EFFECTS OF EXPERIMENTAL MANIPULATION OF TESTOSTERONE LEVELS ON PARENTAL INVESTMENT AND BREEDING SUCCESS IN MALE HOUSE SPARROWS

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ABSTRACT.—Breeding male House Sparrows (*Passer domesticus*) were implanted with testosterone (T), the antiandrogen flutamide (F), or an empty capsule as a control (C). Parental feeding rates by C-treated males were high until nestlings reached 10 days of age, then declined significantly. This is the typical temporal pattern of parental behavior for free-living males. In contrast, F-treated males fed young at a high rate throughout the nestling stage, while T-treated males fed young much less frequently and were more involved in male-male competition during this period of time. There was a significant decrease in the breeding success of T-treated males resulting from increased starvation of their nestlings. Despite lowered levels of testosterone, F-treated males were able to maintain control of their nest boxes and exhibited normal sexual behavior. During the subsequent brood, breeding success of T-treated males again was reduced by nestling starvation. Our results demonstrate that high levels of testosterone inhibit the expression of parental care in male House Sparrows. Moreover, they suggest that the typical pattern of testosterone levels in males (high when mate guarding and low when feeding young) represents an optimal compromise between allocation of effort to male-male competition vs. parental care. *Received 10 July 1986, accepted 1 March 1987.*

CORRELATIONAL and experimental studies on House Sparrows (*Passer domesticus*) have suggested that the activities of breeding males represent a trade-off between investment in male-male competition vs. parental care. In males, circulating levels of testosterone reflect this trade-off, being elevated when male-male competition is high and low when parental investment is high. We have suggested that this pattern maximizes an individual's overall reproductive output, even if it results occasionally in a reduction of fecundity (Hegner and Wingfield 1986a, 1987).

In this study, we tested experimentally whether the variable pattern of male investment represents an optimization by artificially altering that pattern. This was achieved by altering the endocrine and behavioral state of males with subcutaneous hormone implants. We tested specifically whether elevated levels of testosterone during the last portion of the nestling stage, the interbrood interval, and the egg-laying stage are critical for (1) defense of the nesting site, (2) normal sexual behavior, and (3) successful mate guarding. We also tested (4) whether lowered levels of testosterone during incubation and the early portion of the nestling stage are necessary for the expression of parental care.

METHODS

Experiments were conducted in May-July 1985 at several farms in Dutchess Co., New York (42°N). All birds used in the study were breeding in nest boxes that had been present in the study areas since early 1982. Nest-box inspections at 2-3-day intervals enabled us to determine dates of laying, hatching, and fledging, clutch and brood sizes, fledging success, and the growth curves of each nestling. All adult subjects were marked individually with U.S. Fish and Wildlife Service numbered aluminum bands and a unique combination of color bands. All nestlings were marked with ink spots for individual identification.

All adults used in the study were tending their first brood of the season ($n = 28$) or renesting after loss of their first brood ($n = 1$). Males were captured at their nest boxes and given implants when the young were 4-6 days of age. One group of males ($n = 10$) was given a subcutaneous implant of testosterone (T). A second group ($n = 10$) was given an implant of the antiandrogen flutamide (F). Flutamide (α-α-α-trifluo-

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TABLE 1. Feeding rates ($\text{visits}\cdot\text{nestling}^{-1}\cdot\text{h}^{-1}$) during first brood. Values are means ±1 SD. Asterisks denote significantly different rates for adults feeding nestlings aged 8–10 vs. 11–14 days ($P < 0.05$, Mann-Whitney *U*-test). Kruskal-Wallis test denotes significance of differences among treatment groups.

	Flutamide	Control	Testosterone	Kruskal-Wallis test
Age 8–10 days	($n = 6$)	($n = 4$)	($n = 7$)	
Males	2.5 ± 1.1	2.9 ± 1.1*	1.4 ± 1.9	$H = 2.248$, $P > 0.25$
Females	2.7 ± 0.9*	4.1 ± 1.3	6.8 ± 3.3	$H = 8.512$, $P < 0.025$
Total	5.2 ± 2.0	7.0 ± 2.1	8.2 ± 2.7	$H = 4.703$, $0.05 < P < 0.10$
Age 11–14 days	($n = 9$)	($n = 11$)	($n = 7$)	
Males	3.2 ± 0.9	1.1 ± 0.6*	0.2 ± 0.3	$H = 19.912$, $P < 0.005$
Females	4.4 ± 1.2*	3.9 ± 1.2	4.4 ± 2.5	$H = 1.244$, $P > 0.25$
Total	7.5 ± 1.7	4.9 ± 1.5	4.6 ± 2.4	$H = 9.276$, $P < 0.01$

ro-2-methyl-4′-nitro-m-propionotoluidide) is a relatively pure androgen antagonist that inhibits androgen uptake or nuclear binding of androgens in target tissues, or both (Peets et al. 1974, Neri and Peets 1975, Adkins-Regan and Garcia 1986). Although F may not affect circulating levels of T *per se*, it has the biological effect of lowering them by blocking the effects of T in target tissues. A third group of males ($n = 9$) received an empty implant as controls (C). We thus compared the patterns of investment and breeding success of males with tonic high levels of T, effectively tonic low levels of T, and levels of T that fluctuated in the normal seasonal pattern. All implants were identical 20-mm lengths of Silastic tubing (internal diameter 1.47 mm, external diameter 1.96 mm; Dow Corning, Midland, Michigan) packed with crystalline T or F or left empty (C). Nests were chosen to control for clutch and brood size, nestling age, and date of hatching at each local site (see Table 3).

The activities of adults during the first brood were monitored using a focal-nest protocol. Data reported are from 70.0 h of observations conducted when nestlings were 8–14 days of age. For both adults, rates of feeding visits were recorded as a measure of parental investment. For males, two measures of investment in male-male competition were determined: relative amount of nest-site defense and mate-guarding activity. Both were aggregate, normalized measures ranging from 0 to 2 (see Hegner and Wingfield 1987).

Reproductive activities at each nest were monitored by nest inspections through the completion of the second (subsequent) brood. When nestlings in this brood were 6–13 days old, breeding adults were captured at the nest boxes. A small blood sample (400 μl) was collected within 3–9 min of capture (mean = 4.7, SD = 1.3), body mass was determined to the nearest 0.1 g, and fat levels in the furculum and abdomen were estimated on a scale of 0–5. At the time of recapture, the implant was removed from each male and checked visually for effectiveness (disappearance of content). All were effective.

From blood samples, plasma concentrations of the following steroid hormones were measured by radioimmunoassay after separation and partial purification on diatomaceous earth : glycol microcolumns: testosterone (T), estradiol-17β (E2) (females only), and corticosterone. For additional information on these procedures, see references cited by Hegner and Wingfield (1986a, b).

RESULTS

PATTERNS OF INVESTMENT

Parental care.—The experimental implants had a significant effect on the rate of feeding visits made by males (Table 1). T-treated males fed younger nestlings (aged 8–10 days) at about half the rate of the other males, although this difference was not statistically significant. Females apparently compensated for the reduced feeding contribution of their T-treated mates by increasing their feeding rates.

After young House Sparrows reach 9–10 days of age, male feeding rates decline significantly (Hegner and Wingfield 1986a, 1987). The same pattern was exhibited by the C-treated males in this study ($U = 3$, $P < 0.005$, Table 1). In contrast, neither the F-treated nor T-treated males exhibited a significant decline in feeding rates as the nestlings got older. There was an important contrast, however, between the two groups of males. The F-treated males continued to feed at a high rate as the nestlings matured, while the low feeding rates of the T-treated males declined even further. The result was a significant difference in feeding rates among the three groups of males.

In normal House Sparrow nests, feeding rates by females generally remain high after the young reach 9–10 days of age (Hegner and Wingfield 1986b). A similar pattern was exhibited by these females, with the exception that females paired with F-treated males actually fed

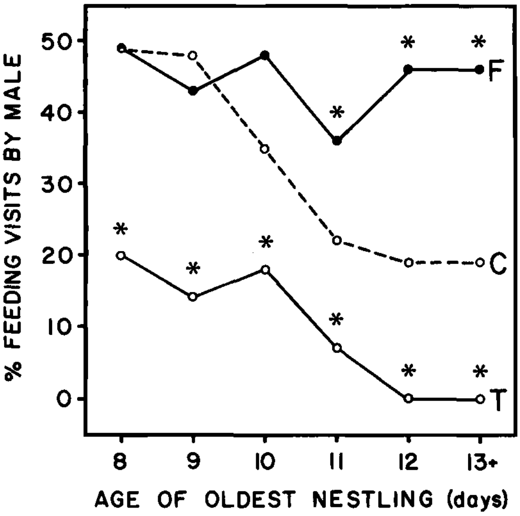

Fig. 1. Relationship between feeding contribution of males and nestling age. Each point represents the proportion of feeding visits by males relative to females; hence, 50% represents an equal contribution by both sexes. Proportionate contributions of T-treated males differed significantly from those of F-treated males at each nestling age ($P < 0.05$, Chi-square tests). Asterisks denote significant differences ($P < 0.05$, Chi-square tests) between C-treated and F-treated or T-treated males at a given nestling age.

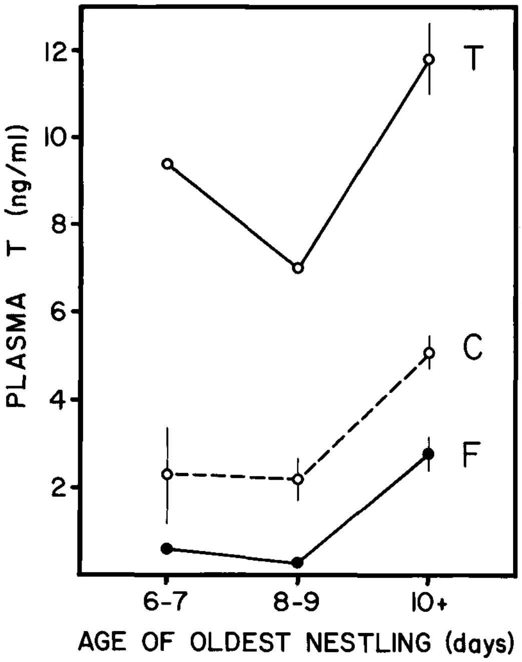

Fig. 2. Relationship between circulating levels of testosterone (ng/ml) and nestling age in males given experimental implants. Values are means ±1 SE. Analysis of variance indicated a significant relationship between testosterone concentrations and both nestling age and type of implant (see Table 5).

older nestlings at a significantly higher rate ($U = 8.5$, $P < 0.05$). This increase perhaps was due to their unusually low feeding rate earlier in the nestling stage.

The effect of the implants on the feeding behavior of males is best summarized as a plot of the feeding contribution of males relative to their mates at each nestling age (Fig. 1). The feeding rates of C-treated males equaled those of their mates until the young were 9 days old, then declined significantly to about 20% of the total feedings in the next 2 days. This is the typical pattern for free-living House Sparrow males (Hegner and Wingfield 1986a). In contrast, the patterns of the F-treated and T-treated males were very different. F-treated males continued to bring food at the same rate as their mates up to the time the young fledged, while the rates of T-treated males, already down to about 20% of the total when the young were 8 days old, declined to near zero 4 days later.

Male-male competition.—The experimental implants had a significant effect on the patterns of male-male competition (Table 2). When nestlings were 8–10 days old, T-treated males spent considerably more time singing, courting, and defending the nest boxes than did the other males. When the chicks were older, there was a significant difference in the allocation of effort to nest defense among the groups of males. The C-treated males exhibited increased investment in nest-site defense ($U = 7$, $P < 0.05$), the typical pattern for free-living males in our study area (Hegner and Wingfield 1986a). In contrast, the investment in nest-site defense did not increase in the F-treated males, and the already high investment by the T-treated males increased, but not significantly.

During the nestling stage, all males showed little tendency to follow females closely, and females rarely spent more than a minute or two near the nest. There was no observable mate-guarding activity in 77% of the focal samples, and no differences among groups (Table 2). This was expected because mate-guarding activity typically peaks after the young have fledged (Hegner and Wingfield 1986a).

There were no differences among groups in

TABLE 2. Investment in male-male competition. Values are means ±1 SD. Sample sizes are given in Table 1. Asterisk denotes significant difference ($P < 0.05$, Mann-Whitney *U*-test). Kruskal-Wallis test denotes significance of differences among treatment groups.

	Flutamide	Control	Testosterone	Kruskal-Wallis test
Nest defense				
Age 8–10	0.16 ± 0.12	0.06 ± 0.10*	0.57 ± 0.43	$H = 5.736$, $0.05 < P < 0.10$
Age 11–14	0.16 ± 0.19	0.47 ± 0.41	0.94 ± 0.57	$H = 10.078$, $P < 0.01$
Mate guarding				
Age 8–10	0.01 ± 0.02	0.00 ± 0.00	0.03 ± 0.08	$H = 0.655$, $P > 0.75$
Age 11–14	0.40 ± 0.52	0.12 ± 0.27	0.07 ± 0.17	$H = 2.168$, $P > 0.75$

the ability of the males to maintain control of their nest boxes. One C-treated and 1 F-treated male lost their boxes; all others retained them. There also was no indication that sexual behavior was affected by the implants. Males in each group were seen copulating (data not shown), and there was no difference among groups in the interbrood interval (see Table 3).

EFFECT ON BREEDING SUCCESS

In the first brood, there was a significant decline in the success of nests tended by T-treated males (Table 3). A greater proportion of their broods starved, resulting in fewer young fledged. Despite these higher starvation losses, the peak mass of surviving young from the first brood did not differ among groups. There also were no differences among groups in the interbrood interval or size of the subsequent clutch or brood.

In most nests the subsequent clutch was either larger (56%) or the same size (37%) as the first clutch, reflecting the normal seasonal pattern for House Sparrows (Murphy 1978, McGillivray 1983, Hegner and Wingfield unpubl. data). Although both nests in which the subsequent clutch was smaller were in the T-treated group, there was no difference among groups in the size of the second clutch relative to the first ($H = 3.563$, $P > 0.10$).

Three females disappeared after young in the second brood hatched. Two were paired with F-treated males, the third with a C-treated male. All young died in these nests, and they were deleted from further analyses. In the remaining nests the T-treated males again fledged significantly fewer young. In this group, half of the

TABLE 3. Effects of hormone implants on reproduction. Values are means ±1 SD.

	Flutamide	Control	Testosterone	Kruskal-Wallis test
Brood 1	($n = 10$)	($n = 9$)	($n = 10$)	
Clutch size	4.7 ± 0.5	5.0 ± 0.7	5.1 ± 0.7	$H = 1.929$, $P > 0.25$
Brood size	4.3 ± 0.8	4.6 ± 1.1	4.3 ± 1.1	$H = 1.337$, $P > 0.50$
% brood starve	6.5 ± 14.2	2.2 ± 6.7	37.0 ± 44.7	$H = 6.778$, $P < 0.05$
No. fledged	3.8 ± 1.0	4.2 ± 0.8	2.6 ± 1.9	$H = 4.717$, $0.05 < P < 0.10$
Nestling mass (g)[a]	23.2 ± 2.6	24.0 ± 2.8	23.0 ± 3.6	$H = 1.215$, $P > 0.50$
No. surviving young[b]	3.4 ± 0.8	3.9 ± 1.1	1.9 ± 1.6	$H = 8.376$, $P < 0.025$
Brood 2	($n = 9$)	($n = 8$)	($n = 10$)	
Interbrood interval (days)	8.9 ± 2.5	7.6 ± 2.3	6.9 ± 2.0	$H = 3.458$, $P > 0.10$
Clutch size	5.6 ± 0.9	6.0 ± 0.5	5.3 ± 0.7	$H = 4.240$, $P > 0.10$
Brood size	5.1 ± 1.6	4.9 ± 1.6	3.9 ± 1.7	$H = 3.839$, $P > 0.10$
% brood starve[c]	24.8 ± 15.6	37.6 ± 17.8	66.5 ± 37.1	$H = 5.450$, $0.05 < P < 0.10$
No. fledged[a]	3.7 ± 1.0	3.0 ± 1.0	1.6 ± 1.8	$H = 6.245$, $P < 0.05$
Nestling mass (g)[d]	21.7 ± 2.4	23.9 ± 2.4	21.4 ± 2.4	$H = 9.293$, $P < 0.01$
No. surviving young[b]	3.0 ± 0.6	3.0 ± 1.0	1.3 ± 1.7	$H = 5.835$, $0.05 < P < 0.10$

[a] $n = 38, 38, 26$.

[b] Surviving = maximum mass ≥20.1 g.

[c] $n = 7, 7, 10$.

[d] $n = 26, 21, 16$.

TABLE 4. Physiological effects of hormone implants. Hormones listed are testosterone (T), estradiol-17β (E2), and corticosterone (B). Values are means ±1 SD. Fat level was estimated on a linear scale from 0 to 5 (see text).

	Flutamide	Control	Testosterone	Kruskal-Wallis test
Males	($n = 9$)	($n = 8$)	($n = 6$)	
T (ng/ml)	1.3 ± 0.2	3.7 ± 0.3	10.6 ± 0.5	$H = 15.012, P < 0.005$
B (ng/ml)	11.9 ± 4.3	8.3 ± 3.0	11.2 ± 5.0	$H = 1.974,\ P > 0.25$
Body mass (g)	26.7 ± 1.5	27.6 ± 1.7	26.7 ± 1.2	$H = 1.093,\ P > 0.50$
Fat level	0.9 ± 0.5	0.7 ± 0.4	0.6 ± 0.2	$H = 1.883,\ P > 0.25$
Length of cloacal protuberance (mm)	5.5 ± 1.1	5.9 ± 0.4	6.9 ± 1.3	$H = 5.691,\ 0.05 < P < 0.10$
Beak color	3.7 ± 0.2	3.8 ± 0.1	3.9 ± 0.2	$H = 5.617,\ 0.05 < P < 0.10$
Females	($n = 7$)	($n = 7$)	($n = 7$)	
T (pg/ml)	76 ± 50	96 ± 110	44 ± 74	$H = 2.319,\ P > 0.25$
E2 (pg/ml)	100 ± 62	75 ± 26	183 ± 110	$H = 4.054,\ P > 0.10$
B (ng/ml)	11.9 ± 4.3	12.7 ± 12.0	11.2 ± 5.0	$H = 0.557,\ P > 0.50$
Body mass (g)	26.0 ± 1.5	26.5 ± 1.3	27.5 ± 1.1	$H = 5.424,\ 0.05 < P < 0.10$
Fat level	1.3 ± 0.6	0.9 ± 0.3	1.0 ± 0.5	$H = 1.557,\ P > 0.50$

nests failed completely, with all nestlings starving. No other nests failed completely.

Curiously, the maximum mass of the surviving nestlings in the second brood was significantly higher in the C-treated group than in the other groups. All of the young in this group were heavier than the 20.1-g threshold for post-fledging survival (Dawson 1972), while a disproportionate number of young in the F-treated ($n = 7$) and T-treated ($n = 3$) groups fell below this threshold ($G = 8.771$, $P < 0.025$). Taking this into account, birds in the T-treated group still produced fewer offspring that were likely to survive.

ENDOCRINE EFFECTS

The majority (79%) of males were recaptured at the nest boxes while tending the second brood. As expected, T-treated males had significantly higher circulating levels of T (Table 4). These levels are high, but within the range of peak levels recorded in free-living males (Hegner and Wingfield 1986a), indicating that the testosterone treatment was not a pharmacological dose. Circulating levels of T in the F-treated males appeared to be lower than average, although this was not necessarily expected from flutamide treatment. As a further verification of the effectiveness of flutamide administration, we examined the length of the cloacal protuberance and the beak color of males, both of which are androgen-dependent characters in this species (Hegner and Wingfield 1986a). Males treated with T tended to have darker beaks and longer cloacal protuberances, and F-treated males tended to have lighter beaks and shorter cloacal protuberances, the expected result of the implant treatment (Table 4).

In all groups of males, there was evidence that circulating levels of T continued to fluctuate in the typical pattern during the nestling stage (Fig. 2). Levels of T were higher in males captured when young were 10 or more days old than in males captured when nestlings were younger. Two-way ANOVA indicated a significant effect of nestling age despite the different average levels of T resulting from the implants (Table 5). This is further evidence for the importance of rising levels of T during the later parts of the nestling stage for breeding male House Sparrows.

Other endocrine and physical measurements provided no evidence for increased stress on males or females in any group resulting from the experiment (Table 4). Circulating levels of corticosterone, a hormone often associated with stress (e.g. Siegel 1980), were normal in all adults. Similarly, body mass and fat depots did not differ among groups.

TABLE 5. Analysis of variance for testosterone levels in males.

Source	df	F	Significance
Implant	2	32.125	$P < 0.001$
Nestling age	2	5.036	$P < 0.025$
Interaction	4	0.169	$P > 0.10$
Error	14		

DISCUSSION

In free-living birds, circulating levels of testosterone and other reproductive hormones fluctuate dramatically during the breeding season (Wingfield and Farner 1978a, b). These fluctuations are related to events critical to the breeding success of individual males. High levels of testosterone occur when males establish breeding territories, attract mates, and copulate with fertile females. Low levels of testosterone occur when males provide parental care to nestlings and fledglings. This suggests that testosterone levels are elevated during periods of intense male-male competition (e.g. for control of breeding resources and defense of fertile females) but lowered when demands for parental care are high (e.g. when young require care from the male). We recently presented correlational evidence from free-living House Sparrows to support this suggestion (Hegner and Wingfield 1986a, b), and many other studies point to the same conclusion (see Wingfield and Moore 1987).

We tested whether or not the fluctuating pattern of testosterone levels in male House Sparrows represented an optimal compromise between conflicting demands of male-male competition and parental care. In some males, concentrations of testosterone were elevated artificially to maximal levels from early in the nestling stage of the first brood of the season to late in the nestling stage of the second brood. In another group of males, concentrations of testosterone were effectively lowered by blocking androgen receptors in target tissues with flutamide. The behavior and breeding success of these males were compared with those of control males during the same period.

We found that tonic, elevated testosterone levels were detrimental to a male's fecundity. By failing to feed their nestlings, T-treated males produced significantly fewer fledglings than did males in the other groups. Half of the T-treated males lost their entire second brood to starvation. Hence, elevated levels of testosterone at the inappropriate time (e.g. when feeding young nestlings) results in lower reproductive output. Our experiment also provides evidence that low levels of testosterone at the appropriate time (e.g. when feeding young nestlings) increase reproductive output, although this was less conclusive. By providing more food to nestlings, F-treated males produced more fledglings during the second brood than did control males. Many of these young were lighter than average, however, and hence were more likely to perish shortly after fledging (Dawson 1972). Nestling mortality was unusually high for this time of year, even in control nests, which suggests this was a particularly unfavorable nesting season. Perhaps in a more favorable year, nestling mass in the F-treated group would be higher.

Our experiment does not indicate, however, that tonic low levels of testosterone at the inappropriate time (e.g. during the interbrood interval and egg laying) lower reproductive output. F-treated males were able to maintain control of their nesting sites and exhibited normal copulatory behavior. Hence, elevated levels of testosterone do not appear to be necessary for maintenance of an established nesting site and pair bond, or for copulation in House Sparrows (see also Moore and Kranz 1983). High testosterone levels, however, may be required for establishing these or for defense when challenged.

An important parameter missing from this study was whether the F-treated males were able to maintain a high confidence of paternity during the second brood. Correlational evidence suggests a great deal of male-male competition for fertile females in our study area (Hegner and Wingfield 1986a, b). If F-treated males were unable to guard their mates properly, the young they fed so frequently may not have been their own. Future studies are planned to address this point.

Our data suggest that males maximize their reproductive output through a compromise between investment in male-male competition and parental care. Part of the mechanism appears to involve varying circulating levels of testosterone. Testosterone is involved in regulating aggressive behavior in birds, including territoriality and mate guarding (e.g. Balthazart 1983; Moore 1984; Wingfield 1984b, 1985; Wingfield and Ramenofsky 1985; Wingfield et al. 1987). Correlational studies have shown repeatedly that testosterone levels are low when males are engaged in parental activities (e.g. Wingfield and Farner 1978a, b; Wingfield 1984a; Hegner and Wingfield 1986a). Moreover, recent experimental evidence, including this study, suggests that elevated levels of testosterone inhibit the expression of parental care in male birds.

Silverin (1980) implanted male Pied Flycatchers (*Ficedula hypoleuca*) with testosterone early in the breeding season. In this species, many males are bigamous, establishing defense of a second nesting site after their first mate begins incubation (von Haartman 1956). All implanted males were able to attract a second female, but because they failed to provide parental care, their overall reproductive output was lower than that of monogamous birds (Silverin 1980). Similarly, Wingfield (1984c) found that normally monogamous male Song Sparrows (*Melospiza melodia*) became polygamous when implanted with testosterone because they were able to defend larger territories. No reproductive data were available in that study, although male Song Sparrows normally provide substantial amounts of parental care, particularly after young fledge. This study provides further experimental evidence that high levels of testosterone and high rates of parental care are incompatible in male birds.

ACKNOWLEDGMENTS

We are grateful to the Bradbury, Van Tassel, and Wheeler families for their gracious hospitality in providing access to nest boxes on their farms. Greg Ball, Al Dufty, Mike Moore, and an anonymous reviewer provided constructive criticism on earlier drafts. Chris Levesque drafted the figures and helped with the assays. Research support was provided to R.E.H. by NRSA postdoctoral fellowship 3F32MH08837 and to J.C.W. by NSF grant PCM8316155, a Charles H. Revson Fellowship in Biomedical Research, and an Irma T. Hirschl Career Scientist Award.

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The **North American Bluebird Society** announces the **5th annual grants in aid** for ornithological research on cavity-nesting species of North America, with emphasis on the genus *Sialia*. Presently, three annual grants of single or multiple awards totaling $7,500 are awarded: **J. L. Williams Memorial Bluebird Research Grants.**—Available to student, professional, or individual researchers for a suitable research project focused on any of the three species of the genus *Sialia*. **General Research Grant.**—Available to student, professional, or individual researchers for a suitable research project focused on a North American cavity-nesting species. **Student Research Grant.**—Available to full-time college or university students for a suitable research project focused on a North American cavity-nesting species. Guidelines and application materials are available on request from **Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 59846.** Completed applications must be received by **1 December 1987**; decisions will be announced by 15 January 1988.

The **Hawk Mountain Sanctuary Association** is accepting applications for its **11th annual award** for raptor research. To apply for the $750 award, the applicant should submit a brief description of his or her research program (5 pages maximum), a *curriculum vitae*, and two letters of recommendation to **Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529.** The deadline for applications is **15 October 1987.** The Association's board of directors will make a final decision early in 1988. Only students in degree-granting institutions are eligible to apply; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of North American raptor populations.