 1990, 1991). Testosterone-implanted juvenile males showed an increased tendency to build bowers, perform displays and related behaviors, and molt into adult plumage, when these birds were compared with a control group. However, the behaviors of implanted birds were uncoordinated and these birds were not tolerated by bower-holding males. These results suggest that, although adult-like behaviors can be induced by testosterone implants, these birds suffer from an inability to produce fully coordinated behaviors, and, because of their early attainment of adult plumage, they may be denied opportunities to observe displays of older males. Thus, it is possible that a combination of hormonal factors (e.g., testosterone) and hormone independent factors (e.g., experience) may regulate courtship and bower construction in Satin Bowerbirds. It is also possible that circulating corticosterone levels may be important since this adrenocortical steroid hormone is known to suppress reproductive behavior either directly or indirectly by inhibiting secretion of reproductive hormones (e.g., Wingfield and Silverin 1986, Wingfield 1988).

In this study we report levels of testosterone and corticosterone in individual male birds of different age classes in a wild population. We compare juvenile plumage and adult males and assess age-related changes in testosterone and corticosterone levels. We test the specific predictions that circulating concentrations of these two hormones affect the performance of bower-holding males in producing displays and in ob-

taining matings. We also evaluate the possible relationship between hormone levels and male advertising and bower destruction tendencies.

METHODS

This study was carried out at Wallaby Creek, in the Beaury State Forest, 120 km NW of Lismore, New South Wales, Australia, and the study site has been described elsewhere (Borgia 1985b). Satin Bowerbirds at Wallaby Creek have been the subject of an intensive field study from 1980 to 1987, and general information about the birds was collected over that period. Data for the comparisons reported here were collected from August 1984–December 1984.

Birds were captured in baited traps and removed immediately. The birds were color-banded (if not previously captured), scored for plumage characters and numbers of ectoparasites, weighed, measured for wing length, and immediately released. Plumage characters and measurements of wing length allowed sexing and aging of birds (Vellenga 1970). Individual birds were banded with unique combinations of colored bands. Our records allowed us to estimate the ages of males based on when they obtained adult plumage. Males exhibit a green female-like plumage with dark beaks until four years of age, at which time the beak begins to gradually turn completely yellow. At five years, males exhibit a mottled blue and green plumage which, after the final molt, becomes entirely blue at seven years of age. We classified individual males as juveniles if they were less than seven years old.

Male ranks were established by observation of male interactions at trapping sites. We recorded the identity of birds that were involved in interactions, including the band combinations of birds that initiated and received the attack. Aggressiveness was measured as the ratio of the number of attacks by a bird to the total number of encounters by a bird. Encounters are the total number of times a bird was an attacker plus the number of times it was attacked. This aggressiveness index was used to order males into ranks. Our aggressiveness index was highly correlated with dominance value (see Collis and Borgia 1990, 1991; Borgia and Loffredo, MS) based on a total of 2,176 interactions recorded in 1984.

Each permanent bower site was monitored by a camera controlled by an infrared device that was triggered when birds entered the bower (see Borgia 1985a, 1986a). Matings occur in the bow-

er, and our camera monitoring at bower season. Behavioral havior around the and display calls w 15 m from the bo number of courtsh were determined (1985a). Females ty Rarely females mat moving out of the as a single mating.

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HORMONE ANALY

Blood samples for h as birds were captu The birds were cap operated by a hidde processed the bird in to four heparinized mm i.d.) blood sam veins punctured by dle. All of the bir captured numerous were taken. Birds w ing been captured handled, and most r trap immediately af effect on their behav trifuged, and the se separated and held frozen. Samples we ice to the laborator

The steroid horm costerone were mea after partial purifica diatomaceous earth and free moieties

er, and our camera system provided continuous monitoring at bowers through the entire mating season. Behavioral observations including behavior around the bower and male advertising and display calls were made from hides located 15 m from the bowers. Male mating success, number of courtships, and identity of visitors were determined by review of films (Borgia 1985a). Females typically mate once per season. Rarely females mated twice with a male without moving out of the bower and these were scored as a single mating.

Nine categories of decorations were counted and bower quality estimates were made on daily visits to bowers (see Borgia 1985a). These data were reduced by taking seasonal means of decorations counts to represent values for individual decoration variables. In 1984, one-half of the bowers on the study site were regularly destroyed as part of another experiment. Measures of bower quality are based on mean estimates of bower quality in the three week period preceding the experimental bower destruction experiment. To test if this experiment affected the results reported here, we compared treatment and control bowers and found no significant difference in testosterone levels ($t = 1.18$, $df = 13$, $P > 0.30$).

HORMONE ANALYSIS

Blood samples for hormonal analysis were taken as birds were captured at feeding sites in 1984. The birds were captured in cage traps that were operated by a hidden observer who removed and processed the bird immediately after capture. Two to four heparinized capillary tube (75 mm \times 1.4 mm i.d.) blood samples were taken from wing veins punctured by a 27 gauge hypodermic needle. All of the birds in our sample had been captured numerous times before blood samples were taken. Birds with a previous history of having been captured tended not to struggle when handled, and most returned to the vicinity of the trap immediately after release with no noticeable effect on their behavior. Blood samples were centrifuged, and the serum and RBC fractions were separated and held on ice until they could be frozen. Samples were transported frozen on dry ice to the laboratory for analysis.

The steroid hormones testosterone and corticosterone were measured by radioimmunoassay after partial purification of steroid fractions on diatomaceous earth/glycol microcolumns. Bound and free moieties were separated by dextran-

coated charcoal. Standard curves covered the range 2–500 pg for testosterone and 7.8–2,000 pg for corticosterone. All samples were processed within a single assay, and intra-assay variation was <10%. For further details of procedure, assay validation, and reliability criteria see Wingfield and Farner (1975); Wingfield et al. (1982b); Ball and Wingfield (1986).

STATISTICAL ANALYSIS

Spearman rank correlations (r_s), Student's t -test (t), and combined probability tests (Sokal and Rohlf 1969) were used for statistical comparisons. Means are expressed as $\bar{x} \pm SD$ except where noted. One-tailed tests were used for initial comparisons of testosterone and corticosterone levels with male and mating success and for other tests of a priori predictions.

RESULTS

HORMONE LEVELS AND CLASS

Differences in testosterone levels were found between bower-holding and nonbower-holding males (Fig. 1a) and these were statistically significant ($t = 2.9$, $df = 23$, $P < 0.03$). Similar trends were found for corticosterone levels between bower-holding (Fig. 1b) and nonbower-holding males, but they were not significant ($t = 1.43$, $df = 23$, $P > 0.10$).

HORMONE LEVELS AND MATING SUCCESS

We predicted that testosterone levels might be significantly correlated with male mating success and this result was supported ($r_s = 0.47$, $n = 14$, $P = 0.023$, Fig. 2), however there was no significant correlation with corticosterone levels ($r_s = 0.22$, $n = 14$, $P = 0.111$, Fig. 3). There was no correlation with rank as determined by aggressive interactions at feeding sites with either testosterone ($r_s = 0.009$, $n = 14$, $P > 0.50$) or corticosterone ($r_s = -0.253$, $n = 14$, $P = 0.19$) levels, and number of copulations were marginally correlated with rank ($r_s = 0.33$, $n = 14$, $P = 0.065$). There was no significant correlation between corticosterone and testosterone levels ($r_s = 0.173$, $n = 14$, $P > 0.25$).

HORMONE LEVELS AND DISPLAY CHARACTERS

Visitation and courtship at bowers were both strongly associated with hormone levels (Table 1). There was a strong positive correlation between testosterone levels and visitation at males'

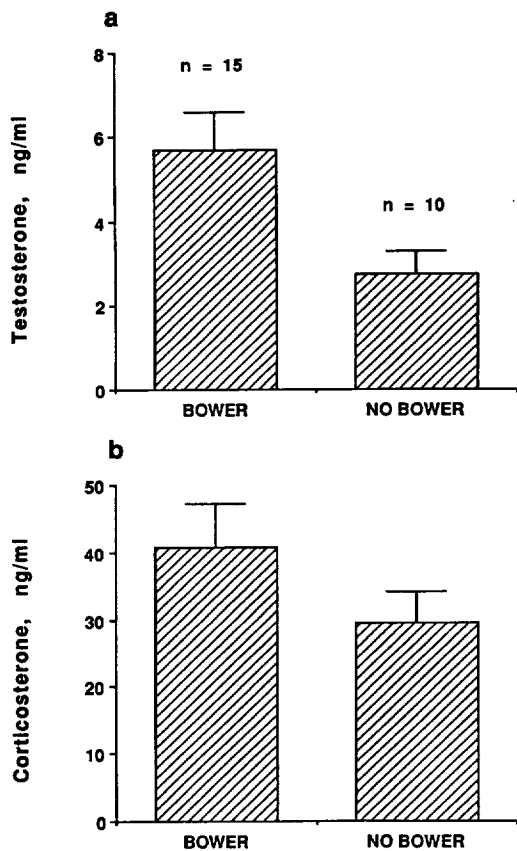


FIGURE 1. Plasma levels of testosterone (a) and corticosterone (b) in males with and without bowers.

bowers, the number of courtships by a male and courtships without copulations. Negative correlations were found for corticosterone levels and these same variables.

Two of four bower quality variables (Table 2) were significantly correlated with testosterone, but none showed correlations with corticosterone. The high *P* values for these probability tests suggest that these results are robust even with multiple comparisons. A combined probability test showed the overall correlation of bower variables and testosterone was highly significant ($\chi^2 = 26.36$, $df = 8$, $P < 0.005$).

The summary variable for decorations (the total number of decorations) was positively correlated with testosterone levels ($r_s = 0.64$, $n = 14$, $P = 0.01$) but not corticosterone ($r_s = 0.161$, $N = 14$, $P = 0.15$). This result is also supported in an analysis in which results from Spearman correlations based on contrasts between testos-

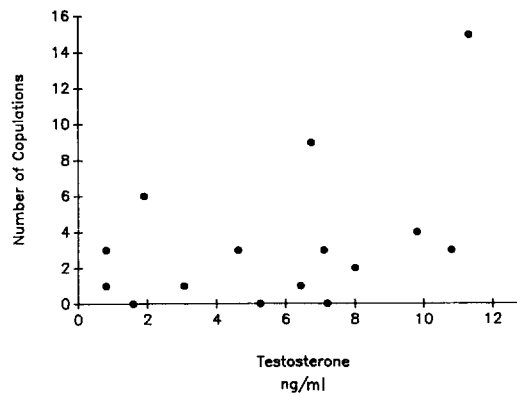


FIGURE 2. Circulating testosterone levels and male mating success in 1984.

terone and individual decoration variables (Table 3) were combined. Each decoration type had a positive correlation coefficient, and when combined, there was a highly significant association between decorations and testosterone levels (combined probability test $\chi^2 = 49.7$, $df = 18$, $P < 0.001$). Adjusting for multiple comparisons (by dividing by the number of contrasts) caused these individual comparisons to become nonsignificant. None of the nine individual decoration types showed a significant (unadjusted) correlation with corticosterone (Fig. 4) and correlation coefficients show no clear pattern (only six of nine of these are in the positive direction).

Male advertising. Table 4 shows the relationship between advertising calls and hormone levels. Neither the frequency of scratch or whistle calls showed significant correlations with testosterone or corticosterone levels.

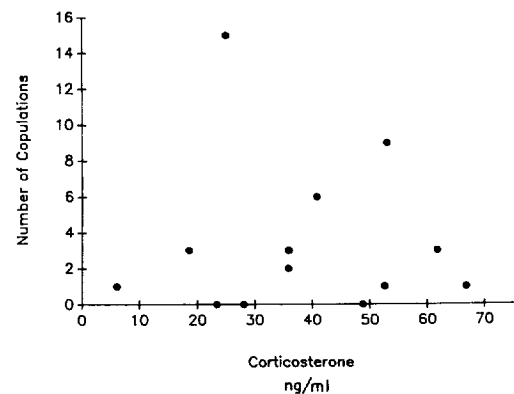


FIGURE 3. Circulating corticosterone levels and male mating success in 1984.

TABLE 1. Relations

Total visitors at bowers
Total courtships at bowers
Courtships without copulations

Bower destruction. The relationship between hormone levels and bower destruction. A male was a victim of destruction if he was mated and the number of copulations was zero. There was no relationship between hormone or testosterone levels and bower destruction. A male was a destructor if he destroyed a bower. Bower destruction was negatively correlated with corticosterone levels. The relationship to testosterone was not significant.

DISCUSSION

Our results, which show that the number of male mating successes and testosterone are consistent, suggest that testosterone affects male mating success. These comparisons showed that testosterone was marginally correlated with mating success. Significant correlations between testosterone and bower quality variables in holding males (a group of males that had higher testosterone levels than other males) showed significant positive correlations between testosterone levels and male ability to attract females for courtship, two variables. The relationship between testosterone and the number of copulations and the overall pattern suggest that testosterone on display by the bowerbird. In general,

TABLE 2. Relations

Bower symmetry
Bower stick size
Bower stick density
Bower quality of construction

* The highest quality bower quality.

TABLE 1. Relationships of plasma testosterone and corticosterone levels to behavior at the bower.

	Visitors and display			
	Corticosterone		Testosterone	
	Spearman correlation (n = 14)	P	Spearman correlation (n = 14)	P
Total visitors at bower	-0.521	0.013	0.333	0.032
Total courtships at bower	-0.452	0.023	0.537	0.006
Courtships without copulations	-0.531	0.012	0.410	0.017

Bower destruction. Table 5 shows the relation between hormone levels and the frequency that a male was a victim of bird-caused destructions and the number of times he was a destroyer. There was no relationship between corticosterone or testosterone and the number of times a male was a destruction victim. Male tendency to destroy was negatively correlated (marginally) with corticosterone levels, but showed no relationship to testosterone levels.

DISCUSSION

Our results, which show a significant correlation of male mating success with levels of testosterone, are consistent with the hypothesis that testosterone affects male mating success. Additional comparisons showed that testosterone levels were marginally correlated with rank. There was no significant correlation of testosterone or corticosterone with absolute male age, but bowerholding males (a group that includes the oldest males) had higher testosterone and corticosterone levels than other males. There were significant positive correlations between testosterone levels, and male ability to attract females to bowers for courtship, two measures of bower quality, and the number of decorations on bowers. This overall pattern suggests an important effect of testosterone on display and mating in the satin bowerbird. In general, contrasts involving cor-

ticosterone were less often significant than those involving testosterone.

Display variables that showed significant negative correlations with corticosterone levels also showed significant positive correlations with testosterone. Courtship displays of Satin Bowerbirds have been suggested to be energetically demanding because of the extreme postures taken by males. These include puffing of feathers, harshness of their calls, and the protrusion of their eyes (Marshall 1954, Vellenga 1970, Lofredo and Borgia 1985). However, the observation that display activity is inversely related to corticosterone levels suggests the possibility that active displaying by males is not severely stressful. This implies that, contrary to earlier suggestions and what is implied from some recent sexual selection models (Zahavi 1975; Lande 1981; see Borgia 1991 for a full discussion) male Satin Bowerbird displays are not costly in terms of impairing overall male function or survivorship. This result is supported by the observation that successful male Satin Bowerbirds tend to live longer and have high quality displays relative to other males (Borgia 1991). The inverse relationship between corticosterone and male display behavior is also consistent with the hypothesis that male display itself may lower stress in males (but see Marler and Moore 1988; Moore and Marler 1987, 1988). If so, this may account for the common tendency among male Satin Bowerbirds to

TABLE 2. Relationships of plasma testosterone and corticosterone levels to bower quality.

	Bower quality measures*			
	Corticosterone		Testosterone	
	Spearman correlation (n = 14)	P	Spearman correlation (n = 14)	P
Bower symmetry	-0.039	ns	-0.258	0.10
Bower stick size	-0.212	ns	-0.622	0.012
Bower stick density	-0.002	ns	-0.505	0.016
Bower quality of construction	-0.188	ns	-0.261	0.10

* The highest quality bowers received the low scores so a negative correlation indicates a positive relationship between hormone level and bower quality.

TABLE 3. Relationships of plasma testosterone and corticosterone to bower decorations.

	Bower decoration			
	Corticosterone		Testosterone	
	Spearman correlation (n = 14)	P	Spearman correlation (n = 14)	P
Yellow leaves	0.129	0.165	0.380	0.045
Yellow straw	0.013	0.24	0.498	0.017
Blue feathers	0.232	0.11	0.140	0.16
Blue blossoms	-0.369	0.05	0.084	0.19
Snail shells	0.141	0.16	0.346	0.055
Yellow blossoms	0.123	0.17	0.435	0.03
Man made objects	-0.178	0.14	0.326	0.065
Cicadas	-0.122	0.17	0.399	0.04
Other natural objects	0.016	0.25	0.127	0.16

display in bowers with no other birds present. Another possibility is that males who fail to display do so because they are intimidated by other males.

The observed correlations support a model suggesting that intrapopulational differences in testosterone levels can account for differences in male ability to produce display characters and ultimately affect male reproductive success. It should be noted, however, that the correlations involving testosterone levels generally failed to explain a large proportion of the total variation in either male display characters or mating success. This suggests that a simple increase in testosterone levels may not be sufficient to cause large changes in male reproductive success. Alternatively, daily cycling in testosterone may have contributed to variation in measured levels of testosterone and thereby reduced the total level of variation that could be explained in our comparisons.

The experiments described above involving implants of testosterone in juvenile males (Collis and Borgia 1990, 1991) showed significant effects on male aggression against other juvenile males. Even so, implanted juvenile males with levels of circulating testosterone in excess of adult plumage males could not dominate the adult plumage

males nor produce high quality displays. Similarly in the red-winged blackbird, *Aegalanus phoeniceus*, implants increase the likelihood that they would obtain a territory and mates (Beletsky et al., 1990).

The tendency for male Satin Bowerbirds to frequently practice displays (Loffredo and Borgia 1986), the long delay in their attainment of secondary sexual traits, and the finding that older males produce the highest quality displays (Borgia 1986, Borgia, in preparation) support the hypothesis that experience is critical for high male mating success. High levels of testosterone might then only be one of several determinants of male mating success. Marshall (1950) also showed that testosterone injections only partially restored bower-building behavior, suggesting that other factors may also be involved.

This model may explain why males have not evolved to produce high levels of testosterone at a young age. Increases in testosterone production in immature males might be costly in forcing them into high risk activities before they have sufficient experience to produce a display competitive with those of older and more practiced males (see Collis and Borgia 1990). The variation in testosterone levels explained only a relatively small part of the total variation in male success

TABLE 4. Relationships of plasma testosterone and corticosterone to male advertising behaviors.

	Advertising calls			
	Corticosterone		Testosterone	
	Spearman correlation	P	Spearman correlation	P
Whistle call frequency	0.270	0.09	0.149	0.24
Scratch call frequency	0.154	ns	0.070	ns

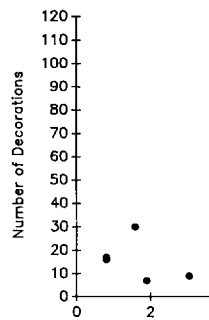


FIGURE 4. Circulating testosterone and total number of bowers.

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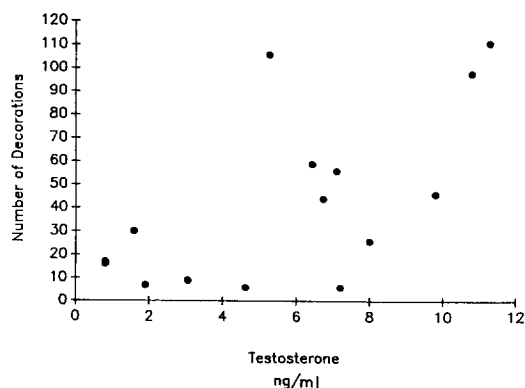


FIGURE 4. Circulating testosterone levels and the total number of bower decorations in 1984.

(and less than decoration variables, see Borgia 1985a), suggesting that testosterone and experience may act independently to affect male mating success. This view is further supported by patterns among variables showing strong correlations with testosterone levels that tended not to be those that measure artistic experience. Thus, stick density, stick size, and total numbers of decorations that show strong correlations with testosterone levels, all require that males be very active in pursuing specific types of sticks or decorations, but do not directly reflect male experience. By contrast, variables such as quality of bower construction show nonsignificant correlations with testosterone levels even though this is one of the best predictors of male reproductive success (Borgia 1985a, in preparation).

Our findings from earlier studies showing an important role for bower quality, bower decoration and male display affecting male mating success (Borgia 1985, Loffredo and Borgia 1986) and testosterone-implant studies showing an increase in these activities in juvenile birds suggests that testosterone may be part of an enabling mechanism that allows the correct level of expression of these traits by males that differ in dominance and experience. While it may be possible that mating experience is the cause of high testosterone-levels (e.g., Wingfield and Moore 1987) that hypothesis would less adequately explain both increases in display behavior by implanted juvenile males (Collis and Borgia 1990) and changes in male mating success at bowers where decorations have been manipulated (e.g., Borgia 1985, Borgia in preparation). Moreover, it leaves unresolved the function of high testos-

TABLE 5. Relationships of plasma testosterone and corticosterone levels to bower destruction.

	Natural bower destructions			
	Corticosterone		Testosterone	
	Spearman correlation	P	Spearman correlation	P
Destruction victim	-0.234	ns	-0.109	ns
Destroyer	-0.405	0.05	-0.252	ns

Two-tailed tests.

terone levels and seasonal cycling of testosterone levels with large increases occurring in anticipation of the mating season (see Marshall 1954). Increases of testosterone in anticipation of the breeding season could be induced by male-male competition over bower sites (see Wingfield and Moore 1987), a point not addressed in this study.

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LITERATURE CITED

- BALL, G. F., AND J. C. WINGFIELD. 1987. Changes in plasma levels of luteinizing hormone and sex steroid hormones in relation to multiple-broodedness and nest site density in male starlings. *Physiol. Zool.* 60:191-199.
- BALTHAZART, J. 1983. Hormonal correlates of behavior, p. 221-365. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*, Vol. 7. Academic Press, New York.
- BELETSKY, L., G. H. ORIAN, AND J. C. WINGFIELD. 1990. Effects of exogenous androgen and antiandrogen on territorial and non-territorial red-winged blackbirds (*Aves: Icterinae*). *Ethology* 85:58-72.
- BORGIA, G. 1985a. Bower quality, number of decorations and mating success of male Satin Bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* 33:266-271.
- BORGIA, G. 1985b. Bower destruction and sexual

- competition in the Satin Bowerbird (*Ptilonorhynchus violaceus*). Behav. Ecol. Sociobiol. 18:91-100.
- BORGIA, G. 1986. Sexual selection in Bowerbirds. Sci. Am. 254:92-100.
- BORGIA, G. 1991. The cost of display in the non-resource based mating system of the Satin Bowerbird. Am. Nat.
- BORGIA, G., AND M. A. GORE. 1986. Feather stealing in the Satin Bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. Anim. Behav. 34:727-738.
- COLLIS, K., AND G. BORGIA. 1990. Experimental advancement of display character development in juvenile male Satin Bowerbirds and its effects on display function. Chapter 2. M.S.thesis, Department of Zoology, Univ. of Maryland, College Park, USA.
- COLLIS, K., AND G. BORGIA. 1991. Immediate and long term effects on males aggression from testosterone implants in juvenile male Satin Bowerbirds. Auk.
- DONAGHEY, R. 1981. The ecology and evolution of bowerbird mating systems. Ph.D.diss., Monash University, Clayton, Victoria.
- HARDING, C. 1981. Social modulation of circulating hormones in the male. Am. Zool. 21:223-232.
- HARDING, C. F., M. J. WALTERS, D. COLLADO, AND K. SHERIDAN. 1988. Hormonal specificity and activation of social behavior in male red-winged blackbirds. Horm. Behav. 22:402-418.
- HEGNER, R. F., AND J. WINGFIELD. 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. Auk 104:462-469.
- LANDE, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Nat. Acad. Sci. USA 78:3721-3725.
- LOFFREDO, C. A., AND G. BORGIA. 1985. Male courtship vocalization as cues for mate choice in the Satin Bowerbird (*Ptilonorhynchus violaceus*). Auk 103:189-195.
- LOFFREDO, C., AND G. BORGIA. 1986. Sexual selection, mating systems, and the evolution of avian acoustical displays. Am. Nat. 128:733-794.
- MARLER, C. A., AND M. C. MOORE. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav. Ecol. Sociobiol. 23:21-26.
- MARSHALL, A. J. 1950. The function of the bower of the Satin Bowerbird in the light of experimental modifications of the breeding cycle. Nature 165:388-389.
- MARSHALL, A. J. 1954. Bower-birds: their displays and breeding cycles. Clarendon Press, Oxford, England.
- MOORE, M. C., AND C. A. MARLER. 1987. Effects of testosterone manipulations on nonbreeding season territorial aggression in free-living male lizards, *Sceloporus jarrovi*. Gen. Comp. Endocrinol. 65:225-232.
- MOORE, M. C., AND C. A. MARLER. 1988. Hormones, behavior and the environment: an evolutionary perspective, p. 71-84. In M. H. Stetson [ed.], Processing of environmental information in vertebrates. Springer-Verlag, New York.
- ROHWER, S., AND J. C. WINGFIELD. 1981. A field study of social dominance, plasmas levels of luteinizing hormone, and steroid hormones in wintering Harris' sparrows. Z. Tierpsychol. 57:153-183.
- SOKAL, R., AND F. ROHLF. 1969. Biometry. Freeman, San Francisco.
- VELLENGA, R. 1970. Behavior of the male Satin bowerbird at the bower. Aust. Bird Bander 1:3-11.
- WINGFIELD, J. C. 1984. Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. II. Agonistic interactions as information stimulating secretion of testosterone. Gen. Comp. Endocrinol. 56:417-424.
- WINGFIELD, J. C. 1988. Changes in reproductive function of free-living birds in direct response to environmental perturbations, p. 121-148. In M. H. Stetson [ed.], Processing of environmental information in vertebrates. Springer-Verlag, Berlin.
- WINGFIELD, J. C., G. F. BALL, A. M. DUFTY, R. E. HEGNER, AND M. RAMENOFSKY. 1987. Testosterone and aggression in birds. Am. Sci. 75:602-608.
- WINGFIELD, J. C., AND D. S. FARNER. 1975. The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. Steroids 26:311-327.
- WINGFIELD, J. C., AND M. C. MOORE. 1987. Hormonal, social, and environmental factors in the reproductive biology of free-living male birds, p. 149-175. In D. Crews [ed.], Psychobiology of reproductive behavior: an evolutionary perspective. Prentice-Hall, NJ.
- WINGFIELD, J. C., AND B. SILVERIN. 1986. The effects of corticosterone on territorial behavior of free-living male song sparrows, *Melospiza melodia*. Horm. Behav. 20:405-417.
- WINGFIELD, J. C., J. P. SMITH, AND D. S. FARNER. 1982a. Endocrine response of white-crowned sparrows to environmental stress. Condor. 84:399-409.
- WINGFIELD, J. C., A. NEWMAN, G. L. HUNT, AND D. S. FARNER. 1982b. Endocrine correlates of female-female pairing in the western gull, *Larus occidentalis wymani*, of Santa Barbara Island. Anim. Behav. 30:9-22.
- ZAHAVI, A. 1975. Mate selection—a selection for a handicap. J. Theor. Biol. 53:205-214.

BROOD SIZE
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Abstract.

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INTRODUCTION

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