

SINGING IN RELATION TO SOCIAL DOMINANCE AND TESTOSTERONE IN WHITE-THROATED SPARROWS

by

R. HAVEN WILEY, W. H. PIPER¹⁾, MANEE ARCHAWARANON²⁾ and ELIZABETH WYRICK THOMPSON³⁾

(Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, U.S.A.)

(With 3 Figures)

Summary

Singing by white-throated sparrows *Zonotrichia albicollis* during the winter in natural situations occurred most frequently among birds with high rank in a dominance hierarchy. Genetic morph, age and sex had no significant influence on singing during winter. Among testosterone-implanted birds in small groups in large aviaries, dominance rank strongly influenced singing. Testosterone-treated birds with top rank sang most frequently, those with second rank less, and those with lower rank never. As a testosterone-treated bird's rank changed in the course of regroupings with new opponents, its frequency of singing also changed. Dominance in a group thus interacted with testosterone to promote singing. In addition, grouped birds in May before treatment with testosterone did not sing. As a consequence, it seems likely that the normal seasonal development of territorial behavior and singing involves cascading interactions of endocrine states and social circumstances.

Introduction

The influence of testosterone on singing in many passerines is widely recognized (SILVER *et al.*, 1979; BALTHAZART, 1983; HARDING, 1983; PRÖVE, 1983). Experiments involving castration and testosterone administration (PRÖVE, 1974; ARNOLD, 1975; POHL-APEL & SOSSINKA, 1984; HEID *et al.*, 1985; DEVOOGD, 1986; HARDING *et al.*, 1988; SELIER & GÜTINGER, 1988;), as well as correlations between annual gonadal cycles, circulating testosterone, and singing (DAVIS, 1958; HARDING, 1981; MARLER *et al.*, 1987, 1988; NOTTEBOHM *et al.*, 1987; ROST, 1990), all provide

evidence for the hormonal activation of singing. The influence of testosterone on singing is more problematic in species in which singing occurs regularly in females or outside the breeding season. Although administration of testosterone to females and to nonbreeding males induces singing in a variety of species (NOTTEBOHM, 1980; NOWICKI & BALL, 1989; KRINER & SCHWABL, 1990), these individuals do not normally experience such high levels of testosterone.

During a decade of research on the behavior of white-throated sparrows *Zonotrichia albicollis* during winter, we noted that individuals occasionally sang, although testosterone titers during winter were less than 20% those during the breeding season (ARCHAWARANON *et al.*, 1991). At the same time, experiments with captive birds suggested that dominance in small groups strongly affected singing among testosterone-treated birds.

We report here an analysis of singing by free-living birds during winter, together with the results of further experiments on singing and dominance in captive birds. In both of these situations singing is closely associated with high rank in dominance hierarchies. On this point, our results confirm those of a more limited recent study (SCHLINGER, 1990). We could not, however, confirm that singing by white-throated sparrows during winter was associated with one of this species' two plumage morphs. Instead, our experiments on testosterone-treated birds in small groups suggest that social dominance has a fundamental influence on singing in this species.

Methods

Field study of wintering birds.

We observed singing by wintering white-throated sparrows at the Mason Farm Biological Reserve near Chapel Hill, NC, from October to March during four winters, 1983-1984 through 1986-1987. This study was part of a larger program to investigate the behavioral correlates and ecological consequences of dominance in this population. Because we have already described our procedures in several previous publications (PIPER & WILEY, 1989a,b, 1990a,b, 1991; PIPER, 1990a,b; WILEY & PIPER, 1992), we include only a summary here. Our study area included 17 trapping stations 25 m apart along 400 m of hedgerow beside cultivated or weedy fields (PIPER & WILEY, 1989a). All birds using this area each winter were trapped, examined, and marked for individual recognition. For each bird, we obtained the length of its wing chord, its age as indicated by pneumatization of the cranium (WILEY & PIPER, 1992), the extent of black and white in its crown stripes (PIPER & WILEY, 1989b), and its sex by laparotomy (PIPER & WILEY, 1991). The coloration of the crown stripes in basic (winter) plumage allowed us to determine the morph with greater than 90% accuracy (PIPER & WILEY, 1989b); in addition, about half of all birds were examined

¹⁾ Present address: National Zoological Park, Smithsonian Institution, Washington, D. C. 20008-2598.

²⁾ Present address: Department of Biology, Ramkhamhaeng University, Bangkok, Thailand.

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following the prealternate molt in March and April when coloration of the two morphs was distinctly different. We recaptured birds repeatedly throughout each winter, so that we also obtained each bird's mean fat score in January and February (as computed by PIPER & WILEY, 1990a), the size of its range along the hedgerow (as computed by PIPER & WILEY, 1990b), years of residence in the study area, and arrival date in autumn (as computed by PIPER & WILEY, 1989a).

Observations of the birds' behavior were obtained at four sites 75-100 m apart along the hedgerow and within the 400-m trap line. Each of these sites included a small blind for an observer and 6 feeding positions (cement blocks on end) each baited 3-6 days/week with about 15 ml of millet, usually enough to last for 30-60 min of observation.

One bird was considered dominant over another at a particular observation site, if it dominated that opponent in at least 75% of its interactions (PIPER & WILEY, 1989a). Each winter we observed 8000-21000 interactions between identified individuals. From this information, we calculated a dominance proportion for each individual at each observation site (the proportion of that individual's dyadic relationships in which it was dominant). In the present analysis, as in our previous ones, we have included only those individuals for which we determined dominance relationships with 10 or more opponents at a single site in one year. During the four years of this study, 536 individuals satisfied these criteria.

During observations of behavioral interactions, we recorded the identity of singing individuals whenever possible. Most singing occurred while birds perched on the cement blocks or in shrubs immediately adjacent to them, so that singing individuals were readily identified.

For statistical analysis of the correlates of singing, our criterion (dependent) variable was the number of times each bird was seen singing at one site in one winter. For birds that met the criteria for calculation of dominance proportions at more than one site, we used only that site at which it had the largest number of defined dyadic relationships, unless it was only observed singing at another site, in which case we used that site in the analysis. Thus each individual entered these analyses only once. We included 14 predictor (independent) variables: year, age (first winter or older), sex, coloration of crown stripes, morph, length of wing chord, mean fat score in January and February, arrival date, years of residence, size of range, observation site, distance between this site and the individual's mean trapping location, number of dyadic relationships, and dominance proportion (logit transformed as described by PIPER & WILEY 1989a). First, we used stepwise multiple regression, as implemented by SYSTAT with $\alpha = 0.15$ for acceptance (WILKINSON, 1988), to identify variables for further analysis. Finally, we used multiple regression as implemented by the multivariate general linear hypotheses in SYSTAT for evaluation of the significance of predictors of singing. Because of the number of independent variables considered, we adjusted significance levels in accordance with the Bonferroni procedure.

Studies of captive birds.

A preliminary experiment conducted in May-June 1985 indicated that dominance strongly modified the activation of singing in white-throated sparrows by exogenous testosterone. This experiment involved birds captured in early May. Because of the lateness of the season for this experiment, a similar experiment was conducted in January-March 1992.

For both experiments, we captured birds in the Mason Farm Biological Reserve 200-500 m from the area used for the field study, collected the same data explained above, placed colored bands on each bird for individual identification, and then introduced 4-6 birds of mixed age and sex, depending on availability, into outdoor aviaries located at least 6 m apart. Each aviary was 2.4 m on a side, with a one-way mirror in an enclosed chamber on one side to permit undisturbed observation of the birds at close range. Each aviary had a standardized arrangement of perches and shelter. Mixed seeds and water with vitamins were provided in excess in several containers except during observations. At the end of each experiment, birds were given numbered bands for permanent identification and released.

Implants consisted of 10-mm lengths of crystalline testosterone (Sigma Chemical Co.) in the centers of 20-mm lengths of Silastic tubing (1.5 mm internal, 2.0 mm external diameter). Both ends of the tubes were sealed with the tips of wooden toothpicks and Dow Corning medical adhesive. These doses were chosen because in earlier experiments we had found that such implants produced circulating titers of testosterone equal to 11.95 ± 4.39 ($N = 3$) and 9.26 ± 2.89 ng/ml ($N = 2$) in males and females respectively. These implants thus resulted in testosterone levels comparable to those in breeding birds of related species (WINGFIELD & FARNER, 1978a, 1978b; WINGFIELD, 1984, 1985). Controls received 20-mm lengths of Silastic tubing prepared in the same way except that they contained no hormone. All implants were inserted beneath the skin on the back; all remained in place without complications until removed at the end of each experiment.

Each experiment involved several stages in which individuals were grouped with different partners in different aviaries. Experiment I in 1985 included 6 groups of 4-6 birds. We determined dominance relationships during the first week in captivity (stage 1). Then all birds were removed from the aviaries, the two or three highest-ranking individuals in each aviary (half the birds in groups of 4 and 6 respectively) received implants of testosterone, and the remainder received empty implants. The birds were released simultaneously in their original aviaries within two hours of capture. After dominance relationships and singing were again determined (stage 2), all birds were again captured. The assortment of individuals in aviaries was then permuted, so that each bird was in a new aviary with new opponents. We released the new inhabitants of each aviary simultaneously within one hour of capture. Similar permutations were conducted 4 more times, so that altogether there were six stages (stages 2-7) in each of which individuals confronted new opponents in new aviaries.

Experiment II in 1992 included five groups of 4-6 birds. Stages 1 (before implantations) and 2 (birds in their original groups after implantations) proceeded like those in Experiment I. Stages 3 and 4 involved rearranging birds with each aviary always having 2 or 3 T-implanted birds and 2 or 3 control birds.

Prior to observations, food was removed from an aviary for 50-75 min to increase the rate of interaction once food was returned. During observations only one food dish was present. In Experiment I each bird was the subject of a 15-min focal sample on two days during each stage of the experiment. In Experiment II all individuals' songs were noted during 30-min periods on two days during each stage. As each individual had a distinctive song pattern and we could watch the birds from such close range, it was not difficult to determine which bird sang. All observations were conducted between 0800 and 1200.

Dominance relationships in an aviary were determined during each stage of an experiment by observing interactions at the single food dish and elsewhere in the aviary. Dominance interactions followed patterns reported in other experiments in similar conditions (ARCHAWARANON & WILEY, 1988; ARCHAWARANON *et al.*, 1991). Most dyads had consistent relationships in numerous interactions, although a few pairs interacted infrequently or not at all. Occasional groupings (5/35 in Experiment I, 7/20 in Experiment II) included a nontransitive (triangular) relationship; in these cases we accepted the hierarchy that minimized the number of entries below the diagonal in a standard interaction matrix.

At the end of Experiment I we collected blood from a dorsal branch of the jugular vein in heparinized hematocrit tubes. We employed solid-phase radioimmunoassays (Count-A-Count, Diagnostic Products Corp., Los Angeles, CA) to determine concentrations of testosterone in these samples after extraction of lipids with methylene chloride. These procedures exactly followed those we have reported previously (ARCHAWARANON & WILEY, 1988; ARCHAWARANON *et al.* 1991).

All statistical comparisons included each individual only once. The different stages of each experiment allowed us to observe most individuals in different positions in a dominance hierarchy and thus to compare singing by an individual as its rank changed.

Results

Field study of wintering birds.

This species' song consists of several unmodulated tones at different frequencies usually followed by several triplets of brief tones at the same frequency (BORROR & GUNN, 1965). Some songs heard during winter had unsteady frequencies in the tonal notes, and about one third included no triplets. Nevertheless, many songs sounded very similar to those produced during the breeding season. Overall, 17% of birds in our sample of 536 were seen singing, and some of these sang regularly.

Stepwise multiple regression identified only one variable as a predictor of the number of times a bird was observed singing during winter, its dominance proportion. The result was the same if the analysis was restricted to the 92 individuals actually observed singing. Furthermore, dominance remained the only strong correlate of singing if the dependent variable was a binary classification of individuals, those observed and those not observed singing. Linear regression yielded a highly significant influence of a bird's transformed dominance proportion on the number of times it was observed singing (Table 1).

Three other predictor variables, age, wing chord, and morph, reached marginal levels of significance (Table 2). If we adopt the Bonferroni procedure for adjusting significance levels by dividing by the number of variables tested, so that $\alpha = 0.05/14 = 0.004$, then none of these three variables satisfied this criterion.

The association of singing with dominance was indeed striking (Fig. 1). Of seven birds with dominance proportions equal to 1.0, we observed five singing (71%); of 38 with dominance proportions > 0.9 , we observed 53% singing. In contrast, only 3% of those with dominance proportions ≤ 0.25 were seen singing.

TABLE 1. Regression of number of times observed singing on dominance proportion

Variable	Coefficient	SE	t	p
Constant	0.413	0.052	7.99	<<0.001
Dominance proportion	0.304	0.031	9.69	<<0.001

N = 532, R² = 0.150

TABLE 2. Regression of number of times observed singing on four independent variables including dominance proportion

Variable	Coefficient	SE	t	p
Constant	4.86	1.73	2.81	<0.01
Dominance proportion	0.375	0.041	9.08	<<0.001
Age	-0.141	0.071	-1.97	0.05
Wing chord	-0.054	0.024	-2.28	0.02
Morph	-0.253	0.123	-2.07	0.04

N = 468, R² = 0.174; sample size is somewhat smaller than in Table 1 because of missing data for some individuals.

If we consider those individuals observed singing in more than one year, 26 of 34 sang more or sang only in the year in which their dominance proportion was highest (binomial test, $p < 0.01$).

Experiment I.

Although testosterone titers in wild white-throated sparrows normally rise sharply in April (ARCHAWARANON & WILEY, 1988), no birds sang in our aviaries during May until implanted with exogenous testosterone. No control birds sang at any time during the experiment. Of 16 testosterone-implanted birds, 13 sang during at least one of the 6 stages following implantation.

Testosterone had a strong influence on dominance among unfamiliar opponents, as reported previously (ARCHAWARANON *et al.*, 1991). Consequently, during stages 3-7 the testosterone-implanted birds usually had the highest ranks in their aviaries. Nevertheless, testosterone-implanted birds varied in rank, and each individual often changed rank when grouped with new opponents. In each stage after implantation, particularly from stage 3 onward, top-ranking birds sang more often than second-ranking birds (Fig. 2). Third- and lower-ranking birds with testosterone implants never sang.

For 10 of the 13 birds that sang, the number of songs/sample correlated positively across stages with their dominance ranks (mean $r_s = 0.89$, range 0.84-0.97, N = 6 stages, $p < 0.05$ in each case). For the remaining three, the correlation was not significant. Five individuals that both sang and had wide variation in ranks during the stages of the experiment illustrate the changes in singing as individuals' ranks changed (Table 3).

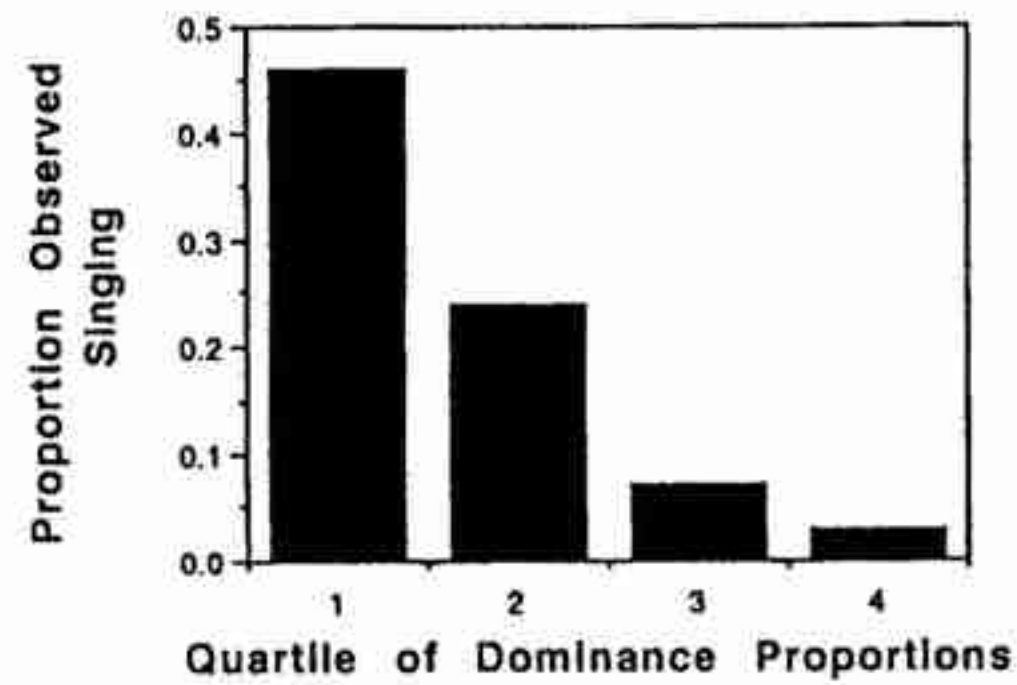


Fig. 1. The proportion of individuals observed singing during winter in relation to their dominance.

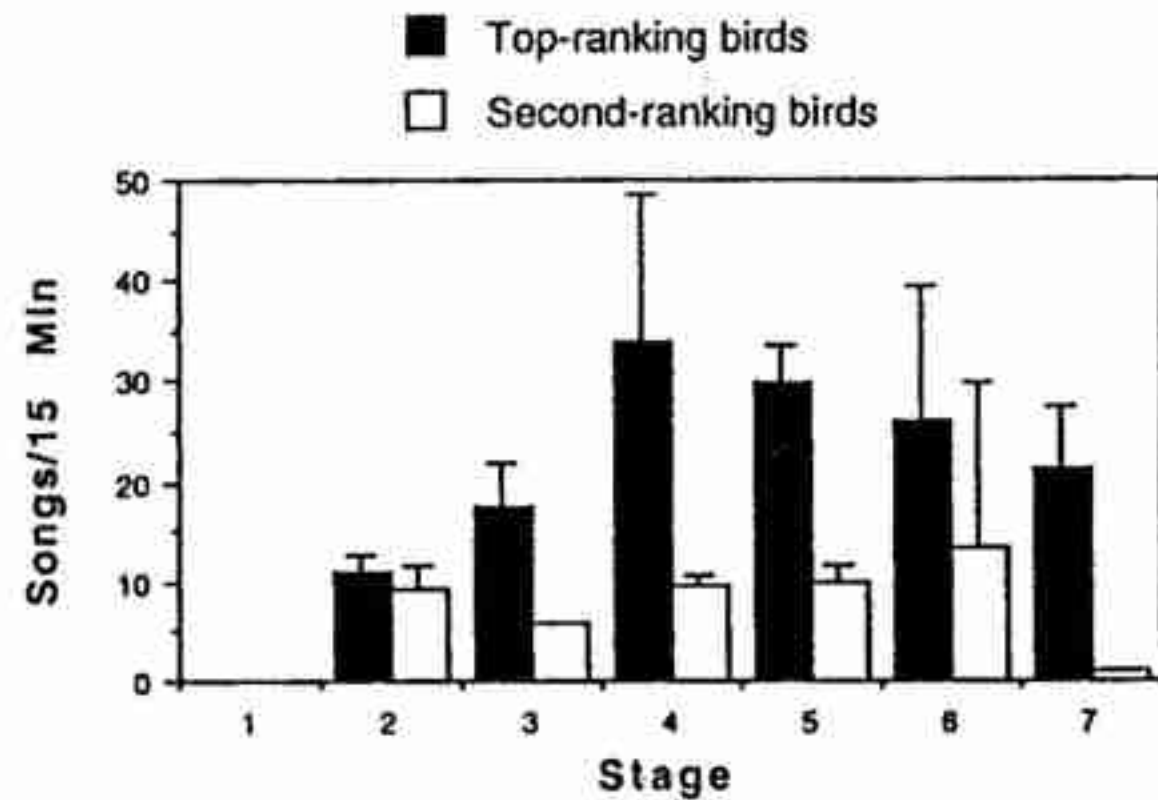


Fig. 2. Rates of singing (mean and SD) by testosterone-treated birds with top and second rank in groups in successive stages of Experiment I. Stage 1 preceded testosterone treatment; opponents were permuted following Stages 2-6. Only testosterone-treated birds with top or second rank sang.

Testosterone-implanted birds at the end of the experiment in June had titers of circulating testosterone similar to those reported previously for birds that had received the same size of implants for similar periods of time (ARCHAWARANON & WILEY, 1988) (Fig. 3). Testosterone-treated males and females did not differ, and both had 4-5 times the concentrations of testosterone in controls. The controls did not differ significantly from untreated birds in January.

TABLE 3. Examples of changes in dominance ranks and singing by five individuals during experiment I

Stage	1	2	3	4	5	6	7
Rank	2	2	3	1	1	1	4
Singing ¹⁾	-	+	-	+	+	+	-
Rank	2	2	3	1	1	3	1
Singing	-	-	-	+	+	-	+
Rank	2	2	1	2	3	4	1
Singing	-	+	+	+	-	-	+
Rank	1	1	5	3	1	1	1
Singing	-	+	-	-	+	+	+
Rank	1	1	3	1	2	1	3
Singing	-	+	-	+	+	+	-

Implantations followed Stage 1; opponents permuted following Stages 2-6.

¹⁾ +, individual was observed singing during this stage of the experiment; -, not observed singing.

Experiment II.

This experiment served to confirm the preceding findings. Ten of 14 testosterone-treated birds sang during stage 3 or 4 of the experiment; no control bird sang at any time. Of the 10 birds that sang, eight had different ranks in stages 3 and 4. Each of these birds sang more when higher in rank than when lower. On occasions when a testosterone-treated bird ranked lower than second in its group's hierarchy ($N = 4$ and 7 in stages 3 and 4, respectively), it never sang.

During stages 3 and 4, top-ranking testosterone-treated birds sang on average 1.15 and 0.80 songs/min, while second-ranked birds sang 0.20 and 0.40 songs/min, respectively. Combining these two stages, top-ranked birds sang on average 0.99 songs/min and second-ranked birds sang 0.30 songs/min ($U = 7$, $N_1 = 7$, $N_2 = 5$, $p = 0.05$, Mann-Whitney U Test; two individuals that occupied the same rank in both stages were counted once each, with their singing rates in the two stages averaged).

The reduction in singing by second- and lower-ranking birds did not result from immediate interference by top-ranking birds. Top-ranking

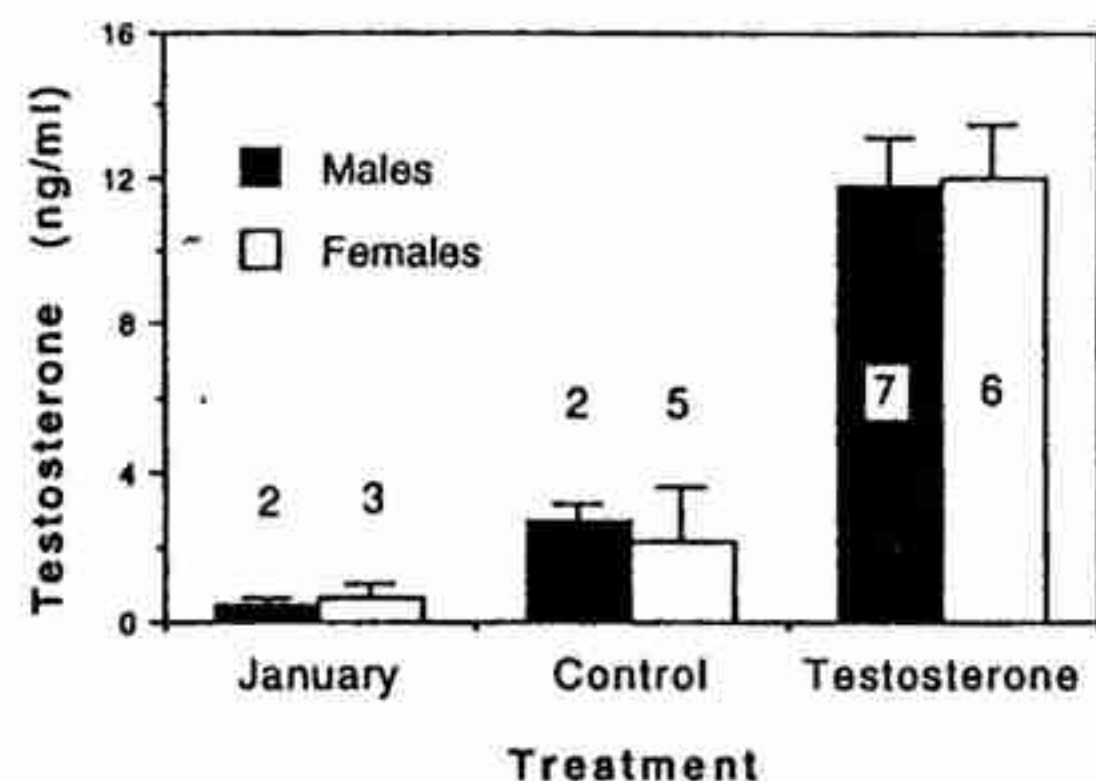


Fig. 3. Concentrations of testosterone (mean and SD) measured in the blood of experimental (with testosterone implant) and control (with empty implant) birds in Experiment I compared with those of wild birds in January. Numbers indicate sample sizes.

birds never interrupted singing subordinates. Furthermore, singing by top-ranking birds was not associated with immediate supplantations or attacks on subordinates. For instance, during stage 4, we observed 81 bouts of singing by top-ranking birds, of which only 27 (33%) were followed by supplantation or attack by these individuals before any other. As top-ranking birds performed 46% of 454 supplantations and attacks observed during this stage, aggressive behavior by top-ranking birds followed singing less frequently than expected. This pattern held separately for each of the aviaries, as well as overall. Birds usually sang from high perches in the aviaries, while most aggression occurred near food. Probably for this reason, birds did not often switch rapidly from one to the other activity.

Although fewer second-ranking birds were available for analysis, they too appeared less likely than expected to switch immediately from singing to aggression. In addition, their singing never provoked immediate supplantation or attack from their top-ranking opponent. Neither did it elicit immediate singing by the top-ranking bird. We thus concluded that the immediate social consequences of singing could not explain the lower frequencies of singing by second-ranked birds.

Social status, on the other hand, clearly influenced singing. Two individual cases serve to emphasize the interaction between social status and

hormonal state in activation of singing. First, consider an individual that changed status dramatically. YP held rank 4 in its aviary in stage 3 and, despite testosterone treatment, never sang then. In stage 4 it remained in the same aviary but with 4 new opponents from elsewhere. Within one day, a testosterone-treated newcomer, BS, established top rank and became extremely aggressive toward all other birds in the aviary. YP became the second-ranking bird and began to sing frequently. The observation session on this day was the only occasion on which a second-ranking individual sang more frequently than the top-ranking. Two days later, however, YP had ceased singing, while BS continued its frequent aggression and less frequent singing. To prevent further harassment of the low-ranking birds in this aviary, BS was then removed. Two days later, YP had top rank and had resumed frequent singing. YP's early surge of singing, after the introduction of new opponents, quickly disappeared as it continued in rank 2; singing began again when it could take top rank.

1993
1993
Another case dramatically illustrated the suppression of singing in testosterone-treated birds with low rank. Two control birds, YY and YP, occupied the top two positions in one aviary in stage 3, perhaps because they had remained in the same aviary as in the preceding stage; neither they nor two testosterone-treated birds below them ever sang. For stage 4, YY and YP were returned to the same aviary with two new testosterone-treated opponents. Perhaps because of their continued familiarity with the aviary (WILEY, 1990; DEARBORN & WILEY, *in press*) or because of the testosterone-treated opponents' lack of experience as top-ranking birds, YY and YP again established dominance over the testosterone-treated birds; again the testosterone-treated birds did not sing. Thus the subordinate testosterone-treated birds did not sing even when no other bird in the aviary sang. It is also clear from these cases that future investigations should consider prior residence as an influence on the activation of singing as well as on dominance (PIPER & WILEY, 1989; WILEY, 1990; DEARBORN & WILEY, *in press*).

Discussion

In our experiments and observations, dominance in social relationships had a strong influence on singing in white-throated sparrows, both in the

field during winter when testosterone titers were low and in aviaries when birds had testosterone titers approximating the highest levels during the breeding season. As expected, testosterone administration to captive birds clearly increased singing, but primarily among birds with the top rank in their groups. Testosterone-treated birds with second rank sang less, and those with lower rank never sang. Thus a combination of top rank and high testosterone titer most strongly activated singing.

Our results confirm SCHLINGER's (1990) observation that social dominance influences singing in wintering white-throated sparrows. They do not confirm, however, any association of singing during winter with white morph or intense interactions. His experiments consisted of pair-wise tests in small cages (35 × 40 × 60 cm) between birds otherwise held indoors in isolation. The association of singing in 19/108 pairwise interactions with intense interactions might have resulted from the previous isolation of the subjects and the small sizes of the cages. The observation that all six singing birds were white morph cannot be evaluated statistically without information about the relative proportions of morphs among all subjects, but the small number of individuals suggests that the result might have occurred by chance.

Does dominance have a direct influence on singing, or is its influence mediated indirectly by an increase in testosterone titers? Our observations in the field cannot decide this issue. White-throated sparrows wintering in our study area had low titers of circulating testosterone, less than one quarter the levels attained by April (means for males and females, January-February, 0.5-1.5 ng/ml) (ARCHAWARANON *et al.*, 1991), but we do not yet have enough information to determine whether individual differences in testosterone titers correlate with singing or dominance.

Our experiments in aviaries indicated a direct influence of testosterone on dominance and singing. As in our previous experiments (ARCHAWARANON *et al.*, 1991), testosterone-treated birds with new opponents tended to have high rank. Only testosterone-treated birds ever sang. The low rates of singing in the field during winter, in contrast to the high rates among many treated birds in aviaries, provided additional evidence that testosterone influenced singing.

It also seems probable that dominance had a direct influence on singing. The administration of exogenous testosterone presumably inhibited secretion of gonadotropins and, consequently, endogenous tes-

tosterone as well. If so, circulating testosterone in treated birds in our aviaries would have remained constant at levels set by their implants. Our results would then require some direct influence of dominance on singing, without the mediation of changes in circulating testosterone. There remains an unexplored alternative, however. If social status modulated the inhibition of gonadotropin secretion by exogenous testosterone, then the influence of dominance on singing might have been mediated by changes in circulating testosterone.

Regardless of the physiological mechanisms involved, there remains a question about the nature of the interaction between testosterone and dominance in controlling singing. Note that high rank in combination with low levels of circulating testosterone, as among dominant birds in the field or in groups in aviaries without testosterone treatment, resulted in low levels of singing. Conversely, high levels of testosterone in combination with low rank, as among treated birds with second or third rank in aviaries, also resulted in low levels of singing. Thus full activation of singing resulted only from the combined influences of testosterone and high rank. To confirm that this joint influence of endocrine and social state on singing is truly multiplicative as opposed to additive, as the present observations suggest, will require a more complete dose-response study, both in the field and in aviaries.

An unexpected result was the absence of singing among grouped birds in aviaries during May before treatment with testosterone. Even top-ranking birds failed to sing without exogenous testosterone. Some isolation from conspecifics is evidently needed for normal seasonal endocrine and behavioral development in this species. A direct test of this hypothesis would require a comparison of grouped and isolated birds in aviaries during May and June.

This result suggests that the seasonal development of territorial behavior might require reciprocal influences of behavior and hormones. In particular, photoperiodic stimulation of gonadal activity in early spring, by increasing both aggression toward and avoidance of rivals, could lead to isolation and dominance, eventually within a territory, which in turn could provide conditions for further endocrine and behavioral development, including full activation of territorial defense and singing.

An influence of isolation on seasonal endocrine and behavioral development would contrast with the immediate influence of aggressive inter-

actions between territorial neighbors, as demonstrated in song sparrows *Melospiza melodia* and possibly red-winged blackbirds *Agelaius phoeniceus* during the breeding season in natural populations (WINGFIELD, 1984, 1985; WINGFIELD *et al.*, 1987; HARDING *et al.*, 1988). An environmental "challenge", such as aggression by a neighboring rival, can stimulate endocrine responses appropriate for meeting the "challenge". In this case, aggressive interactions lead to an increase in circulating testosterone, which in turn might increase aggressiveness. The physiological mechanisms of seasonal territoriality might thus involve both tonic effects of isolation and phasic effects of interaction on endocrine development.

In many species singing and territoriality outside the breeding season do not depend on hormonal activation. Great tits *Parus major* sing at least occasionally in all months of the year, despite low titers of circulating testosterone during winter (ROST, 1990). European robins *Erithacus rubecula* of both sexes sing on territories during the winter (LACK, 1946). In this species testosterone activates singing in both sexes (KRINER & SCHWABL, 1990), but frequency of singing during winter, when titers of gonadal hormones are low, is apparently not influenced by testosterone (SCHWABL & KRINER, 1991; SCHWABL, 1992). Northern mockingbirds *Mimus polyglottos* of both sexes also defend territories during winter, although singing ceases entirely. As in the European robin, territorial aggression at this time has no relationship with circulating testosterone (LOGAN & WINGFIELD, 1990). Territorial behavior during the nonbreeding season without relation to circulating testosterone probably occurs in many other species as well (BURGER & MILLAR, 1980; MOORE, 1988). In many tropical birds, both sexes sing year-round on permanent territories. In at least one of these species, as expected, singing is not correlated with hormonal state (SCHWABL & SONNENSCHNEIN, 1992).

Our results with white-throated sparrows have suggested a number of interactions between social situation and hormonal state in the control of singing. In this species testosterone does not invariably activate singing. Instead, testosterone interacts with dominance to promote singing. Furthermore, some isolation from frequent encounters with rivals, such as that provided by dominance within a territory, evidently contributes to full endocrine development. Many previous studies, mostly on socially isolated birds, have suggested that gonadal recrudescence leads directly to territoriality and singing. Our results here suggest that seasonal endo-

crine and behavioral development might instead be a cascading interaction between hormonal effects on social behavior and social effects on hormonal activity.

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