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SOCIAL INERTIA AND HORMONAL CONTROL OF AGGRESSION AND DOMINANCE IN WHITE-THROATED SPARROWS

by

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(With 5 Figures)
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Introduction

The influence of testosterone (T) on social dominance in birds varies with circumstances. Recent experiments, for instance, have shown that treatment of wintering birds with T does not change previously established dominance relationships, unless visual signals normally correlated with dominance are also changed concommitantly (ROHWER & ROHWER, 1978; JÄRVI *et al.*, 1987). This interaction of concurrent changes in hormonal status and external appearance recalls earlier reports that dominance relationships do not change when T-treated birds confront familiar social partners (ALLEE *et al.*, 1939; BENNETT, 1940; EMLEN & LORENZ, 1942; BEVAN *et al.*, 1960; GUHL, 1964, 1968; TROBEC & ORING, 1972; LUMIA, 1972; WINGFIELD & MOORE, 1986), a phenomenon for which GUHL (1968) coined the term "social inertia".

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Although familiarity with social partners is now routinely controlled in many experiments on behavioral endocrinology, few studies have directly addressed the effects of familiarity with opponents on hormonal control of aggression and dominance. In the present study, we investigated social inertia in small groups of captive white-throated sparrows *Zonotrichia albicollis* and in addition considered whether social inertia occurs in a free-living population.

In white-throated sparrows, as in a variety of other birds, treatment with T can increase the frequency and intensity of aggressive behavior (ADKINS & PNIEWSKI, 1978; ADKINS-REGAN, 1981; WINGFIELD *et al.*, 1987; ARCHAWARANON & WILEY, 1988; HARDING *et al.*, 1988). T can also increase an individual's dominance ranking among unfamiliar opponents (ALLEE *et al.*, 1939; BENNETT, 1940; MOSS *et al.*, 1979; SEARCY & WINGFIELD, 1980; BAPTISTA *et al.*, 1987). In addition, a number of studies have shown that concentrations of circulating T correlate positively with aggressiveness or dominance, although often not after stable relationships have formed (WINGFIELD & FARNER, 1978a, b; SCHWABL *et al.*, 1980, 1988; HARDING, 1983; SILVERIN & WINGFIELD, 1982; RAMENOVSKY, 1984; WINGIELD & MOORE, 1986; HEGNER & WINGFIELD, 1987).

White-throated sparrows during winter form loose foraging flocks with predominantly linear dominance hierarchies (WATT, 1986a; SCHLINGER, 1987; PIPER & WILEY, 1989a). The ability to dominante other birds in aggressive encounters affects access to feeding sites, movements, accumulation of subcutaneous fat, and survival (SCHNEIDER, 1984; PIPER, 1990a, b; PIPER & WILEY, 1990a, b). This species has two genetic morphs, which are distinguishable on the basis of plumage brightness in winter (PIPER & WILEY, 1989b). In free-living birds in North Carolina, sex and age, but not wing length or morph, influence dominance, but the single strongest influence on a bird's dominance is the location of encounters with respect to the center of its range (PIPER & WILEY, 1989a).

The experiments described here address three questions: (1) does familiarity with opponents in captivity alter the effects of T on aggression and dominance? (2) do untreated birds in captivity tend to retain their ranks in encounters with strangers? and (3) do free-living birds show evidence of social inertia? In the field, each bird has many more opponents to confront. Because social inertia suggests an ability to recognize opponents, the cognitive difficulties should increase when the number of opponents increases.

General methods

Experiments with captive birds.

Subjects.

During January 1985 and 1986, white-throated sparrows of all age and sex classes were captured in mist nets or in seed-baited treadle-traps at 8 locations 50-100 m apart in the Mason Farm Biological Reserve near Chapel Hill, North Carolina. They were individually marked with colored bands and their weights and wing chords measured. Sex was determined by laparotomy and age by examining the pneumatization of the cranium. Measurements of plumage brightness and determinations of morph followed procedures described earlier (PIPER & WILEY, 1989b). Birds were initially kept in visual isolation for 1-5 days in individual cages in a room with a natural photoperiod and fed a mixed diet. Following each experiment, the birds were given permanent bands and released.

Plan of experiments.

For these experiments, groups of 5 or 6 birds were placed in 12 outdoor aviaries (each 2.4 × 2.4 × 2.6 m and at least 6 m apart). On one side of each aviary, an enclosed observation chamber with one-way glass permitted close study of the birds without disturbing them. Each experiment consisted of several stages lasting 14-16 days each. At the beginning of each stage, birds were released simultaneously into each aviary. In most cases, birds combined in one aviary were trapped at different locations. Between stages birds were caught, weighed and examined, and then regrouped either with new opponents not previously encountered or with their previous opponents. During this process they were held visually isolated indoors in individual cages for 1-3 h.

Behavioral observations.

Observations were undertaken between 0900 and 1200 following 60 min deprivation of food. Each bird was the subject of two focal-individual samples for 15-min periods approximately one week apart during each stage of the experiment. Aggressive interactions included supplanting, in which one bird displaced another from a perch or from a water or food tray at the center of an aviary, and attack, in which one bird pursued another. If one bird supplanted or attacked another in 75% or more of their interactions, the first bird was considered dominant over the second. Using this criterion, dominance relationships were always clear. We recorded 22-137 interactions by each bird in each stage.

These captive birds formed predominantly linear dominance hierarchies, with an occasional nontransitive triad (triangle). In addition, subordinate birds occasionally supplanted or attacked dominant birds, interactions classified as reversals of the normal relationship. When an aviary included a nontransitive triad, we determined each bird's rank by arranging the dominance matrix to minimize the number of interactions below the principal diagonal of the interaction matrix.

Scores for aggression and dominance.

In each stage of an experiment, we calculated an aggression score for each bird by dividing its total number of supplantations and attacks by the number of birds subordinate to it in the same aviary. This aggression score represented the rate of aggressive actions by an individual per available recipient and thus did not depend on differences in opportunities associated with differences in a bird's rank.

Each bird's dominance rank was scaled to the number of birds in its aviary. For example, if there were six birds in an aviary, the top-ranking bird was given a score of 1.0, and the others scores of 0.8, 0.6, 0.4, 0.2, and 0, respectively; if there were 5 birds in an aviary, they were given scores of 1.0, 0.75, 0.5, 0.25, and 0, respectively. In each aviary we classified the bottom three birds in the hierarchy as low-ranking birds, and the other two or three as high-ranking birds.

Statistical analysis.

The aggression scores and scaled ranks for each individual were averaged across the relevant stages of an experiment, to yield averaged aggression scores or averaged ranks. Thus in each statistical test, each individual contributed only one observation or one pair of observations. To compare the behavior of birds in different stages of an experiment, we used Wilcoxon matched-pairs signed-ranks tests; to compare different treatment groups, we used Mann-Whitney U tests.

Experiments with free-living birds.

In these experiments, conducted between December 1985 and February 1986, we observed birds from a plywood blind at an artificial feeding site consisting of six concrete blocks placed on end 0.7 m apart beside a hedgerow of multifloral rose *Rose multiflora*. This site was over 250 m from the locations at which birds were trapped for aviary experiments and 175 m from a series of trapping and feeding sites used for concurrent field studies of unmanipulated birds (PIPER & WILEY, 1989a). Food consisted of mixed millet and sunflower seeds. All but a few of the birds using this feeding site were trapped, banded and examined as explained above.

Hormonal implants.

Procedures followed those already reported in greater detail (ARCHAWARANON & WILEY, 1988). Subcutaneous implants each consisted of a 10-mm length of crystalline T (Sigma Chemical Co.), in the center of a 20-mm length of Silastic tubing (I.D. 1.50 mm, E.D. 1.99 mm, Dow Corning Silastic Medical Grade Tubing). In preliminary experiments, we used radioimmunoassays to determine the titers of T in males and females that received implants of this size. Levels of circulating T after implants had been in place 6 weeks were 11.9 ± 4.39 (N = 3) and 9.3 ± 2.89 ng/ml (N = 2) in males and females, respectively (ARCHAWARANON, 1987). These implants thus resulted in mean T levels somewhat higher than those normally found in breeding males of related species (4-10 ng/ml; white-crowned sparrows *Zonotrichia leucophrys*, WINGFIELD & FARNER, 1978a, b; song sparrows *Melospiza melodia*, WINGFIELD, 1984a; WINGFIELD & GOLDSMITH, 1990). For controls, 20-mm lengths of empty Silastic tubing were prepared in the same way. Implants were placed under the skin of the upper back and were checked periodically to make sure that they were still in place and contained hormone. The tubes were weighed before and after implantation in order to determine the amounts of hormone absorbed by the birds.

Radioimmunoanalysis of hormones.

After each experiment, we drew blood from each subject for radioimmunoassay of T. Our procedures have been described previously in detail (ARCHAWARANON & WILEY, 1988). Radioimmunoassays were performed in the laboratory of the Endocrinology Section, U.S. Environmental Protection Agency, Research Triangle Park, N.C., following methods described by JACKSON & FRANKLIN (1984) and GOLDMAN *et al.* (1986). Measurement of T employed solid-phase radioimmunoassay kits (Coat-A-Count, Diagnostic Products Corp., Los Angeles, CA 90045), which measured both bound and unbound hormone. A resuspended methylene chloride extract of plasma was added to each sample tube. The standard curves were run in triplicate and the unknowns in duplicate.

According to literature from the manufacturer, the cross-reaction with 5 α-dihydrotestosterone in these assays is less than 9% and with other natural androgens less than 4%. In this study, inter- and intra-assay variances were 4% and 3%, respectively, and recovery of known amounts of these hormones added to sparrow plasma was about 85%.

Experiment 1: hormonal treatment of captive birds

Introduction.

In this experiment, we implanted T in white-throated sparrows in order to determine how this hormone affected aggression and dominance with familiar opponents. In a previously published series of experiments conducted from October through May 1985-86 (ARCHAWARANON & WILEY, 1988), T was implanted, following methods identical to those described above, in male and female white-throated sparrows. Following implantation, these birds were held indoors in indiviaul cages in visual isolation for one week and then grouped with unfamiliar opponents in the same outdoor aviaries used in the present experiments. The treated birds had significantly higher dominance ranks and aggression scores than controls. Responses to hormones did not depend on the subject's sex. These experiments thus demonstrated that no more than one week's treatment with T resulted in significant changes in dominance with unfamiliar opponents in unfamiliar aviaries. The question in the present experiment was whether or not the same results would be obtained with familiar opponents in familiar locations.

Methods and materials.

During January 1985, five or six white-throated sparrows were placed in each of three aviaries (Stage 1). After aggression scores and dominance rankings were determined for each bird as described above, the three lowest-ranking birds in each of the groups were implanted with T. The two or three highest-ranking birds of each group were implanted with empty tubes. The birds were returned within 2 h to the same groups and aviaries (Stage 2) and in the following two weeks aggression scores and dominance ranks were again determined.

Subsequently, at intervals of two weeks, we caught all birds and regrouped each with new opponents in a different aviary and once again determined aggression scores and dominance ranks (Stages 3 and 4). Each new group in these two stages consisted of three controls and three T-implanted birds. At the same time, four additional groups received implants of 17β-estradiol in the same way; the results from these groups were similar to those with T implants, although less pronounced, and are not reported in detail here (see ARCHAWARANON, 1987).

Each bird was first observed prior to any implants (Stage 1) and then during three two-week periods following implants, first with familiar opponents (Stage 2), then twice with new ones (Stages 3 and 4).

Results.

Before implantation, all three groups had linear hierarchies without triangles. Most interactions occurred at the food trays and did not differ from those elsewhere in the aviaries. After low-ranking birds were implanted with hormones and regrouped with new opponents (Stages 3 and 4), hierarchies were again mostly linear with only a few reversals and triangles; in Stages 2 and 4, two groups included triangular relationships. In the original groups, there were no significant associations of rank with sex, age, size, or plumage brightness (Table 1), although the differences between high- and low-ranking birds in sex and age resembled significant differences in larger samples of free-living birds (PIPER & WILEY, 1989a). The subjects absorbed T at an average rate of 0.24 ± 0.03 mg/day (n = 9). There was no difference between males and females in the effects of this hormone on our behavioral measures.

TABLE 1. Dominance rank in relation to sex, age, wing length, brightness of crown stripes and weight in Experiments 1 and 2 (Stage 1 only)

Experiment	1		2	
N (groups)	7		5	
Ranks[1])	High	Low	High	Low
N (individuals)	18	18	12	18
Sex (% male)[2])	61	33	42	44
Age (% >1 year)[2])	83	67	58	39
Wing (mm ± SD)	71.0 ± 2.7	69.0 ± 2.6	70.9 ± 2.4	69.6 ± 2.5
Brightness (± SD)[3])	19.0 ± 8.6	15.9 ± 4.4	21.5 ± 8.3	16.7 ± 5.2
Weight (g ± SD)	27.8 ± 2.3	27.8 ± 3.2	27.3 ± 2.7	27.1 ± 3.1

[1]) High = top two or three birds in the dominance hierarchy; low = bottom three birds (see text). [2]) All birds sexed by laparotomy and aged by skull ossification (see text). [3]) Brightness of crown stripes (PIPER & WILEY, 1989b).

No statistical comparisons between high and low ranks in the two experiments are significant (χ^2 tests for sex and age, t tests for remaining measures).

T-implanted birds remained low-ranking in Stage 2 (same opponents as before implantation); their scaled ranks did not change significantly. In Stages 3 and 4 (after regrouping with new opponents), T-implanted birds had significantly higher averaged aggression scores and dominance ranks than in Stages 1 and 2 ($T = 0$, $n = 9$, $p < 0.01$, Figs. 1B and 1D).

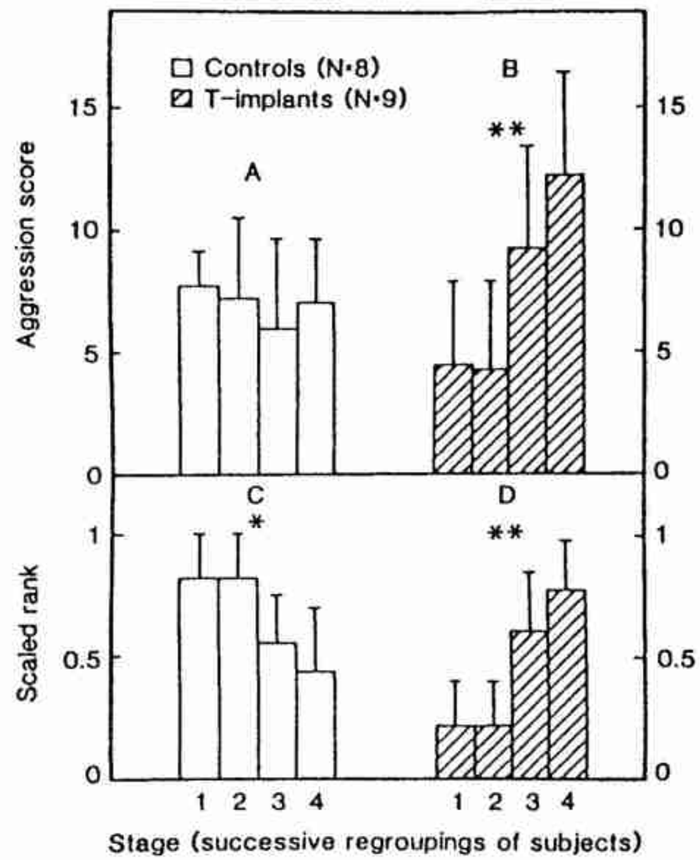

Fig. 1. Overall mean aggression scores (upper) and scaled dominance ranks (lower) of controls (open bars) and testosterone-implanted birds (hatched bars) in Stages 1 through 4 of Experiment 1. Note that Stage 1 was before implantations. Vertical lines indicate one SD. Stages 1 and 2 combined compared with Stages 3 and 4 combined: $^{*}p<0.05$, $^{**}p<0.01$ (two-tailed Wilcoxon matched-pairs signed-ranks tests); for other statistical comparisons, see text.

In contrast, birds implanted with empty tubes did not change significantly between stages in averaged aggression scores (Stages 1 and 2 versus 3 and 4, $T = 10$, $n = 8$, $p > 0.05$, Fig. 1A). Their dominance ranks in Stages 3 and 4 were significantly lower than in Stages 1 and 2 ($T = 3$, $n = 8$, $p < 0.05$, Fig. 1C).

In comparisons of birds with empty implants and those with T implants, the latter had significantly higher averaged aggression scores following regrouping with new opponents (Fig. 1, $n_1 = 8$, $n_2 = 9$; Stage 3, $U = 15$, $p = 0.05$; Stage 4, $U = 10$, $p < 0.02$). In Stage 4, T-implanted birds also ranked significantly higher than those with empty implants

($U = 11$, $p = 0.02$). On the other hand, in Stages 1 and 2, birds with T implants, which had been selected for lower initial dominance ranks, had significantly lower averaged aggression scores than did those with empty implants ($U = 15$, $p = 0.05$).

Thus T-implanted birds with familiar opponents in a familiar setting did not change in dominance rank or averaged aggression scores; when moved to new opponents in a new situation, both their dominance rankings and aggression increased.

Experiment 2: regrouping of birds in the absence of hormonal treatment

Introduction.

This experiment considered whether or not birds are likely to retain their ranks after regrouping in different aviaries with different opponents, in the absence of hormonal manipulations. Since the birds implanted with hormones in Experiment 1 were selected for low dominance ranks in Stage 1, it is possible that their rise in rank in Stages 3 and 4 might have occurred simply because there was little correlation among an individual's rankings in different groups of opponents.

Methods and materials.

During January 1986, five untreated birds were placed in each of six aviaries (Stage 1). Aggression scores and dominance were determined for each individual as described above. Then twice, at intervals of two weeks, birds were regrouped with new opponents, in new aviaries, and once again observed (Stages 2 and 3).

Results.

As in Experiment 1, hierarchies had few reversals and triangles. Again dominance ranks were not significantly associated with sex, age, size, or plumage (Table 1).

Birds that were high-ranking in Stage 1, regardless of how many times they were regrouped with new opponents, did not change significantly in their aggression scores ($T = 31.5$, $n = 12$, $p > 0.05$, Fig. 2A), although they did have significantly lower ranks in the later stages ($T = 6.5$, $n = 12$, $p < 0.01$, Fig. 2C). Low-ranking birds in Stage 1 did not change either in aggression scores or in dominance ranks in later stages (Fig. 2B and 3D; for dominance ranks, $T = 74$, $n = 18$, $p > 0.05$). Note that, although high-ranking birds tended to drop progressively in rank in later stages,

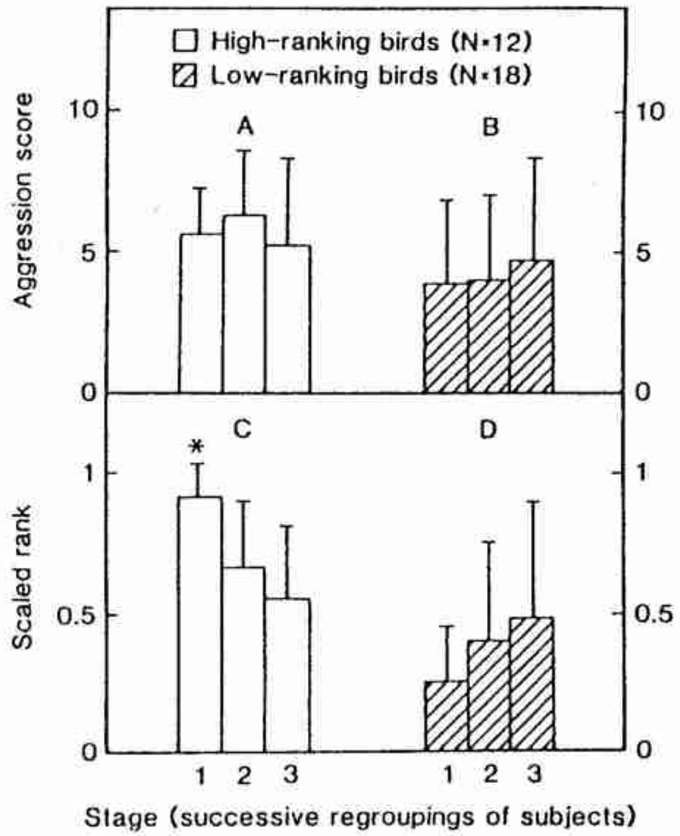

Fig. 2. Overall mean aggression scores (upper) and scaled ranks (lower) of high- (open bars) and low-ranking (hatched bars) birds in Stages 1 through 3 of Experiment 2. Vertical lines indicate one SD. Stage 1 compared with Stage 3, *$p<0.01$ (two-tailed Wilcoxon matched-pairs signed-ranks tests).

their averaged ranks never became as low as those of low-ranking birds from Stage 1. Conversely, although low-ranking birds in Stage 1 tended to have higher ranks in later stages, their average never rose as high as that of high-ranking birds from Stage 1.

High-ranking birds in Stage 1 tended, in subsequent stages, to have higher averaged aggression scores and dominance ranks than those that had been low-ranking ($U = 37$, $n_1 = 12$, $n_2 = 18$, $p<0.05$). Thus birds with high rank initially were more likely than initially low-ranking birds to retain high rank with new opponents in a new location, but this effect decreased with successive exposures to new opponents.

Experiment 3: hormonal treatment of birds in the field

Introduction.

In this experiment we observed interactions between individually marked, free-living birds before and after implanting them with Silastic tubes. Birds received either tubes with T or empty tubes.

Materials and methods.

Between 12 December and 29 January, before implanting any birds, we observed 1269 interactions among 80 individually marked birds. If a bird supplanted or attacked another in at least 75% of their interactions, it was considered dominant in that dyadic relationship. Since other studies had shown that the first interaction observed between any pair of birds agreed, in 93% of cases, with the pattern in the remainder of their observed interactions, we considered a single interaction sufficient to characterize a dominance relationship (PIPER & WILEY, 1989a).

Between 1 and 10 February we implanted Silastic capsules in the 23 individuals with the largest numbers of recorded interactions. Twelve, selected at random, received T implants (9 females, 3 males), and 11 others received empty implants (2 females, 9 males). We prepared and administered the implants as described above.

From 3 to 24 February, we recorded 1359 interactions among 76 identified birds at the same site. In about 30% of these interactions, both opponents were implanted subjects or controls. We determined dyadic relationships as described above.

Results.

In the period following implantation of capsules, the frequency of fighting and vigorous attacks approximately doubled from 3.4% to 7.5% of all interactions. Two of the birds with T implants became extremely aggressive, and at different times each attempted to defend the area within several meters of the feeding site against all others. One bird repeatedly attacked higher-ranking conspecifics and engaged in aggressive behavior to the exclusion of feeding.

Following implantations, we observed interactions of 26 dyads each consisting of a T-implanted bird and a previously higher-ranking control with an empty implant. In four dyads, following implantation neither bird consistently dominated the other by our criteria. In four other dyads, previously dominant controls were subordinate. In the remaining 18 dyads, there were no changes in dominance relationships.

These data serve to reject the hypothesis that dominance relationships after implantation were equally likely to change or to remain stable (binomial test, $p<0.05$). In addition, even though the four relationships that did change were all cases of T-treated subordinates achieving dominance over previously dominant controls, this number is insufficient

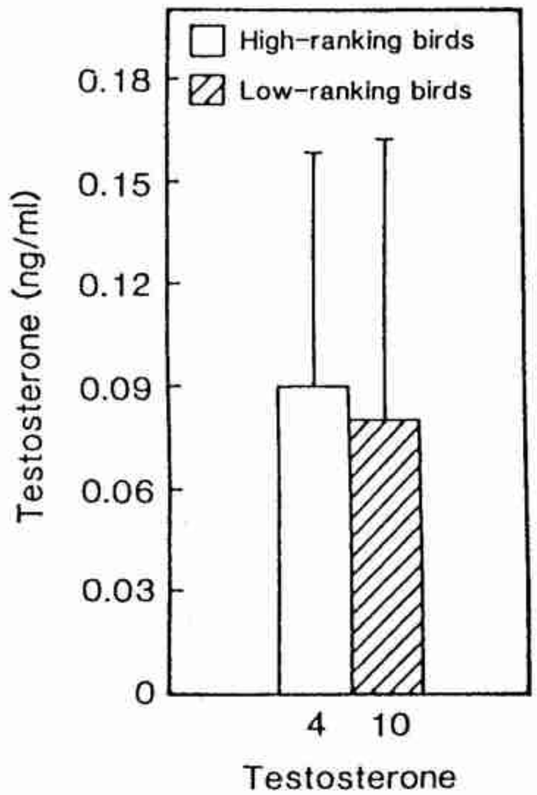

Fig. 3. Mean testosterone concentrations in high- (open bars) and low-ranking (hatched bars) birds at the end of Experiment 2. Number under each bar indicates N; vertical lines indicate one SD. No significant differences (Mann-Whitney U-tests).

to reject the hypothesis that change in each direction was equally likely (binomial test, $p > 0.15$). Thus treatment with T had little or no effect on dominance relationships in free-living birds.

Circulating levels of hormones in untreated birds

In the untreated birds at the end of Experiment 2, titers of circulating T in high-ranking birds did not differ significantly from those in low-ranking birds ($U = 12$, $n_1 = 4$, $n_2 = 10$, $p > 0.05$, Fig. 3). Males had significantly higher levels of T than females among both high- and low-ranking birds ($U = 4$, $n_1 = 6$, $n_2 = 8$, $p = 0.004$, Fig. 4).

To study levels of circulating hormones in free-living birds during the months of January and April, 8-10 white-throated sparrows were caught in the field once a month during 1986. Blood from these birds was then

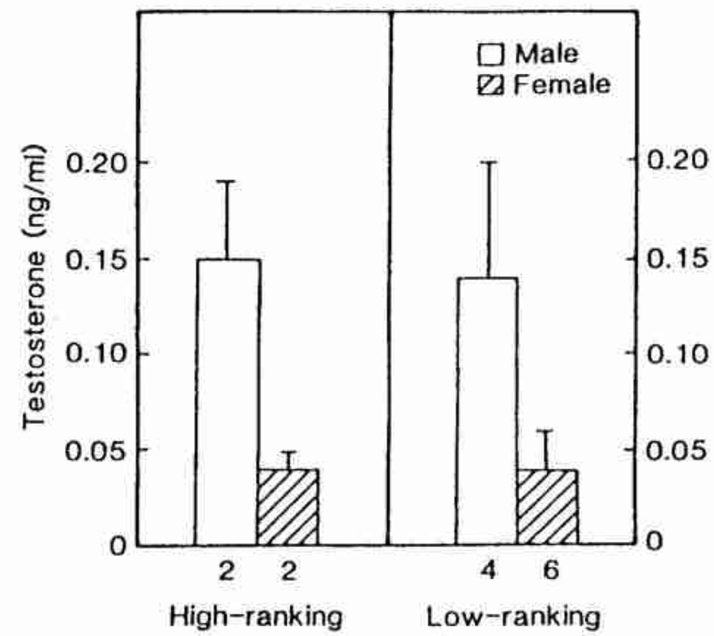

Fig. 4. Mean testosterone concentrations of male (open bars) and female (hatched bars) high- and low-ranking birds at the end of Experiment 2. Number under each bar indicates N; vertical lines indicate one SD. Comparison of males and females; high- and low-ranking birds combined, $p = 0.004$ (two-tailed Mann-Whitney U-tests).

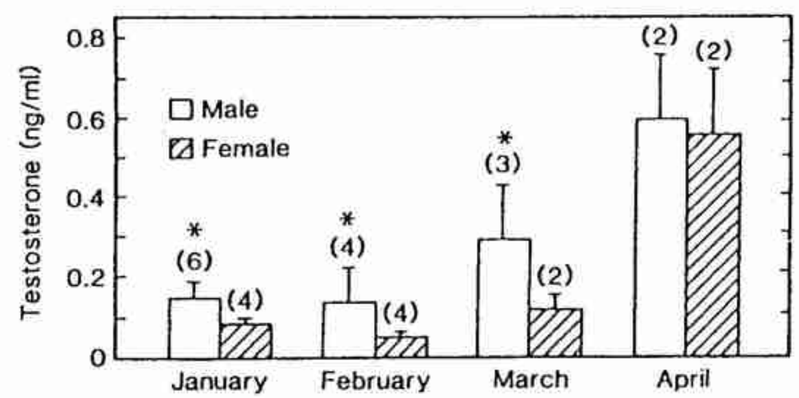

Fig. 5. Concentrations of testosterone in plasma of male (hatched bars) and female (open bars) free-living birds from January to April. Number under each bar indicates N; vertical lines indicate one SD. $^*p < 0.05$ (comparison of males and females, three months combined, two-tailed Mann-Whitney U test).

assayed for T. Circulating levels of T in free-living males during January and February were significantly lower than in April ($U = 0$, $n_1 = 2$, $n_2 = 10$, $p < 0.05$, Fig. 5) and during January, February and March were significantly higher than in females ($U = 16$, $n_1 = 10$, $n_2 = 13$, $p < 0.05$).

Discussion

These experiments are pertinent to several issues in understanding dominance hierarchies in birds. We consider in turn (1) the consequences of familiarity with opponents and locations for hormonal control of aggressiveness and dominance, (2) recognition of opponents in dominance hierarchies, and (3) evolutionary implications of these influences on dominance ranks.

Hormonal influences on social relationships in relation to familiarity of opponents.

When our subjects interacted with unfamiliar opponents in new locations, T-treatment significantly increased aggression scores and dominance. There were no indications that sex influenced the activation of behavior by this hormone. These findings are similar to those in separate experiments reported earlier (ARCHAWARANON & WILEY, 1988). On the other hand, when T-implanted birds were returned to familiar opponents in familiar locations, there were no significant changes in their aggression scores or dominance. Interpretation of these results requires consideration of two additional factors: (1) the activation of behavior as a function of time following implantation; and (2) the consequences of successive rearrangements of the birds in the absence of hormonal treatment.

Activation of behavior as a function of time and unfamiliarity of opponents.

It is unlikely that the implants had much effect on circulating titers of T in the 1-2 h before the birds were returned to their original aviaries in Stage 2 of this experiment. In this stage, subjects encountered opponents with which they had already established dominance relationships in the same aviaries. By minimizing the delay before returning birds to their aviaries, we assured that the birds in each aviary retained familiarity with each other. Thus as circulating levels of hormones rose, the birds continued to interact with familiar opponents in a familiar location. During this stage, there were no indications that hormonal treatment affected either aggression scores or dominance ranks. The similarity of aggression scores in Stages 1 and 2 suggests that these scores did not change progressively with time during Stage 2.

The absence of any indication of changes in dominance rankings or aggression scores over the two weeks of Stage 2 contrasts with the results from previously reported experiments in which implanted birds were grouped after one week with new opponents (ARCHAWARANON & WILEY, 1988). Although these two experiments were conducted with different birds in successive winters, the birds came from the same population at nearly the same time of year and the two experiments employed the same aviaries and procedures for implantations. Thus two weeks' treatment with T in the present experiments did not result in changes in dominance rankings or aggressiveness of birds with familiar opponents in their original locations, while only one week's treatment in isolation did so when opponents and locations were novel. Likewise, beginning in Stage 3 of the present experiments, when birds were regrouped with different opponents in different aviaries, the implanted hormones significantly influenced dominance rankings and aggression scores. We can conclude that T treatment had no significant effect on dominance ranks and aggressiveness when treated individuals interacted with familiar opponents in familiar aviaries, but that it did have these effects within no more than one week when individuals interacted with unfamiliar opponents in unfamiliar aviaries.

It remains uncertain whether the effects of hormones on ranks and aggressiveness depend entirely on the unfamiliarity of opponents or also on the unfamiliarity of the location. It is also possible that the availability and distribution of food, which affect the intensity of competition (THEIMER, 1987; SCHWABL *et al.*, 1988), would affect the influence of hormones on established relationships. Further studies are needed to determine what aspects of the situation result in hormonal effects on behavior and how quickly the effects on relationships with unfamiliar opponents appear.

Regroupings in the absence of hormonal treatment.

For untreated birds regrouped with unfamiliar opponents in unfamiliar aviaries in Experiment 2, initially high- and low-ranking birds converged somewhat in their aggression scores and dominance ranks after the first

regrouping, but the changes were not statistically significant. Low-ranking birds tended to remain low-ranking. However, after two regroupings with new opponents in new locations, initially high- and initially low-ranking birds tended to achieve similar ranks on average. Apparently, a bird's ranking in any one group correlated with its ranking in another group. Such a correlation of rankings could result either from experience with dominance in the earlier grouping or from intrinsic behavioral or other features of individuals that contributed to dominance. Since dominance rankings of initially high- and low-ranking birds tended to converge eventually, the influences on dominance seem likely to have been experiential rather than intrinsic. In any case, we can conclude that birds treated with T in Experiment 1 had higher dominance rankings after regrouping because of effects of the hormones, and not because of consequences of the regroupings alone.

Previous experience might also modify the dominance of T-treated birds in interactions with unfamiliar opponents. This possibility could explain the progressive change in dominance of treated birds during Stages 3 and 4 of Experiment 1. The alternative possibility that slow activation of behavior by T might explain this result is inconsistent with previously published experiments (ARCHAWARANON & WILEY, 1988).

Aggressiveness in relation to dominance rank.

Averaged aggression scores of high-ranking birds were significantly higher than those of low-ranking birds in initial groupings. Our measure of a bird's aggressiveness was adjusted for the number of subordinate opponents and therefore did not necessarily vary with its dominance. We thus measured aggressiveness of individuals independent of confounding effects of differences in opportunities for aggression associated with differences in dominance rank (SEARCY & WINGFIELD, 1980). This measure revealed increases in aggressiveness of hormone-treated birds between Stages 3 and 4, concurrent with increases in dominance ranks.

The finding that aggression did not change progressively with time during interactions with familiar opponents during Stage 2 of Experiment 1 was unexpected. Other studies have suggested that frequencies of aggression increased in stable groups of birds following T treatments, even though rankings did not change (GUHL, 1964, 1968; ROHWER & ROHWER, 1978). These studies, however, did not determine which individuals were responsible for the increased aggression. Our aggression scores based on focal observations of treated birds would not have reflected any increase in aggression directed toward them by higher-ranking opponents. Greater activity or more persistent approaches to feeding sites by the treated subjects could have provoked aggression by opponents.

In our experiments with free-living birds, a few of the subjects had noticeably increased rates of aggression following T treatment. In the field, however, the familiarity of the subjects with their opponents was not controlled. Although many opponents were undoubtedly familiar with our subjects, at least some undoubtedly were not. Field studies on this population have shown that individuals vary considerably in the extent of their movements during winter (PIPER & WILEY, 1990b). Thus the increased aggressiveness shown by these unconfined birds, as well as by those observed by ROHWER & ROHWER (1978), might have been directed at less familiar opponents.

Behavior in relation to circulating titers of hormones.

Our assays of circulating T at the end of Experiment 2 showed no indication of correlations with dominance. Males differed significantly from females in T levels, but there was no difference between high- and low-ranking birds. Several studies have previously reported that levels of circulating T correlated with aggressiveness or dominance only during the initial establishment of relationships with unfamiliar opponents (DIXSON, 1980; BERNSTEIN *et al.*, 1983; RAMENOVSKY, 1984; SILVERIN *et al.*, 1984; WINGFIELD, 1985; HEGNER & WINGFIELD, 1987). In stable groups of familiar opponents, the maintenance of social relationships is evidently independent of differences in circulating levels of these hormones.

In interactions with novel opponents, correlation between circulating T and aggressiveness could result either from effects of hormones on behavior or vice versa. Agonistic interactions are now known to result in rapid rises in circulating T in a variety of birds and mammals (ROSE *et al.*, 1971; BERNSTEIN *et al.*, 1983; SAPOLSKY, 1982; SACHSER & PRÖVE, 1984; WINGFIELD, 1984b, 1985). In combination with experiments demonstrating effects of T on aggressiveness, these results suggest reciprocal stimulation of T levels and aggressive behavior in interactions with novel opponents.

Once social relationships become well established, on the other hand, not only do circulating levels of T often decrease and cease to correlate with rank but, as the results of Experience 1 indicate, established social relationships can suppress changes in aggressive behavior and dominance rank in response to increased T. These findings suggest that

familiarity with opponents attenuates the reciprocal stimulation of T and aggressive behavior.

In free-living birds as well as in untreated captives, T levels were higher in males than in females. Since sex had no effect on responses to hormones in our experiment, the finding that the sexes differed significantly in T levels suggests that this small difference might explain in part why males rank slightly higher on average than females in populations wintering in North Carolina (PIPER & WILEY, 1989a; but see SCHWABL *et al.*, 1988).

In our implanted birds, on the other hand, hormonal levels were much higher than in unmanipulated birds in winter. These treated birds had titers comparable to those in males of closely related species in the breeding season (WINGFIELD & FARNER, 1978a, b; WINGFIELD, 1984a; WINGFIELD & GOLDSMITH, 1990), when males are territorial. Indeed, the despotic behavior of topranking, T-implanted birds both in later stages of Experiment 1 and in the field included some features of territorial behavior. Unlike other individuals in winter, they chased and attacked opponents repeatedly without regard to their proximity to food. The top-ranking, T-treated birds also often sang frequently, like territorial birds. The relationship between T treatment and singing was complex; we reserve a full discussion of this issue for elsewhere. It is not clear, however, that implants of T in wintering birds induced only quantitative changes in the frequencies of previously occurring categories of behavior rather than inducing some qualitatively new ones.

Recognition of opponents.

The stability of dominance ranks with familiar opponents, despite hormonal manipulations, suggests some form of recognition of opponents' relative dominance. Birds continue to behave toward opponents in accordance with their previously established associations of opponents with success or failure in encounters.

It is important to emphasize how difficult it is to confirm that individuals in a dominance hierarchy can recognize their opponents. Although it is often argued that "individual recognition" is necessary for the stability of dominance hierarchies, this reasoning is clearly incorrect. Stable intrinsic characteristics of individuals, such as status signals or differences in aggressiveness, could produce stable dominance relationships. In addition, learned differences in general aggressiveness or avoidance as a result of previous encounters (COLLIAS, 1943; JACKSON, 1988) could generate stable, linear hierarchies without any need for recognition of opponents. Furthermore, experiments that have purported to demonstrate "recognition of individuals", by modifying subjects' appearance (for example, GUHL & ORTMAN, 1953), have not established individual recognition at all, but only recognition of familiar individuals as opposed to strangers. A number of observations that suggest "individual recognition", such as decreased aggressiveness with time after a group is formed (for example, WATT, 1986a), also require no more than habituation to familiar opponents.

These examples make it clear that it is important to differentiate several levels of recognition of social partners. Recognition requires (1) discrimination of stimulus configurations and (2) association of different responses with each configuration on the basis of past experience with them. Different levels of comprehensiveness in the stimulus configurations discriminated create a hierarchy of different forms of recognition (Table 2). At one extreme, there is recognition of familiarity, a discrimination between cues encountered more and less frequently. This form of recognition, which can result from either habituation or sensitization to repeatedly encountered cues, is sufficient, for instance, to produce increased aggression towards opponents with modified appearance. At the other extreme is strict recognition of individuals. To demonstrate this, it is necessary to show that subjects respond in different ways to cues associated with a number of separate individuals. Between these two extremes is a continuum of possibilities in which subjects recognize sets of other individuals of varied scope.

In this scheme, social inertia would require at least the intermediate level of recognition: recognition of sets of higher- and lower-ranking

TABLE 2. Three levels of recognition of social partners

1. Recognition of familiarity: a subject's responses to other individuals depend on the frequency of the subject's previous exposure to them.
2. Recognition of sets of social partners: a subject's responses differ to sets of other individuals, as a result of previous experience with them, regardless of differences in frequency of exposure to them; a subject's responses do not differ to the individuals within these sets.
3. Recognition of individuals: a subject's responses differ to other individuals separately, as a result of previous experience with them, regardless of differences in frequency of exposure to them.

opponents. It cannot be explained simply by recognition of familiarity, as exposure to higher- and lower-ranking opponents is approximately equal. Either the behavior of the opponents or the behavior of the hormonally modified subjects, or both, instead depends on their relative ranks. On the other hand, social inertia in dominance hierarchies does not necessarily require strict individual recognition. Present information leaves that possibility open.

All forms of recognition depend on classification of other individuals by the cues they present, and such classification becomes more demanding the larger the numbers of individuals. In our experiment in the field, the numbers of interacting individuals at any one feeding site were clearly much larger than the six birds in each of our aviaries. For instance, the numbers of regularly interacting birds at four nearby feeding sites in one year ranged from 63 to 99 (PIPER & WILEY, 1989a), although there was a continuum in the frequency with which individuals visited any one site. Consequently, the birds at our feeding site in the present experiment almost certainly varied in familiarity with each other and their capabilities to recognize each other. These uncertainties about the familiarity of each experimental and control bird in a field study makes detailed interpretation of the results problematic. Nevertheless, it is clear that, with few exceptions, most of the 20 birds in our experiment recognized each others' relative ranks, as indicated by the fact that their dominance relationships did not change. We can thus conclude that white-throated sparrows in the field are at least capable of recognizing some 20 other individuals well enough to classify them as higher- and lower-ranking opponents.

Evolutionary implications of social inertia.

Experiments designed to investigate status signals have modified the appearance or hormonal state, or both, of birds interacting with familiar or unfamiliar opponents. The two reports of hormonal manipulations (JÄRVI *et al.*, 1987; ROHWER & ROHWER, 1978) have not clearly separated familiar and unfamiliar opponents, an objective probably impractical in the field. Interpretations of these experiments have failed to consider the effects of familiarity with opponents. Modifications of the plumage of hormonally treated subjects could interfere with recognition by familiar opponents and thus produce effects like those of introducing them to unfamiliar opponents. Thus the finding that ranks changed only when hormonally treated birds were modified in appearance is consistent with

our finding that hormonal treatments affected dominance only in interactions with strangers.

In interactions with strangers, changes in appearance affect dominance particularly when indications of age or sex are altered (MARLER, 1955; FUGLE *et al.*, 1984; ROHWER, 1985; FUGLE & ROTHSTEIN, 1987). Such results are in accordance with many studies that have reported correlations between dominance and sex or age (BALPH *et al.*, 1979; KETTERSON, 1979; JÄRVI & BAKKEN, 1984; WATT, 1986b; JACKSON *et al.*, 1988; PIPER & WILEY, 1989a). It seems plausible that such characteristics are most likely to influence dominance relationships in initial encounters among strangers, when recognition of opponents cannot be involved.

Capabilities for recognition of opponents could evolve as a mechanism to promote stability of social relationships if it were advantageous to remember relationships with opponents rather than to contest them on each encounter. Certainly, it would not pay for an individual to challenge higher-ranking opponents repeatedly if one defeat is likely to predict further defeats. It also would not pay for an individual to harass lower-ranking individuals, if such behavior reduced chances for exploiting subordinate opponents as food-finders. Furthermore, if high- and low-ranking individuals in a dominance hierarchy created mutualistic advantages for each other, as suggested by ROHWER & EWALD (1981), this reciprocity could be evolutionarily stable only among individuals that recognized each other (AXELROD & HAMILTON, 1981). It is important to emphasize that evolutionary stability of reciprocity among unrelated individuals requires strict individual recognition in order to prevent the spread of cheaters; recognition of familiar or other sets of individuals is not sufficient. Available experiments do not establish for certain that birds in dominance hierarchies achieve this level of recognition, despite anecdotal evidence that they might.

Summary

To investigate the effects of familiarity with opponents on the activation of aggression and dominance by testosterone (T) in white-throated sparrows *Zonotrichia albicollis*, we studied birds in groups of five or six in outdoor aviaries and in a free-living population. Experiments were conducted between January and April, when plasma levels of endogenous gonadal hormones were low. Previously published experiments (ARCHAWARANON & WILEY, 1988) showed that when subjects were given subcutaneous implants of T, held individually in cages for one week, and then grouped with unfamiliar opponents, they established dominance over controls with empty implants. In contracts, the present study showed that low-ranking birds given subcutaneous implants of T and returned to their original groups and aviaries did not change in dominance rank nor in

aggression scores over a period of two weeks. When these birds were regrouped with unfamiliar opponents in new aviaries, their dominance ranks and aggression scores increased. This rise in dominance rankings and aggression scores did not result from any effects of regrouping in the absence of hormonal treatments. The sexes did not differ in their responses to these treatments. In the field, T implants markedly increased some individuals' frequencies of aggression but had little or no effect on dominance relationships. The absence of behavioral changes in stable groupings after hormonal treatment, called social inertia, indicates that birds recognize the relative dominance of previous opponents, at least when encountered in familiar locations. Results from the field experiment thus suggest that white-throated sparrows can recognize at least 20 opponents. Hormonal state has more influence on dominance relationships of strangers than on those of opponents familiar with each other in familiar locations.

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