ANDROGENS AND MATING SYSTEMS: TESTOSTERONE-INDUCED POLYGYNY IN NORMALLY MONOGAMOUS BIRDS

JOHN C. WINGFIELD

The Rockefeller University Field Research Center, Tyrrel Road, Millbrook, New York 12545 USA

ABSTRACT.—Recent investigations of the plasma profiles of testosterone (T) in free-living birds suggest that circulating levels of T during the reproductive cycle remain elevated longer in males of polygynous species than in males of monogamous species. When the hormonal profile of polygynous males is mimicked by the administration of subcutaneous implants of T to males of monogamous species, thus maintaining plasma levels of this androgen at high vernal levels, frequencies of territorial aggression and courtship behavior remain elevated, resulting in a marked increase in the size of the territory. A substantial number of T-implanted males also become polygynous, attracting two and sometimes three females to settle on their enlarged territories. These data suggest strongly that the nature of avian mating systems is regulated proximately by temporal patterns of hormone secretion. *Received 2 December 1983, accepted 27 April 1984.*

IN the early spring, males of many passerine birds establish breeding territories to which they then attract a mate or mates. The seasonal development of behaviors associated with the establishment of a territory, courtship, and mate-guarding are regulated by the steroid hormone testosterone (T) (e.g. Hutchison 1978, Farner and Follett 1979, Wingfield and Farner 1980a, Adkins-Regan 1981, Moore 1984). Circulating levels of T in males are elevated throughout the spring, reaching a maximum when females are ovulating and when most copulations occur (Wingfield and Farner 1980a; Wingfield 1980, 1983). In monogamous species there is a rapid decline in plasma levels of T (Wingfield 1980, 1983; Wingfield and Farner 1980a), accompanied by a reduction of territorial and sexual behavior, as soon as the female begins incubation. In polygynous species, however, circulating T remains elevated throughout incubation [e.g. Red-winged Blackbird (*Agelaius phoeniceus*), W. A. Searcy pers. comm.] or at least until the final mate has begun incubation [e.g. Pied Flycatcher (*Ficedula hypoleuca*), Silverin and Wingfield 1982]. In the weakly polygynous Western Meadowlark (*Sturnella neglecta*), plasma levels of T do decline as incubation ensues but then increase for a second time when females are producing a second clutch (Wingfield and Farner 1980b). Monogamous males of captive populations of turtle doves (*Streptopelia* spp.), however, also manifest an elevation of T during the courtship phases of subsequent broods (Feder et al. 1977). This is unlike most monogamous species, such as the White-crowned Sparrow (*Zonotrichia leu-*

cophrys; Wingfield and Farner 1978a, b, 1980a), Eurasian Blackbird (*Turdus merula;* Schwabl et al. 1980), and Song Sparrow (*Melospiza melodia;* Wingfield 1984a), in which plasma levels of T remain depressed, even though up to four clutches may be produced within a single season.

In addition, it has been shown that in the monogamous wild Mallard (*Anas platyrhynchos*) plasma levels of T decrease as soon as the female is incubating. In domesticated and semi-domesticated forms of Mallards, however, the mating system becomes promiscuous, plasma levels of T remaining elevated for longer during the breeding period (Donham 1980, Haase and Donham 1980). Although caution should be exercised in comparing plasma profiles of hormones of truly wild and domesticated forms of the same species, these data do support the hypothesis that, in monogamous males, plasma T is elevated only early in the season when territories and pair bonds are established, whereas, in polygynous forms, plasma T is elevated for longer periods that may overlap the parental phase.

This communication reports the effects of mimicking the hormonal profile of polygynous species by administering subcutaneous implants of T to males of monogamous species and thus maintaining plasma levels of this androgen at high springtime levels.

MATERIALS AND METHODS

Experimental subjects and study sites.—In the spring of 1979, an investigation into the behavioral effects

of experimentally altered temporal patterns of T secretion in male White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) was initiated at a study site near Hart's Lake, Pierce County, Washington (45°N). Free-living populations of this race of White-crowned Sparrow are known to be primarily monogamous (Blanchard 1941, Lewis 1975). In the spring of 1981 this experiment was repeated with free-living male Song Sparrows (*Melospiza melodia*) on the grounds of the Rockefeller University Field Research Center and adjacent lands of the Cary Arboretum of the New York Botanical Society, Millbrook, New York (42°N). Song Sparrows are monogamous, although occasional instances of polygyny are reported (Nice 1943, Smith and Roff 1980).

Hormone implants and sampling procedures.—To alter the temporal pattern of circulating T levels, eight territorial male White-crowned Sparrows were given a subcutaneous implant of crystalline T packed into 20-mm lengths of Silastic tubing (internal diameter 1.47 mm, external diameter 1.96 mm; Dow Corning, Midland, Michigan). Controls ($n = 9$) were given empty implants at a second site some 8 km distant. In the second experiment, a group of 8 territorial male Song Sparrows were given identical implants of T, and in an area 1 km distant a second group of 8 males were given empty implants as controls. All implanted birds were surrounded by untreated but territorial males, and all implants were administered early in spring as territories and pair bonds were being established.

Birds were captured in Japanese mist nets or in Potter traps baited with seeds. Blood samples were collected immediately after capture and before implantation. Sparrows were banded with a U.S. Fish and Wildlife Service aluminum band and a unique combination of colored plastic leg bands for identification of individuals during subsequent behavioral observations. All females captured were also color banded. At each capture, body mass was measured to the nearest 0.1 g, fat depot in the furculum and abdomen was assessed on an arbitrary scale, and wing length was recorded to the nearest millimeter. All of these sampling procedures have been described in detail by Wingfield and Farner (1976, 1978a). At intervals throughout the breeding season, experimental birds and controls were recaptured and further samples were collected. Implants were checked at each capture and, in experimentals, T implants were replaced if the original implant was half empty.

Behavioral observations.—Birds were identified by color-band combinations during regular censuses at least once a week. The bird's location and interactions with conspecifics were also noted. These observations were divided equally between experimental and control sites. Territory size was measured after boundaries had been established (May–July) as follows: tape-recorded songs of Song Sparrows (territory size was not assessed for implanted White-crowned Sparrows) were played to experimental and control males, the position of singing perches was noted on a detailed map, and the area circumscribed by the perches was measured in square meters. Because only singing and display perches were used to identify territory boundaries, these data represent conservative estimates of territory size.

Polygynous associations were indicated by the presence of two or more nests within a territory and by repeated observations of breeding females, identified by color bands, associating with a particular male or carrying food to young on an observed male's territory.

Hormone assays.—Plasma levels of T and corticosterone (B) were measured by radioimmunoassay after partial purification of each steroid on Celite : glycol microcolumns. These assays have been described in detail by Wingfield and Farner (1975) and Wingfield et al. (1982a).

Statistical analysis.—All comparisons of experimental and control birds were made with Mann-Whitney U-tests with the exception of return rates, for which Chi-square tests were employed.

RESULTS

Testosterone-induced polygyny.—Plasma levels of T in control and experimental birds are presented in Fig. 1. In White-crowned Sparrows, circulating T was higher during May and June in males receiving a T implant, but these levels are within the normal physiological range for passerine birds (Wingfield and Farner 1980a). In controls, plasma levels of T declined from high levels in late April and early May to lower levels during the parental phase in May and June. A more detailed investigation was performed with Song Sparrows in which both control and experimental males were recaptured at intervals throughout the season and blood samples collected to check the plasma level of T. Circulating T in control males followed a pattern typical of monogamous species (Fig. 1). Levels were high in April and early May when copulations for the first clutch occurred and then declined during the parental phase in late May and June. In contrast, T levels in experimental males remained elevated throughout the breeding season and were significantly higher than those of controls.

In both White-crowned and Song sparrows, prolonged high levels of circulating T in males were accompanied by significant trends toward polygynous associations (Table 1). This trend was most marked in the Song Sparrow. Of 8 males implanted with T, 6 had 2 mates, 1 had
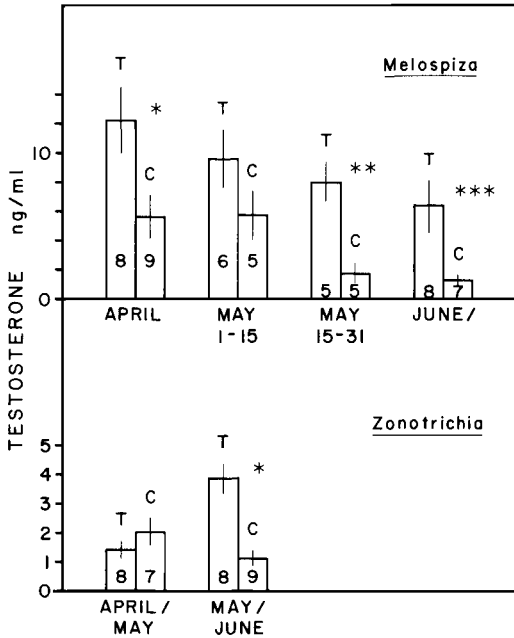
Fig. 1. Plasma levels of testosterone in testosterone-implanted (T) and control (C) Song Sparrows and White-crowned Sparrows. Histograms represent mean levels in ng/ml, and vertical bars are the standard errors. Figures within the histograms indicate sample sizes. $* = P < 0.05$; $** = P < 0.005$; $*** = P < 0.001$; Mann-Whitney U-test.

TABLE 1. Number of females mated to males implanted with testosterone.

	Testosterone implant[a]	Control implant
Zonotrichia		
Mean females/male	1.88*	1.0
Median	2	1
Range	1–3	1–1
n	8	9
Melospiza		
Mean females/male	2.0**	1.0
Median	2	1
Range	1–3	1–1
n	8	8

[a] $* = P < 0.05$; $** = P < 0.001$, Mann-Whitney U-test.

a single mate, and 1 had 3 mates, whereas all controls were monogamous. In some instances, additional color-banded females were sighted once or twice on territories of both experimental and control males, but these were not regarded as permanent associations.

Territory size.—The sizes of territories of male Song Sparrows implanted with T averaged more than twice as large as those controls and neighboring males (Table 2). One T-implanted male defended a territory four times as large as the average territory of controls. There were no dif-

ferences in the sizes of territories among neighbors of T-implanted males or among those of controls and their neighbors.

Consequences of polygynous associations.—To assess the metabolic consequences of defending an enlarged territory and engaging in polygynous associations, I compared plasma levels of corticosterone, body mass in relation to body size [calculated by dividing body mass in grams by wing length in millimeters (mass ratio)], and subcutaneous fat stores between T-implanted males and controls (Table 3). In May and June/July, T-implanted males had less stored fat than controls did, although mass ratio was significantly depressed only in May. Circulating levels of corticosterone, however, did not differ between males implanted with T and controls at any time during the season. Although sample sizes were small, overwinter survival, expressed as the percentage of males that returned to the same area the following year, indicated that T-implanted males were just as likely to return the next spring as control and untreated males (Table 4).

TABLE 2. Effect of testosterone on territory size (m²) of free-living male Song Sparrows. Means ± SE (sample sizes in parentheses) are given.

Control implant	Neighbors of control implant	Testosterone implant[a]	Neighbors of testosterone implant
1,466 ± 145 (8)	1,488 ± 117 (12)	2,955 ± 325* (8)	1,370 ± 87 (16)

[a] $* = P < 0.001$, Mann-Whitney U-test.

TABLE 3. Effect of testosterone on fat depot, mass ratio [body mass (g) divided by wing length (mm)], and circulating levels of corticosterone (B, units = ng/ml of plasma) in free-living male Song Sparrows. Means ± SE (sample sizes in parentheses) are given.

	April			May[a]			June/July[a]		
	Fat	B	Mass ratio	Fat	B	Mass ratio	Fat	B	Mass ratio
Testosterone implant	1.26 ± 0.25 (8)	7.60 ± 1.19 (8)	—	0.19 ± 0.09** (8)	9.32 ± 1.81 (8)	0.310 ± 0.003*** (8)	0.14 ± 0.14* (7)	10.71 ± 1.9 (8)	0.306 ± 0.005 (7)
Control implant	1.44 ± 0.25 (8)	6.24 ± 1.45 (8)	—	0.63 ± 0.21 (8)	13.17 ± 5.24 (5)	0.325 ± 0.007 (8)	0.71 ± 0.29 (7)	6.87 ± 1.55 (7)	0.319 ± 0.008 (7)

[a] * = $P < 0.05$; ** = $P = 0.05$; *** = $P = 0.05$; = $0.05 < P < 0.1$; Mann-Whitney U-test.

TABLE 4. Overwinter survival rates of adult male Song Sparrows.

	Banded in 1981	Returned in 1982	Percentage returned
Experimental	8	4	50
Control	8	3	37
Untreated	12	5	42

DISCUSSION

Clearly, the evidence presented in Fig. 1 and Table 1 suggests a relationship between prolonged high levels of T in the blood of males and polygynous matings. In some instances, as many as three females had nests within the boundaries of a male's territory. Instances of natural polygyny in Song Sparrows and Puget Sound White-crowned Sparrows are rare (Blanchard 1941, Nice 1943, Lewis 1975, Smith and Roff 1980), and I have found no naturally polygynous associations in either species. The site on which male Song Sparrows were implanted with T has subsequently been used as a control area. No further polygynous matings have been observed. Smith et al. (1982), however, did show that, if male Song Sparrows were removed from an insular island population, thus resulting in an excess of females, then polygynous associations were formed.

Because female White-crowned and Song sparrows also defend their territories and in spring may accompany males during boundary disputes (Nice 1943; Wingfield and Farner 1978a, b), it is puzzling that two or even three females would tolerate each other on a single male's territory, unless the territory was sufficiently large to accommodate all females. The territories of T-implanted male Song Sparrows are considerably larger than those of controls. Thus, it appears that the incidence of polygyny in males implanted with T is correlated with an enlargement of the territory that could then accommodate the settlement of two or more females. This strengthens the intriguing possibility that experimental modification of the temporal pattern of T secretion from a monogamous to a polygynous type results in a change in mating system in the same direction.

The increase in the size of the territory is undoubtedly a result of prolonged high circulating levels of T that increase the intensity of

territorial aggression (see Wingfield 1984b). This conclusion is also in accordance with other investigations indicating that elevated levels of T increase the intensity of aggression in male birds (e.g. Trobec and Oring 1972, Searcy and Wingfield 1980, Silverin 1980, Ramenofsky 1982, Moore 1984). Furthermore, Watson and Parr (1981) showed that an implant of T given to a single free-living male Red Grouse (*Lagopus lagopus scoticus*; a species manifesting varying degrees of polygyny) resulted in an increase not only in the number of mates but also in the size of the territory.

Because polygynous matings in normally monogamous systems have the potential for substantially increasing the reproductive success of males, the question now arises as to why polygyny is not more widespread in both White-crowned and Song sparrows. Clearly, other restraints act to conserve monogamy in these species. It is possible that the defense of a larger than normal territory and the increased demand for food by young in two or three nests represent an elevated energetic cost to the male that may be severely debilitating. Decreased fat depot and mass ratio in male Song Sparrows implanted with T suggest that the resulting change in behavior is energetically demanding, although a possible direct effect of T on metabolism cannot be ruled out. By late in the season, however, both fat depot and mass ratio in control males have declined to levels similar to those T-implanted males, suggesting that the change in behavior induced by T implants is not abnormally demanding. Accordingly, it cannot be concluded that males implanted with T are stressed, because circulating levels of corticosterone, a frequently used indicator of stress (Seigel 1980, Wingfield and Farner 1980b), reveal no differences between experimental and control males (Table 3). In addition, four males that were implanted with T returned to the same area in 1982, compared with three controls, suggesting that overwinter survival is not obviously impaired by the administration of hormones. It is possible, however, that slight differences in survivorship, not apparent from the small sample size in these investigations, could provide a significant selective pressure.

A more likely restraint on polygyny is the limited extent to which polygynous males can feed young on their territories. In both White-crowned and Song sparrows, males feed young and, after the young fledge, may provision the offspring to a greater extent than do females (Nice 1943, Blanchard 1941, Lewis 1975). Thus, reproductive success could depend to a large degree on the parental care provided by the male. Polygynous, T-implanted, male White-crowned and Song sparrows were observed feeding young, but it is not known to what extent males provisioned young in each nest. It can be predicted that if males divide their efforts among 2 or 3 nests, the decrease in net input per nest will result in reduced production of independent young. Additionally, T-implanted males could spend much time singing and patrolling the territory (Silverin 1980, Moore 1984), reducing the time spent foraging and feeding young even further. Support for these predictions comes from Silverin (1980), who administered T to male Pied Flycatchers during the parental phase when endogenous plasma levels of T are low (Silverin and Wingfield 1982). Treated males spent most of their time singing and patrolling the territory, and they failed to feed young, which resulted in a dramatic reduction of reproductive success. Currently, I have no data on fledging success for Song Sparrows, but this prediction is being tested. Smith et al. (1982) induced polygynous associations in male Song Sparrows by removing some males from an insular population, which resulted in an excess of females. They found that polygynous males tended to feed young only in the nest of the primary female. The secondary females were able to raise young alone, although growth rates of these young were decreased and fewer reached independence, compared with young from nests in which males also provided food.

It should be borne in mind that, because in these experiments high circulating levels of T were maintained artificially, it is possible that the subsequent development of polygynous associations was artifactual. It is of interest, however, to relate the T-induced polygyny hypothesis and predictions to the "polygyny threshold" model (Orians 1969, Wittenberger 1976), through which, in part, it is asserted that, if some of the breeding habitat is sufficiently rich in trophic resources to enable females to gather sufficient food to raise young without the help of a mate, then females will choose to mate with males occupying richer or larger territories, irrespective of whether or not these males are already mated and despite the pres-

ence of unmated males in possession of poor territories. Also, the tendency of females of passerine species to perform most or all of the incubation enables males to respond to slight changes in environmental quality and to become opportunistically or facultatively polygynous (Emlen and Oring 1977). Thus, if the habitat requirements of the above models are met, then it seems reasonable to assume that selection would act on the neuroendocrine and endocrine systems by favoring males that tend to have high levels of circulating T for longer periods. This, in turn, would increase the intensity of aggressive territorial behavior, perhaps resulting in a larger than normal territory that might favor the settlement of more than one female. Note, however, that the larger territories of T-implanted males are not gained at the expense of untreated neighbors, because the latter have territories identical in area to those of controls (Table 2). Moreover, it appears that neighbors of T-implanted males are able to defend their territories against these "aggressive" males (see also Wingfield 1984b), and, thus, the expansion of the territory following the male's treatment with T would be difficult unless the implants were administered early in the breeding season before all males had arrived. In these investigations, the implants were given in March and April as territory boundaries were being established. It should also be noted that prolonged high plasma levels of T would also tend to maintain courtship behavior, which would facilitate the attraction of additional mates.

Finally, it should be pointed out that it is unlikely that implants of T would induce polygyny in all monogamous avian species, because some, such as long-lived colonial species (e.g. larids) often form permanent pair bonds, and a high degree of behavioral interaction between mates is required for successful breeding. Thus, prolonged high plasma levels of T in males of these species could disrupt the intricate behavioral interactions leading to the onset of the nesting phase. Nevertheless, the clear correlation of extended periods of high plasma levels of T in naturally polygynous species with the polygyny experimentally induced by administration of T to normally monogamous species suggests that, at least in some avian groups, the endocrine mechanisms underlying reproductive behavior are quite malleable. Accordingly, the use of hormone im-

plants to manipulate behavior in free-living individuals could prove to be a useful tool for investigations of social systems.

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