

SHORT COMMUNICATIONS

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TAN AND WHITE COLOR MORPHS OF WHITE-THROATED SPARROWS DIFFER IN THEIR NON-SONG VOCAL RESPONSES TO TERRITORIAL INTRUSION¹

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Abstract. White-throated Sparrows (*Zonotrichia albicollis*) occur in two distinct color morphs indicated by the color of the bird's median crown stripe. Tan-striped (TS) and white-striped (WS) sparrows differ in their aggressive behavior, with WS males generally behaving more aggressively than TS males. We measured the number and type of songs and call vocalizations used by TS and WS males in response to simulated territorial intrusion. TS males used significantly more "low aggression" calls compared to WS males. These results suggest that non-song call vocalizations, in addition to measures of song, may be valuable for future studies of territorial behavior and communication in birds.

Key words: aggression, playback, territory defense, vocalizations, White-throated Sparrow, *Zonotrichia albicollis*.

White-throated Sparrows (*Zonotrichia albicollis*) are polymorphic in plumage during the breeding season and can be divided into two distinct phenotypes: white-striped (WS) or tan-striped (TS) according to the color of the bird's median crown stripe (Lowther 1961, Lowther and Falls 1968). This phenotypic difference is a consequence of an autosomal polymorphism on chromosome 2 (Thornycroft 1976). Negative assortative mating maintains this balanced polymorphism so that WS birds of either sex mate with TS birds of the opposite sex over 90% of the time (Falls and Kopachena 1994, Houtman and Falls 1994). Associated with the phenotypic difference are striking behavioral differences in territorial and agonistic behavior (Falls 1969, Ficken et al. 1978, Knapton and Falls 1984). When presented with a WS stuffed model territory intruder, WS males are more likely to attack the model than TS males although the two morphs are equally likely to attack a TS model (Kopachena and Falls 1993). WS males have higher spontaneous singing rates early in the breeding season and approach playbacks more readily than do TS males (Lowther 1962,

Kopachena and Falls 1993, Falls and Kopachena 1994).

White-throated Sparrows usually have a repertoire of only one song type (Borror and Gunn 1965). Variation in song expression may convey information about the motivational state of the singer (Falls and Kopachena 1994) and perhaps introduce communicative range in a bird with only one song type. For example, low-volume whisper songs are thought to indicate a male's ambivalence about a territorial encounter (Falls and Kopachena 1994). Song is clearly not the only means to understand how a bird will defend a territory. Although song is correlated with territory maintenance and high levels of aggression in the White-throated Sparrow, non-song call vocalizations also are used in territory defense. Field observations have established that a territory-holding male White-throated Sparrow will respond to an intrusion by singing, calling, approaching, and attacking the intruder (Falls 1988). White-throated Sparrows of both color morphs maintain and use a complex repertoire of call types, which may afford an important additional means for understanding territory defense in this species.

The songs and call vocalizations of the White-throated Sparrow have been thoroughly described by Lowther and Falls (1968) and more recently by Falls and Kopachena (1994). Based on these descriptions and the contexts in which each call normally occurs, we have classified the most commonly observed call types into two categories, "low aggression" and "high aggression" calls, in order to use these calls as a response measure during simulated territorial intrusion. Although our categorization is along a single dimension (aggression), we are confident that our dichotomy can be reliably measured. Previous descriptions of White-throated Sparrow call vocalizations have outlined the contexts in which different calls are used, the message each call is likely to be sending, and behaviors with which particular calls commonly occur (Lowther and Falls 1968, Falls and Kopachena 1994). We used this information to define our two call categories. For example, the "pink" call is known to be used as an aggressive vocalization during agonistic encounters. Because pinks are accompanied by other

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postural cues, like crest raising and tail flicking as well as flyovers and attacks, the intent of the bird is clearly aggressive and hence pinks are categorized as high aggression calls. Each vocalization is described and categorized below.

Both song and call vocalizations are used in territory defense by both WS and TS males. Because TS males are known to be less aggressive in their response to territorial intrusion than WS males (Kopachena and Falls 1993, Falls and Kopachena 1994), we predicted that WS males would respond to playback with more full songs, and a greater number of high aggression call vocalizations, whereas TS males would respond with fewer full songs, more whisper songs, and a greater number of low aggression call vocalizations.

METHODS

Territorial intrusion was simulated by playing song on 41 White-throated Sparrow territories in Algonquin Provincial Park, Ontario, Canada. The sample consisted of 19 white striped (WS) and 22 tan striped (TS) birds. Each playback lasted 5 min during which White-throated Sparrow song was played at 10-sec intervals from a Uher 4200 Report Stereo. One or two songs were played on territories either known or likely to be inhabited by White-throated Sparrows. The presence of a White-throated Sparrow was confirmed either when the bird approached or when any white-throat vocalization was heard. The Uher was then placed in a visible location, switched on, and observed from a distance of at least 10 m for a 5-min trial. All vocalizations were tallied. An effort was made to place the Uher in a central location in the territory. All playbacks were conducted during the first week of June to eliminate any changes in response levels due to season. Two different recorded songs were used in this experiment, each for approximately 50% of playback trials, balanced across subjects. Both song samples were high quality recordings from the tape library of J. B. Falls (University of Toronto). All birds were classified as either naive or non-naive, where the non-naive type were known to have been exposed to playback earlier in the season (see details below). Approximately 59% of TS males and 42% of WS males were naive.

In our sample of 41 White-throated Sparrows, there were 19 non-naive males that had been netted and banded earlier in the breeding season. The remaining 22 naive birds in the sample consisted of 13 TS males and 9 WS birds which were presumed to be males based on their behavior. Because TS females do not sing and do not respond to territorial intrusion (Falls 1969, Falls and Kopachena 1994), any TS bird responding to playback was assumed to be male. The majority of the TS males responding to playback sang, confirming the fact that they were males. When WS females respond to song playback, they are often accompanied by their TS male mate (Kopachena and Falls 1993, Falls and Kopachena 1994). None of the naive WS birds in our sample was accompanied by a TS bird. WS females also tend to respond to song playback with trill vocalizations (Lowther 1962, Falls and Kopachena 1994). The nine naive WS birds did not trill more frequently or differ in any of their vocal responses from the known, non-naive WS males. All

of the naive WS birds responded to playback with song and various high and low aggression calls. Six of the nine naive WS birds also flew at and attacked the speaker broadcasting song, which is a highly aggressive response not observed in female WS White-throated Sparrows during territory defense. Based on these criteria, we are confident that all of the naive TS and WS birds in our sample were male.

DESCRIPTION OF VOCALIZATIONS

Low aggression vocalizations. Whisper songs (or quiet songs) are commonly heard from males responding to playback at the boundaries of their territories (Lowther and Falls 1968, Falls and Kopachena 1994). Whisper songs are thought to indicate ambivalence about a territorial encounter and may elicit weak responses from other males (Falls and Kopachena 1994).

The trill vocalization consists of a series of short notes which can occupy a wide frequency range. Trills are mainly uttered by females either spontaneously or in answer to male song and are often associated with a copulation solicitation (Lowther 1962). Male White-throated Sparrows will sometimes trill in response to territorial intrusion before they begin singing (Lowther and Falls 1968, Falls and Kopachena 1994).

The seep (*tseet*) is a high pitched call note. Seeps are commonly used as contact calls when individuals are closer to the ground (feeding) and are visually isolated from one another. Seeps can be variable in volume, difficult to localize, and may indicate a mild warning when used during a territorial encounter (Lowther and Falls 1968).

High aggression vocalizations. The pink note is a loud and easily localized call that functions both as an alarm call and as an aggressive vocalization in an agonistic encounter. The loudest pink notes occur during agonistic encounters. Pink notes indicate excitement or alarm and are often accompanied by crest-raising, tail flicking, flyovers, and occasionally attacks (Falls and Kopachena 1994).

The use of full song in territory defense has been extensively studied (Krebs 1977, Krebs et al. 1978) and is used more frequently by WS males than TS males in response to territorial intrusions in the early portion of the breeding cycle (~1 May to 1 June) (Lowther and Falls 1968, Kopachena and Falls 1993). Singing of full songs commonly occurs before and after chasing or fighting when territory boundaries are being established and defended. Speaker replacement experiments have demonstrated that the sound of full song alone is effective in maintaining a territory for a short time in the absence of a territory holding male (Krebs 1977, Falls 1988).

Other common White-throated Sparrow vocalizations include the chip-up call and the partial song. These are not described here or included in our analyses, even though they were measured in this experiment. In the majority of playback trials of both color morphs neither the chip-up call nor partial song were used. For sonograms of calls, see Falls and Kopachena (1994).

Vocalization rates were analyzed for the two color morphs using nonparametric Mann-Whitney *U*-tests. A layered Bonferroni method was used to correct for multiple comparisons (Darlington 1990). All values re-

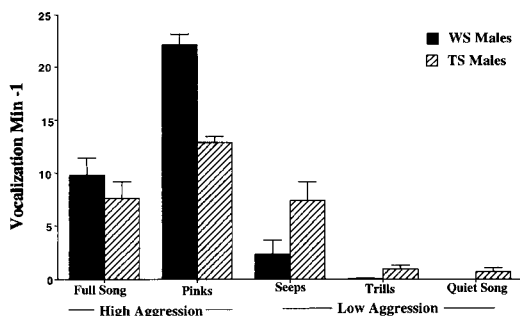


FIGURE 1. Mean (\pm SE) vocalization rates of white-striped (WS, $n = 19$) and tan-striped (TS, $n = 22$) male White-throated Sparrows responding to simulated territorial intrusion.

ported below are means \pm SE. Probability values less than 0.05 are considered statistically significant.

RESULTS

Three vocalizations which appear to reflect ambivalence or lower levels of aggression about a territorial encounter, seeps, trills, and whisper (quiet) songs were more prevalent in TS males than in WS males (Fig. 1). TS males "seeped" significantly more than WS males during playback trials (WS: 2.4 ± 1.3 seeps, $n = 19$; TS: 7.4 ± 1.8 seeps, $n = 22$; $z = 2.71$, $P < 0.01$). TS males also "trilled" more than WS males in response to song playback (WS: 0.05 ± 0.05 trills, $n = 19$; TS: 0.95 ± 0.32 trills, $n = 22$; $z = 2.68$, $P < 0.01$) and sang more whisper songs (WS: 0, $n = 19$; TS: 0.68 ± 0.39 songs, $n = 22$; $z = 1.93$, $P = 0.054$). When corrected for multiple comparisons using a layered Bonferroni method, the trill ($P < 0.04$) and seep ($P < 0.04$) vocalizations, but not the whisper song ($P = 0.16$), remained statistically significant. Because all of the low aggression calls differed significantly in the same direction before Bonferroni correction, the hypothesis that TS males use more low aggression calls than WS males is supported.

White-striped males, on average, sang more full songs in response to playback than did tan-striped males, but this difference was not statistically significant (WS: 9.8 ± 1.7 songs, $n = 19$; TS: 7.6 ± 1.6 songs, $n = 22$; $z = -1.09$, $P = 0.27$). WS males also "pinked" more than TS males, although again this difference did not reach statistical significance (WS: 22.1 ± 10.6 , $n = 19$; TS: 12.9 ± 5.8 , $n = 22$; $z = 0.28$, $P = 0.77$).

DISCUSSION

Tan-striped White-throated Sparrow males respond to playback with more low aggression calls than white-striped males during the second month of the breeding season, supporting our hypothesis that TS males produce more low aggression calls in response to simulated territorial intrusion. Production of high aggression calls did not differ significantly between TS and WS males in this study. Our hypothesis that WS males produce more high aggression calls in response to playback was not supported. However, WS males have been found to be more aggressive and have a higher spontaneous rate

of singing in the first month of the breeding season (Lowther 1962, Kopachena and Falls 1993). Our study was conducted during the first week of June (the second month of the breeding season). It is possible that the rate of production of high aggression calls declines in WS males just as the use of full song, a high aggression signal, declines in WS males in the second month of the breeding season. The advantage of measuring territorial behavior using call vocalizations is that we are still able to detect differences in aggressive behavior between TS and WS males at a time of year when significant differences in song no longer exist.

Full song alone does not provide as much information as full song plus call vocalizations when attempting to identify differences in territorial or other aggressive behavior. This study supports earlier results which demonstrated differences in territorial behavior between the two White-throated Sparrow color morphs and illustrates the importance of examining the use of both call vocalizations and song to evaluate the territorial and aggressive vocal behavior in any species. Whereas we know song alone will deter territory invaders, even in the absence of the resident male (Krebs 1977, Krebs et al. 1978), it may be possible for other aggressive vocalizations, such as the "pink" call, to contribute as a deterrent. Studies which test the effectiveness of calls alone or calls and song in territory maintenance and the proportion of call types used in territory defense could greatly increase our understanding of the role of call vocalizations.

Call vocalizations are used by many bird species to indicate alarm, but may be used in more contexts in species with only one song type. Single-song species, like the White-throated Sparrow, may use calls in combination with song in aggressive encounters to communicate information such as level of aggression or motivation to attack, whereas species with larger song repertoires may not need to rely as heavily on calls. For example, the territorial Field Sparrow (*Spizella pusilla*) has two song types, the multi-purpose *simple* song and the highly aggressive *complex* song, which is used exclusively in agonistic contexts when the birds are highly motivated to defend their territory (Nelson and Croner 1991). Whereas White-throated Sparrow calls communicate level of alarm, or motivation to attack, calls may be able to communicate additional information. Much more study is needed before we can fully understand all of the functions of call vocalizations in this species.

Studies of variation in the use of calls with motivational state and information content of calls have tended to be conducted in non-songbird species (vervet monkey, *Cercopithecus aethiops*, Seyfarth and Cheney 1990; Eastern chipmunk, *Tamias striatus*, Weary and Kramer 1995; Chicken, *Gallus gallus*, Marler and Evans 1996). Perhaps this is because studies in songbirds have been largely focused on the rich song variation across and within species. The results of this study suggest that it may be useful to attend to call vocalizations of songbirds in further studies of communication in birds. The White-throated Sparrow, with its two color morphs, is an ideal species in which to demonstrate the benefits of examining calls because more is known about their call vocalizations and the

contexts in which they are commonly used. Further study is necessary to determine how the results of an investigation like this one are affected by season, to what extent complex information can be conveyed through call vocalizations in birds, and how reliance on calls may vary with song repertoire size.

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MICROGEOGRAPHIC SONG DISCRIMINATION IN A NONTERRITORIAL PASSERINE, THE BOAT-TAILED GRACKLE¹

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Abstract. We used playback in the field to test Boat-tailed Grackles (*Quiscalus major*) for the ability to discriminate local songs from foreign songs. Male grackles responded more strongly to songs recorded at

their own colony than to songs recorded at colonies 4–13 km distant. Female grackles showed little response to either local or foreign song.

Key words: bird song, Boat-tailed Grackle, *Quiscalus major*, song discrimination.

Female Boat-tailed Grackles (*Quiscalus major*) nest colonially in reeds or trees. A male Boat-tailed Grackle

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