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Wilson Bull., 99(1), 1987, pp. 86-91

Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows. – The effects of testosterone on dominance hierarchies differ among avian species, and it is difficult to predict how particular species will respond. Selinger (1967) found that androgen injections increased the number of head grabs and pecks in Japanese Quail (*Coturnix coturnix japonica*), in some cases leading to a reversal in dominance. Androgen injections also led to a reestablishment of original dominance relationships in quail that had previously lost their dominance due to castration. Gottier (1968) reported that chickens (*Gallus gallus*) injected with androgens moved up in their hierarchy. In the polymorphic Harris Sparrow (*Zonotrichia querula*) darker birds are dominant to lighter colored birds (Rohwer, 1978). Low-ranking birds disguised to resemble high-ranking individuals by painting did not move up in the hierarchy, unless they were also treated with testosterone (Rohwer and Rohwer 1978). Testosterone injections, however, had no effect on low-ranking Red-billed Queleas (*Quelea quelea*), European Starlings (*Sturnus vulgaris*), or domestic Rock Doves (*Columba livia*) (Mathewson 1961, Crook and Butterfield 1968, Lumia 1972).

Here we report on post-testosterone treatment hierarchies in migratory Gambel's Whitecrowned Sparrows (*Zonotrichia leucophrys gambelii*).

Methods.-In the fall of 1979, hatching-year Gambel's White-crowned Sparrows (aged by crown color) were captured in the Los Angeles, California area, sexed by laparotomy, and held for several weeks in outdoor aviaries. On 9 January 1980, control and experimental groups of six males each were color-banded for individual recognition and put in separate rooms in $1.2 \times 0.9 \times 0.5$ m cages. Photoperiod was held at 10L:14D and room temperature at 20 ± 1°C. Birds were fed seeds, pheasant starter, grit, greens, and vitamins. From 13 January through 28 January (Period 1) each of us independently observed the two captive flocks. For 1 h each observation morning we counted displacements as described by Parsons and Baptista (1980). We then compared our tabulations. Because we found that we agreed on the positions of the birds in the two hierarchies, we pooled our data throughout the experiment. On 28 January the two lowest ranking birds in one hierarchy (birds 5e and 6e in the experimental group) were given intramuscular injections of testosterone (Searle SC-16148, 0.15 cc at 50 mg/cc). Previously, this dosage was found to be effective in inducing song (Baptista 1974) (see below). Birds 5c and 6c in the control group were injected with placebo (the peanut oil vehicle). Four days later birds 5 and 6 in the experimental group were given a second injection (0.10 cc), and their counterparts in the control group were injected with placebo. We observed the birds for 45 days, during which time 4819 aggressive interactions were recorded (2181 in the control group and 2638 in the experimental group).

Observations were made between 13 and 28 January. Before injections, straight-line hierarchies were established in both groups (Period 1) (Fig. 1). The ratio of wins to losses between any two birds indicates which of the two is dominant, although subordinate birds occasionally won encounters with dominants.

Behavior following injections. - In the control group, no changes in behavior occurred after placebo injections of the two lowest ranking birds (5c and 6c). In the experimental group, three types of changes were observed. First, the injected birds, 5e and 6e, initiated



(* indicates injection.)

FIG. 1. Dominance hierarchies of control (left column) vs experimental (right column) groups of White-crowned Sparrows. Period 1 illustrates hierarchies before injections. Individual percent wins appear in the column to the right of each hierarchy. Periods 2 and 3 (combined) illustrate hierarchies after injection with testosterone or placebo. Asterisks denote injected birds. Period 4 illustrates the hierarchy beginning 4 days after the second injections.

many more aggressive encounters than they had prior to treatment. Second, they won a much higher percentage of interactions in the total time span following injections than they had before injections (Fig. 2), and several reversals in dominance relationships occurred (Fig. 1). The third change involved the nature of interactions between the two injected birds and their cage-mates. Following androgen treatment, 5e and 6e often pulled at the wings



FIG. 2. Percentage of wins of injected birds 5e and 6e combined (gray bars) versus control birds 5c and 6c combined (open bars). Each bar represents the mean \pm SE percentage of wins over total number of encounters in which these birds were involved.

and tails of their opponents. This high-intensity aggressive behavior was rarely exhibited by any bird before injections. No wing or tail pulling was observed in the control birds (5c and 6c) during Periods 1 to 3. During Period 4 the mean number of wing or tail pulls in the control groups was 0.2 per day. No wing or tail pulling was observed in the experimental group (5e and 6e) during period one. Following androgen injection, however (Periods 2 and 3), the mean number of wing or tail pulls in the experimental group increased to 4.5 per day. During Period 4 wing and tail pulling in the experimental group was maintained at a rate of 1.4 per day, a higher level than that observed in the control group (0.2 per day). These data contrast with those for pigeons. No increased aggression was found by Lumia (1972) in testosterone-treated low-ranking pigeons, which are strongly influenced by prior experience.

Our observations suggest that, following testosterone treatment, subordinates may direct attacks at cage-mates regardless of rank. This may result in temporary persecution by the dominant. Reversals in rank may ensue. For example, from 6 to 21 February, Bird 6e, originally the bottom-ranking bird, won 79 of 86 encounters with the previously 2nd-ranked bird, 2e (Fig. 1).

In Period 4 the androgen-injected birds remained intensely aggressive. Bird 5e won 214 out of 215 encounters with 2e, and 6e remained dominant to 1e and 2e (Period 4) (Fig. 1). Also, the number of encounters in the control group that fell outside a straight-line hierarchy increased over those in Periods 1 to 3. For example, 5c won 68 out of 71 encounters with 1c (Fig. 1). We have no explanation for these changes, although changes in dominance hierarchies may be spontaneous (Marler 1955), and they have been observed in late winter-early spring in several species (Samson 1977, Parsons and Baptista 1980).

How may the effects of changing season be separated from those of actual androgen injections? We computed the number of interactions won by the fifth and sixth-ranking birds (combined) in control and experimental groups as a percentage of the total number of encounters in which these birds were involved. In Periods 2 and 3, following injections, experimental birds 5e and 6e won more than twice the percentage of encounters that they won in Period 1, before injection (38.6 vs 14.5%). In contrast, in control birds (5c and 6c) the percentage of wins in Periods 2 and 3 was lower than in Period 1.

Hierarchy after metabolism of injected testosterone.—We know from observations that birds treated with androgens initiate many more encounters and that they may rise in dominance status. But what happens after the artificially introduced androgens have been metabolized?

Ramenofsky (1984) studied dominance relationships of male Japanese Quail by subjecting them to short-term dyadic encounters in a round-robin tournament over 19 days. Radioimmunoassays indicated that high plasma testosterone levels were correlated with fighting success only in the earlier encounters. By day 15 testosterone levels of winners and losers were similar. She concluded that higher androgen levels influenced the outcome of initial encounters, but that learned response biases took precedence once dominance relationships stabilized. Our study indicates that testosterone injections may effect reversals of dominance in a White-crowned Sparrow flock, but that testosterone is not required to maintain the new hierarchical relationships as developed below.

We noted in earlier studies (unpubl. data) that White-crowned Sparrows engaged in long bouts of whisper singing after testosterone treatment. In this study we counted songs of birds 5 and 6 in both groups in the early afternoon of each observation day. We use rate of whisper singing (cf. Baptista 1974) as a crude index of changes in testosterone levels. Singing by a control bird was heard on only one occasion, before placebo injection. In contrast, on the days following injections with androgen, experimentals 5e and 6e sang frequently. For example, bird 5e sang over 60 songs per half-h following injections (Fig. 3). By Period 4 the amount of singing decreased, probably corresponding with the decrease of synthetic andro-



FIG. 3. Relationship of number of songs and number of wins in birds 5c and 5e. Vertical bars represent percentage of wins of experimental bird 5e (gray bars) versus control bird 5c (open bars) at four-day intervals beginning 13 January and ending 21 February. Dots represent mean number of songs sung per half-h by experimental bird 5e during those periods. Abscissa represents observations during periods 1 to 4: Periods 1 and 4 are divided into 4-day intervals. Periods 2 and 3 consist of two 4-day intervals of observation.

gens. Treated birds continued to win encounters, however, suggesting that these wins are the result of experience gained by winning encounters during Periods 2 and 3.

Summary. – Testosterone injections rendered low-ranking birds more aggressive thus increasing the number of wins following injections and effecting some status reversals. Following reversal (Period 4) the newly subordinate birds are conditioned through the experience of repeatedly losing encounters to retain their new status, despite the fact that testosterone titers are no longer high in their opponents.

Acknowledgments. — The studies were completed while all three authors were in residence at the Moore Laboratory of Zoology, Occidental College, Los Angeles, California. We thank the Biology Department for use of space and Occidental College equipment. We thank M. Balph for critical comments on an earlier version of the ms, M. Morton who performed the laparotomies, and G. Nusse who prepared the figures. Searle Laboratories provided the testosterone used in these studies.

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Wilson Bull., 99(1), 1987, pp. 91-94

Growth characteristics of Wood Ducks from two southeastern breeding locations. – Recently, advances have been made in the application of the Richards sigmoid model to the study of avian growth. These studies (White and Brisbin 1980, Brisbin et al. 1986) have provided a means of evaluating bird growth by making independent estimates of the three major components of the growth process: (1) *size*, or asymptotic limit approached, (2) *rate*, a measure of the total amount of time required for growth to be completed, and (3) *shape*, a quantity which expresses the specific path or trajectory taken by the growth process to approach asymptote within the time constraints of the total growing period. In this reparameterized process error model, these three characteristics are quantified by the parameters W_{∞} , T, and m, respectively (Brisbin et al. 1986).

Preliminary studies that used these procedures to analyze the growth of waterfowl and other organisms have suggested that, following exposure to a variety of environmental stressors, changes in growth curve shape (m) are more likely to occur than are changes in either size (W_{∞}) or growth rate (T) (Brisbin et al. 1986). Fendley and Brisbin (1977), however, found that sigmoid growth characteristics of captive-reared Wood Ducks (*Aix sponsa*) also can vary according to the breeding location. In that study, growth rates were found to vary between birds from different locations, but no difference was found in asymptotic sizes. There was also a suggestion of a change in the shapes of the growth curves, as evidenced by a shift in the ages at the point of inflection, although this could not be tested conclusively as analyses in that study were based on the use of the logistic rather than the Richards sigmoid model. (The logistic model is a special case of the Richards model that is obtained by constraining m = 2, and therefore changes in the value of m cannot be detected.)

We report here the use of the reparameterized Richards process error model to analyze the sigmoid growth characteristics of captive-reared Wood Ducks that were collected as