

- AU, D.W.K., AND R. L. PITMAN. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88:304-317.
- BROWN, R.G.B. 1988. The influence of oceanographic anomalies on the distributions of storm-petrels (*Hydrobatidae*) in Nova Scotian waters. *Colonial Waterbirds* 11:1-8.
- BROWN, R.G.B., S. P. BARKER, AND D. E. GASKIN. 1979. Daytime surface swarming by *Meganyctiphanes norvegica* (M. Sars) (Crustacea, Euphausiacea) off Brier Island, Bay of Fundy. *Can. J. Zool.* 57:2285-2291.
- CLARKE, T. A. 1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *U.S. Fish. Bull.* 72:337-351.
- CROSSIN, R. S. 1974. The storm petrels (*Hydrobatidae*). *Smithson. Contrib. Zool.* 158:154-205.
- CROXALL, J. P., H. J. HILL, R. LIDSTONE-SCOTT, M. J. O'CONNELL, AND P. A. PRINCE. 1988. Food and feeding ecology of Wilson's storm petrel *Oceanites oceanicus* at South Georgia. *J. Zool. (Lond.)* 216: 83-102.
- HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. *Wildl. Monogr.* 85:1-171.
- LINTON, A. 1978. The food and feeding habits of the Leach's Storm-Petrel (*Oceanodroma leucorhoa*) at Pearl Island, Nova Scotia and Middle Lawn Island, Newfoundland. M.Sc.thesis, Dalhousie Univ., Halifax, Nova Scotia.
- MÖRZER BRUYNIS, W.J.F., AND K. H. VOOUS. 1965. Night feeding by Sooty Tern (*Sterna fuscata*). *Ardea* 53:79.
- PITMAN, R. L. 1986. Atlas of seabird distribution and relative abundance in the eastern tropical Pacific. Southwest Fisheries Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, Administrative Report LJ-86-02C.
- SHEVCHENKO, N. F. 1986. Feeding of *Vinciguerria nimbaria* (Gonostomatidae) in the tropical zone of the Atlantic Ocean. *J. Ichthyol.* 26(4):50-56.
- VERMEER, K., AND K. DEVITO. 1988. The importance of *Paracallisoma coecus* and myctophid fishes to nesting fork-tailed and Leach's storm-petrels in the Queen Charlotte Islands, British Columbia. *J. Plank. Res.* 10:63-75.
- WATANUKI, Y. 1985. Food of breeding Leach's Storm-Petrels (*Oceanodroma leucorhoa*). *Auk* 102:884-886.

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## SONG AS PART OF HIGH INTENSITY AGGRESSIVE INTERACTIONS OF WINTERING WHITE-THROATED SPARROWS<sup>1</sup>

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*Key words:* Song; White-throated Sparrow; aggressive behavior; seasonal differences; behavioral polymorphism.

Bird song is generally considered a component of reproductive and territorial behavior of breeding birds (Falls 1969, Thorpe 1961). Some songbirds sing outside of the breeding season in defense of nonbreeding territories (e.g., Lack 1943) yet the functions of these songs is not always known (Saunders 1947, Thorpe 1961). In the northeastern United States, White-throated Sparrows (*Zonotrichia albicollis*) occur in small flocks and are reported to sing fall songs until the end of November and spring songs as early as mid-January though not regularly until mid-February (Saunders

1947, 1948). Breeding birds sing spontaneously on territory or as part of fights or boundary disputes (Falls 1969). I report here of midwinter singing by White-throated Sparrows (WTSPs) during high intensity aggressive interactions under both field and laboratory conditions.

Song of wild WTSPs was observed incidentally during the course of experiments on aggressive behavior of captive flocks of WTSPs (Wasserman et al. 1984). Several groups of six WTSPs were being held in outdoor aviaries (1.2 × 1.8 × 2.4 m) set in a clearing amongst dense scrub vegetation between 13 December 1979 and 15 January 1980. Birds had been captured during October and November 1979 near our observation site at the Manomet Bird Observatory, Manomet, Massachusetts, and then randomly assigned to flocks composed of white-striped (WS) and tan-striped (TS) individuals (Lowther 1961). Birds experienced ambient photoperiods and environmental conditions and were fed Agway mixed seed and water ad libitum.

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Periodically, while we observed these birds from a blind, a wild flock of WTSPs would approach the front of the cages to consume waste seed. On such occasions captive birds would fly to the front of their cages and although separated by 1.27-cm mesh hardware cloth, wild and captive birds would engage in intense aggressive interactions. These interactions on several occasions produced whistled song (Lemon and Harris 1974) from both wild and captive birds. Songs were surprisingly loud and clear but contained fewer notes as compared with breeding birds. During these interactions WS birds from the different flocks were the first to engage each other in aggressive bouts and were the only birds observed singing. Song was not heard during our observations of caged bird aggressiveness, presumably because dominance hierarchies of captive groups were established prior to the start of our studies.

In a subsequent laboratory study on aggression and plasma androgens in nonbreeding WTSPs (Schlinger 1987), singing was again observed so I recorded the behavioral context associated with song under these conditions. For these experiments, individually caged WTSPs were held indoors under light cycles adjusted to ambient winter photoperiod during December and January of 1981–1982 and 1983–1984. Two groups of birds ( $n = 13$ ,  $n = 12$ ) were tested as pairs to determine dominance relationships ( $n = 108$  tests). To record behaviors, two birds were simultaneously released into a cage ( $35 \times 40 \times 60$  cm) and allowed to interact for 10 min. Aggressive disputes between birds were noticeably intensified by adding several mealworms to a tray in the center of the test chamber. Birds were otherwise maintained on a diet of mixed seed and water ad libitum. Six classes of behavioral interactions were identified (Schlinger 1987). The least intense involved avoidance of one bird by another and the most intense involved a challenge at the food tray followed by a prolonged chase throughout the cage. Very aggressive bouts with a clear winner were terminated more quickly and bouts with no interactions were allowed to continue for an additional 5 min. The bird more frequently supplanted during a test was considered subordinate. Following all testing, birds were sexed and gonadal regression confirmed by laparotomy (males = 10WS/5TS, females = 3WS/7TS). Plasma androgen levels were also determined (Schlinger 1987). Total androgen levels were slightly elevated ( $\bar{x} \pm SE = 785 \pm 152.5$  pg/ml) in November 1 week before behavioral testing began but declined to basal levels ( $372 \pm 18.8$  pg/ml) by mid-January 1 week after behavioral testing was terminated. These data do not exclude the possibility that circulating androgens were elevated in some birds during the context of a fight (e.g., Wingfield 1985).

Whistled songs of one to four note duration and moderate amplitude were heard during 19 of the 108 pair tests from six individual singers. Typically, songs of breeding WTSPs include from five to 14 notes consisting of a singlet of sustained frequency followed by singlets, doublets, or triplets generally at a higher pitch (Lemon and Harris 1974). At no time were songs of this length heard. All singing birds (males:  $n = 5$ , females:  $n = 1$ ) were WS. Recipients of song were male ( $n = 7$ ) or female ( $n = 7$ ) and WS ( $n = 4$ , all male) or TS ( $n = 10$ ). Song was associated only with the most intense behavioral encounters that involved a chal-

lenge for proximity to the food tray. In 15 of the 19 interactions in which a bird sang, song occurred simultaneously with a "head dance" or "bill up" display ( $\chi^2 = 5.26$ ,  $df = 1$ ,  $P < 0.05$ ). This display is given by some passerines during agonistic interactions, particularly in a sexual context, but may also be a component of winter aggressive interactions (Balph 1977). Song was also an indication of dominance. In 15 of the 19 tests in which song was heard the singer was later determined to be the dominant individual ( $\chi^2 = 5.26$ ,  $df = 1$ ,  $P < 0.05$ ). Song was not heard in tests in which dominance was determined without a dispute (i.e., avoidance by the subordinate) and not all disputes produced whistled song.

Singing behavior of passerine birds has become an extremely rich area of study for both ethologists and neurobiologists (e.g., Thorpe 1961, Arnold 1982) and the observations reported here are noteworthy for several reasons. First, they combine both field and laboratory observations of song used within the context of extremely aggressive interactions by midwinter WTSPs suggesting that singing plays a role in determining dominance status within or between flock members.

These observations also show that some birds can sing despite having regressed gonads and basal levels of circulating androgens. Song is ordinarily under the control of circulating androgens (for review see Arnold 1982) and it is not unexpected that reduced androgen levels were correlated with reduced quality (e.g., fewer notes and apparent reduced amplitude). Under these conditions, however, song was only heard during the most intense behavioral encounters. During the breeding season when circulating androgens are elevated, birds sing frequently as part of territorial defense (Falls 1969). This suggests that one mechanism whereby androgens increase song is to intensify the aggressiveness of birds. In this way, birds sing more often because they experience a greater frequency of intensely arousing behavioral interactions. Another possibility is that brain regions which control song are made more sensitive by androgens. As a consequence, birds sing under less arousing situations. In the avian brain, regions have been identified which independently control aggression and singing behavior: a group of interconnected nuclei in the telencephalon controls song (Nottebohm et al. 1976), and the hypothalamus/preoptic area (HPOA) seems most important in controlling aggressive behavior (Harding 1983). Paradoxically, however, connections between the HPOA and song-related brain regions have not been identified. Nevertheless, because these regions both contain steroid-concentrating cells (Arnold et al. 1976, Gahr et al. 1987), steroids acting at two or more brain regions may function together to determine the circumstances in which birds sing.

Singing behavior was restricted to WS individuals. This species exhibits plumage variability as a consequence of a chromosomal polymorphism (Thornycroft 1975). Birds with a white-central stripe through the crown (WS) in alternate plumage have an inverted second chromosome which is not found in TS birds (a tan median crown stripe). Lowther and Falls (1968) and Falls (1969) previously reported that WS males sing more frequently than TS males and that WS females sing whereas TS females do not. Although in

some species females can sing a song of similar or reduced complexity when compared with males, and this even in winter (Lack 1943), in most species only males sing (see Brenowitz et al. 1986). The observations that song of breeding or nonbreeding WTSPs is a behavior fundamentally produced by birds of a particular morph of either sex is unique and suggests that song, and the organization of brain regions which control song, are coupled to genetic differences between morphs rather than exclusively linked to the sex chromosomes per se. It is relevant that there are no reported differences in circulating levels of androgens between males and females or WS and TS birds in midwinter to account for the observed differences in singing behavior (Schlinger 1987, Schwabl et al. 1988). In the Zebra Finch (*Poephila guttata*), only adult males sing and male-typical song can be induced in adult females after exposure to sex steroids during development (Arnold 1982). It is possible then that developmental differences in patterns of steroid hormone secretion between the morphs in the WTSP may account for differences in singing behavior during adulthood.

Seasonal differences in singing behavior have also been correlated with seasonal differences in the volumes of the song-control nuclei in some species (Nottebohm 1981, Arai et al. 1989, Kirn et al. 1989). The observation that only WS birds retain the capacity to produce some song elements in midwinter despite plasma androgen levels similar to TS individuals suggests that birds of different morphs may show unique seasonal patterns of growth or steroid sensitivity within brain regions that control song. Interestingly, in the closely related White-crowned Sparrow (*Zonotrichia leucophrys*), despite seasonal differences in overall song performance, there are no seasonal changes in the size of the song-control nuclei (Baker et al. 1984). These birds may retain the neural capacity to produce song for use in winter aggressive interactions.

In conclusion, this report presents evidence that song is part of winter aggressive interactions of WTSPs and points to this species as an interesting model in which to investigate questions about the organization and activation of singing in birds.

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#### LITERATURE CITED

- ARAI, O., I. TANIGUCHI, AND N. SAITO. 1989. Correlation between the size of song control nuclei and plumage color change in Orange Bishop Birds. *Neurosc. Letts.* 98:144-148.
- ARNOLD, A. P. 1982. Neural control of passerine song, p. 75-94. In D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 1. Academic Press, New York.
- ARNOLD, A. P., F. NOTTEBOHM, AND D. W. PFAFF. 1976. Hormone concentrating cells in vocal control and other areas of the brain of the zebra finch (*Poephila guttata*). *J. Comp. Neurol.* 165:487-512.
- BAKER, M. C., S. W. BOTTJER, AND A. P. ARNOLD. 1984. Sexual dimorphism and lack of seasonal changes in vocal control regions of the white-crowned sparrow brain. *Brain Res.* 295:85-89.
- BALPH, M. H. 1977. Winter social behavior of dark-eyed juncos: communication social organization, and ecological implications. *Anim. Behav.* 25:859-884.
- BRENOWITZ, E. A., A. P. ARNOLD, AND R. N. LEVIN. 1986. Neural correlates of female song in tropical duetting species. *Brain Res.* 343:104-112.
- FALLS, J. B. 1969. Functions of territorial song in the White-throated Sparrow, p. 207-235. In R. A. Hinde [ed.], *Bird vocalizations*. Cambridge Univ. Press, London.
- GAHR, M., G. FLUGGE, AND H-R. GUTTINGER. 1987. Immunocytochemical localization of estrogen-binding neurons in the songbird brain. *Brain Res.* 402:173-177.
- HARDING, C. F. 1983. Hormonal influences on avian aggressive behavior, p. 435-467. In B. Svare [ed.], *Hormones and aggressive behavior*. Plenum Press, New York.
- KIRN, J. R., R. P. CLOWER, D. E. KROODSMA, AND T. J. DEVOOGD. 1989. Song-related brain regions in the Red-winged blackbird are affected by sex and season but not repertoire size. *J. Neurobiol.* 20:139-163.
- LACK, D. 1943. *The life of the Robin*. Witherby, London.
- LEMON, R. E., AND M. HARRIS. 1974. The questions of dialects in the songs of white-throated sparrows. *Can. J. Zool.* 52:83-98.
- LOWTHER, J. K. 1961. Polymorphism in the white-throated sparrow. (*Zonotrichia albicollis*). *Can. J. Zool.* 38:281-292.
- LOWTHER, J. K., AND J. B. FALLS. 1968. White-throated Sparrow, p. 1364-1392. In O. L. Austin, Jr. [ed.], *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies*. Am. Nat. Mus. Bull. 237.
- NOTTEBOHM, F. 1981. A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. *Science* 214:1368-1370.
- NOTTEBOHM, F., T. M. STOKES, AND C. M. LEONARD. 1976. Central control of song in the canary, *Serinus canarius*. *J. Comp. Neurol.* 165:457-486.
- SAUNDERS, A. A. 1947. The season of bird song—the beginning of song in spring. *Auk* 64:97-107.
- SAUNDERS, A. A. 1948. The seasons of bird song—the cessation of song after the nesting season. *Auk* 65:19-29.
- SCHLINGER, B. A. 1987. Plasma androgens and aggressiveness in captive winter white-throated sparrows (*Zonotrichia albicollis*). *Horm. Behav.* 21:203-210.
- SCHWABL, H., M. RAMENOFSKY, I. SCHWABL-BENZINGER, D. S. FARNER, AND J. C. WINGFIELD. 1988. Social status, circulating levels of hormones, and competition for food in winter flocks of the White-throated Sparrow. *Behavior* 107:107-121.
- THORNEYCROFT, H. B. 1975. A cytogenetic study of

- the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). *Evolution* 29:611-621.
- THORPE, W. H. 1961. Bird song. Cambridge Univ. Press, London.
- WASSERMAN, F. E., C. DOWD, B. A. SCHLINGER, D. BYMAN, S. P. BATTISTA, AND T. H. KUNZ. 1984. The effects of microwave radiation on avian dominance behavior. *Bioelectromagnetics* 5:331-339.
- WINGFIELD, J. C. 1985. Short-term changes in plasma levels of hormones during establishment and defense of a breeding territory in male Song Sparrows, *Melospiza melodia*. *Horm. Behav.* 19:174-187.

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## SEXUAL DIFFERENCES IN ANTI-PREDATOR BEHAVIOR OF BREEDING AMERICAN AVOCETS AND BLACK-NECKED STILTS<sup>1</sup>

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**Key words:** *American Avocet; Recurvirostra americana; Black-necked Stilt; Himantopus mexicanus; Recurvirostridae; antipredator behavior; sexual dimorphism.*

One hypothesis for the evolution of biparental care in species with precocial young is that two adults are needed for predator defense (Pitelka et al. 1974, p. 194, Lenington 1980). However, even when both parents participate in predator defense, their contributions are unlikely to be equal because of differences in selective pressures on males and females (Trivers 1972, Montgomerie and Weatherhead 1988). In a review of sexual differences in nest protection behavior in shorebirds, Gochfeld (1984) listed 42 species for which differences have been reported and 40 species for which relatively equal participation by the sexes has been reported. Neither the American Avocet (*Recurvirostra americana*) nor the Black-necked Stilt (*Himantopus mexicanus*) appear on the lists but their Eurasian congeners, the Eurasian Avocet (*R. avocetta*) and the Black-winged Stilt (*H. himantopus*), are included as species in which the sexes have relatively equal antipredator roles.

American Avocets and Black-necked Stilts are relatively monomorphic, monogamous shorebirds that exhibit biparental care of eggs and young. They produce a wide variety of mobbing and diversionary displays, which are associated exclusively with breeding (Sordahl 1986). The displays, which are similar for these two members of the Recurvirostridae, have been well described (Gibson 1971a, Hamilton 1975, Sordahl 1986). They include aerial displays such as dive-bombing or circling a predator and ground displays such as crouch-running, false-incubation, and displays in which the wings are extended and moved erratically. No sex-specific displays or other sexual differences in antipredator behavior have been reported in avocets or stilts.

Gibson (1971a, 1978) found no difference between male and female American Avocets in the amount of time spent in diversionary behavior. However, during parts of five field seasons in which I observed many interactions between recurvirostrids and natural predators and staged hundreds more with models of eight predator species or myself as predator, males seemed more aggressive than females. In this paper I describe quantitatively this sexual difference in antipredator behavior.

### METHODS

I spent about 1,000 hr studying American Avocets and Black-necked Stilts in northern Utah during the 1977 and 1978 breeding seasons. Additional observations were made in 1979, 1980, and 1987. My two study sites, the Barrens Company Hunting Club in Cache County and the Bear River National Wildlife Refuge in Box Elder County, are described in Sordahl (1982). About 85 avocet and 25 stilt pairs nested at the Barrens (Sordahl 1981a); breeding populations at the Bear River Refuge were much larger, probably numbering about 2,500 avocet and 1,000 stilt pairs (pers. comm. with refuge personnel). Potential predators of eggs or young were abundant and diverse at both sites, enabling me to record over 500 interactions between recurvirostrids and more than 20 predator species. Predators included at least three species in each of the following groups: ardeids, raptors, gulls, corvids, and mammals. For each observed instance of mobbing, I attempted to record the sex and number of mobbers. Although both avocets and stilts are relatively monomorphic, the sexes usually can be distinguished in the field (Hamilton 1975). However, the distances at which predator interactions were observed often precluded identification of a mobber's sex.

I further studied the antipredator behavior of avocets and stilts experimentally, using myself as a stimulus. Nineteen avocets (13 males, six females) and seven stilts (four males, three females) were nest-trapped (Sordahl 1980) and color-marked. I used a standardized procedure for testing marked adults, which con-

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