

AGE-RELATED EFFECTS OF TESTOSTERONE, PLUMAGE, AND EXPERIENCE ON AGGRESSION AND SOCIAL DOMINANCE IN JUVENILE MALE SATIN BOWERBIRDS (*PTILONORHYNCHUS VIOLACEUS*)

KEN COLLIS AND GERALD BORGIA

Department of Zoology, University of Maryland, College Park, Maryland 20742, USA

ABSTRACT.—We investigated the relationship between age and dominance in the Satin Bowerbird (*Ptilonorhynchus violaceus*) to understand why young males delay maturation. Testosterone implants were used to experimentally advance the expression of adult characteristics in juvenile-plumaged males. Testosterone implants increased both aggression and dominance among juvenile-plumaged males. In the year following implantation, treated males molted into full adult plumage and maintained their dominance over controls at feeding sites even though their implants were probably empty. Despite the changes in circulating androgens, aggression, and plumage brought on by the testosterone treatment of juvenile-plumaged males, age-related differences remained in aggression and social dominance between the treated and untreated birds. These age effects are consistent with the hypothesis that male experience in male aggressive encounters plays an important role in determining dominance relationships and, ultimately, affects the development of male adult-plumaged characters.

Received 12 September 1990, accepted 13 January 1992.

THE EVOLUTION of exaggerated male display traits common in many polygynous species has attracted much attention and discussion (see Bradbury and Andersson 1987). It is known for several of these species that exaggerated male display traits are fully expressed only after a relatively long developmental delay (e.g. Marshall 1954, Gilliard 1969, Selander 1972, Vellenga 1980, Studd and Robertson 1985, Foster 1987). For birds, the ultimate causes of this delay are not well understood. For most birds, unlike mammals (e.g. Clutton Brock et al. 1982), physical characters (e.g. size) that might directly affect male success in aggression (and, hence, their ability to influence displays of other males) do not change with age after early juvenile development. There is, however, much evidence that experience can affect display traits (Shettleworth 1984), and delays associated with gaining this experience may be important in the development and deployment of elaborated displays.

Satin Bowerbirds (*Ptilonorhynchus violaceus*) are especially suited for the study of delayed development of male display characters. Adult males build elaborate structures called bowers, where males court females (Vellenga 1970, Donaghey 1981, Borgia 1985a). Young males do not hold bowers and undergo a long delay in both plumage and behavioral development. Although young males produce viable sperm while

still in juvenile plumage (Marshall 1954), they do not acquire a full-adult blue plumage until their seventh year (Marshall 1954, see also Vellenga 1980). Prior to that time, young males maintain a green plumage and are behaviorally subordinate while feeding in flocks and when visiting the bowers of older males (Vellenga 1970, Collis 1990). Young males spend a great deal of time observing older males at their bowers, and practice bower building and display behaviors when the owner is absent from the bower site (Vellenga 1970, Borgia in prep.). As young males grow older, they become more aggressive and involved in the behaviors performed by adult males, constructing temporary bowers at sites removed from the bowers of adult males (Vellenga 1970). Both male dominance and age are important factors in a male's ability to hold a bower site, and to become successful in attracting females by maintaining a bower of high relative quality (Borgia 1985b, 1986, in prep., Borgia and Gore 1986). Among adult males, mating success is skewed in favor of a small minority of males who are able to build high-quality bowers with many decorations on their display courts (Borgia 1985a).

Two hypotheses provide plausible explanations for why there is delayed maturation of display characters in male Satin Bowerbirds. First, previous experience in aggressive inter-

actions may be important in the development of aggressive dominance. In turn, may be necessary to display sites or to attract mates. Young males may not be able to assert dominance until they have gained experience in aggression necessary to compete with older males for dominance. Aggression in birds may be important in social hierarchy in fowl (*Gallus gallus*). Ratner (1961) have shown that a way of learned dominance position. A combination of testosterone and aggressive condition may lead to increasing aggression in male pigeons. Experience alone had no effect on aggression and dominance. Prior experience in aggression had an effect on social hierarchy (*Lagopus lagopus*; Marshall 1954, *Coturnix coturnix*; and White-crowned and *Zonotrichia leucophrys* 1985, Baptista et al. 1985).

Second, young males may need to gain experience in display characters to produce effective displays. This is critical in producing a display until it is gained, complex traits needed for the display traits. The hypothesis, delayed development of the limited advantage, age, and not because males to become a mature age development of reproductive success. Age-related factors of display, or why adult characters build bowers. Costs leading to the display traits include: (1) increased pressing display traits. In 1972, Marler and tolerance of young experienced males, ability to learn display learning hypothesis.

actions may be important in determining male aggressive dominance. Aggressive dominance, in turn, may be necessary to allow males access to display sites or other prerequisites for attracting mates. Young males may delay maturation until they have gained the experience in aggression necessary to compete successfully with older males for mates. Previous studies of aggression in birds suggest that experience may be important in social dominance. In domestic fowl (*Gallus gallus*), Smith and Hale (1959) and Ratner (1961) have shown that conditioning, by way of learned dominance or submission, had a significant effect on an individual's dominance position. Lumia (1972) found that the combination of testosterone treatment and aggressive conditioning led to the greatest effect in increasing aggression and dominance position of male pigeons. Testosterone treatment alone had no effect on aggression, and conditioning alone led to only small changes in aggression and dominance of the treated birds. Prior experience in aggressive encounters also had an effect on social dominance in Red Grouse (*Lagopus lagopus*; Moss et al. 1979), Japanese Quail (*Coturnix coturnix*; Ramenofsky 1984), and Song and White-crowned sparrows (*Melospiza melodia* and *Zonotrichia leucophrys*; Arcese and Smith 1985, Baptista et al. 1987).

Second, young males may fail to develop adult display characters because they have insufficient experience in using these characters to produce effective displays. Experience can be critical in producing effective displays and, until it is gained, costly investment by young in traits needed for aggressive dominance and in the display traits is avoided. Under this hypothesis, delayed maturation occurs because of the limited advantages of dominance at a young age, and not because of the inability of young males to become aggressively dominant. Plumage development may be delayed when male reproductive success depends strongly upon age-related factors, such as learned components of display, or when precocial development of adult characters brings significant costs, or both. Costs leading to delayed maturation may include: (1) increased risk to young males expressing display traits (Lack 1954, Selander 1965, 1972, Marler and Moore 1988); or (2) reduced tolerance of young males by older, more experienced males, that may impair young males' ability to learn display (termed the facilitated-learning hypothesis by Collis and Borgia 1990)

or to reproduce (Rohwer et al. 1980, Lyon and Montgomerie 1986, Foster 1987). These alternatives need not be mutually exclusive.

Here we investigate the first of the above hypotheses. We used testosterone implants to induce premature maturation of adult characters in juvenile-plumaged males. After treatment, we compared levels of aggression and dominance position of the treated birds with the levels found in controls and untreated adult-plumage males. We tested the prediction that aggressive experience is important in overall social dominance: that young birds treated with testosterone are expected to remain subordinate to older, experienced males. We investigated both the immediate effects of implants and the effects of implants one year later on males that had prematurely obtained adult plumage.

METHODS

This study was conducted from August through December (1986 and 1987) as part of an investigation of Satin Bowerbirds that began in 1980 (see Borgia 1986). The field site is located 150 km southwest of Brisbane in the Beaurty State Forest, New South Wales, Australia, and has been described elsewhere (Borgia 1985a). This work was carried out in a valley formed by Wallaby Creek, adjacent to a system of ridges where bower sites have been located over eight previous years (Donaghey 1981, Borgia 1986). From August to October, Satin Bowerbirds are commonly found in the morning and late afternoons in open paddocks in predominantly single-sex flocks (5-50 birds). In paddocks, the birds generally feed on grass shoots. Satin Bowerbirds may move singly or in flocks to forage along the creek in flowering trees (e.g. *Gravellia* sp.), fruiting trees, and shrubs (e.g. *Rubus* sp.). In late October and early November, the flocks begin to disperse, and males spend more time visiting and tending bowers. The breeding season begins in mid-November and continues through mid-December.

Three feeding sites were established in mid-August and maintained through October in paddocks where birds had fed previously. Interactions were recorded daily at two of the three sites between 0600 and 1200 (see below). Sites were occasionally monitored in the afternoon. Birds were attracted to traps set in these locations that were baited with bread. The traps were operated by an observer in a blind 20 m away. We measured wing length, tarsus length, bill length, and weight of captured birds. Also, they were scored for plumage characters. Birds were banded with individually distinct color-band combinations. Birds were aged and sexed based on plumage and wing length (see Vellenga 1980). Blood was drawn from the wing vein of all experimental birds prior to treatment (see

below). Blood samples were collected in two to four heparinized capillary tubes (75 mm × 1.4 mm i.d.), and were centrifuged soon after collection. Plasma was frozen for hormone analysis in the laboratory.

Behavioral sampling.—Behavioral interactions at feeding sites were recorded to estimate individual dominance rank before and after treatment. We recorded the identity of both the initiator and the recipient of each interaction, and a description of the initiated behavior and response of the recipient.

There were four categories of initiated behaviors noted: move toward, mild attacks, threats, and severe attacks. Move toward is an aggressive approach of the initiator toward the target bird with the apparent intent of displacing the target. Mild attacks were rapid movements (e.g. lunge) that did not involve contact of the initiator with the target.

Four kinds of threats accompanied aggressive displays: puff threats, open-beak threats, wing-flip threats, and vocal threats. Puff threats involved males puffing their feathers while in an erect posture. Open-beak threats involved a bird holding its beak partially open as it approached another bird without vocalizing. Wing-flip threats were quick movements of the wings away from the body and back again. Vocal threats were harsh-sounding calls (with the beak held open) directed at a target bird. Severe attacks were attacks that involved contact (e.g. hit, strike, maul).

There were four types of responses by target birds to directed aggression: yield to initiator, held ground, mild displacement of the initiator, and severe displacement of the initiator. Yield to the initiator involves the target bird being displaced. Held ground means the target bird failed to yield or retaliate in response to the directed aggression of the initiator. Mild and severe displacements involved mild and severe attacks, respectively, by the target bird in response to the approach, threat, or attack of the initiator. An all-occurrence sampling method (Altmann 1974) was used to record behaviors of all birds used in the experiment in 1986 and 1987. Interactions occurred in or close to the traps, and happened infrequently enough so that nearly all interactions could be recorded by experienced observers. Individuals in the flock were censused for each observation period.

Experimental procedure.—Behavioral interactions were recorded for two weeks prior to treatment. Juvenile-plumaged males of similar rank (determined by number of "interactions won/total interactions" prior to treatment) and plumage condition (age class) were then paired and randomly assigned to a treatment group (see Table 1). This was done to assure that birds of different rank and plumage condition were distributed equally across all treatment groups. The treatments consisted of a control group and three testosterone-treated groups. The testosterone-treated birds received either one, two, or three implants of testosterone. Crystalline testosterone (Steraloids, Wilton, New Hampshire) was packed into Dow-Corning Silastic tubing (length 20 mm, inside diameter 1.47

mm, external diameter 1.96 mm), and the open ends were sealed with silicone (silastic adhesive). Implants were soaked in methanol to insure they were adequately sealed. Controls were given empty implants. A 12-gauge needle was inserted at the nape of the neck, and the implants were pushed under the skin where they remained throughout the experiment. This procedure took from 5 to 10 min from capture to release. Birds showed few outward signs of disturbance as a result of this procedure. They had been frequently handled in previous years, and most were active around traps soon after release.

Birds were recaptured and weighed at various times throughout the experiment. Blood samples were taken on all testosterone-treated and control birds to determine their post-treatment blood-hormone levels. In 1987 the birds were censused and interaction data was taken to determine the dominance status of birds that were treated in 1986. To determine the effects of testosterone implants on various measures of condition, birds were recaptured at this time so that the birds could be weighed and checked for changes in plumage condition.

Measuring dominance.—Dominance status was determined for each individual by calculating the number of opponents dominated using dominance values (DV):

$$DV = \arcsin X^{0.5}, \quad (1)$$

where X is the proportion of individuals dominated (see Beilharz and Mylrea 1963). Dominance values allow assignment of rank so that frequent interactions among particular dyads are not given undue weight. Dominance values were calculated before and after implantation for all individuals that interacted with five or more nontreated opponents.

Hormone assays.—Hormone assays were carried out with a single antibody RIA kit (Amersham, Arlington Heights, Illinois). We measured total androgen (TA), testosterone (T), and dihydrotestosterone (DHT). These measures were validated for Satin Bowerbird plasma and found to be accurate. Precision of replicate assay from pooled serum was 8.6% (coefficient of variability within assay). Serial dilution curves for the serum were parallel to the standard curve ($P < 0.05$), which insures no interference from other components in the serum. The sensitivity for T was 2 pg/tube and for DHT was 5 pg/tube (M. A. Ottinger pers. comm.; for further details on general assay procedure, see Ottinger and Mahlke 1984).

Statistical analyses.—We determined the effect of testosterone treatment on behavior by comparing within-subject differences (before and after implant) among treatments. Comparisons of changes within individuals among treatment groups allowed for the control of: (1) hormonal and behavioral differences prior to treatment; and (2) time-dependent changes in variables. Statistical comparisons involved GLM repeated-measures analyses (Winer 1971, SAS Insti-

TABLE 1. Individual condition, and rank

Bird	Rank
myd	
wwl	
dop	
lol	
Mean	
rgm	
rrn	
ymr	
ogn	
kny	
ypd	
dkn	
dlv	
Mean	
rdo	
nyk	
dno	
gnr	
dgw	
ddp	
wnp	
rnw	
ryl	
moy	
rkm	
mkk	
lyr	
Mean	
Grand mean	

* The different number groups were pooled in d

^b db = dark-billed, green

^c This measurement of

tute 1985), Spearman Whitney U -tests (Siegal and Rohlfs 1981). One-tailed P -values were used.

Hormone implants.—Testosterone and DHT were measured before treatment and treatment. No significant difference was found between the pooled testosterone levels ($\bar{x} = 2.0$ ng/ml, $n = 23$; DHT, $\bar{x} = 5.0$ ng/ml, $n = 19$; T, $\bar{x} = 5.0$ ng/ml, $n = 19$) and the control group ($\bar{x} = 4.0 \pm 1.6$ ng/ml, $n = 19$).

TABLE 1. Individual birds in testosterone-treated and control groups arranged by treatment, plumage condition, and rank (number of interactions won/total interactions) before implantation in 1986.

Testosterone				Control*			
Bird	Implants	Plumage ^b	Rank ^c	Bird	Implants	Plumage ^b	Rank ^c
myd	1	y ^b	0.306	grp	1	y ^b	0.409
wwl	1	y ^b	0.333	ryg	1	y ^b	0.458
dop	1	y ^b	0.544	Mean			0.433
lol	1	y ^b	0.682				
Mean			0.466				
rgm	2	db	0.070	wmk	2	db	0.071
rrn	2	db	0.092	owo	2	db	0.077
ymr	2	db	0.223	gpk	2	db	0.267
ogn	2	db	0.331	mkr	2	db	0.316
kny	2	db	0.337	rrr	2	db	0.358
ypd	2	db	0.401	mnr	2	db	0.411
dkn	2	db	0.506	nnk	2	db	0.613
dlv	2	db	0.580	rng	2	db	0.690
Mean			0.317	Mean			0.350
rdo	3	db	0.116	dyo	3	db	0.053
nyk	3	db	0.160	pyo	3	db	0.054
dno	3	db	0.200	wnk	3	db	0.270
gnr	3	db	0.311	odp	3	db	0.304
dgw	3	db	0.361	mkm	3	db	0.444
ddp	3	db	0.679	lnp	3	db	0.533
wnp	3	db	0.824	glw	3	db	0.643
rnw	3	db	0.909				
ryl	3	y ^b	0.304	dkl	3	y ^b	0.374
moy	3	y ^b	0.377	ppk	3	y ^b	0.455
rkm	3	bg	0.286	lrp	3	bg	0.327
mkk	3	bg	0.345	pmo	3	bg	0.552
lyr	3	bg	0.409	Mean			0.364
Mean			0.406				
Grand mean			0.387	Grand mean			0.365

* The different number of empty implants given to control birds did not have an effect on measured behaviors. Hence, the different control groups were pooled in determining treatment effects.
^b db = dark-billed, green-plumaged male; y^b = yellow-billed, green-plumaged male; bg = yellow-billed, mixed blue- and green-plumaged male.
^c This measurement of rank carried out so that birds of different ranks before implantation were distributed evenly across treatments.

tute 1985), Spearman (r_s) rank correlations, Mann-Whitney U -tests (Siegel 1988), and Student t -tests (Sokal and Rohlf 1981). Means are expressed as $\bar{x} \pm SE$. One-tailed P -values are cited when positive treatment effects were expected; otherwise, two-tailed P -values are used.

RESULTS

Hormone implants.—Plasma levels of TA, T, and DHT were measured in individuals in control and treatment groups before and after implantation. No significant differences were found between the mean androgen levels of the pooled testosterone-treated groups (TA, $\bar{x} = 8.0 \pm 2.0$ ng/ml, $n = 23$; T, $\bar{x} = 7.2 \pm 2.0$ ng/ml, $n = 23$; DHT, $\bar{x} = 3.6 \pm 1.6$ ng/ml, $n = 23$) and the control group (TA, $\bar{x} = 5.6 \pm 1.6$ ng/ml, $n = 19$; T, $\bar{x} = 5.0 \pm 1.6$ ng/ml, $n = 19$; DHT, $\bar{x} = 4.0 \pm 1.6$ ng/ml, $n = 19$) before implantation

(TA, $t = 0.90$, $n = 42$, $P = 0.37$; T, $t = 0.84$, $n = 42$, $P = 0.41$; DHT, $t = -0.15$, $n = 42$, $P = 0.88$; two-tailed P -values). The mean androgen levels measured for the testosterone-treated group (TA, $\bar{x} = 10.7 \pm 1.3$ ng/ml, $n = 19$; T, $\bar{x} = 9.5 \pm 1.3$ ng/ml, $n = 19$; DHT, $\bar{x} = 2.4 \pm 0.6$ ng/ml, $n = 19$) were significantly higher than those of the control group (TA, $\bar{x} = 1.8 \pm 0.6$ ng/ml, $n = 15$; T, $\bar{x} = 1.7 \pm 0.6$ ng/ml, $n = 15$; DHT, $\bar{x} = 0.6 \pm 0.2$ ng/ml, $n = 15$) after implantation (TA, $t = 5.65$, $n = 34$, $P < 0.001$; T, $t = 4.97$, $n = 34$, $P < 0.001$; DHT, $t = 2.55$, $n = 34$, $P = 0.008$; two-tailed P -values). The testosterone implants consistently raised the measured blood androgens above basal levels. A significant positive correlation was found between the change in androgen levels and dose supporting the hypothesis for a dose-response effect (TA, $r_s = 0.53$, $n = 30$, $P = 0.002$; T, $r_s = 0.48$, $n = 30$, $P = 0.005$; DHT, $r_s = 0.39$, $n = 30$, $P = 0.02$; Fig. 1). The

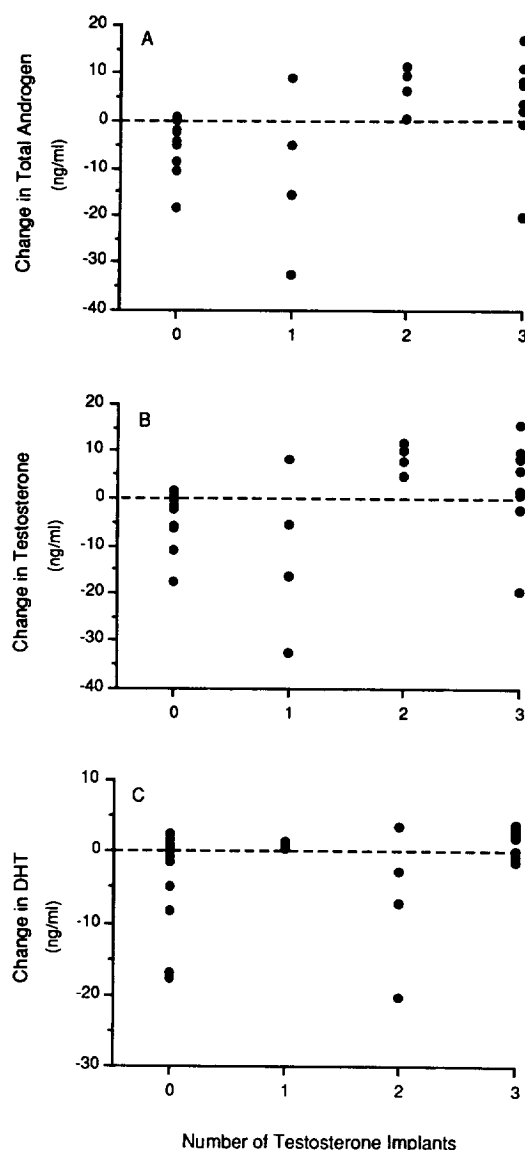


Fig. 1. Effect of dose (number of testosterone implants) on blood androgen before and after implantation. Dose of zero (0) signifies birds in control group, which were given empty implants. Hormones measured were: (A) total androgens; (B) testosterone; and (C) dihydrotestosterone (DHT).

measured blood androgen levels of testosterone-treated birds after implantation, although above that of nontreated birds (see above), overlapped with levels measured for adult-plumaged 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, $n = 19$).

Androgens, aggression, and dominance.—We used

a repeated-measures ANOVA to determine the effects of the testosterone treatment on aggressive behavior. Means were compared within subjects for each class of aggressive behavior (see above) over time (before and after implant). Differences between treatments then were analyzed within the model by the treatment-by-time interaction. We analyzed aggressive encounters of treatment birds with adult-plumaged males (blue plumage) separately from those encounters with females and juvenile-plumaged males (green plumage) to determine whether or not changes in aggressive behavior due to treatment are dependent upon the plumage color (signaled status) of the target.

Significant differences were observed between the treatment groups in initiated aggression (see Table 2). Testosterone-treated birds were more aggressive than controls and tended more often to approach, to threaten in the form of wing flips, and to attack severely green birds (Table 2). Testosterone treatment, on the other hand, had no effect on the tendency of birds to initiate aggressive behaviors toward blue birds (Table 2). The response of treatment birds when approached, threatened, or attacked by green birds showed no significant differences between the treatments (Table 3). Testosterone-treated birds held their ground against the initiated aggression of blue birds significantly more often than controls (Table 3).

We compared the change in hormone level with change in dominance values after implant for all birds in treatment groups, and found significant relationships in interactions involving treated birds and untreated green birds (TA, $r_s = 0.63$, $n = 14$, $P = 0.01$; T, $r_s = 0.59$, $n = 14$, $P = 0.02$; DHT, $r_s = 0.31$, $n = 14$, $P = 0.13$). When blue birds were included in the analysis, relationships between change in hormones and change in dominance value were marginally significant (TA, $r_s = 0.31$, $n = 25$, $P = 0.06$; T, $r_s = 0.29$, $n = 25$, $P = 0.08$; DHT, $r_s = 0.02$, $n = 25$, $P = 0.46$). Further evidence of a treatment effect was found by the significant treatment-by-time interaction in a repeated-measures ANOVA (Table 4). In an analysis of interactions between treatment birds and untreated green birds, testosterone-treated birds had a significant increase in dominance over controls after treatment (Table 4). When blue birds were included in the analysis, the change was not significantly different (Table 4). We demonstrated a dose effect by a significant correlation between dose

TABLE 2. Comparison of aggressive behaviors initiated by testosterone-treated and control birds toward adult-plumaged males (blue plumage) and juvenile-plumaged males (green plumage). Probabilities of

Behavior
Direct approach
Threat
Puff
Open-beak
Wing-flip
Vocal
Mild attack
Severe attack
Direct approach
Threat
Puff
Open-beak
Wing-flip
Vocal
Mild attack
Severe attack

* F- and P-values associated with treatment and after implant. Means

and change in dominance values after implant in green plumaged males (see above, Fig. 2A). This relationship was significant when blue birds were included in the analysis ($r_s = 0.12$, $n = 35$).

The failure to find a significant difference affects when blue males were included in the analysis to the high rate of aggression by adult-plumaged males and the overall dominance of green males. Adult-plumaged males over juvenile-plumaged males in aggressive interactions ($t = 6.1$, $P < 0.001$). Juvenile-plumaged males initiated aggressive interactions with adult blue-male significantly more often than adult blue-male initiated interactions with juvenile-plumaged males (see above, Table 1). Testosterone treatment had no effect on the tendency of birds to initiate aggressive interactions toward adult-plumaged males. Aggressive dominance was not affected by the number of implants. In 1987, 85.0% of initiated aggressive interactions resulted in a suppression of the initiator. In 1987, 96.6% of

TABLE 2. Comparison between pooled testosterone-treated groups and control group in the change (after implantation minus before implantation) in mean numbers of initiated interactions directed towards females and juvenile-plumaged males, and adult blue-plumaged males. Total frequency of each behavior given in parentheses. Probability values (*P*) are two-tailed.

Behavior	Treatment-by-time interaction ^a		Control			Testosterone		
	<i>F</i>	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>
Interaction with females and juvenile-plumaged males								
Direct approach	4.36	0.04	6.12 (120)	5.82 (99)	0.92	8.96 (218)	16.50 (396)	0.002
Threat								
Puff	2.56	0.12	0.47 (8)	0.00 (0)	0.13	0.37 (9)	0.54 (13)	0.52
Open-beak	0.00	0.99	4.47 (101)	3.88 (66)	0.75	5.83 (142)	5.25 (126)	0.71
Wing-flip	4.88	0.03	0.23 (4)	0.06 (1)	0.28	0.12 (3)	0.42 (10)	0.04
Vocal	0.91	0.35	0.18 (3)	0.29 (5)	0.67	0.17 (4)	0.62 (15)	0.05
Mild attack	0.54	0.47	9.65 (224)	8.71 (148)	0.82	14.50 (357)	17.54 (421)	0.39
Severe attack	6.12	0.02	1.00 (17)	0.06 (1)	0.08	0.25 (6)	1.00 (24)	0.10
Interaction with adult blue-plumaged males								
Direct approach	0.34	0.56	1.64 (33)	0.94 (16)	0.44	2.96 (71)	2.96 (71)	1.00
Threat								
Puff	2.36	0.13	0.18 (4)	0.06 (1)	0.52	0.25 (6)	0.50 (12)	0.11
Open-beak	0.46	0.50	3.23 (70)	0.82 (14)	0.17	4.79 (115)	3.92 (94)	0.55
Wing-flip	1.01	0.32	0.23 (4)	0.00 (0)	0.05	0.12 (3)	0.04 (1)	0.40
Vocal	2.72	0.11	0.12 (2)	0.00 (0)	0.30	0.04 (1)	0.17 (4)	0.19
Mild attack	1.27	0.27	4.52 (111)	1.94 (33)	0.53	7.58 (183)	11.08 (266)	0.32
Severe attack	1.80	0.19	0.12 (2)	0.06 (1)	0.82	0.17 (4)	0.58 (14)	0.07

^a *F*- and *P*-values associated with treatment-by-time interaction in a repeated-measures ANOVA. Time represents effects on aggression before and after implant. Means are least-squared means computed by SAS Proc GLM (SAS Institute 1985).

and change in dominance value among birds in green plumage ($r_s = 0.48$, $n = 19$, $P = 0.02$; Fig. 2A). This relationship was not significant when blue birds were included in the analysis ($r_s = 0.12$, $n = 35$, $P = 0.25$; Fig. 2B).

The failure to find significant treatment effects when blue males are included may be due to the high rate of interaction with blue males and the overall dominance of blue males over green males. Adult blue males were dominant over juvenile-plumaged males in agonistic interactions ($t = 6.24$, $n = 123$, $P < 0.001$). Juvenile-plumaged males were often the target of adult blue-male interactions; green males infrequently initiated, and appeared to avoid, interactions with adult blue males (Collis pers. observ.). Testosterone treatment had no effect on the tendency of the treated birds to initiate interactions towards adult blue males (Table 4). Aggressive dominance was strongly influenced by the number of interactions initiated. In 1986, 85.0% of initiated interactions were won by the initiator, 12.2% resulted in a tie, and 2.8% resulted in a supplant of the initiator by the target. In 1987, 96.6% of initiated interactions by all

birds were won by the initiator, 1.7% resulted in a tie, and 1.7% were lost by the initiator to the target. We suggest that changes in overall dominance of testosterone-treated juvenile-plumaged males might not be expected in flocks that consist mostly of adult blue males.

Plumage, aggression, and dominance.—We compared treatment groups in aggression directed towards all birds in 1987, the year after implantation. The birds treated with testosterone returned to traps in 1987 in full-adult blue plumage. The birds in the control group remained in juvenile green plumage. In all cases the testosterone-treated birds were more aggressive than the controls. Significant differences were observed in the mean number of initiated interactions ($t = 2.57$, $n = 26$, $P = 0.008$), direct approaches ($t = 2.63$, $n = 26$, $P = 0.007$), puff threats ($t = 1.93$, $n = 26$, $P = 0.03$), open-beak threats ($t = 2.47$, $n = 26$, $P = 0.01$), vocal threats ($t = 2.17$, $n = 26$, $P = 0.02$), mild attacks ($t = 2.60$, $n = 26$, $P = 0.008$), and mild displacements of the initiator of an interaction by the target ($t = 2.13$, $n = 26$, $P = 0.04$). These differences may not be attributable to differences in

TABLE 3. Comparison between pooled testosterone-treated groups and control in the change (after implantation minus before implantation) in number of aggressive responses to initiated interactions of females and juvenile-plumaged males, and adult blue-plumaged males. Total frequency of each behavior given in parentheses. Probability values (*P*) are two-tailed.

Behavior	Treatment-by-time interaction ^a		Control			Testosterone		
	<i>F</i>	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>
Interactions with females and juvenile-plumaged males								
Yield to initiator	0.11	0.74	20.88 (426)	15.76 (268)	0.31	27.50 (682)	24.62 (591)	0.50
Recipient held ground	0.55	0.46	1.56 (36)	1.94 (33)	0.65	2.46 (62)	3.58 (86)	0.10
Mild displacement	0.20	0.66	0.12 (3)	0.06 (1)	0.73	0.46 (11)	0.50 (12)	0.78
Severe displacement of initiator	0.70	0.41	0.00 (0)	0.00 (0)	1.00	0.00 (0)	0.04 (1)	0.20
Interactions with adult blue-plumaged males								
Yield to initiator	0.01	0.94	26.29 (507)	21.53 (366)	0.54	39.87 (963)	34.29 (823)	0.39
Recipient held ground	5.15	0.03	4.59 (87)	2.00 (34)	0.41	6.12 (147)	12.87 (309)	0.01
Mild displacement of initiator	0.84	0.37	0.35 (13)	0.09 (2)	0.67	1.62 (40)	0.50 (41)	0.06
Severe displacement of initiator	0.00	0.96	0.12 (2)	0.00 (0)	0.35	0.17 (4)	0.04 (4)	0.24

^a *F*- and *P*-values associated with treatment-by-time interaction in a repeated-measures ANOVA. Time represents effects on aggression before and after implantation. Means are least-squared means computed by SAS Proc GLM (SAS Institute 1985).

hormone levels so much as to differences in plumage between the treatment groups in 1987.

We separated the directed aggression of the treated birds towards birds in green plumage (females and juvenile males) and in blue plumage (adult males) to determine if plumage color of the target affected the treated birds' propensity to initiate interactions in 1987 (Table 5). The testosterone-treated birds tended to be more aggressive towards both green- and blue-plumaged birds (Table 5).

The plumage change experienced by the tes-

tosterone-treated males the year after treatment may be a cost to those males in that an adult plumage incites increased aggression from older males. To test this hypothesis we compared the initiated aggression of adult-plumaged males toward males in the treatment groups in 1987 (see Table 6). Testosterone-treated males received more puff threats and mild attacks than controls by adults (Table 6). Testosterone-treated males tended to be involved in a greater total number of interactions. Comparison of attack ratios (initiated/total interactions involving

TABLE 4. Comparison between pooled testosterone-treated groups and control in the change (after implantation minus before implantation) in dominance value among females and juvenile-plumaged males, and adult blue-plumaged males. The number of treatment birds included in calculation of dominance value given in parentheses. Probability values (*P*) are two-tailed.

Group	Treatment-by-time interaction ^a		Control			Testosterone		
	<i>F</i>	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>	$\bar{x}_{\text{bef}}$	$\bar{x}_{\text{aft}}$	<i>P</i>
Dominance among all untreated birds (including adult males)	0.35	0.56	29.64 (14)	30.71 (14)	0.76	33.38 (21)	37.09 (21)	0.19
Dominance among untreated juvenile males and females (excluding adult males)	5.16	0.04	44.29 (7)	36.71 (7)	0.04	51.08 (12)	53.33 (12)	0.40

^a *F*- and *P*-values associated with treatment-by-time interaction in a repeated-measures ANOVA. Time represents effects on aggression before and after implantation. Means are least-squared means computed by SAS Proc GLM (SAS Institute 1985).

adult males) between the two groups showed that testosterone-treated males were significantly higher than controls ($Mann-Whitney U = 25$, $P = 0.03$). Testosterone-treated males also bear a slightly increased risk of being directed at them by

To determine if testosterone treatment affected dominance, we compared dominance values of all testosterone-treated males before and after they returned to feeding. Testosterone-treated birds in green plumage were dominated by adult males in juvenile plumage. Any effect of testosterone treatment on dominance in 1987 may be unlikely that the testosterone-treated males were more dominant than testosterone at the time of treatment. Testosterone impairs dominance (Kincl and Rudel 1987). Testosterone made one year after treatment. Furthermore, the effect of testosterone on dominance is directly or indirectly related to testosterone independent of external factors. Dominance relationships are

We tested the hypothesis that testosterone-treated males in green plumage are less dominant than untreated males. In a paired-samples *t*-test, untreated adult males were more dominant than testosterone-treated birds that attained adult plumage ($n = 42$, $P = 0.05$).

An interaction between testosterone treatment and experience affected dominance patterns in olive-backed and Satin Bowerbirds. Testosterone treatment had a dependent effect on dominance relationships. Testosterone treatment affected dominance in juvenile-plumaged males, which led to changes in dominance among untreated males. Testosterone treatment affected dominance in juvenile-plumaged males, which led to changes in dominance among untreated males. Testosterone treatment affected dominance in juvenile-plumaged males, which led to changes in dominance among untreated males. Testosterone treatment affected dominance in juvenile-plumaged males, which led to changes in dominance among untreated males.

Changes in dominance relationships after testosterone treatment in juvenile-plumaged males were demonstrated in

adult males) between the treatment groups showed that testosterone-treated birds had a significantly higher attack ratio than control birds (Mann-Whitney *U*-test, $Z = -2.22$, $n = 25$, $P = 0.03$). Testosterone-treated birds may bear a slightly increased cost in aggression directed at them by older males.

To determine the effects of plumage type on dominance, we calculated dominance values for all testosterone-treated and control birds that returned to feeding sites in 1987. The testosterone-treated birds that developed an adult plumage were dominant over the controls still in juvenile plumage ($t = 2.82$, $n = 19$, $P = 0.006$). Any effect of testosterone treatment on dominance in 1987 must be considered indirect. It is unlikely that the implants were supplying testosterone at the time dominance was measured. Testosterone implants typically last two months (Kinch and Rudel 1971), and these measures were made one year after the initial implant. Furthermore, the effect of testosterone either directly or indirectly on plumage had an effect, independent of endogenous hormone levels, on dominance relationships in 1987.

We tested the prediction from the experience hypothesis that testosterone-treated birds in blue plumage are less dominant than naturally occurring males. In accordance with this hypothesis, untreated adult blue-plumaged males were more dominant than the testosterone-treated birds that attained a blue plumage ($t = -1.66$, $n = 42$, $P = 0.05$).

DISCUSSION

An interaction of androgen levels, plumage, and experience appears to determine age-related patterns in overall social dominance in the Satin Bowerbird. Furthermore, we showed independent effects of androgens and plumage on dominance relationships within an age class. Testosterone treatment alone increased aggression in juvenile-plumaged Satin Bowerbirds, which led to changes in their dominance position among untreated juvenile males and females. Testosterone treatment of juvenile-plumaged males did not affect aggression or dominance reversals among adult-plumaged males.

Changes in dominance as a result of testosterone treatment among birds of similar age, plumage condition, and experience have been demonstrated in White-crowned Sparrows

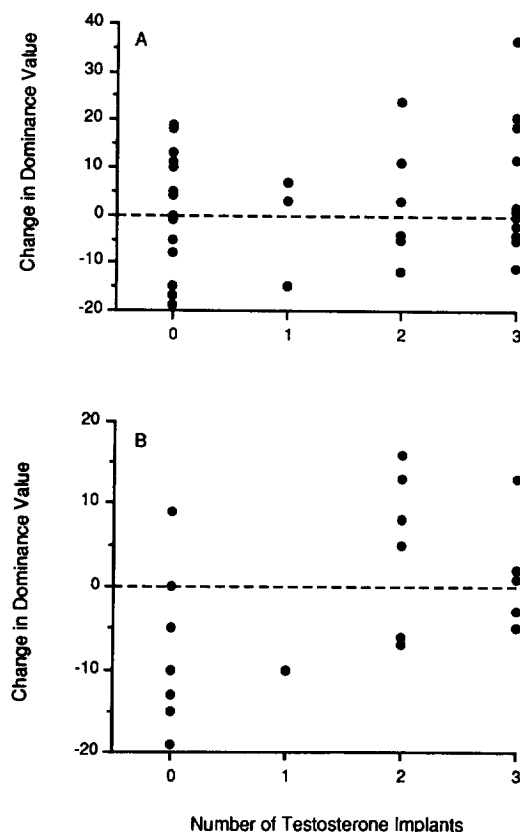


Fig. 2. Change in dominance value (dominance measured after implantation minus dominance measured before implantation) relative to dose (number of testosterone implants). Dose of zero (0) signifies birds of control group, which were given empty implants. Plots are: (A) among birds in green plumage; and (B) among all birds (including adult blue-plumaged males).

(Baptista et al. 1987), Japanese Quail (Selinger and Bermant 1967), Herring Gulls (*Larus argentatus*; Boss 1943), Red-winged Blackbirds (*Agelaius phoeniceus*; Searcy and Wingfield 1980), and Ringed Turtle-Doves (*Streptopelia risoria*; Bennett 1940). Studies that failed to show any relationship between androgen levels and dominance status did not control for the confounding effects of plumage, age, and experience on dominance, suggesting the importance of multiple factors in overall dominance (Lumia 1972, Rohwer and Wingfield 1981, Ramenofsky 1984, Holberton et al. 1989). It has been proposed that correlations between testosterone and dominance status exist only during heightened periods of male-male interaction (referred to as the challenge hypothesis; see Wingfield et al.

TABLE 5. Comparison between testosterone-treated group and control group in mean numbers of aggressive interactions initiated by treatment birds toward females and juvenile-plumaged males, and adult blue-plumaged males in 1987.

Behavior	Control ^a			Testosterone ^b			t	P
	$\bar{x}$	SE	n	$\bar{x}$	SE	n		
Interactions directed at females and juvenile-plumaged males								
Total interaction	4.50	1.98	12	11.85	2.84	13	2.09	0.02
Direct approach	2.08	0.85	12	5.69	1.66	13	1.89	0.04
Threat								
Puff	0.00	0.00	12	0.38	0.21	13	1.73	0.05
Open-beak	0.42	0.23	12	1.38	0.45	13	1.88	0.04
Wing-flip	0.08	0.08	12	0.08	0.08	13	-0.06	0.48
Vocal	0.00	0.00	12	0.61	0.21	13	2.77	0.005
Mild attack	1.83	0.97	12	3.92	0.82	13	1.66	0.06
Severe attack	0.33	0.19	12	0.31	0.21	13	-0.09	0.46
Interactions directed at adult blue-plumaged males								
Total interactions	2.91	2.14	12	11.08	4.26	13	1.72	0.05
Direct approach	0.82	0.51	12	2.77	1.12	13	1.59	0.06
Threat								
Puff	0.09	0.08	12	0.54	0.27	13	1.56	0.07
Open-beak	0.09	0.08	12	1.00	0.48	13	1.81	0.04
Wing-flip	0.27	0.25	12	0.08	0.08	13	-0.68	0.25
Vocal	0.00	0.00	12	0.00	0.00	13	—	—
Mild attack	0.91	0.75	12	7.23	2.93	13	2.04	0.03
Severe attack	0.73	0.67	12	0.38	0.31	13	-0.39	0.35

^a Controls that had molted to a blue plumage in 1987 were removed from analysis. Only controls having a juvenile green plumage included.

^b Testosterone-treated males that returned to traps in 1987 had molted to a full-adult blue plumage.

1987). When levels of aggression among males are low, other factors (i.e. individual recognition, territoriality) may mediate social dominance in birds (Wingfield et al. 1987). Our work on Satin Bowerbirds shows that testosterone levels can have an overriding effect on dominance relationships among juvenile-plumaged males. However, dominance status across age classes appears to involve other factors in addition to androgens.

We showed that plumage had a significant effect on dominance status. Testosterone-treated juvenile males underwent a premature change into a blue plumage, not observed in control birds, the year following treatment (Collis and Borgia unpubl. manuscript). In the year following implant these males were dominant over the controls who remained in juvenile plumage, but were subordinate to untreated blue males. Convincing experimental evidence exists in support of plumage effects on dominance status within age and sex classes in other species (Fugle et al. 1984, Rohwer 1985, Watt 1986).

Juvenile birds dyed to resemble brightly col-

ored dominant adults were dominant over other untreated juvenile males in both White-crowned Sparrows and Harris' Sparrows (*Zonotrichia querula*; Fugle et al. 1984, Rohwer 1985). In similar experiments, where juvenile birds dyed to resemble adults interacted with birds of all ages (including adult-plumaged males), the treatment had no effect on dominance rank (Rohwer 1977, Fugle and Rothstein 1987, Möller 1987). Rohwer (1977) argued that the inability of dyed birds to dominate adult birds was due to an incongruence between the behavior and signaled status of the treated birds. Although signaling a high status, the treated birds were intrinsically subordinate. Consequently, the treated birds lost in agonistic encounters when challenged repeatedly by adult birds. This "incongruence hypothesis" (Rohwer 1977) explains how a status signaling system can remain evolutionarily stable and cheating can be prevented by subordinate individuals carrying a plumage signaling a high status. Given the advantages associated with carrying an adult plumage, plumage variation could not be maintained without some control of cheating. To test

TABLE 6. Comparison between testosterone-treated group and control group in mean numbers of aggressive interactions received by treatment birds from females and juvenile-plumaged males, and adult blue-plumaged males in 1987.

Behavior
Total interaction
Direct approach
Threat
Puff
Open-beak
Wing-flip
Vocal
Mild attack
Severe attack
Total interactions
Direct approach
Threat
Puff
Open-beak
Wing-flip
Vocal
Mild attack
Severe attack

^a Controls that had molted to a blue plumage in 1987 were removed from analysis.

^b Testosterone-treated males that returned to traps in 1987 had molted to a full-adult blue plumage.

the incongruence hypothesis (Rohwer 1977) dyed to resemble adults interacted with birds of all ages (including adult-plumaged males), the treatment had no effect on dominance rank (Rohwer 1977, Fugle and Rothstein 1987, Möller 1987). Rohwer (1977) argued that the inability of dyed birds to dominate adult birds was due to an incongruence between the behavior and signaled status of the treated birds. Although signaling a high status, the treated birds were intrinsically subordinate. Consequently, the treated birds lost in agonistic encounters when challenged repeatedly by adult birds. This "incongruence hypothesis" (Rohwer 1977) explains how a status signaling system can remain evolutionarily stable and cheating can be prevented by subordinate individuals carrying a plumage signaling a high status. Given the advantages associated with carrying an adult plumage, plumage variation could not be maintained without some control of cheating. To test

We present a study of the effects of testosterone implants on dominance status in Satin Bowerbirds (Ptilonorhynchidae) that were implanted with testosterone implants when they were juveniles and remained in juvenile plumage for the rest of their lives. This implies the effects of testosterone on dominance status. These results, compared with those of males in different plumage classes (Borgia and Loffredo 1986), experience is important for understanding dominance. Satin Bowerbirds, like Harris' Sparrows, have differences between juvenile and adult plumage. Behavioral experience in Satin Bowerbirds, like Harris' Sparrows, may have

aggressive
alt blue-

TABLE 6. Comparison between testosterone-treated group and control group in mean numbers of aggressive interactions received by females and juvenile-plumaged males, and adult blue-plumaged males in 1987.

P	Behavior	Control ^a			Testosterone ^b			t	P
		$\bar{x}$	SE	n	$\bar{x}$	SE	n		
	Interactions initiated by females and juvenile-plumaged males								
0.02	Total interaction	4.50	1.25	12	2.46	0.59	13	-1.51	0.07
0.04	Direct approach	2.08	0.80	12	0.38	0.18	13	-2.14	0.02
	Threat								
	Puff	0.00	0.00	12	0.08	0.08	13	0.96	0.17
0.05	Open-beak	0.33	0.14	12	0.38	0.18	13	0.22	0.41
0.04	Wing-flip	0.00	0.00	12	0.08	0.08	13	0.96	0.17
0.48	Vocal	0.00	0.00	12	0.15	0.10	13	1.42	0.08
0.005	Mild attack	2.08	0.62	12	1.46	0.39	13	-0.86	0.20
0.06	Severe attack	0.00	0.00	12	0.15	0.10	13	1.42	0.08
0.46									
	Interactions initiated by adult blue-plumaged males								
	Total interactions	14.00	3.15	12	28.08	8.21	13	1.55	0.07
0.05	Direct approach	3.83	1.10	12	6.85	2.20	13	1.19	0.12
0.06	Threat								
	Puff	0.17	0.17	12	1.61	0.63	13	2.16	0.02
0.07	Open-beak	1.17	0.65	12	1.00	0.47	13	-0.21	0.42
0.04	Wing-flip	0.08	0.08	12	0.23	0.12	13	0.98	0.17
0.25	Vocal	1.00	0.43	12	0.69	0.17	13	-0.69	0.25
—	Mild attack	8.33	1.99	12	18.30	5.31	13	1.70	0.05
0.03	Severe attack	0.50	0.29	12	0.77	0.39	13	0.54	0.30
0.35									

^a Controls that had molted to a blue plumage in 1987 were removed from analysis. Only controls having a juvenile green plumage included.^b Testosterone-treated males that returned to traps in 1987 had molted to a full-adult blue plumage.

ver oth-
White-
ws (Zo-
er 1985).
e birds
h birds
(males),
ce rank
7. Möll-
inabil-
ds was
behavior
ds. Al-
ed birds
uently,
ounters
ds. This
977) ex-
remain
be pre-
rying a
the ad-
n adult
e main-
To test

the incongruence hypothesis, Rohwer and Rohwer (1978) dyed subordinate birds to look like dominant adults and, at the same time, implanted them with testosterone to render them more aggressive. These individuals experienced a significant increase in overall dominance rank, winning most of their interactions with previously more dominant birds.

We present a somewhat different pattern. The year after treatment, birds given testosterone implants were behaviorally aggressive and had an adult plumage. Despite these changes, these birds remained subordinate to true adult males. This implies the existence of additional factors. These results, coupled with the finding that males in different age groups are similar in size (Borgia and Loffredo in prep.), suggest that experience is important in overall social dominance. Satin Bowerbirds are long lived relative to Harris' Sparrows. The potential for large differences between individuals in age-related behavioral experience may be much greater in long-lived versus short-lived species. Thus, for Satin Bowerbirds, age-related differences in experience may have a greater role in both dom-

inance relationships, as well as the timing of when a male attempts to become dominant.

Other evidence supports the suggestion that age-related differences in experience are important to explain variation in male Satin Bowerbird aggressive behavior. First, birds treated with testosterone continued to avoid adult blue males after treatment. Controls and testosterone-treated birds did not differ in the mean number of initiated interactions directed at blue birds after implant. We know that juvenile green males typically lose in interactions with adult blue males. Second, although testosterone treatment raised the frequency of aggressive and display behaviors initiated by juvenile-plumaged males and caused them to attain adult blue plumage, the form and quality of these behaviors was not affected (Collis and Borgia unpubl. manuscript). Testosterone-treated males continued to give crude displays typical of birds in their age class (Collis and Borgia unpubl. manuscript). Furthermore, the bowers built by the testosterone-treated males were of a lower overall quality compared to the bowers of older more experienced males (see Collis and Borgia un-

publ. manuscript). The low-quality displays of testosterone-treated males, coupled with age-related improvements observed in bower building (Borgia 1986, in prep.) and display (Loffredo and Borgia 1986) in untreated males, support the hypothesis that experience affects the development of displays important to females. The significance of experience in the development of adult male patterns of display has been well documented in other species. The ontogeny of display behaviors such as song (Rice and Thompson 1968), repertoire size (Nottebohm and Nottebohm 1978, Derrickson 1987), and motor patterns involved in courtship (Marshall 1954, Kruijt and Hogan 1967, Groothuis 1989) depends on practice and experience gained by young birds (see Shettleworth 1984).

It appears that experience has a critical effect on male dominance and, ultimately, the development of male display traits. The elevation of testosterone levels and plumage change of juvenile males were insufficient to raise the dominance status of juvenile males to levels found in older males; thus, advantages associated with increased testosterone levels and an adult plumage may be realized only if these characters are associated with a sufficient level of experience. Elsewhere, Borgia and Loffredo (unpubl. manuscript) have found an age-related increase in dominance both among juvenile and adult male Satin Bowerbirds. The failure of young males to elevate their testosterone levels to render themselves more aggressive may occur because such a change fails to provide an advantage in dominance relations with older, more experienced males. Elsewhere, we have shown that premature plumage development caused by testosterone implants in Satin Bowerbirds reduces opportunities for males to learn important elements in male display (Collis and Borgia unpubl. manuscript). The combined effect of experience on male success in aggression and on a male's ability to acquire effective display traits contributes to the prolonged delay in attainment of adult plumage and display characters in Satin Bowerbirds.

ACKNOWLEDGMENTS

This research was supported by funds awarded to G.B. by the American Philosophical Society, Harry Frank Guggenheim Foundation, and the National Science Foundation (BNS 81-13477, BNS 83-08154, BNS 85-10483, and BSR 89-11411). Additional support was

provided by the University of Maryland and the University Computer Center. Logistical support was provided by the University of Melbourne Zoology Department and, in particular, M. J. Littlejohn and J. Hook. Invaluable assistance was provided in the field by D. Bond, R. Carscadden, M. Collis, A. Day, C. Depkin, A. Rosenthal, and S. Webb. We thank the N. and J. Hayes, Mulkay, and Bell families, along with the N.S.W. Forestry Commission for their assistance and for allowing us access to their property. Hormone analysis was performed by M. A. Ottinger and T. Hargrove. Statistical and SAS consultation was provided by S. and L. Douglas, C. Denman, and J. Ott. Valuable criticisms of this manuscript were made by L. Chao, E. S. Morton, J. Ott, M. A. Ottinger, M. Shea, and anonymous reviewers. K.C. thanks M. Collis for her patience and support throughout all stages of this work.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:227-267.
- ARCESE, P., AND J. N. M. SMITH. 1985. Phenotypic correlates and ecological consequences of dominance in Song Sparrows. *J. Anim. Ecol.* 54:817-830.
- BAPTISTA, L. F., B. B. DEWOLFE, AND L. AVERY-BEAUSOLEIL. 1987. Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows. *Wilson Bull.* 99:86-91.
- BEILHARZ, R. G., AND P. J. MYLREA. 1963. Social position and behavior of dairy heifers in yards. *Anim. Behav.* 11:522-528.
- BENNETT, M. A. 1940. The social hierarchy in Ring Doves. II. The effects of treatment with testosterone propionate. *Ecology* 21:148-165.
- 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(6):92-100.
- 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.
- BRADBURY, J., AND M. ANDERSSON. 1987. Sexual selection: Testing the alternatives. Wiley, New York.
- BOSS, W. R. 1943. Hormonal determination of adult characters and sex behavior in Herring Gulls (*Larus argentatus*). *J. Exp. Zool.* 94:181-209.
- CLUTTON-BROCK, T., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: Behavior and ecology of two sexes. Univ. Chicago Press, Chicago.
- COLLIS, K. 1990. The role of hormones and experience in the development of male display in the Satin Bowerbird (*Ptilonorhynchus violaceus*). M.S. thesis, University of Maryland, Park, Maryland.
- DERRICKSON, K. C. 1987. Changes in the behavior of Northern Mockingbirds (*Mimus polyglottos*). *104:198-207.*
- DONAGHEY, R. 1981. Catbird (*Ailuroedus*) Bowerbird (*Ptilonorhynchus violaceus*) dissertation, Monash University, Victoria, Australia.
- FOSTER, M. S. 1987. Social system and social system of the genus *Chiroxiphus*.
- FUGLE, G. N., AND S. I. ROSE. 1981. On the control of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*).
- FUGLE, G. N., S. I. ROSE, AND M. A. MCGINLEY. 1981. Mating White-crowned Sparrows (*Zonotrichia leucophrys gambelii*).
- GILLIARD, E. T. 1969. The social behavior of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*).
- GROOTHUIS, T. 1989. The behavior in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) and the emergence of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*).
- HOLBERTON, R. A., AND K. C. DERRICKSON. 1989. Status signaling in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*): Plumage correlates of dominance.
- KINCL, F. A., AND H. A. KINCL. 1981. The release of hormones in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Suppl. 151.*
- KRUIJT, J. P., AND J. A. HOGAN. 1967. On the lek in Bowerbirds (*Ptilonorhynchus violaceus*). *Ardea* 55:203-210.
- LACK, D. 1954. The numbers of Bowerbirds (*Ptilonorhynchus violaceus*). *Clarendon Press, Oxford.*
- LOFFREDO, C. A., AND G. BORGIA. 1986. Courtship vocalization in Satin Bowerbirds (*Ptilonorhynchus violaceus*). *103:189-195.*
- LUMIA, A. 1972. The role of testosterone in the conditioning of male pigeons (*Columba livia*). *1605-1615.*
- LYON, B. E., AND R. I. LYON. 1981. Plumage maturation and signaling by sex in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *605-615.*
- MARLER, C. A., AND M. A. GORE. 1986. The costs of aggression in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Ecol. Sociobiol.*
- MARSHALL, A. J. 1954. Breeding behavior of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *1954.*
- MÖLLER, A. P. 1990. The role of hormones and experience in the development of male display in the Satin Bowerbird (*Ptilonorhynchus violaceus*). M.S. thesis, University of Maryland, Park, Maryland.

and the Uni-
rt was pro-
ology De-
ohn and J.
in the field
ay, C. Dep-
the N. and
g with the
stance and
Hormone
and T. Har-
s provided
t. Valuable
y L. Chao,
Shea, and
llis for her
ges of this

ff behavior:
-267.

Phenotypic
es of dom-
ol. 54:817-

BEAUSOLEIL.
dominance
ws. Wilson

Social po-
s in yards.

hy in Ring
with testos-
5.

er of deco-
Satin Bow-
experimen-

and sexual
Ptilonorhyn-
18:91-100.
erbirds. Sci.

er stealing
s violaceus):
of display.

Sexual se-
New York.

on of adult
ring Gulls
-209.

D. ALBON.
ogy of two

and experi-

- ence in the development of social dominance and display in the Satin Bowerbird (*Ptilonorhynchus violaceus*). M.S. thesis, Univ. Maryland, College Park, Maryland.
- DERRICKSON, K. C. 1987. Yearly and situational changes in the estimate of repertoire size in Northern Mockingbirds (*Mimus polyglottos*). *Auk* 104:198-207.
- DONAGHEY, R. 1981. Parental strategies in the Green Catbird (*Ailuroedus crassirostris*) and the Satin Bowerbird (*Ptilonorhynchus violaceus*). Ph.D. dissertation, Monash Univ., Melbourne, Australia.
- FOSTER, M. S. 1987. Delayed maturation, neoteny, and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* 41:547-558.
- FUGLE, G. N., AND S. I. ROTHSTEIN. 1987. Experiments on the control of deceptive signals of status in White-crowned Sparrows. *Auk* 104:188-197.
- FUGLE, G. N., S. I. ROTHSTEIN, C. W. OSENBURG, AND M. A. MCGINLEY. 1984. Signals of status in wintering White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). *Anim. Behav.* 32:86-93.
- GILLIARD, E. T. 1969. Birds of paradise and bower birds. Weidenfeld and Nicholson, London.
- GROOTHUIS, T. 1989. On the ontogeny of display behavior in the Black-headed Gull: I. The gradual emergence of the adult forms. *Behaviour* 109:76-123.
- HOLBERTON, R. A., K. P. ABLE, AND J. C. WINGFIELD. 1989. Status signalling in Dark-eyed Juncos, *Junco hyemalis*: Plumage manipulations and hormonal correlates of dominance. *Anim. Behav.* 37:681-689.
- KINCL, F. A., AND H. W. RUDEL. 1971. Sustained release of hormonal preparations. *Acta Endocrinol., Suppl.* 151:1-30.
- KRUIJT, J. P., AND J. A. HOGAN. 1967. Social behavior on the lek in Black Grouse, *Lyrurus tetrix tetrix*. *Ardea* 55:203-240.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LOFFREDO, C. A., AND G. BORGIA. 1986. Male courtship vocalization as cues for mate choice in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Auk* 103:189-195.
- LUMIA, A. 1972. The relationship among testosterone conditioned aggression and dominance in male pigeons. *Horm. Behav.* 3:277-286.
- LYON, B. E., AND R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: Reliable signaling by subordinate males? *Evolution* 40:605-615.
- 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. 1954. Bower-birds: Their displays and breeding cycles. Clarendon Press, Oxford.
- MØLLER, A. P. 1987. Social control of deception among status signalling House Sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.* 20:307-311.
- MOSS, R., H. H. KOLB, M. MARQUISS, A. WATSON, B. TRECA, D. WATT, AND W. GLENNIE. 1979. Aggressiveness and dominance in captive Red Grouse. *Aggressive Behav.* 5:59-84.
- NOTTEBOHM, F., AND M. E. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary, *Serinus canarius*. *Z. Tierpsychol.* 46:298-305.
- OTTINGER, M. A., AND K. MAHLKE. 1984. Androgen concentrations in testicular and peripheral blood in the male Japanese Quail. *Poultry Sci.* 63:1851-1854.
- RAMENOFKY, M. 1984. Agonistic behavior and endogenous plasma hormones in male Japanese Quail. *Anim. Behav.* 32:698-708.
- RATNER, S. C. 1961. Effects of learning to be submissive on status in the peck order of domestic fowl. *Anim. Behav.* 9:34-37.
- RICE, J. O., AND W. L. THOMPSON. 1968. Song development in the Indigo Bunting. *Anim. Behav.* 16:462-469.
- ROHWER, S. 1977. Status signalling in Harris Sparrows: Some experiments in deception. *Behaviour* 61:107-128.
- ROHWER, S. 1985. Dyed birds achieve higher social status than controls in Harris' Sparrows. *Anim. Behav.* 33:1325-1331.
- ROHWER, S., AND F. C. ROHWER. 1978. Status signalling in Harris Sparrows: Experimental deception achieved. *Anim. Behav.* 26:1012-1022.
- ROHWER, S., S. D. FRETWELL, AND D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am. Nat.* 115:400-437.
- ROHWER, S., AND J. C. WINGFIELD. 1981. A field study of social dominance, plasma levels of luteinizing hormone and steroid hormones in wintering Harris' Sparrows. *Z. Tierpsychol.* 57:173-183.
- SAS INSTITUTE. 1985. SAS user's guide: Statistics, version 5 ed. Cary, North Carolina.
- SEARCY, W. A., AND J. C. WINGFIELD. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male Red-winged Blackbirds. *Horm. Behav.* 14:126-135.
- SELANDER, R. K. 1965. On mating systems and sexual selection. *Am. Nat.* 99:129-141.
- SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pages 180-230 in *Sexual selection and the descent of man* (B. Campbell, Ed.). Aldine Press, Chicago.
- SELINGER, H. E., AND G. BERMANT. 1967. Hormonal control of aggressive behavior in Japanese Quail. *Behaviour* 28:255-268.
- SHETTLEWORTH, S. J. 1984. Learning and behavioral ecology. Pages 170-194 in *Behavioral ecology: An evolutionary approach* (J. R. Krebs and N. B. Davies, Eds.). Sinauer, Sunderland, Massachusetts.

- SIEGEL, S. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- SMITH, W., AND E. B. HALE. 1959. Modification of social rank in the domestic fowl. *J. Comp. Physiol. Psychol.* 52:373-375.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman, San Francisco.
- STUDD, M. V., AND R. J. ROBERTSON. 1985. Life span, competition, and delayed plumage maturation in male passerines: The breeding threshold hypothesis. *Am. Nat.* 126:101-115.
- VELLENGA, R. E. 1970. Behavior of the male Satin Bowerbird at the bower. *Aust. Bird Bander* 1:3-11.
- VELLENGA, R. E. 1980. Moults of the Satin Bowerbird. *Emu* 80:49-54.
- WATT, D. J. 1986. Relationship of plumage variability, size and sex to social dominance in Harris' Sparrows. *Anim. Behav.* 34:16-27.
- WINER, B. J. 1971. *Statistical principles in experimental design*, 2nd ed. McGraw Hill, New York.
- WINGFIELD, J. C., G. F. BALL, A. M. DUFTY, JR., R. E. HEGNER, AND M. RAMENOFKY. 1987. Testosterone and aggression in birds. *Am. Sci.* 75:602-608.

ESTIMATING M

Departm

ABSTRACT
hibits a dramatic
all eggs with
laying eggs
cantly and
Because com
by heterosp
cific nest p
parasitized
of parasitiz
nest parasit
of the high
the conclus
Ploceus wea

THE Northern
niopiterus), like ma
a dramatic degre
variability (Mack
Moreau 1960, Free
range from dark
They can be eithe
if speckled, can h
ling. Typically, as
variable eggs, all
alike, suggesting
vidual females do
tial support for
studies of a captiv
(*P. cucullatus*; Vict
laid over a lifetim
males varied little

However, the r
look alike is frequ
ern Masked Weav
In a study of *Plo*
(1988) found that
able eggs, between
a species contain
males produce or
looking eggs mu
parasite. Commur

¹ Present address:
of Washington, Sea