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The Costs of Male Display and Delayed Plumage Maturation in the Satin Bowerbird (*Ptilonorhynchus violaceus*)

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Abstract

The costs associated with the evolution of male display traits has attracted much attention in regard to the type of traits that evolve and the timing of their expression. We investigate these costs by using testosterone implants to alter the development of male display traits in the satin bowerbird (*Ptilonorhynchus violaceus*). Testosterone implants advanced the development of adult display traits in males with juvenile plumage. We then measured the costs of early expression of these characters in treated males. Testosterone implants caused young males to (1) become more involved in behavior normally carried out by older males when visiting bowers, (2) build bowers, and (3) molt prematurely into an adult plumage. No difference was observed between the testosterone-treated birds and controls in return rate or condition the year following treatment, suggesting that the physical costs of display are not high. We found that males in adult plumage are tolerated less, and are not displayed to as frequently as juvenile plumage males at the bowers of established bower holders. The causes of delayed plumage maturation are most consistent with the facilitated-learning hypothesis. That is, early development of adult characteristics reduces the opportunity of young males to learn display behavior critical for later reproductive success.

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Introduction

Evolutionary biologists have long been interested in the study of sexually selected traits, especially in species where males have highly elaborated characters and provide no assistance to females in the rearing of young (e.g. FISHER 1930; TRIVERS 1972; ZAHAVI 1975; BORGIA 1979; LANDE 1981; HAMILTON & ZUK 1982; KIRKPATRICK 1982; BRADBURY & GIBSON 1983). Recently, there has been much emphasis placed on the study of the costs associated with exaggerated display characters and how these costs might be important in sexual selection (POMIANKOWSKI 1987; HEISLER et al. 1987; PRICE et al. 1987). For instance, in Zahavi's

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good genes model, costs are important in guarenteeing honest advertisement (ZAHAVI 1975; KODRIC-BROWN & BROWN 1984). Costs associated with display traits may not only limit the degree to which a trait is expressed in adult males, but may cause the delayed maturation of adult display characters observed in many species with exaggerated characters (SELANDER 1965, 1972; WILEY 1974). Here we investigate the costs of male display in the satin bowerbird, particularly how these costs may be important in explaining delays in plumage and display development in juvenile males.

The costs most often discussed in association with extreme sex-limited display characteristics are related to reduced survivorship (LACK 1954; SELANDER 1965, 1972; MARLER & MOORE 1988). Males with exaggerated characters may experience a higher risk of mortality due to (1) the high energetic costs that might be associated with display, (2) increased risk of injury, and (3) increased predation pressure on the more conspicuous males (MARLER & MOORE 1988). Few empirical studies have measured mortality costs of male display in birds, and these studies differ in the importance they assign to these costs. DUFTY (1989) showed that testosterone implants caused increased aggressiveness in male cowbirds resulting in reduced survivorship the year following treatment. Other studies on birds have shown display traits to be costly, but were unable to show that exaggeration of these traits cause increased mortality risks (MØLLER 1989; WINGFIELD 1984). Mortality costs associated with the display of bower-holding satin bowerbirds were investigated and the results suggest that these costs are not large (BORGIA 1992). Even so, the premature expression of display characters may be high, and such costs may limit character development in young males.

In species where learning plays a critical role in the development of display behaviors, as seems true for some polygynous bowerbirds (MARSHALL 1954; VELLENGA 1970; LOFFREDO & BORGIA 1986; BORGIA 1986; COLLIS & BORGIA 1992) and grouse (KRUIJT & HOGAN 1967; KRUIJT et al. 1972; WILEY 1974), early maturation may be costly for young males because adult plumage attracts aggression from older males. We propose the facilitated learning hypothesis, a subset of the more general status-signalling hypothesis (see ROHWER 1975, 1977; LYON & MONTGOMERIE 1986). The status-signalling hypothesis suggests that variation in plumage evolved as a reliable signal of status within social groups, where bright plumage correlates with a male's ability to be aggressively dominant. Under this hypothesis, males with bright plumage incur both physical and reproductive costs resulting from the increased aggression received from rival males. Young males with dull plumage do not experience these physical costs, and by signalling a subordinate status, are tolerated by older males allowing them increased access to unmated females and/or resources that are important to male mating success (i.e. territories, experience). The facilitated-learning hypothesis suggests that young males delay development of adult plumage characteristics to enhance their opportunity to learn courtship behavior from adult males. Under this hypothesis, the early development of adult characters (e.g. plumage) is a cost to young males because it impairs young males' ability to learn display.

Satin bowerbirds are especially suited for a study of the costs of display because males undergo long delays in the maturation of plumage, and have easily quantifiable, complex displays that improve with age (MARSHALL 1954; VELLENGA 1970; BORGIA 1985a, 1986; LOFFREDO & BORGIA 1986; COLLIS & BORGIA 1992). Males in this species are highly polygynous, with male mating success dependent upon the ownership of a high quality bower (BORGIA 1985a, b), a structure constructed from sticks where males court females (see BORGIA 1986). Most males do not acquire a full adult plumage until their 7th year, even though they produce viable sperm while still in juvenile plumage (MARSHALL 1954; see also VELLENGA 1980). Males do not mate until they have molted in a full adult plumage and are established on a permanent bower site (BORGIA 1986). Females do not show a similar delay in reproduction (MARSHALL 1954; VELLENGA 1970, 1980). Prior to their 7th year, males maintain a female-like plumage and spend a great deal of time visiting the bowers of older males (VELLENGA 1970, 1980). At these sites young males may be courted by the bower owner, and when the owner is absent, they practice display and bower building behavior themselves (VELLENGA 1970; BORGIA unpubl. data). As males age various graded changes are observed in their behavior and plumage. During their 5th and 6th years, males (1) pass through a series of transitional plumages before molting in a full adult blue plumage (VELLENGA 1980), (2) become more aggressive both while in flocks feeding and when visiting bowers (BORGIA 1985b, 1986; COLLIS & BORGIA 1992), and (3) begin building temporary bowers at sites removed from the permanent sites of older males (VELLENGA 1970, 1980).

Previous studies of satin bowerbirds have shown that age, dominance, and experience are all important in the development of displays important to male reproductive success (MARSHALL 1954; VELLENGA 1970; BORGIA 1985a, 1986; LOFFREDO & BORGIA 1986; COLLIS & BORGIA 1992). Treatment of juvenile plumage males with testosterone increased both aggression and dominance status among birds in juvenile plumage, but it did not affect agressive dominance between the treated juveniles and untreated adult males, which were similar in size and plumage condition the year following treatment (COLLIS & BORGIA 1992). These results suggested a role for experience in overall dominance relationships in the satin bowerbird.

Here we report the effects of testosterone treatment done to accelerate male development so that we could measure the costs of expressing adult display characters in juvenile males. We investigated the development of plumage, bower building, and other behavior related to male display in juvenile plumage males, and measured the effect of testosterone treatment on male condition and survivorship. We then used this information to test hypotheses concerning the costs associated with full display development in the satin bowerbird.

Methods

This study was carried out in 1986 and 1987 as part of a long-term study that began in 1980 on satin bowerbirds at Wallaby Creek in the Beaury State Forest, New South Wales, Australia (DONAGHEY 1981; BORGIA 1986). The study site is in a valley formed by Wallaby Creek and extends roughly 1.5 km into a system of ridges that surround the valley to the north and east. The site can be characterized as open canopy eucalyptus forest with patches of subtropical rain forest found along low lying creeks and on the east side of the higher ridges. Bowers are located in and around the ridge system surrounding the valley and are attended by males throughout the breeding season, from early Nov. through Dec. Prior to the breeding season, from Aug. through Oct., birds are commonly found foraging in large, single-sexed flocks in open paddocks and in trees and shrubs surrounding the creek. A more complete description of the study site and the general ecology of the satin bowerbird can be found elsewhere (BORGIA 1985a, 1986).

Experimental Procedure

Birds were captured from late Aug. to Oct. prior to the breeding season at established feeding sites using ground traps baited with bread. Once captured, the birds were color banded (if not previously banded), weighed, measured for wing length, tarsus length, and bill length, scored for plumage differences, and aged and sexed (based on plumage and wing length, see VELLENGA 1980). Behavioral interactions were recorded at feeding sites to determine the relative dominance ranks of juvenile plumage males before they were assigned to a treatment group (see COLLIS & BORGIA 1992). Birds of similar rank, age, and plumage condition were paired and randomly assigned to either a testosterone-treated, or control group. Implants were administered in 1986 over a 4-wk period, from mid-Sep. through mid-Oct. The testosterone-treated birds received either one, two, or three implants of testosterone where controls were given the same number of empty implants. Different levels of treatment were administered to determine if a dose-response relationship existed between hormones and the measured behavior. There were a total of 25 birds in the testosterone-treated group and 21 birds in the control group (see COLLIS & BORGIA 1992). Sample sizes between treatment groups were not equal because we could not capture all males that were initially assigned to groups. Blood samples were collected from all birds immediately after capture to determine blood androgen levels both before (0—7 d) and after (7—14 d) implant. Hormonal analysis was carried out using single-antibody radioimmunoassay techniques (see OTTINGER & MAHLKE 1984). The handling and treatment of birds caused few outward signs of disturbance. Birds had been handled frequently in previous years and most birds returned to traps immediately after release. Further details on the implanting procedure, blood collection, and hormone analysis can be found elsewhere (COLLIS & BORGIA 1992).

Body, wing, and tail feathers (1—3 in each area) were removed from the treatment birds at the time implants were administered and at first recapture following treatment. At various times after the removal of feathers, birds were recaptured to determine the color and growth rate of the replacement feathers. To determine the effects of treatment on plumage change at annual molt, treatment birds were censused a year after implant at feeding sites. Birds were checked for changes in plumage color, and weighed.

Behavioral Sampling

From late Aug. through Nov. in 1986 and 1987 we recorded behavioral interactions at provisioned feeding sites. For each two-way interaction we recorded the identity of both the initiator and recipient of the interaction, as well as a description of the directed action and response. Several types of agonistic interactions in the form of approaches, threats, and attacks were observed and the effect of testosterone treatment on these types of behavior has been discussed elsewhere (COLLIS & BORGIA 1992). In addition, males occasionally engaged in courtship display to males and females at the feeding sites.

The study site was thoroughly searched for both permanent and temporary bower sites. Throughout the breeding seasons from 1981—1986, the behavior of established adult male bower holders and their visitors were continuously monitored using a remote control camera system erected at their bowers (BORGIA 1985a). In addition, behavioral observations were carried out by observers at both the permanent bower sites of older males and the temporary sites of younger males. Bower observations carried out in 1986 allowed us to determine whether or not testosterone treatment had an effect on the kinds of behavior carried out by young males when visiting the bowers of older males. The behaviors that were measured were displays and courtships carried out by the visiting bird, courtship of the visiting bird by the bower owner, and bouts of building, painting, bower destructions, and stealing of decorations carried out by the visiting bird.

Bower observations carried out by observers from 1982—1986 were analyzed to determine if the plumage color of a visiting bird affected that bird's ability to observe the bower owner at his bower. The relationship between the tolerance of bower-owning males and plumage color of visiting

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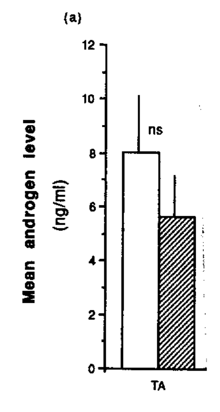

Fig. 1: A comparison
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males was investigated by comparing the proportion of bouts in which visiting birds in different plumages were chased away and courted at bowers by the resident bower holder. We controlled for the effects of behavior on tolerance by removing all bouts from the analysis that were preceded by an aggressive behavior carried out by the visiting bird (i.e. stealing of decorations, bower destruction, courtship or display, vocalizations).

On daily visits to bowers, observers noted the number of 9 different types of decorations found on bowers and estimated four different characteristics of bower quality (see BORGIA 1985a). Bowers were rated for symmetry, stick density, size of sticks used, and overall quality (see BORGIA 1985a). Bowers that had well sculpted, symmetrical walls, constructed from densely packed fine sticks, with an overall neat appearance were given a top score of one, with the lowest quality bowers receiving a score of six. Further details on bower decoration and quality measures can be found elsewhere (BORGIA 1985a).

Statistical Analyses

No measurable differences were observed between the testosterone-treated groups in the behavior measured here, so the different levels of testosterone treatment were pooled in all comparisons. Statistical comparisons are by Student t-test (t), Mann-Whitney U-tests (U), and Chi-square (χ^2) and Fisher's exact tests for independence (SOKAL & ROHLF 1981; SIEGEL 1988; SAS INSTITUTE INC. 1985). Means are expressed as $\bar{X} \pm$ SE. When positive treatment effects were expected one-tailed p values are cited, otherwise p values are two-tailed and are noted as such.

Results

Effects of Testosterone Treatment

Hormones. Plasma levels of total androgen (TA), testosterone (T), and dihydrotestosterone (DHT) were measured for individuals in control and testosterone-treated groups before and after implant. The testosterone implants consistently raised the measured blood androgens above basal levels, causing significant differences between experimental groups in endogenous androgens after implant (Fig. 1). The measured blood androgen levels of testosterone-treated birds after

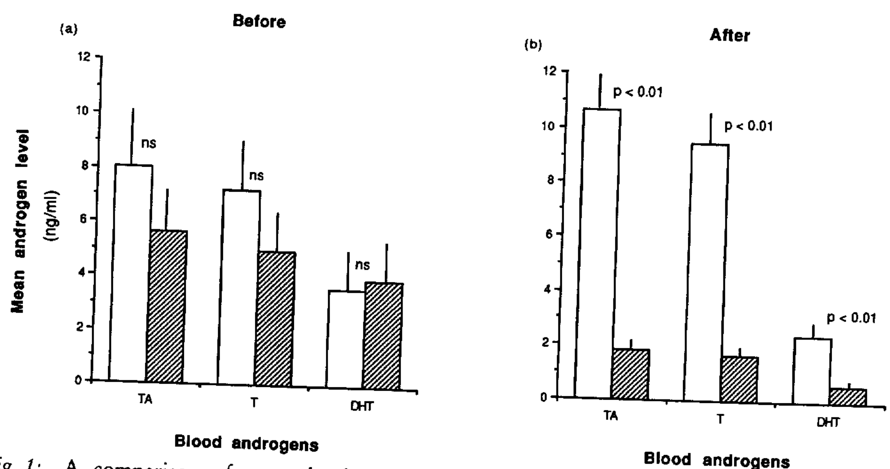

Fig. 1: A comparison of mean levels (± SE) of total androgens (TA), testosterone (T), and dihydrotestosterone (DHT) for pooled testosterone treated groups (white columns) and controls (hatched columns). Measures on androgens were made (a) before implant and (b) after implant

Table 1: Plumage changes observed in treatment birds the year following implant compared to the normal pattern of plumage change. Numbers represent the number of birds in each treatment group and their plumage condition at implant. Changes in plumage are indicated with arrows. Numbers not followed by arrows were birds that did not undergo a change in plumage

Normal pattern of plumage change	Age (yrs) Plumage Bill	1—4 green dark	5 green yellow	6 mixed blue-green yellow	7 blue yellow
Testosterone		10 →	→	→	→
			2 →	→	→
				2 →	→
Control		5			
			2		
			2 →	→	
			1 →	→	→
				1 →	→

implant (see Fig. 1) were significantly above levels measured for adult-plumage males (TA: $\bar{X} = 4.6 \pm 0.7$ ng/ml, n = 19; T: $\bar{X} = 4.3 \pm 0.7$ ng/ml, n = 19; DHT: $\bar{X} = 0.6 \pm 0.2$ ng/ml, n = 19). These levels however, were not outside the range normally exhibited by adult males.

Plumage. In 1987, the year following treatment, differences were observed between the treatment groups in plumage color. Of the 14 testosterone-treated birds that were re-sighted in 1987, all had molted into an all-blue adult plumage (Table 1). Of these 14 birds, 10 had changed from a dark-billed, green plumage directly into all-blue plumage skipping two transitional phases (depending on the age of these dark-billed, green males at time of implant, this transition into all-blue plumage was observed 2—5 yr before what would normally be expected); two birds skipped one transitional phase, changing from a yellow-billed, green plumage to an all-blue plumage; and two treatment birds molted into an all-blue plumage from a mixed blue-green plumage (Table 1). Of the 11 controls that were re-sighted in 1987, 7 birds did not change plumage type; two birds molted to a blue-green mixed plumage from a yellow-billed, green plumage; one bird molted to an all-blue plumage from a mixed blue-green plumage; and only one bird skipped a transitional phase by molting to an all-blue plumage from a yellow-billed, green plumage (Table 1). The bird in the control group that skipped a transitional phase was observed to have the highest mean testosterone level of all the controls whose hormone levels were measured in 1986. 12 of 14 testosterone-treated birds and only 1 of 11 controls skipped at least one transitional phase in plumage providing evidence for an effect of treatment on plumage type (Fisher's exact test, $p < 0.001$).

Feathers were removed from all treatment birds at implant, and 3 to 10 d after implant. Birds were then recaptured in 1986 and the color of the replacement feathers was noted. In all cases, for both treatment and control birds, the replacement feathers showed the same juvenile color as the feathers removed.

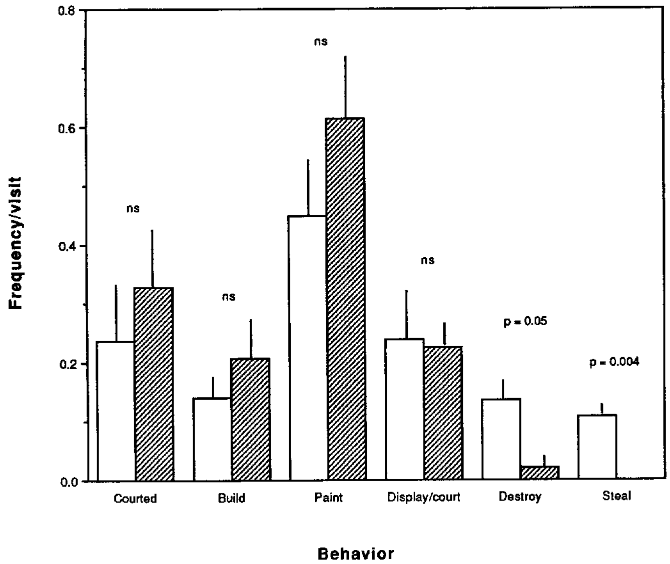

Fig. 2: A comparison of the mean (± SE) frequency of display and bower-building behavior per visit in 1986 between the pooled testosterone-treated groups (white columns) and the control group (hatched columns)

Display and Bower-building Behaviors. Display behaviors were exhibited in three different contexts and each was investigated to determine the effects of testosterone treatment on sexual behavior. First, throughout the breeding season juvenile males visit the bowers of established adult male bower holders. Significant differences were observed between the treatment groups in the types of behavior carried out while visiting the permanent bowers of older males (Fig. 2). We controlled for differences in visitation rates by comparing the frequency of occurrence of each behavior (as listed in Fig. 2) per visit between the treatment groups. Birds treated with testosterone stole decorations (T-implant: 0.11 ± 0.05, n = 15; controls: 0.00 ± 0.00, n = 12, U = 132, p = 0.004) and destroyed bowers (T-implant: 0.14 ± 0.06, n = 15; control: 0.02 ± 0.02, n = 12, U = 114, p = 0.05) more often than controls. No other significant differences were observed between the treatment groups in the behavior carried out by visiting birds at bowers.

Second, male satin bowerbirds occasionally display to one another at feeding sites prior to the breeding season. Comparisons between treatment groups following treatment in 1986 showed that the testosterone-treated birds tended toward more display behavior at the traps than the controls, but this difference was not significant (Fisher's exact test, p = 0.09). Testosterone-treated birds also tended to display at a greater frequency than controls at these sites, this difference approached significance (T-implant: 1.83 ± 0.63, n = 23; control: 0.67 ± 0.39, n = 18, t = 1.46, p = 0.07).

Finally, testosterone treatment affected bower building. Of the 25 juvenile males that were treated with testosterone, five were observed to build and hold bowers in 1986, where that same year none of 21 controls built bowers (Fisher's exact test, $p = 0.04$).

Measurable differences existed between the bowers built by the testosterone-treated males and the established bowers of older males. The bowers of older males ranked higher in overall quality of construction (T-implant: 5.40 ± 0.82, $n = 3$; established bower holders: 3.38 ± 0.27, $n = 19$, $U = 49$, $p = 0.05$, two-tailed) and were more elaborately decorated, having a greater total number of decorations (T-implant: 36.00 ± 7.90, $n = 3$; established bower holders: 92.35 ± 11.88, $n = 19$, $U = 49$, $p = 0.05$, two-tailed).

Costs of Display

Tolerance. A possible cost associated with increased testosterone levels in juvenile plumage males is that these birds may have a reduced opportunity to observe display of older males if elevated testosterone levels lead to changes in their perceived status by these males. We tested this hypothesis by comparing the frequency of unprovoked chases (chases that were not preceded by a behavior that may be perceived by the bower holder as aggressive) around bowers in years 1982—1986 by established adult blue male bower holders of birds in juvenile and adult plumage (Table 2). Adult blue plumage males were chased more often than were juvenile plumage males ($\chi^2 = 11.74$, $n = 109$, $p < 0.001$) and females were chased less often than juvenile plumage males ($\chi^2 = 9.89$, $n = 145$, $p = 0.002$).

Table 2: Visits to bowers by individual birds in different plumage classes from 1982—1986 that result in either no chase (tolerance) or an unprovoked chase. Only visits when resident bower holder known to be present are incluced in the analysis

Class	Birds chased	Birds not chased	Total visitors*	% chase
Females	4	48	52	7.7
Juvenile plumage males (dark-billed green and transitional plumage males)	30	63	93	32.2
Dark-billed green males	13	34	47	27.6
Transitional plumage males (yellow-billed green and blue-green mixed plumage males)	17	29	46	36.9
Yellow-billed green males	15	25	40	37.5
Blue-green mixed plumage males	2	4	6	33.3
Adult blue plumage males	13	3	16	81.2
Adult blue plumage males without bowers	10	1	11	90.9
Adult blue plumage males with bowers	3	2	5	60.0

* Only individually identified (color-banded) birds included in the analysis. Individual birds are the units of replication, and are included only once in the analysis.

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There were no significant differences among males in different transitional plumages in their tendency to be chased away from bowers. Furthermore, there was no difference between bower-holding and non-bower-holding adult blue plumage males in the frequency in which they were chased away while visiting bowers.

Observation of Display. Differences in tolerance of males in different plumage are expected to affect male ability to observe displays at the bowers of established males. We tested this hypothesis by comparing the frequency of courtship of birds in different plumage classes by established bower holders in the years 1982—1986 (Table 3). These results indicate that juvenile plumage males were courted more often than blue plumage males ($\chi^2 = 22.33$, $n = 109$, $p < 0.001$). No other comparisons proved to be significantly different, including the comparison between females and juvenile plumage males.

Survivorship. The effects of treatment on survivorship were tested by comparing the return rates of control and testosterone-treated birds to feeding sites the year following implant. Of the 25 birds that were treated with testosterone in 1986, 13 returned to feeding sites in 1987, where 13 of 21 controls were observed at these sites 1987 (Fisher's exact test, $p = 0.19$). We could detect no effect of testosterone treatment on male survivorship.

Condition. The effects of testosterone on condition was investigated by comparing the change in weight (weight at recapture — weight at implant) of the treatment birds that returned to traps the year following treatment. Birds in both

Table 3: Visits to bowers by individual birds in different plumage classes from 1982—1986 that result in either a courtship or no courtship. Only visits when resident bower holder known to be present are incluced in the analysis

Class	Birds courted	Birds not courted	Total visitors*	% courted
Females	47	5	52	90.4
Juvenile plumage males (dark-billed green and transitional plumage males)	78	15	93	83.9
Dark-billed green males	40	7	47	85.1
Transitional plumage males (yellow-billed green and blue-green mixed plumage males)	38	8	46	82.6
Yellow-billed green males	32	8	40	80.0
Blue-green mixed plumage males	6	0	6	100.0
Adult blue plumage males	4	12	16	25.0
Adult blue plumage males without bowers	4	7	11	36.4
Adult blue plumage males with bowers	0	5	5	0.0

* Only individually identified (color-banded) birds included in the analysis. Individual birds are the units of replication, and are included only once in the analysis.

the testosterone-treated and the control group were observed to lose weight in 1987 and there was no difference between treatment groups in weight loss (T-implant: 11.14 ± 5.02, n = 7; control: 11.25 ± 3.79, n = 4, U = 14.5, p = 0.46).

Discussion

Our results show that testosterone treatment had a significant effect in advancing the development of both behavioral and morphological characteristics in juvenile male satin bowerbirds. While visiting bowers, treated birds became more involved in behavior typically carried out by older male visitors (i.e. bower destructions and the stealing of decorations). Testosterone treated birds also built their own bowers and prematurely molted into a full adult plumage the year following treatment. Elsewhere, we have shown that testosterone treatment caused increases in both aggression and dominance position of the treated birds (COLLIS & BORGIA 1993).

Despite these changes, behavioral differences remained between the juvenile males treated with testosterone and "natural" adult plumage males. The quality of the bowers built by the testosterone-treated males were of a lower overall quality and had fewer total decorations than the bowers built by older males. Furthermore, testosterone treatment did not affect the quality of courtship display of treated males, which were of similar quality to the displays of untreated juvenile males (K. COLLIS & G. BORGIA, pers. obs.). Birds treated with testosterone remained subordinate to adult plumage males despite observed increases in androgens, aggression, and changes in plumage (COLLIS & BORGIA 1992). We suggest that this evidence, coupled with age-related improvements observed in bower building (BORGIA 1986, 1993) and display (LOFFREDO & BORGIA 1986) in untreated males, are consistent with the hypothesis that experience is an important component in the full development of male display and social dominance in the satin bowerbird.

The delayed development of male display characters in the satin bowerbird is likely due to costs associated with the early expression of these traits. These costs may be expressed in two ways. First, early plumage development may hinder the ability of young males to observe and learn display behavior at bower sites of older males (the facilitated-learning hypothesis). Our evidence showing that males in juvenile green plumage were less often chased and more often courted than blue plumage males is consistent with this hypothesis.

A second hypothesis is that there may be high direct physical costs associated with the attainment of adult plumage. Some of these costs may result from increased risk from predators, and others from the reactions of older, more dominant males (SELANDER 1965, 1972; FOSTER 1987). Several lines of evidence suggest that these costs may not be severe. There was no difference between the testosterone-treated birds and the controls in the rate of return the year following treatment, even though the returning testosterone-treated birds were more aggressive and carried a brighter plumage than the controls. These treatment

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C. thanks M. COLLIS for her patience

groups did not differ in condition as measured by the change in body mass the year following treatment. In general, mortality rates of adult plumage males are generally low (BORGIA 1993). Other evidence suggests that there might be physical costs of display. Young males with testosterone-induced blue plumage were subject to a higher proportion of attacks in encounters with "natural" blue plumage males than controls at feeding sites (COLLIS & BORGIA 1992). However, the testosterone-treated males also initiated more interactions than did the controls. Consequently, the increase in received aggression by the testosterone-treated birds may have resulted from their own heightened aggressiveness.

Juvenile plumage in the satin bowerbird may serve as a reliable signal of subordinance, allowing young males access to adult male bower sites. Fitness benefits to young males having access to adult bower sites could be immediate or long-term (ROHWER 1975, 1977; LYON & MONTGOMERIE 1986). Since juvenile male satin bowerbirds do not mate or build bowers in the vicinity of adult male bowers (BORGIA 1986), and based on the evidence that the physical costs of display may be limited, the benefits associated with signalling subordinance are more likely long-term. We suggest that male satin bowerbirds delay plumage maturation to increase their ability to learn display behaviors important in female choice. Reproductive benefits are then realized by males later in life after they have perfected these displays.

The above evidence is most consistent with the hypothesis that the major costs of early plumage maturation in satin bowerbirds are due to limitations placed on early maturing birds in acquiring information needed to produce successful displays (facilitated-learning hypothesis). These results, however, are not conclusive. For example, characters other than male plumage may account for the higher rate of chasing of blue males by bower holders from their bowers, and the number of birds in treatment and control groups was probably too small to show anything but extremely high mortality costs. More tests will be necessary to determine the extent to which one or both of the above types of costs have influenced the evolution of male plumage displays.

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