# Social inertia in white-throated sparrows results from recognition of opponents

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Social inertia is a term for the stability of dominance relationships despite changes in the intrinsic dominating abilities of opponents. In a standard test for social inertia, low-ranking birds in an established hierarchy receive implants with testosterone (treated) and high-ranking birds receive empty implants (untreated). Social inertia occurs when the treated birds remain subordinate to untreated opponents in these groups, despite evidence that similarly treated birds dominate untreated strangers. In previous demonstrations of social inertia, however, treated and untreated birds were returned to their original aviaries and tested with familiar opponents, and thus the effects of familiarity with the location and those of familiarity with opponents were not separated. To address this issue, we investigated social inertia in 16 groups of white-throated sparrows, *Zonotrichia albicollis*. When low-ranking treated birds were placed in new aviaries with familiar high-ranking, untreated opponents (treatment S, same opponents), dominance relationships showed social inertia. When such birds were placed in new aviaries with unfamiliar opponents (treatment N, new opponents), testosterone influenced dominance. When groups of high-ranking, untreated birds acquainted with each other were placed with unfamiliar treated opponents (treatment G, grouped dominants), 'coat-tail' effects (dominance by association with high-ranking individuals) sometimes outweighed the effects of testosterone. Social inertia in this species is thus a result of familiarity with opponents, rather than familiarity with locations of encounters. Measurements of aggressive tendencies confirmed a previous report that social inertia suppresses activation of aggression by testosterone. White-throated sparrows can thus recognize their opponents, and this ability affects the expression of both dominance and aggression.

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The term 'social inertia' was used by Guhl (1968) to describe an unexpected stability in the dominance hierarchies of hens. Subordinate hens in an established hierarchy retained their low rankings after treatment with testosterone, despite the demonstrated effect of testosterone on dominance over unfamiliar opponents. In other words, in established flocks, treated birds failed to show their expected dominating ability.

This phenomenon also occurs in white-throated sparrows, *Zonotrichia albicollis*, both in small groups of birds held in outdoor aviaries and in unconfined birds in the field (Archawaranon et al. 1991). For instance, after

hierarchies had stabilized in groups of six birds in aviaries, the two or three lowest-ranking birds in each aviary received implants with testosterone (T), while the remaining higher-ranking birds received empty implants. When the birds were returned to their original aviaries, the hierarchies remained nearly unchanged. In contrast, when birds were reassembled with previously unfamiliar opponents, the T-treated birds almost always dominated the untreated birds.

One implication of this result is that birds must recognize their familiar opponents. Social inertia currently provides some of the clearest evidence for recognition of opponents in dominance hierarchies. Note that the formation of linear hierarchies does not alone imply recognition of opponents, because such hierarchies could also result from status signalling or assessment without need for recognition of opponents (Archawaranon et al. 1991). Social inertia thus raises questions about the relationships between status signals and recognition of opponents in the formation of hierarchies.

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These experiments with hens and sparrows leave open an important question: because treated and untreated birds were returned to groups of familiar opponents in familiar locations, it is not clear to what extent the location of interactions influenced the expression of social inertia. In white-throated sparrows, in particular, the location of encounters is known to have a pronounced influence on the birds' dominance both in the field and in aviaries (Piper & Wiley 1989a; Dearborn & Wiley 1993; Piper 1998). The present experiment was designed to address this issue.

Another open question about social inertia concerns possible changes in aggressive tendencies of individuals. In Archawaranon et al.'s (1991) experiment, the frequency of aggression did not increase under conditions of social inertia, but did increase when treated birds faced unfamiliar opponents. To check the generality of this result, we compared both the overall rates of aggression and the behavioural tendencies of individuals in standardized situations in each experimental condition.

This experiment also addressed the possibility that dominance relationships might be influenced by 'coat-tail' effects (Wiley 1990; Cristol 1995). Coat-tail effects occur when subordinates familiar with a high-ranking individual have an advantage over strangers. As a result, groups of familiar individuals can attain dominance over unfamiliar opponents (Wiley 1990).

The initial stages of the present experiment followed the design introduced by Archawaranon et al. (1991). After small groups of white-throated sparrows had established stable hierarchies, the lowest-ranking members of each group received T implants and the higher-ranking birds empty implants. Birds were then returned to their original aviaries for further observation. Subsequently, all birds were moved to new aviaries, in three different arrangements: some groups of familiar opponents were moved intact, some groups consisted entirely of unfamiliar opponents, and some were combined groups of familiar untreated birds with unfamiliar treated opponents. In the latter case, any coat-tail effect opposed any effect of testosterone on dominance.

The results provided clear evidence that social inertia results from familiarity with opponents, regardless of the locations of encounters. These results also show that social inertia suppresses the activation of aggressive behaviour by testosterone. Finally, these results suggest an alternative interpretation of 'double-treatment' experiments on status signals, in which birds are either changed in appearance or treated with testosterone, or both.

## METHODS

### Experimental Subjects

In each of two winters (1995 and 1996) we captured 48 white-throated sparrows without regard to age or sex at seed-baited treadle traps along 500 m of hedgerow in the Mason Farm Biological Reserve near Chapel Hill, North Carolina. We used birds in their first winter for these experiments, but otherwise used the first birds captured

each year. No attempt was made to determine the sex of subjects by laparotomy. Previous field studies at this site have shown that dominance among free-living birds is affected by both age and sex (Piper & Wiley 1989a). In previous studies of small groups of captives, there has been no significant influence of sex on rankings (Archawaranon & Wiley 1988; Archawaranon et al. 1991), although differences in wing lengths of high- and low-ranking birds suggest trends in the same direction as those in larger samples in the field. These previous experiments have also shown that birds of both sexes respond similarly to implants of steroid hormones, at least during winter, when gonads have fully regressed (Archawaranon & Wiley 1988).

We marked each bird individually with coloured plastic bands and recorded its mass, wing chord length, and scores for crown brightness and subcutaneous fat (following procedures explained by Piper & Wiley 1989a, b). We then randomly sorted birds into groups of five or six, with the stipulations that no birds trapped within 50 m of each other were placed together (groups in 1996 included a few exceptions) and that each group have at least one older bird (in its second winter or older). The birds in each initial group had a chance to establish dominance relationships and familiarity with each other in the first stage of the experiment.

Most birds had been trapped, marked and released in the same area during the preceding autumn to determine their ages by the extent of cranial development. Birds in their first winter had incomplete cranial pneumatization at least until December (Wiley & Piper 1992). Many older birds had been marked in previous years. Unmarked birds with complete cranial pneumatization after December were of unknown age. We used seven such birds in 1995 and none in 1996. No birds used in these experiments had been the subjects of previous experiments.

We conducted the experiments in late winter and early spring each year (in 1995, birds were trapped 31 January–1 February and released 16–17 March; in 1996, they were trapped 29 February–2 March and released 6 April). Birds were released well before migration (mid-April–early May).

### Aviaries

Groups of birds were placed in large outdoor aviaries (2.4 × 2.4 × 2.6 m) with observation chambers equipped with one-way glass. Wild-caught birds could thus be studied without disturbing them. We used a total of nine different aviaries, all with nearly identical dimensions. Birds had continual access to food (a mixture of seeds, chick starter mash and parsley greens) except for a period just prior to and during observations (see below). Food was provided ad libitum in three locations in open pans under small shelters in each aviary. Each aviary also had one water dispenser and four to five horizontal perches.

Food, shelter, water and perches were in similar, but not identical, locations in different aviaries. The aviaries were about 4 m apart along both sides of a narrow field, so some had woodland on the east side and others had woodland on the west. Birds in any one aviary could see

those in another on the other side of the field about 10 m away but could not see birds in nearer aviaries. Our subjects could also usually see wild white-throated sparrows near the aviaries.

## Plan of Experiments

The experiments each year consisted of three stages: (I) initial observations of groups; (II) continued observations of the same groups in the same aviaries after low-ranking birds had received testosterone implants; and (III) final observations after changes of aviaries and opponents. The second stage allowed time for any effects of testosterone to develop before the final tests with different combinations of opponents. Between successive stages, we caught and weighed all birds, regrouped them and then, nearly simultaneously, released the birds of each group into an aviary. Between capture and release, birds were held for 30–60 min in visual isolation in cages with food and water.

During stage I, we determined the initial dominance relationships and behavioural tendencies in each aviary. At the end of this stage, the two or three lowest-ranking birds in each aviary received implants of testosterone in Silastic tubing (see below), and the three highest-ranking birds received empty implants. We refer to the former as 'treated' birds and to the latter as 'untreated'. All birds were then released into the same aviaries with the same opponents for stage II, and observations of dominance relationships and behavioural tendencies continued. At the end of stage II, we recaptured all birds, checked their implants, and regrouped them for stage III.

For stage III, we moved all birds to new aviaries in three different arrangements: some aviaries contained birds with the same opponents as in stages I and II (treatment S, 'same' opponents, N=4 aviaries); other aviaries contained birds facing all new opponents (treatment N, 'new' opponents, N=6); and still others contained three birds with empty implants from the same aviary facing T-implanted opponents each from a different aviary (treatment G, 'grouped' dominants, N=6). In the last treatment, we thus kept together groups of untreated high-ranking birds familiar with each other (unlike treatment N) but pitted them against T-treated opponents unacquainted with them or with each other (unlike treatment S). A comparison of treatments S and N should reveal any influence of familiarity with opponents on interactions in a neutral (new) location. Conversely, a comparison of stage II with treatment S in stage III should isolate any influence of location on interactions between familiar opponents (see Fig. 1 for a summary).

Aviaries were randomly assigned to treatments at the start of stage III, subject to the requirements of the experimental design. Then, from the aviaries assigned to a particular treatment, we randomly assembled the occupants for the corresponding aviaries in stage III. For instance, for treatment G, the untreated birds from one of the original aviaries were placed together as a group in one of the new aviaries, along with two or three randomly chosen T-treated birds each from a different aviary in stage II. We chose aviaries for each group to maximize
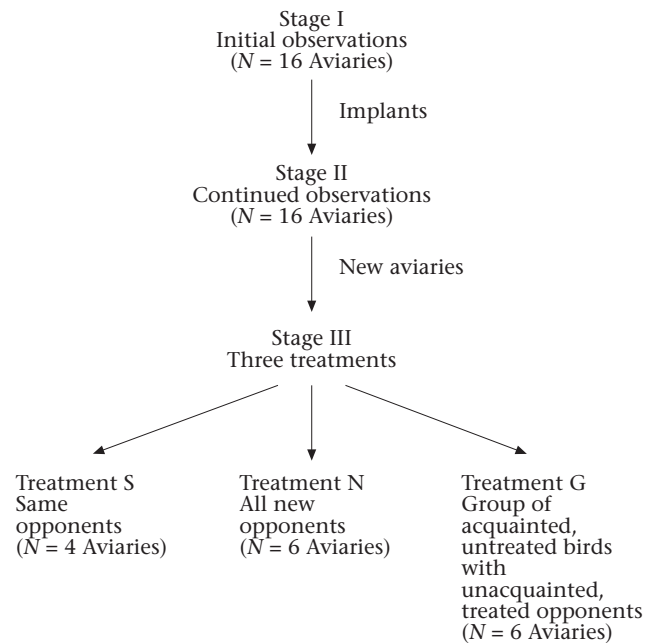


**Figure 1.** Plan of the experiment (see text for details).

the change in external surroundings for the new occupants (by assuring that the arrangement of trees, the narrow field, and other aviaries around the new aviary differed from that of the occupants' original aviaries).

We conducted half of each treatment in each of the 2 years. After completion of our observations each year, we removed all implants and then permanently banded and released the birds.

## Testosterone Implants

Procedures followed those of Archawaranon et al. (1991). The implants consisted of 10 mm of crystalline testosterone (Sigma Chemical Corp., St Louis, Missouri) placed within a 20-mm length of Silastic tubing (internal diameter 1.50 mm, external diameter 1.99 mm, Silastic Medical Grade Tubing: Dow Corning, Midland, Michigan) with the ends sealed by Dow Corning Medical Adhesive. In previous studies, these implants were sufficient to raise circulating titres of testosterone to maximal levels in the breeding season in related species (Archawaranon et al. 1991). Untreated birds received identical, except empty, implants. We placed the implants beneath the skin of the upper back. The birds remained in visual isolation in individual cages for 30–60 min after implantation and were checked before release to ensure the implants were properly positioned.

During stage III of the experiment in 1996, several birds lost their implants for unknown reasons: seven untreated birds lost implants but were retained in the analysis because the surgery and the presence of the implant for at least 8 days seemed sufficient control for the experiment; two T-implanted birds also lost their implants at this time and were excluded from the analysis. One bird escaped in 1996.

## Observations of Dominance Relationships

We observed each aviary on three to five mornings during each stage between 0800 and 1200 hours. Each of these sessions lasted 15–45 min depending on the rate of interaction. To increase the birds' activity, we removed all food from an aviary for a period of 1–2.5 h prior to observations (shorter periods in colder weather). During observations we focused on interactions at a single shallow dish of mixed seeds (millet and sunflower) 20 cm in diameter, although we recorded any aggressive interactions observed elsewhere as well.

Aggressive interactions fell into four categories of increasing intensity. A Stand-off consisted of one bird approaching within 30 cm of an opponent at the food but not feeding when threatened (feeding bird faced its opponent or called); a Supplantation occurred when one bird left the source of food following the approach of an opponent; an Attack was similar to a Supplantation but involved direct, rapid approach by the opponent; and a Chase included pursuit by the opponent. We combined these interactions in determining dominance relationships. In those cases in which the usual relationship between two birds occasionally reversed, one bird was considered to be dominant over the other if it prevailed in over 75% of their interactions.

In some cases a dominance relationship changed during the experiments. We concluded that a change in a dominance relationship had occurred when one participant won all encounters for one or more successive days and then the other won all encounters for the remainder of the stage of the experiment (in all cases at least 2 more days of observation). These changes in dominance were also characterized by interactions of higher intensity.

We calculated each bird's dominance score as the number of opponents that it dominated divided by the total number of opponents in the aviary. For relationships that did not meet our criterion for dominance ($N=8$ in 1995, none in 1996), we credited each opponent with 0.5 opponents dominated. As a measure of the overall intensity of interactions in an aviary, we computed the proportion of high-intensity interactions (Attacks and Chases) among all interactions observed.

## Observations of Behavioural Tendencies

We assessed individuals' behavioural tendencies during interactions with opponents in eight groups of birds in 1996. We followed Wiley & Hartnett (1976) in arranging feeders to produce relatively standardized encounters between opponents, and in defining a mutually exclusive and exhaustive classification of possible terminations of these encounters. An encounter consisted of two birds feeding simultaneously at small dishes 10 cm apart. Each dish measured 4 cm in diameter and fit snugly into a three-sided stall of clear plastic (thin Plexiglas). These stalls permitted only one bird at a time to feed at each dish and forced birds feeding simultaneously at the two dishes to take positions parallel to each other. This apparatus standardized three features of encounters: birds' distances from opponents, their orientations towards their opponents, and their positions with respect to the opponents' headings. In addition to encounters (both stalls occupied simultaneously), there were also alone periods (one stall occupied and the other available).

To compare treated and untreated birds' behavioural tendencies towards lower-ranking opponents, we focused on actions that terminated encounters and alone periods. Thus for each combination of treated and untreated opponents, we determined the proportions of encounters terminated by Supplants (an approaching bird caused a feeding bird to leave) and Leaves (a feeding bird left its dish without interacting with an opponent) and the proportions of alone periods terminated by Supplants and Joins (a bird started feeding at the dish adjacent to a bird already feeding).

To increase the rate of interactions, we removed food from an aviary 60–90 min before observations. We conducted observations of behavioural tendencies and dominance interactions, as described above, on alternate days.

## Statistical Analysis

We used Spearman rank correlations to compare the birds' dominance scores in successive stages of the experiment. Stable dominance relationships would result in correlations significantly greater than zero. Either unpredictable changes in dominance or a tendency for treated birds to rise in rank (and hence untreated birds to drop) would produce correlations near or below zero. For each aviary, we calculated the probability of obtaining a value of Spearman's correlation as large as or larger than the one observed, based on probabilities tabulated for small $N$ by Olds (1938). We then combined these probabilities (one for each of 16 aviaries, eight each year) by the method for independent samples (Sokal & Rohlf 1995). This procedure computes a statistic ($-2\Sigma\ln P_k$ with $P_k$ probabilities from $k$ independent tests) distributed as $\chi^2$ with $df=2k$. To avoid confusion, we label this statistic $C^2$.

To allow a more intuitive grasp of the results, we also report the number of dyadic relationships between T-treated and untreated birds that changed between stages I and II or between stages II and III. We did not compute statistics for these changes in dyadic relationships, however, because each individual was involved in four to five dyadic relationships at a time. The Spearman correlations, discussed above, used each individual's rank in each stage only once.

To assess changes in intensities of interactions or in behavioural tendencies in the same groups of birds in different stages of the experiment, we used nonparametric Wilcoxon signed-ranks tests. Comparisons of aviaries with different treatments in stage III did not involve paired observations, so we used Mann–Whitney $U$ tests in these cases. To compare characteristics of high- and low-ranking birds in the initial groups (stage I), we performed separate Mann–Whitney $U$ tests for each year and then combined the probabilities, as described above.

## RESULTS

### General Features of the Initial Hierarchies

During each stage of the experiment, we observed 1–42 interactions between each pair of opponents. Although some pairs of opponents interacted much more frequently than others, we discerned no pattern to this variation. The 16 aviaries observed in stage I included 94 birds (14 aviaries with six birds each, and two aviaries with five birds each) in 230 dyadic relationships. In 17 of these dyads, we recorded one to three reversals (an interaction that reversed the usual relationship of the opponents), after excluding those cases in which subsequent observations revealed the relationship had changed. Nine aviaries included one or two nontransitive relationships (triangles), which involved a total of 12 dyads and 21 individuals.

The initial hierarchies were thus predominantly linear with some reversals and triangles. The numbers of birds in each aviary were small, so a single reversal or triangle in an aviary resulted in nonsignificance in tests for linearity of the hierarchy (Appleby 1983). However, when probabilities were combined across aviaries for each year, the results indicated significantly linear hierarchies (1995: eight aviaries, $C_{16}^2=35.2$, $P<0.01$; 1996: eight aviaries, $C_{16}^2=28.7$, $P<0.05$).

In the initial hierarchies, the three highest- and two or three lowest-ranking birds differed significantly in mass when both years were combined as independent samples ($C_4^2=13.0$, $P<0.02$). No other measure, including wing chord, fat scores, or scores for brightness of crown stripes, had a significant association with high and low rank in the initial groups, although wing chord was close ($C_4^2=9.1$, NS). Most of our subjects were in their first winter, so rankings were not associated with age.

### Dominance Scores

A bird's rank in stage II, after implanting, correlated strongly with its rank in stage I. Among the Spearman correlation coefficients for the 16 aviaries in the 2 years (Fig. 2), all but five exceeded 0.9, and all but two differed significantly from 0 at the 0.05 level (for the combined probabilities, $C_{32}^2=158.0$, $P<0.001$). Across both years, only eight of 145 relationships between untreated and treated birds changed between stages I and II after implantation. These changes involved five of 52 treated birds that managed to reverse their relationships with one or more higher-ranking, untreated opponents (see Fig. 3 for the ranks of individual birds in these two stages).

When birds were moved to a new location, their subsequent ranks depended on the social situation they faced. In aviaries containing the same individuals in stages II and III (treatment S), birds' ranks in their new locations depended strongly on their ranks in their previous locations. Three of the four aviaries with this treatment had Spearman correlation coefficients exceeding 0.9, and all had correlation coefficients that differed significantly from 0 (Fig. 2; for the combined probabilities, $C_8^2=44.3$, $P<0.001$). In this case, only one of 30 relationships
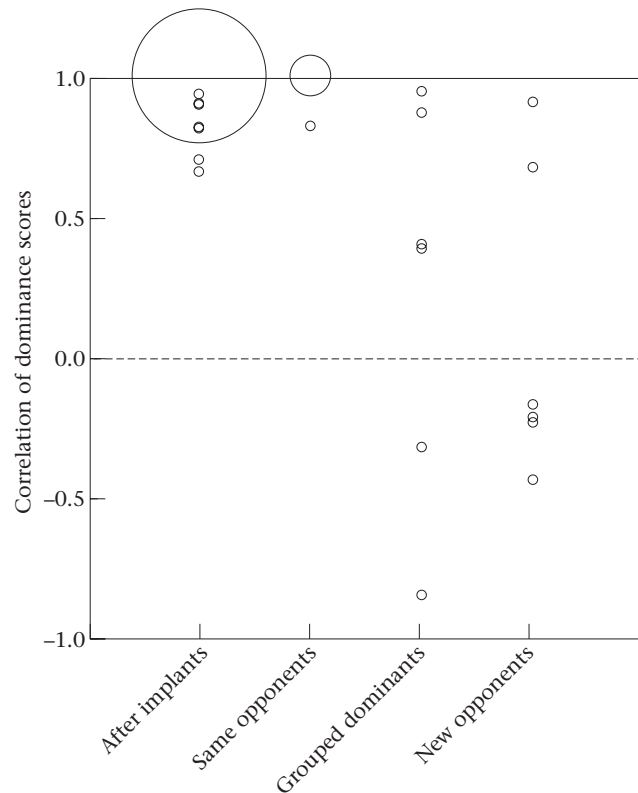


**Figure 2.** Spearman correlation coefficients between the dominance scores of birds in different stages of the experiment. Correlations were calculated for each aviary in the experiment (diameters of circles are proportional to the numbers of aviaries with the same values). After implants: correlations between rankings in stages I and II (N=16 aviaries, 8 each year); Same opponents: correlations between rankings in stage II and treatment S of stage III (same opponents in new aviary) (N=4 aviaries); Grouped dominants: correlation between rankings in stage II and treatment G of stage III (untreated high-ranking birds moved as a group) (N=6 aviaries); New opponents: correlations between rankings in stage II and treatment N of stage III (all new opponents in new aviary) (N=6 aviaries). See text for details.

between untreated and T-treated birds changed between stages II and III. In addition, three such relationships that had already changed between stages I and II remained stable in stage III (see Fig. 4 for the ranks of individual birds in stages II and III for treatment S).

When T-treated birds faced a group of previously dominant birds moved together as a unit (treatment G), the birds' new ranks were also predicted by their previous ranks, an indication of some stability in the birds' rankings. However, the Spearman correlations between the birds' ranks in stages II and III for these six aviaries included only one that exceeded 0.9, and only two that differed significantly from 0 (for the combined probabilities, $C_{12}^2=23.5$, $P<0.05$). Clearly, much more change occurred in this treatment than in the preceding one. Altogether, in 48 relationships between untreated and T-treated birds, the latter dominated in 25, and a majority (11/16) of T-treated birds managed to dominate at least one untreated opponent (see Fig. 5 for the ranks of individual birds in stages II and III for treatment G).
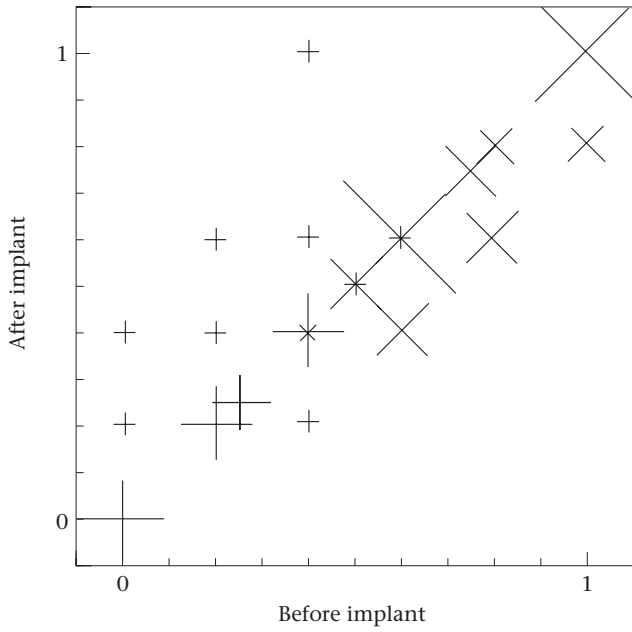
**Figure 3.** The dominance scores of individual birds before and after they received implants (stages I and II, respectively). Dominance scores are proportions of opponents dominated (see text). +: treated birds; ×: untreated birds. The size of the symbol at each point is proportional to the number of individuals.
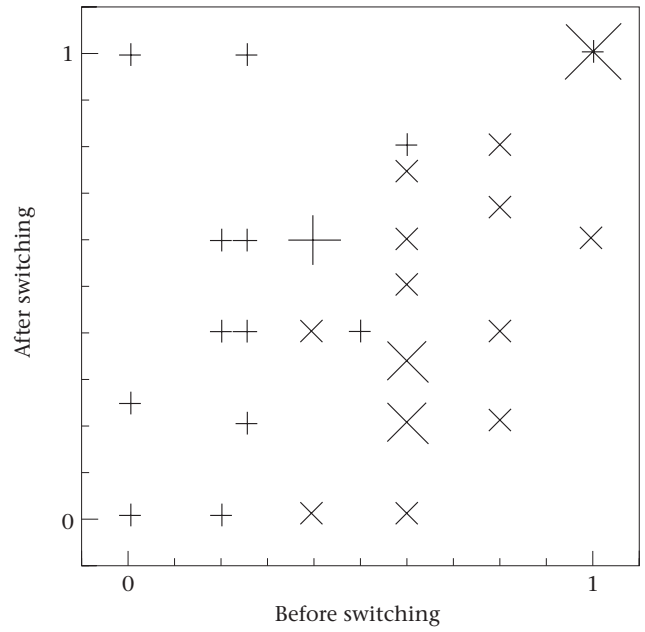


**Figure 5.** The dominance scores of individual birds before and after switching aviaries (stage II and treatment G of stage III, respectively). For explanation of symbols, see Fig. 3.
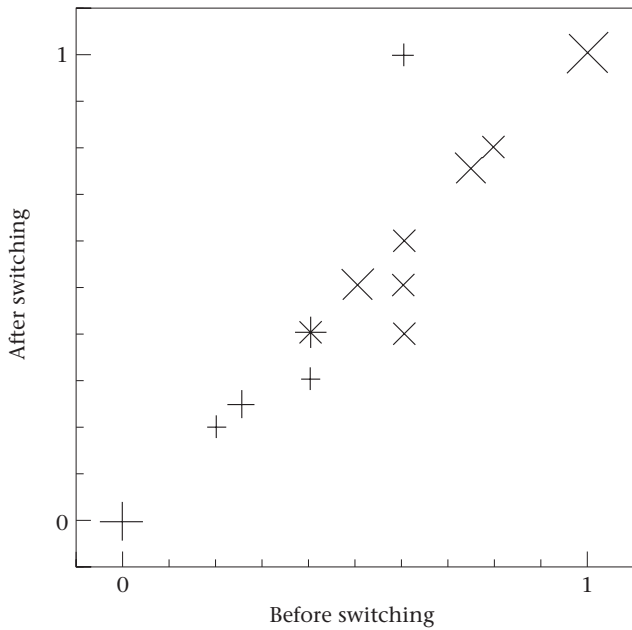


**Figure 4.** The dominance scores of individual birds before and after switching aviaries (stage II and treatment S of stage III, respectively). For explanation of symbols, see Fig. 3.
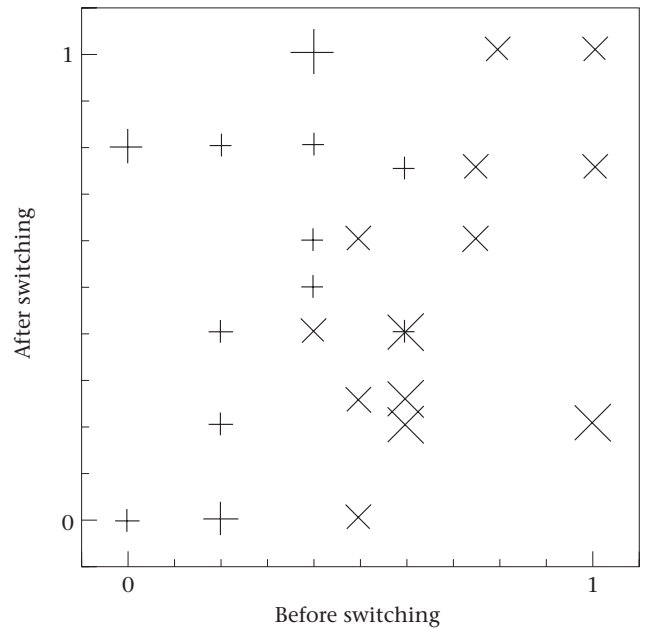


**Figure 6.** The dominance scores of individual birds before and after switching aviaries (stage II and treatment N of stage III, respectively). For explanation of symbols, see Fig. 3.

T-treated birds did even better in aviaries in which all birds were previously unacquainted (treatment N). Ranks in stage III were not correlated with ranks in stage II. Although one aviary had a Spearman correlation of 0.9, which differed significantly from 0 (Fig. 2), the combined probabilities from all six aviaries in this treatment did not reach significance ($C_{12}^2=13.0$, NS). Altogether, in 48

relationships between T-treated and untreated birds, the former dominated in 33, and 14 of 17 T-treated birds dominated at least one untreated opponent (see Fig. 6 for the ranks of individual birds in stages II and III for treatment N).

The overall result for treatment G (untreated dominant birds moved as groups) obscured a pattern of strikingly divergent results. Each year, in one of these aviaries all untreated birds dominated all T-implanted opponents,
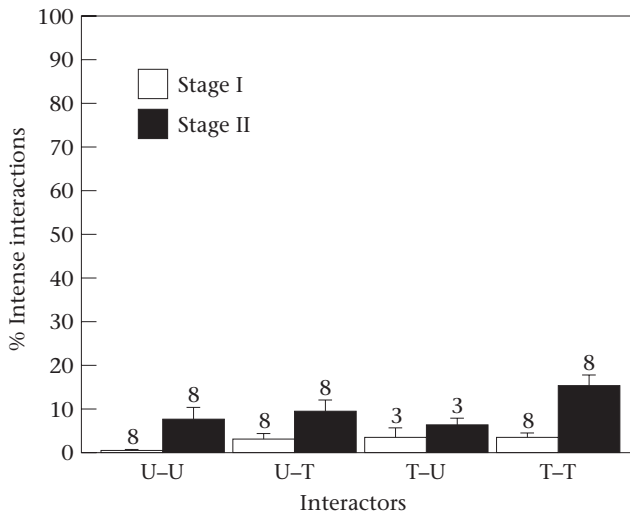
**Figure 7.** Percentages of intense interactions (Attacks and Chases, see text) in stages I and II (before and after treatment of low-ranking birds with testosterone) for four combinations of actor–recipient: U–U, untreated birds initiating interactions with untreated opponents; T–T, treated birds with treated opponents; T–U, treated birds with untreated opponents; and U–T, untreated birds with treated opponents. Numbers above bars indicate the numbers of aviaries in which these estimates could be obtained (maximum=8). Statistical analysis (nonparametric comparisons of means for each aviary, not the overall means shown here, as explained in the text) showed no significant differences between stages I and II.
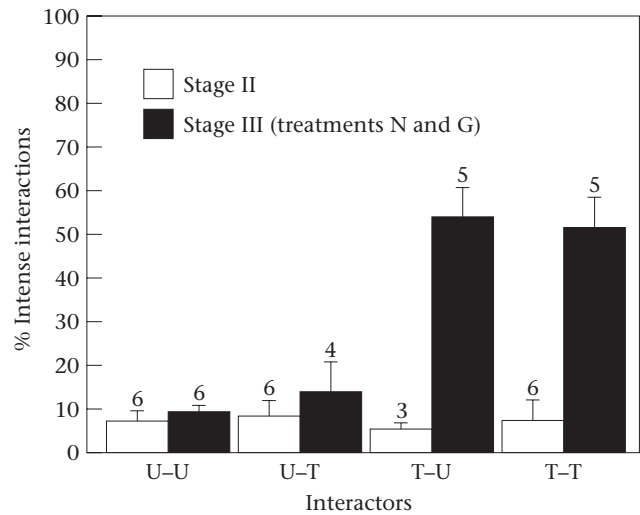


**Figure 8.** Percentages of intense interactions (Attacks and Chases, see text) in stages II and III (before and after the birds were moved to new aviaries) for treatments N and G combined (treated birds with unfamiliar, untreated opponents). For further explanation, including the four combinations of actor–recipient (U–U, U–T, T–U, U–T), see Fig. 7. Maximum possible number of aviaries for each estimate=6. Statistical analysis (see text) showed significant differences between stages for interactions initiated by treated birds (T–U and T–T).

whereas in the other two aviaries with this treatment, T-implanted birds had greater success (25 of 33 relationships between T-treated and untreated birds were dominated by T-treated birds). In contrast, in none of the aviaries in which all birds were unacquainted (treatment N) did all untreated birds ever dominate all T-treated opponents. In short, most of the birds in treatment G responded like those in treatment N, but birds in two aviaries responded like those in treatment S.

## Intensity of Interactions

To compare proportions of high-intensity interactions between stages I and II, we separated the four possible pairings of untreated (U) and T-treated birds (T): U–U, U–T, T–U, T–T (each pairing in the order actor–recipient). In Wilcoxon signed-ranks tests on the eight aviaries in 1996, only untreated birds showed a significantly increased proportion of intense interactions (U–U, $z=2.24$, $P<0.025$; U–T, $z=1.82$, NS; T–U, $z=0.54$, NS; T–T, $z=1.52$, NS; Fig. 7).

In a comparison of the intensity of interactions in stages II and III, for the two aviaries with treatment S, there was no change in the proportions of high-intensity interactions for any pairing (Wilcoxon signed-ranks tests, NS, for each aviary). We used Mann–Whitney $U$ tests to compare the six aviaries with treatments N or G with those aviaries in stage II that provided the birds for treatments N and G. In these comparisons, untreated birds did not increase the proportion of intense interactions they initiated (U–U, $U=15.5$, $N_1=N_2=6$, NS; U–T,

$U=22.0$, $N_1=N_2=6$, NS). In contrast, T-treated birds in these aviaries initiated a higher proportion of intense interactions against untreated birds (T–U, $U=4.5$, $N_1=N_2=6$, $P=0.03$; T–T, $U=7.0$, $N_1=N_2=6$, $P=0.08$; Fig. 8).

## Behavioural Tendencies

Interaction rate, the total number of Joins and Supplants/min per bird, is a measure of the level of activity in an aviary. This measure did not change between stages I and II (eight aviaries, Wilcoxon test, $z=-0.17$, NS; there were no observations of behavioural tendencies during stage III).

The tendency to supplant an opponent in a standardized situation was measured by the proportion of Encounters that terminated with a Supplant by the dominant bird. We determined these proportions for each type of pairing (U–U, U–T, T–U, T–T, each listed as actor–recipient) in each aviary and tested the significance of any changes from stage I to stage II with Wilcoxon signed-ranks tests ($N=8$ aviaries studied in 1996). Because untreated birds (U) usually outranked those with implants (T) in stages I and II, there were few T–U pairings. In none of the four pairings did tendencies to supplant a subordinate opponent change significantly from stage I to stage II, although T–T pairs were close (U–U, $z=1.49$, NS; U–T, $z=-0.51$, NS; T–U, $z=1.34$, NS; T–T, $z=1.84$, $P=0.07$; Fig. 9).

Another measure of the aggressive tendencies of dominants was obtained from their behaviour when approaching a subordinate feeding alone. The dominant in our standardized situation could either Join the subordinate by occupying the remaining empty place, or it could
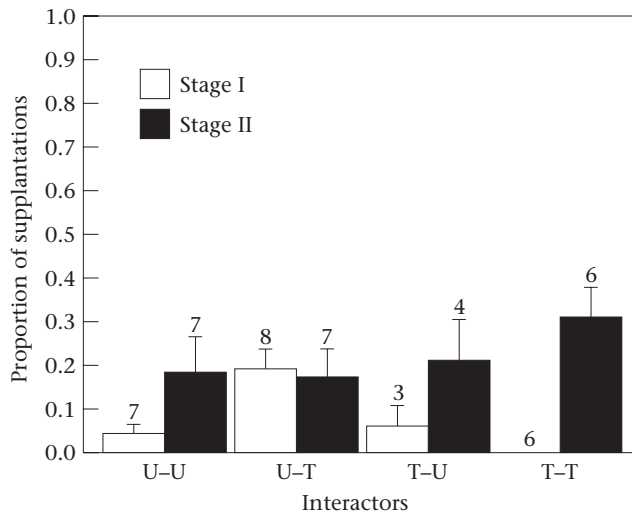
**Figure 9.** Proportions of Supplantations in standardized encounters between opponents in stages I and II (before and after treatment of low-ranking birds). For further explanation, including the four combinations of actor–recipient (U–U, T–T, T–U, U–T), see Fig. 7. Maximum possible number of aviaries for each estimate=8. Statistical analysis (see text) showed significant differences between stages for interactions between treated birds (T–T).

Supplant the subordinate and take its place. The proportion of such occasions in which the dominant Supplanted rather than Joined a subordinate did not change between stage I and II for any of the kinds of pairings (eight aviaries, Wilcoxon tests: U–U, $z=0.85$, NS; U–T, $z=1.07$, NS; T–U, $z=-0.63$, NS; T–T, $z=-1.09$, NS).

Thus treatment of the low-ranking birds in an aviary with testosterone did not significantly change the behaviour of individuals towards their familiar subordinates in standardized situations. This result applied equally to interactions between treated birds (T–T pairings) and to those between untreated birds (U–U pairings).

## DISCUSSION

### Influences on Rankings in Initial Groups

The initial dominance hierarchies in stage I were similar to those obtained in previous studies of this species in captivity (Archawaranon & Wiley 1988; Archawaranon et al. 1991; Dearborn & Wiley 1993; Wiley et al. 1993). As a rule, mass and wing chord are weakly associated with dominance in unfamiliar birds placed in an unfamiliar aviary. In wild populations of this species, sex (strongly correlated with wing length) and age are significant correlates of dominance (Piper & Wiley 1989a). These studies have also failed to find any relationship between crown brightness and dominance. It should be emphasized that the correlates of dominance in aviaries are not necessarily identical to those in the field. Birds placed with unfamiliar opponents in unfamiliar locations are deprived of any situational influences on dominance, such as prior experience in particular locations or with particular opponents.

### Social Inertia

Our results in stage II matched those obtained in similar experiments on white-throated sparrows by Archawaranon et al. (1991): dominance relationships rarely changed when low-ranking treated birds and high-ranking, untreated birds were returned to familiar opponents in familiar locations. In contrast, birds implanted with testosterone and placed in aviaries with unfamiliar opponents almost always dominated untreated birds. The almost universal success of treated birds in interactions with unfamiliar untreated opponents suggests that the influence of testosterone among unfamiliar opponents usually outweighs any effects of previous experience with dominance (Jackson 1991).

This stability of dominance relationships could result from familiarity with opponents (social inertia) or familiarity with the locations of encounters. Stage III of the present experiment was designed to resolve this issue. Treatment S in stage III showed what happens when familiar opponents were placed in a new location. The persistence of dominance relationships clearly indicated social inertia among familiar opponents, despite changes in the locations of encounters.

These experiments only examined relatively small changes in the locations of encounters. Our aviaries differed slightly in internal arrangements and external environment but, nevertheless, shared many similar features. It remains possible that a more substantial change in the context of encounters would affect the stability of dominance relationships.

In comparison with treatment S, treatment N (new opponents in new locations) confirmed that familiarity with opponents is essential for social inertia. The conclusion that birds recognize their dominance relationships with familiar opponents, independent of immediate context, seems robust.

### Coat-tail Effects in Dominance Hierarchies

Treatment G in stage III provided weak evidence for a coat-tail effect on dominance. Earlier studies of coat-tail effects in white-throated sparrows, following Wiley (1990), also produced equivocal results (J. E. R. Perry & R. H. Wiley, unpublished data). In these studies, different replicates often yielded all-or-nothing results. In the present experiment, the results of treatment G fit this pattern, as evidenced by the striking persistence of rankings in two of the six aviaries.

Possible mechanisms for coat-tail effects include (1) joint effects of familiar birds on opponents (coordinated attacks or intimidation by greater aggregation), (2) fewer unfamiliar opponents to fight, (3) increased aggressiveness towards strangers stimulated by proximity of familiar opponents, or (4) safe zones for familiar opponents of the highest-ranking bird (because the latter permits familiar subordinates to approach more closely than strangers; Wiley 1990; Cristol 1995). Especially in the last case, the ranks of all familiar opponents might depend entirely on the overall status of the one top-ranking bird. This situation could produce an all-or-nothing outcome

in interactions with strangers, depending on whether or not the top-ranking bird among the familiar opponents achieved highest rank overall. Some such mechanism might have produced the inconsistent outcomes in treatment G in our experiment. Clearly we need more work on coat-tail effects in dominance hierarchies.

## Recognition of Opponents

Linear dominance hierarchies might result from assessment and scaling of individuals' attributes, either aggressive tendencies, fighting capabilities, or status signals, without any need for recognition of opponents or for any influence of third parties on dyadic interactions. Scaling of aggressive tendencies or capabilities could result from intrinsic differences among individuals or from acquired differences, which may result from prior experience in interactions (for some discussion of these possibilities see Chase 1986; Jackson & Winnegrad 1988; Archawaranon et al. 1991; Rothstein 1992).

In contrast, both coat-tail effects and social inertia require some recognition of opponents. Coat-tail effects might require no more than discrimination of familiar and unfamiliar opponents. Social inertia, however, requires that individuals recognize the relative ranks of opponents or at least categories of high- and lower-ranking opponents.

Social inertia is thus particularly interesting because it provides evidence that birds can recognize their dominance relationships with particular sets of familiar opponents. Social inertia does not require that a bird recognize each of its opponents individually, for instance by discriminating the differences in rank between itself and various opponents, but it does require that a bird can classify familiar opponents into at least two classes, those ranking higher and lower than itself.

This ability to classify opponents by their relative ranks is not the same as using status signals or assessment to determine relationships with opponents, because it applies only to familiar opponents. Thus the initial determination of dominance relationships and their eventual stability have at least partially different mechanisms. Social inertia shows that testosterone affects the initial determination but not the eventual stability of dominance.

## Intensity of Interactions and Behavioural Tendencies

The comparisons of interactions and behavioural tendencies in stages I and II provide no evidence that testosterone changed the behaviour of individuals when they were returned to groups of familiar opponents in familiar locations. They thus confirm the similar finding in an earlier study of social inertia in white-throated sparrows by Archawaranon et al. (1991).

The results in stage III show that it is familiarity with opponents, rather than familiarity with location, that prevents activation of aggression by testosterone. Only in groups in which treated birds met new opponents in stage III (treatments N and G) were there clear increases in the intensity of interactions initiated by treated birds. Untreated birds did not show any significant increases. Interactions with unfamiliar opponents thus revealed previously latent aggressiveness in the treated birds.

That this aggressiveness by treated birds was indeed inhibited in the presence of familiar opponents is further confirmed by the groups of familiar opponents in stage III (treatment S). In these groups, treated birds showed no increase in intensity of interactions from stage II to III, just as they had shown no such increase from stage I to II.

Interaction with familiar opponents thus not only resulted in stable dominance relationships despite treatment of subordinate individuals with testosterone, but also inhibited the activation of aggression in treated individuals. It seems probable that social inertia resulted, at least in part, from a failure of testosterone to activate aggression by subordinates in groups of familiar opponents. In our experiments, high-ranking individuals did not face repeated challenges from familiar testosterone-treated subordinates.

It remains unclear whether treated subordinates refrained entirely from challenges of familiar dominants or whether infrequent interactions with familiar dominants served to suppress further challenges. Our measures of the intensity of interactions and of agonistic tendencies in standardized situations aggregated the outcomes of many interactions and thus would not reflect the importance of a few crucial events.

Other studies have reported increases in aggression within stable groups of birds following treatment of low-ranking individuals with testosterone (Guhl 1964, 1968; Rohwer & Rohwer 1978). Similar changes occur in white-throated sparrows when low-ranking birds are treated with testosterone in the field (Archawaranon et al. 1991). These different results could arise from different possibilities for recognition of opponents and are best considered in combination with 'double treatment' experiments on status signals.

## Status Signals and Recognition of Opponents

Studies of status signalling in a congener of the white-throated sparrow, the Harris' sparrow *Zonotrichia querula*, have included manipulations of hormonal state or appearance or both (a double treatment). For instance, one individual implanted with testosterone and then released where it had been captured, failed to increase in dominance; in contrast, two others observed before and after they were both implanted and painted to look like older males, did increase in rank (Rohwer & Rohwer 1978).

The bird that was only implanted received more attacks from dominant opponents, but apparently did not initiate any more attacks (Rohwer & Rohwer 1978). In white-throated sparrows, some implanted birds returned to wild flocks also engage in more frequent aggression, in part initiated by themselves (Archawaranon et al. 1991). Birds released into wild flocks confront opponents that no doubt vary in familiarity. Presumably, as in stage III of the

present experiment, testosterone activates aggression when opponents are unfamiliar with each other.

Painting a bird might well affect its previous acquaintances' ability to recognize it. This new situation might also quickly affect the subject's behaviour. As a result, the rise in dominance of Harris' sparrows following double treatment (with both implants and paint) might result either from direct effects of the painting on its status signals or from indirect effects of the painting on recognition of opponents. In the latter case, when recognition is diminished, testosterone could produce an increase in dominance. Such double-treatment experiments might thus be explained by the effects of testosterone on the behaviour of unfamiliar opponents, in effect by an absence of social inertia.

## Comparative Study of the Mechanisms of Dominance

The plumage of Harris' and white-crowned sparrows, *Zonotrichia leucophrys*, unlike that of white-throated sparrows, differs with age and, to a lesser extent, with sex. In these two species there is apparently no overlap in the appearance of first-winter and older birds (Rohwer et al. 1981; Fugle et al. 1984; Fugle & Rothstein 1987), and young birds in their first winter painted to resemble older birds become dominant over other young birds (Rohwer 1985; Fugle & Rothstein 1987; Slotow et al. 1993).

In contrast, in white-throated sparrows, there is much greater overlap in the winter plumages of age classes and sexes (Piper & Wiley 1989b). Both in the field and in aviaries, age and size (a close correlate of sex) influence dominance. When these factors are controlled statistically, plumage differences have no significant influence on dominance (Piper & Wiley 1989a).

Furthermore, an experiment in which first-winter, white-throated sparrows were painted to resemble the two extremes of plumage (black and white stripes or brown and tan stripes) failed to reveal any effects on dominance (L. Steadman & L. Chadwick, unpublished data). These experiments included eight groups of first-winter birds, six birds in each group, and employed procedures and materials for painting that closely matched those in experiments with white-crowned sparrows (Fugle & Rothstein 1987). All of these lines of evidence suggest that status signalling does not have a clear influence on dominance in white-throated sparrows.

At present, we have evidence for status (age class) signalling in two species of *Zonotrichia* and evidence for social inertia and recognition of opponents in a third. It is possible that white-throated sparrows use their plumage variation more for recognition, and the other species use it more for status signalling. A comparison of the rate of decrease in aggression in newly formed groups suggests that these species might differ in abilities to recognize opponents (Watt 1986). Further comparisons of these species could clarify the interplay of status signalling and recognition in the formation of dominance hierarchies.

Both status signalling and social inertia produce social stability, in which individuals do not challenge established status. They thus both beg the question of the evolutionary stability of dominance and subordination (Rohwer & Ewald 1981; Møller 1987; Keys & Rothstein 1991). Status signals might have advantages when intrinsic differences among individuals are important predictors of dominating ability, and recognition of opponents might have advantages when situational differences are important. In both cases, it seems likely that evolution has favoured an individual's acceptance of its status with an opponent once established. This 'resignation' might prove advantageous only when situational or intrinsic conditions are likely to remain stable for some time. Further comparative study might well reveal that species differ in meeting the conditions for status signals or social inertia.

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