

THE TERRITORY DEFENSE FUNCTION OF SONG IN SONG SPARROWS:  
A TEST WITH THE SPEAKER OCCUPATION DESIGN

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## SUMMARY

Territory defense is considered one of the primary functions of bird song, but this hypothesis has been directly tested in only a few cases. We used the speaker replacement method to ask whether song functions as a “keep out” signal in song sparrows, a species for there is considerable evidence supporting a mate attraction and stimulation function of song, but only indirect evidence that song functions as a signal to other males. We removed 11 matched pairs of male song sparrows from their territories, replacing one male of each matched pair with loudspeakers broadcasting that male’s song (the “experimental” territory) while leaving the other male’s territory silent (the “control”

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territory). In all cases in which encroachments or takeovers occurred, these occurred first (or solely) on the control territory of a matched pair, supporting the hypothesis that song functions in territory defense in this species. The incidence of intrusions on control territories was very low, however, posing difficulties for the interpretation of speaker replacement experiments designed to ask more specific questions about how song functions in male-male aggressive competition.

## INTRODUCTION

Bird song, as with the calls of frogs and songs of acoustic insects, is thought to have two principal functions: attraction and stimulation of females, and territory defense (Catchpole & Slater, 1995; Searcy & Andersson, 1986). Most of the evidence that bird song functions as a “keep out” signal in territory defense is indirect, however, consisting of observations such as the coincidence of seasonal periods of song with periods of territory defense (e.g., Catchpole, 1973), the tendency of territory owners to increase singing rates when faced with an intruder (e.g., Kramer & Lemon, 1983), and the use of song in interactions between neighboring territory owners (e.g., Krebs et al., 1981). All these patterns are suggestive, but none directly demonstrates that song is effective in keeping rival males off a territory.

This lack of direct evidence reflects the difficulty of finding appropriate and tractable methods for experimentally testing the role of song in territory defense. The predominant method for investigating communication between male birds is territorial playback, in which a song is played from a loudspeaker set on a male's territory and the aggressive response of the owner is measured (Falls, 1992). This technique has been highly successful in answering questions about discrimination, for example questions concerning species or neighbor recognition (Becker, 1982; Stoddard, 1996). Territorial

playback, however, does not directly answer questions about the territory defense function of song. Song is thought to function in territory defense by keeping intruders off the territory, but territorial playback measures the response of owners, rather than intruders, and songs score well if they evoke aggression, rather than avoidance.

Two experimental designs exist that better assess the function of song in territory defense: muting and speaker occupation. In muting experiments, territorial males are rendered unable to sing, either by denervating the syrinx (Peek, 1972) or by puncturing the interclavicular air sac (Smith, 1979). Muting experiments have been performed on three species, red-winged blackbirds (*Agelaius phoeniceus*) (Peek, 1972; Smith, 1979) seaside sparrows (*Ammodramus peninsulæ*) (McDonald, 1989), and ochre-bellied flycatchers (*Mionectes oleagineus*) (Westcott 1992); in all three species muted males experience increased rates of intrusion and territory loss relative to unmuted controls, providing direct evidence for the territorial function of song. The utility of this method is limited, however, to testing the general function of song as a “keep out” signal; it does not provide a means for testing more specific functional hypotheses, such as whether large repertoires are more effective than small repertoires in territory defense.

In speaker occupation experiments, owners are removed from their territories and replaced by speakers broadcasting song (Göransson et al., 1974; Krebs, 1977). Such experiments have been performed with four species: thrush nightingales (*Luscinia luscinia*) (Göransson et al., 1974), great tits (*Parus major*) (Krebs, 1977; Krebs et al., 1978), red-winged blackbirds (Yasukawa, 1981a, b), and white-throated sparrows (*Zonotrichia albicollis*) (Falls, 1988). In all cases, territories defended by broadcast song remained unoccupied longer or suffered lower rates of intrusion relative to control territories from which the male is removed but no song is broadcast (although not all these studies used large enough samples to permit statistical analysis of the effect). The important advantage of speaker replacement experiments is that they offer the possibility of testing more specific hypotheses about how song functions in territory defense,

because one can compare the relative effectiveness of different kinds or patterns of songs in repelling males from the territory.

Our goal in the present study is to test the territory defense function of song in the song sparrow (Melospiza melodia). Song sparrows are monogamous, territorial passerines, widespread in North America (Nice, 1937). Territorial male song sparrows sing throughout their 3 to 4 month breeding season (Nice, 1943). Each male song sparrow has a repertoire of approximately 5 to 14 discrete song types (Borror, 1965), but also sings an apparently unlimited number of variants of each type (Podos et al., 1992). Strong evidence already exists for an intersexual function of song in song sparrows, including the observation that singing rates drop dramatically when males attract a female and rebound if that mate is lost (Nice, 1943; Searcy, 1984), and experimental demonstrations that song stimulates females to perform copulation solicitation display (Searcy & Marler, 1981). Support for an intersexual function of song does not, of course, preclude song from also having an intrasexual function in territory defense (Catchpole & Slater, 1995).

Some patterns of singing behavior shown by male song sparrows have been interpreted as aiding in defense of territory. Kramer and Lemon (1983; Kramer et al., 1985) showed that male song sparrows increase the frequency with which they switch between song types as the context of singing becomes more aggressive, and suggested that switching rate is used as a graded aggressive signal aimed at other males. Beecher et al. (1996) found that male song sparrows in a Washington population interact with neighbors by "repertoire matching," replying to a neighbor with a song in that neighbor's repertoire. Matching is thought to be a tactic that allows an aggressive message to be aimed at a specific individual (Brémond, 1968), and thus is also interpreted as functioning in male-male aggressive competition for territories. These interpretations of song switching and song matching presuppose that song functions in territory defense, an assumption that has not previously been tested in song sparrows.

We chose speaker occupation to test the territory defense function of song because this design can be elaborated to test the relative effectiveness of different types of song or singing behaviors. If initial experiments demonstrated that presence of song is more effective in limiting intrusion onto territories than is absence of song, we planned to move on to look at more complex questions, such as whether variable song is more effective in territory defense than is invariant song, whether faster song rates are more effective than slower rates, and so forth.

## METHODS

Experiments were performed during June, 1995, May and June, 1996, and May, 1997 on Pennsylvania State Gamelands No. 285 in Crawford County, Pennsylvania. The song sparrows used in the experiments held territories on the margins of old fields, in some cases where the old fields bordered second growth deciduous forest, and in other cases where the old fields bordered a lake or marsh.

Our basic procedure was as follows: 1) We chose a pair of nearby territories, and randomly designated one as a control and one as an experimental territory. 2) We removed the owners from both territories as simultaneously as possible. 3) We set out two speakers on the experimental territory, and played recorded songs of the original owner alternately from one speaker and then the other throughout the remainder of the trial, while leaving the second territory as a silent control, unoccupied by speakers. 4) We observed which of the two territories (if either) was first to be wholly or partially taken over by another male song sparrow. We expand on each of these points below.

1) Each pair of experimental and control territories was located in the same old field, and was chosen so that the two territories would be matched as much as possible for size, habitat quality and for the density of local territory owners and floaters. In no case, however, were the experimental and control territories adjacent, i.e. none shared

any boundary. In all cases we had previously color banded the owners of both territories in a pair, so that we could map territory boundaries prior to the trial. Finally, in all cases we had previously recorded songs from the owners of both territories. We recorded owners of control as well as experimental territories so that there could be no bias towards using better singers as experimental rather than control males. Only after recordings of both birds were complete did we choose one of the pair as the experimental territory using a coin flip.

2) We removed owners of experimental and control territories by attracting them to mist nets using playback of song sparrow song. For this purpose, we constructed a playback tape for each experimental and control territory using one song of the owner of that territory; by playing only the owner's song during capture we sought to minimize the chance that playback would seem to neighboring males to represent an intrusion onto the territory. We attempted to capture both the experimental and control males as simultaneously as possible early in the morning on the first day of the trial, using as few playback songs as possible. On two occasions we succeeded in capturing an owner using only three playback songs, whereas at the other extreme we once continued playback intermittently for 70 minutes before succeeding. More typically males were captured with 2-10 minutes of song. During two trials we used playback of swamp sparrow (Melospiza georgiana) distress screams as well as song sparrow song in capturing males. During 3 of 11 pairs of trials we failed to capture one of the two target owners on the initial day, and therefore performed the second removal one or two days later (see Table 1). Experimental males were removed on average at 06:12 (EDT) and control males on average at 06:21. Removed males were held in cages and provided with mealworms, grain, and water, and all were released in good condition at the end of the trial. Most immediately reoccupied their territories.

3) As soon as an experimental male was removed, we set up two speakers 15 m apart on his territory. Speakers were placed in bushes or trees at a height of 1-2 m. A

Sony TC-D5M stereo cassette recorder and two matched SME speakers (Saul Mineroff Electronics, Elmont, NY) were used for playback. Playback tapes were constructed so that 3 minutes of song would be played from one speaker, followed by 1 minute of silence, 3 minutes of song from the second speaker, 1 minute of silence, etc. During the 3 minutes of song, songs were presented at the rate of 1 song per 10 sec. Songs consisted of six variants (Podos et al., 1992) of one song type recorded from the owner of the territory; thus a different playback tape was used in each of the 11 experimental trials. Playback tapes were made using digitized songs recorded previously from the experimental male (25kpts/s, SIGNAL sound analysis software; Beeman, 1996). Amplitude was set at a level that seemed by ear to match that of singing males in the field, and was measured as 89-92 dB (depending on the song) at 1 m. We started playback on the experimental territory on average about 20 minutes after the male was removed.

4) During the eight pairs of trials for which we removed experimental and control males on the same day, one observer watched both territories alternately, spending an equal amount of time watching each during successive 30 min periods. During the three pairs of trials for which the experimental and control removals occurred on separate days, an observer watched the relevant territory continually. During 1995, we continued playback and observations until 20:00 on the day of the removal, and then discontinued the trial whether or not any takeover had occurred on either territory. During 1996 and 1997, we continued trials into a second day if no takeover occurred during the first day. In these cases, we discontinued playback at dusk (ca. 20:30) on the first day, resumed playback at dawn (ca. 05:30) on the second day, and continued the trial to 10:00 on the second day.

We used the presence of a singing male on a removal territory as our criterion for defining a takeover or encroachment. If the intruding male sang throughout the territory, we termed the event a takeover, whereas if the intruder was a neighbor who sang from

only a portion of the removal territory adjacent to his own territory, we termed the event an encroachment. Only neighbors encroached by our definition; invading floaters invariably attempted to take over the entire territory, although they might be prevented from doing so by an encroaching neighbor or another intruding floater. In almost all cases, we had color banded the neighboring territory owners prior to a trial, but even if we had not done so we could tell if an intruder was a neighbor from his behavior on the adjacent territory. Requiring that an intruder sing before counting the event as a takeover or encroachment removed ambiguity about the sex of the intruder and about whether the intrusion was an attempt to annex all or part of the territory, rather than just a foraging visit.

## RESULTS

We carried out 11 pairs of experimental and control trials over three years. A synopsis of the trial outcomes is given in Table 1. During 3 pairs of trials, neither the experimental nor the control territory was taken over or encroached upon. In all 8 of the remaining cases, takeover or encroachment occurred earlier on the control territory than on the matched experimental territory. The difference in outcomes is highly significant by a sign test ( $P < 0.005$ , one-tailed test). Playback of songs thus delayed full or partial takeover of the territory by another male, as predicted by the hypothesis that song functions in territory defense.

In 3 pairs of trials both the experimental and the control territory were fully or partially taken by one or more other males, in five pairs of trials only the control territory was fully or partially taken, and in three pairs neither territory was taken (Table 1). These outcomes are not completely comparable across pairs of trials because territories were exposed to the possibility of takeover for a different length of time in 1995 as compared to 1996 and 1997 (see Methods). Nevertheless, it is clear that song playback



was not absolutely effective in preventing takeover. This conclusion is not surprising; presumably if we had continued the trials long enough, we would expect all or almost all territories eventually to be annexed by other males, whether defended by playback or not. What is more unexpected is that encroachments or takeovers did not occur at all for the duration of our observation period in 3 of 11 control territories and took more than 24 hrs to occur in another 2 control territories.

## DISCUSSION

Our results support the hypothesis that song in song sparrows functions in territory defense. Territories from which we had removed the original owner remained unoccupied longer when defended by playback of the owner's song than when not defended by playback (Table 1). We assume this effect occurs because potential intruders interpret the songs emanating from an experimental territory as indicating that the area is occupied by a male song sparrow who may attack them if they enter his territory. By contrast, the silent control territories give less evidence of being occupied, and neighboring and floater males intrude more readily there. This interpretation is consistent with previous speaker occupation studies, all of which have supported a territorial function of song (Göransson et al., 1974; Krebs, 1977; Krebs et al., 1978; Yasukawa, 1981a, b; Falls, 1988)

Our results differ from earlier work in the relatively low incidence of encroachment and takeover we observed for control territories, where the removed male was not replaced with song. In fact, only 6 of 11 (55%) of the control territories had any incursions within 10 hours of the removal of the male. Our earliest intrusion on a control territory began about 3 hrs after the male was removed. By contrast, Krebs et al. (1978) found that in great tits replacement males occupied the majority of space in all three of the control areas within 6 hrs following removal of resident males. Intrusions rates were

so high in red-winged blackbirds that Yasukawa (1981a,b) was able to confine his observations to a 2-hr period following removal. Neighboring redwings trespassed at an average rate of over 4 trespasses/hr within these first 2 hrs; 6 of 38 trials had to be aborted because the territory was taken over by a floater before there was time to begin the experimental playback (Yasukawa, 1981a). Falls (1988) found that in white-throated sparrows, all eight of his control territories suffered an intrusion less than 5 hrs after the male was removed; the average time to first intrusion was less than 2 hrs. Only in thrush nightingales do intrusion rates appear to be as low as in song sparrows (Göransson et al. 1974).

It is not apparent why we observed such a low incidence of intrusions on our control territories. We would expect competition for territories to positively covary with the number of floaters in the population, and so it may be that there were relatively few floaters present at our study sites. The presence of floaters, however, is usually determined by observing territorial take-overs following the death or removal of territorial males, and we did not have an independent means for assessing the numbers of floaters in our population. It also is possible that male-male competition in our population is greater earlier in the season, when males are first setting up their territories. Some territorial interactions between neighboring males continue to occur through May and into June in our population, however, and territorial males occasionally disappear while others insert into a field, suggesting that male-male competition is still important during the period we conducted our tests.

We chose the speaker occupation design to test the territory defense function of song in song sparrows because the method can be elaborated to address more specific questions, such as whether variable song is more effective in defense than invariant song (e.g., Krebs et al., 1978; Yasukawa, 1981b). We are discouraged, however, about using speaker occupation to pursue these more complex questions in song sparrows because of the difficulties associated with the low intrusion pressure we observed and the resulting

high proportion (27%) of control trials in which incursions never occurred. The effect size for our song versus no song comparison was large enough that we nonetheless observed a significant result, but we expect smaller effect sizes when comparing the effects on defense of one kind of song or singing behavior to another. Suppose, for example, that we wanted to test whether a fast singing rate (e.g., 6 songs/min) was more effective in territory defense than a slow singing rate (e.g., 3 songs/min), and that the actual effect of these treatments was that territories defended by the slow rate would be twice as likely to be taken over first than territories defended by fast rates. With this effect size, we would need a sample of about 30 pairs of control and experimental territories with a takeover to show a significant difference using a (one-tailed) sign test. If 27% of the pairs showed no takeovers at all (as we observed in the present experiment), then the overall sample size would have to be about 41 control and experimental territories in order to have enough statistical power to find an effect. Given the length of the trials, achieving such a sample size would be extremely laborious. In general, speaker occupation should be more tractable when used with species (or populations) having greater intrusion pressure from neighboring or floater males, because high intrusion pressures allow the duration of trials to be shortened while keeping the proportion of trials with no intrusion low. Yasukawa's (1981a, b; Yasukawa et al., 1982) results with red-winged blackbirds, which are polygynous and experience intense male-male territorial competition (Searcy and Yasukawa, 1995), exemplify this point.

Falls (1988) points out another factor affecting the success of speaker occupation experiments — the visual conspicuousness of singing males — and suggests that the method should work best in species in which males are visually inconspicuous, presumably because the illusion of territory occupation can be maintained longer with song alone if the expectation of actually seeing singing owners is low. Our results are consistent with Falls' generalization: song sparrows are small, well-camouflaged birds living in a moderately-vegetated habitat, and speaker occupation does deter intrusions on

empty territories. Male white-throated sparrows, the species tested by Falls (1988), are somewhat larger and less camouflaged than song sparrows, but they occupy a more densely-vegetated habitat. Thrush nightingales (Göransson et al., 1974) and great tits (Krebs, 1977; Krebs et al., 1978) also both live in densely-vegetated habitats and speaker occupation appeared to delay territory takeover in both species (although sample sizes in these studies were too small for the effect to be statistically significant). By contrast, Falls (1978, 1988) reports that speaker occupation has little effect in deterring takeover of empty territories in Australian magpies (*Gymnorhina tibicen*), a species that Falls (1988) characterizes as large, strikingly colored, and occupying open habitat.

The red-winged blackbird provides a possible exception to Falls' generalization. Male redwings have striking red and black plumage and are quite conspicuous when perched, as they normally are, high in the reeds in marshes. Nevertheless, speaker occupation experiments by Yasukawa (1981a,b; Yasukawa et al., 1982) show that song playback does deter intrusion onto empty territories. The effects of song on intrusion in this species, however, are smaller quantitatively than those found in other species studied thus far. That these effects are statistically significant reflects the practical advantages of working with redwings outlined above rather than any greater importance of song in territory defense. Shorter test durations and a higher likelihood of intrusions occurring in redwings permit larger sample sizes than can be readily achieved with species like song sparrows or great tits, and therefore a greater likelihood of finding significance for a subtle effect.

Despite the problems we see with speaker occupation experiments, this design seems essential for examining some central questions in avian communication. As one example, song matching in birds in general, and repertoire matching in song sparrows in particular, have been suggested to function as aggressive signals directed at particular rivals (Brémond 1968; Beecher et al., 1996). It is difficult to see how such a function could be tested directly other than with some form of speaker occupation experiment.

Speaker occupation experiments would also seem to be the most direct method of addressing questions such as whether local song is more effective than foreign dialects in territory defense, whether variable song is more effective than invariant song (Krebs et al. 1978; Yasukawa, 1981b), and whether individual distinctiveness of song benefits males in defense. It may thus be necessary to improve on or elaborate the design of speaker occupation experiments to overcome difficulties inherent with this method.

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Table 1. The outcome of male removal experiments with song sparrows. Experimental territories were occupied by two loudspeakers alternately broadcasting song sparrow song; control territories were not defended by broadcast song.

Year	Trial #	Treatment	Date	Outcome
1995	1	Experimental	June 4	no encroachment/takeover
		Control	June 5	no encroachment/takeover
	2	Experimental	June 6	no encroachment/takeover
		Control	June 6	no encroachment/takeover
3	Experimental	June 8	no encroachment/takeover	
	Control	June 9	encroachment by neighbor starting 9:23 into trial	
4	Experimental	June 12	encroachment by neighbor starting 7:17 into trial	
	Control	June 10	takeover by neighbor starting 5:28 into trial	
1996	5	Experimental	May 18	takeover by floater starting 26:41 into trial
		Control	May 18	takeover by floater starting 24:11 into trial
	6	Experimental	May 23	no encroachment/takeover
		Control	May 23	no encroachment/takeover
7	Experimental	May 30	no encroachment/takeover	
	Control	May 30	takeover by 2 floaters starting 4:58 into trial	
8	Experimental	June 2	no encroachment/takeover	
	Control	June 2	takeover by 2 floaters and 1 neighbor starting 6:02 into trial	

1997	9	Experimental	May 18	no encroachment/takeover
		Control	May 18	encroachment by 2 neighbors starting 27:31 into trial
	10	Experimental	May 23	no encroachment/takeover
		Control	May 23	takeover by floater starting 5:28 into trial
	11	Experimental	May 27	takeover by floater starting 4:00 into trial
		Control	May 27	takeover by floater starting 2:55 into trial