

AN EXAMINATION OF THE INFLUENCE OF SOCIAL INFORMATION ON
TERRITORY SELECTION BY A PARTIALLY MIGRATORY POPULATION OF
SONG SPARROWS (*Melospiza melodia*)

By

Jackson Evans

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A thesis presented to the faculty of the Graduate School of Western Carolina University
in partial fulfillment of the requirements for the degree of Master of Science in Biology

By

Jackson Wesley Evans

Adviser:

Dr. Jeremy Hyman
Assistant Professor of Biology
Biology Department

Committee Members:

Dr. Seán O'Connell, Biology
Dr. Tom Martin, Biology

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ABSTRACT

Territory selection can greatly affect a species' ecology, from density to interactions among individuals. Previously, habitat quality was found to be one of the driving forces in territory selection. However, the use of social information received from other individuals in a population has shown to also play a role in territory selection, especially when habitat is consistent. In a study of black-throated blue warblers, Betts et al. (2008) were able to influence territory selection by playing song in empty potential territories during the post-breeding season when juveniles and males were prospecting for territories. The following year, more males set up territories in the places where song had been played than in places where it had not. I looked to see if a similar effect could be observed in a partially migratory population of song sparrows. Song sparrows have a much longer breeding season than black-throated blue warblers, remaining territorial from early in the spring into the autumn, and many male song sparrows remain year-round residents. Empty territories in suitable habitat were found across the campus of Western Carolina University and song was played in half of them for ten hours a day for ten days during August of 2009. Point counts were done in every territory until April of 2010, and playbacks were done in every territory in May and June of 2010 to test for territoriality. While there was initially a strong presence of birds in the experimental territories compared to the control, ultimately there was no difference in occupancy between experimental and control territories. This could be partially due to density-dependent habitat selection since the population at the field site was very dense. Song sparrows also display a wide variety of territorial behavior, which could result in less

emphasis on social information in territory selection when compared to black-throated blue warblers.

INTRODUCTION

Territory selection in songbirds plays a large role in a species' ecology, affecting population size, density, and interaction among individuals (Morris 2003). For songbirds, correlations between population density and habitat type have been found, leading to the conclusion that habitat quality is the driving factor in territory selection (Anderson et al. 1974, MacArthur et al. 1962). When habitat quality is variable, specific aspects of habitat may play a larger role in territory selection. Bobolinks (*Dolichonyx oryzivorus*) have been found to select territories where there is the least amount of leaf litter present (Wiens 1969), and silver grebes (*Podiceps occipitales*) and Rolland's grebes (*Rollandia rolland*) nested in the densest tules near deep, open water more often than in less dense tules (Burger 1974).

However, more recent studies suggest that observing other individuals for social information, defined as information received from other individuals in a population, may also play a large role in territory selection (Danchin et al. 2004, Betts et al. 2008). Still other studies have suggested that, when habitat quality varies little or predictably from year-to-year, social information may be as or more important than an individual's assessment of habitat in territory selection (Danchin et al. 1998). For instance, in habitats with little or predictable temporal variation, it can be more beneficial to select territories based on social information like conspecific reproductive success, rather than solely on philopatry or the mere presence of conspecifics (Doligez et al. 2003).

Betts et al. (2008) examined the use of social information in territory selection by the migratory black-throated blue warbler (*Dendroica caerulescens*). The authors selected potential territories in both favorable and unfavorable habitats where no males

were present. During the post-breeding season when all offspring were fully fledged, the researchers played song in many of the territories while not playing any song in others. Song was used to mimic the presence of a male and thus potential reproductive success to any males that were prospecting for a new territory. In the following breeding season, significantly more of the experimental territories in both favorable and unfavorable habitat had been settled than in the empty territories where no song had been played. This suggests that in the black-throated blue warbler, social cues may be more important than habitat in territory selection (Betts et al. 2008).

My study further tested the role of social information in territory selection. While Betts et al. (2008) examined the relationship between social and habitat cues in black-throated blue warblers, which are habitat specialists neotropical migrants that leave their breeding grounds during the fall and winter, no studies have examined the role of social cues in territory settlement by songbirds with different habitat use patterns. Song sparrows (*Melospiza melodia*) are edge habitat generalists found over most of North America. While some populations are either long or short-distance migrants, the population at the campus of Western Carolina University is partially migratory with many males remaining year-round (Carroll 2010). In some nonmigratory populations of song sparrows, year-round territory maintenance and defense has been shown to occur (Wingfield et al. 2002), and males at my study site were observed singing well into the autumn. The song sparrows' breeding season in our population is also much larger than that of the black-throated blue warblers, with copulations seen as early as April and as late as August. Given these differences, the consistency of the habitat from year-to-year, and the high density of the song sparrow population at the study site, social information

could play a large role in territory selection since prospecting males could benefit by knowing where males have had reproductive success, which have fully fledged offspring, which have active nests, and which territories are the most highly contested.

Song sparrows have complex song repertoires which serve the functions of defending territories and attracting mates. In previous studies, it has been shown that juveniles learn their songs from adults singing in the area (Hughes et al. 1998, Hill et al. 1999) and that female song sparrows are more likely to mate with males that have larger repertoires (Searcy et al. 1985, Reid et al. 2004). Furthermore, males with larger repertoires are able to maintain larger territories (Hiebert et al. 1989). Territory size and quality can affect reproductive success (Arcese 1989), so it could be that while juvenile males are learning their songs from nearby males, they are also learning which types of habitat are suitable for territories.

Previous research has shown that juvenile song sparrows learn songs from neighboring males, and often set up territories near or replace those neighbors (Beecher et al. 1994), and that neighboring or juvenile males will move into areas that have been abandoned (Knapton and Kregs 1974, Hiebert et al. 1989). I hypothesized that song signals potential reproductive success on the territory to neighboring and juvenile males. Further, if social information plays a large role in territory selection in song sparrows, I should be able to influence territory selection in the local population by using methods similar to those used in the study by Betts et al. (2008).

METHODS

Over the spring and summer of 2009, all song sparrow territories on the campus of Western Carolina University were mapped using point counts and playback experiments. As many song sparrows as possible were caught with mist nets and given both colored bands and U.S. Fish and Wildlife Service bands for later identification. A total of 32 locations were chosen in areas where no territorial behavior, defined as the presence of a singing male in the area, had been seen. Song sparrow territories at the field site were varied but usually consisted of some combination of tall grasses, short trees, hedge rows, shrubs, street lights, signs, roofs, and sidewalks. Each spot was chosen in an area of edge habitat that had some of these characteristics of where song sparrow territories were most often found. Territory quality could not be quantified due to the high variability of habitat in known male territories (e.g., one male might have a linear stretch of hedges along a creek while another had a few small trees and the top of a building). A territory was considered empty if there was no territorial behavior seen during a 10 minute point count followed by 6 minutes of playback at each spot. If there was territorial behavior within a 30 meter radius of a point, it was considered occupied. This distance was chosen because a larger radius would not have been feasible in such a dense population, while a smaller radius could have resulted in unknowingly being in a male's territory since some males will sing from 10 meters or farther away from a speaker placed within their territory.

The 32 locations were divided into two groups: 16 experimental territories where song was played and 16 control territories where no song was played (Figure 1). To try

to reduce any location bias, the territories were spread across the entire campus. Further, most experimental and control territories were paired together in similar habitat.

For each of the 16 experimental territories, a unique repertoire of song sparrow song was played. The songs used were recorded from local birds during the summer of 2008 using digital recorders and microphones. Since song sparrows normally have repertoires of 4-13 songs (Reid et al. 2004), 4 unique songs were chosen for each track to simulate a natural repertoire. Furthermore, varied intervals were used between songs to mimic a song sparrow's natural singing variation throughout the day. The intervals were never any shorter than 6 seconds or longer than 60 seconds. The intervals were kept constant throughout all tracks, so each track was approximately 25 minutes long with each of the songs playing for approximately 6 minutes. The songs were played from MP3 players which were connected to portable speakers and set to play in a loop, amplified to play at approximately 80 decibels, which is the volume used in my playback experiments.

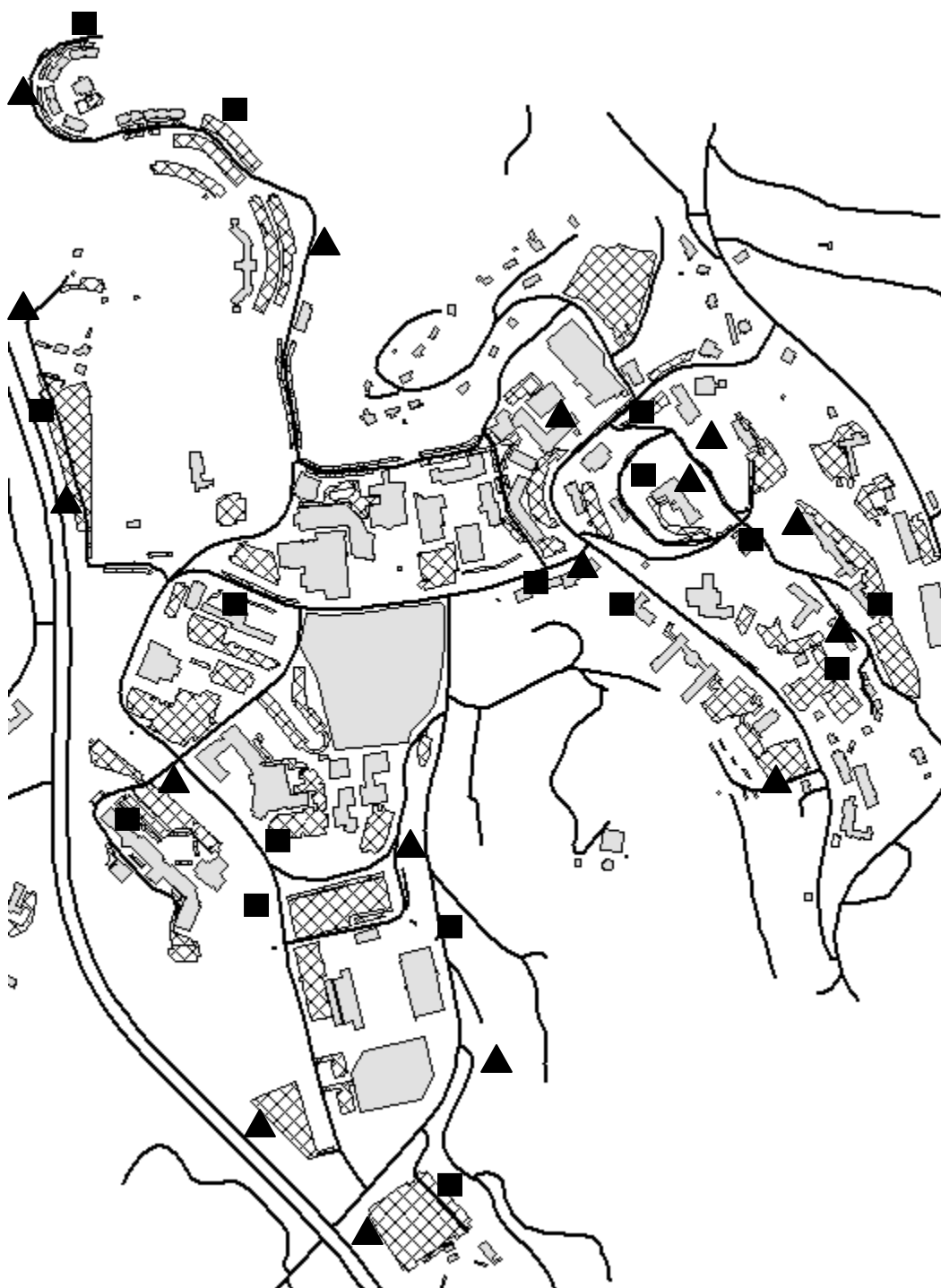


Figure 1: Map of Western Carolina University campus with Control Territories (n=16) marked as squares and Experimental Territories (n=16) marked as triangles. Buildings are indicated by gray, parking lots by the cross-stitch pattern, and roads by black lines.

Between 3 August 2009 and 24 August 2009, song was played in each experimental territory for 10 hours a day for 10 days. Daily observations over the spring and summer revealed that the local population of song sparrows was most active singing in the morning, became less active in the afternoon, and then became more active again in the evening. Based on this, song was played from 06:00 to 11:00 and then from 15:00-20:00. Only half of the experimental territories could receive treatment in a day, so the treatments were divided up so that 8 territories were treated for 5 days, then the next 8 for 5 days, then the first 8 again for 5 days and followed by the last 8 for 5 more days.

After each 5 days of treatment, 10 minute point counts were conducted in the morning on the 8 territories that had received treatment, checking for any activity of prospecting birds. Birds were considered prospecting if they came within 30 meters of the empty territory. I recorded any territorial behavior displayed as well as the identity of the bird if it was banded. Beginning in October of 2009, 10 minute point counts were conducted in all 32 territories. Any territorial behavior displayed as well as the identity of the birds, when possible, were noted. The point counts were made once per month in all territories from October 2009 through April 2010.

During May of 2010, point counts and playback experiments were conducted in all territories to test for a male showing territorial behavior. In the following June, the same was done in every territory that did not have a territorial male present during the May tests. The total number of birds present in territories where song was played was compared to the total number in territories where no song was played using the Fisher's Exact Test to determine if there was a statistically significant difference. I attempted to catch any male song sparrow that displayed territorial behavior the territories using mist

nets. Once caught, I placed color bands and U.S. Fish and Wildlife Service bands on the birds and aged them as a Hatch Year (HY), Second Year (SY), or After Second Year (ASY) bird. I then compared the ages of the males found in experimental versus control territories to see if one age group potentially used social cues in territory selection more than another.

RESULTS

While all of the territories were confirmed to be empty using playback and point counts, during the weeks of playback in the experimental territories, males that had previously not responded to playback in those areas began coming into the test sites in response to song being played (Table 1). The early point counts also found more birds present in the experimental than the control territories (Table 2). Based on the point counts alone, significantly more experimental territories had birds present in them at some point in the non-breeding seasons (Fisher's Exact Test $P = 0.0113$; Table 3).

However, when playbacks were conducted in each territory during the summer of 2010 to test for the presence of a territorial male, there were more males in the experimental territories than the control, but not significantly so (Fisher's Exact Test $P = 0.2890$; Table 4). There was also no difference between the ages of the birds that settled in either the experimental or the control territories (Fisher's Exact Test $P = 1.00$; Table 5).

Table 1: The total number of experimental territories that had song sparrows present in them during the weeks when song was played and during the point counts the week following the playbacks.

Experimental Territories	Birds Present	
	During Experimental Treatments	Post- treatment Point Counts
1	No	No
2	Yes	Yes
3	Yes	Yes
4	No	No
5	Yes	Yes
6	Yes	Yes
7	Yes	No
8	Yes	No
9	Yes	No
10	No	No
11	No	No
12	No	No
13	Yes	No
14	No	No
15	No	No
16	No	No
Total:	8	4

Table 2: Point count results from October through May showing the total numbers of territories with birds present.

Month	Control (n=16)	Experimental (n=16)
October	2	8
November	0	1
December	0	0
January	0	0
February	2	3
March	1	2
April	3	4
May	2	6

Table 3: Total number of individual territories with song sparrows present during the non-breeding season (October through March) (Fisher's Exact Test $P = 0.0113$).

	Birds Present	Birds Absent
Control Territories (n=16)	3	13
Experimental Territories (n=16)	11	5

Table 4: Total number of unique territories that had song sparrows respond to playback during May and June (Fisher's Exact Test $P = 0.2890$).

	Birds Present	Birds Absent
Control Territories (n=16)	6	10
Experimental Territories (n=16)	10	6

Table 5: Number of Second Year (SY) male and After Second Year (ASY) male song sparrows that displayed territorial behavior in the control and experimental territories (Fisher's Exact Test $P = 1.00$).

	SY Males	ASY Males
Control Territories (n=5)	2	3
Experimental Territories (n=6)	2	4

DISCUSSION

Previous work with black-throated blue warblers has shown that social information, in the form of male song, can play a large role in territory selection (Betts et al. 2008). With song sparrows, however, there was not compelling evidence of a difference in territory selection between the experimental territories where song was played and the control territories, casting doubt on the importance of social information in territory selection in this population of song sparrows.

There was an initial surge of activity in the experimental territories during and immediately after song was played in them. In addition, there was initially a greater presence of birds in the experimental territories during October (Tables 1, 2). Many of the birds that began showing up in the experimental territories after song had been played in them for several days were known neighboring males that had been color-banded during the previous summer. Previous studies have shown that new or neighboring males will invade an occupied territory if the original male is removed (Knapton and Kregs 1974, Hiebert et al. 1989). Playing song in unoccupied spaces for ten days may have simulated the presence of a male, and when that male suddenly disappeared after the ten day period, it represented an opportunity for neighboring or new males to expand their own territory.

While there were significantly more experimental territories than control territories that had birds present in them (Table 3), because I used point counts and song sparrows are sexually monomorphic, there was no way to distinguish between a territorial male versus a female, juvenile, or non-territorial foraging bird. As such, I cannot claim that significantly more males had set up territory in the experimental territories than the

controls based on these data. Once playbacks were done to test for territoriality, we found no significant difference between the experimental and control territories (Table 4)

One potential explanation for the lack of a difference between the number of males that settled in the experimental and control territories could be that this population of birds are showing density-dependent habitat selection, in which organisms will choose the most ideal habitat at first, but as the population becomes denser, more individuals will opt for less ideal habitat (Rosenzweig 1991). This behavior has been observed in some bird species such as the coal tit (*Parus ater*) and black-billed magpie (*Pica pica*), but not seen in others such as the common blackbird (*Turdus merula*) (Fernandez-Juricic 2001).

The song sparrow population in this study was very dense, with over 120 known male territories during the summer of 2009 (unpublished data) which, along with much of the area being uninhabitable due to buildings, parking lots, sidewalks, roads, etc., suggest that space is very limited and competition for the best territory locations is high. Additionally, some males had territories in mature conifers, an atypical habitat for the species, which suggests that some males are being forced into less than ideal habitat due to the lack of available space in ideal habitat. Half of the 32 potential territories identified in this study were eventually settled by territorial males, further suggesting that any available space in acceptable habitat is often claimed by a male. There was no difference in the ages of the birds that settled the territories (Table 5), so there is little evidence of one age group using social information more than another. Given the density and potential competition in this population, many males simply may not have the leisure of using social cues to find the ideal spot, but rather have to set up their territory where there is space available, even if it is less than ideal.

The migratory behavior of this population also may influence the value of social information as well. This population is partially migratory with many males being year-round residents (Carroll 2010) which allows for longer breeding and territoriality. There is a very large breeding season with copulations observed as early as April and as late as August. In the study by Betts et al. in 2008, song was played in the post-breeding season when all nest attempts are done, chicks are fully fledged, and both new and experienced males are potentially prospecting for new territories before they migrate. Given the relatively large breeding window of the local song sparrows compared to the black-throated blue warblers in the original study, the post-breeding season for song sparrows when new males are prospecting could range from as early as June to as late as September. As such, there could be fewer prospecting males at any given time in this population of song sparrows, so that when song was played, some juvenile males had fully fledged and left their parents' territories while others had not fledged yet.

There is also evidence of year-round territoriality in some populations of song sparrows (Wingfield et al. 2002) and while there is no evidence of it in the local population, many males are year-round residents (Carroll 2010). This allows them to remain territorial for much more of the year than a migrant would with males responding to playback as early as March and as late as October. By playing song in the unoccupied spots in August when most males are still territorial, it could have represented a male that was still territorial, aggressive, and planning on remaining on his territory throughout the year rather than simply indicating a good breeding territory. Thus males may have been less likely to settle in an experimental territory due to a perceived threat from an aggressive male that was still territorial.

Aggression could have also acted as a deterrent to prospecting males. Males in this population have been shown to be very aggressive, more so than in rural populations and in other urban populations tested (Evans et al. 2010, Scales et al. 2011). Furthermore, studies in many songbirds have shown that neighbor-stranger discrimination exists, where males will respond more aggressively towards strangers than to known neighbors (Lovell and Lein 2004) and this phenomenon has been shown in song sparrows as well (Stoddard et al. 1994). Resident birds have also been shown to act more aggressively towards newer neighbors than more familiar ones (Eason and Hannon 1994). These factors all suggest the possibility that resident, aggressive, neighboring males could have deterred any prospecting males by behaving very aggressively towards them. Playing song for ten days near known territories could have further increased the aggressive responses toward any males that were prospecting around the empty territories after song had been played in them. This could have led to some of the neighboring males expanding their territories into the experimental territories in response to the song being played.

Song sparrow territorial behavior is also highly variable with several alternative strategies. For instance, 25% of males have been found to set up territories much later in the season than the rest of the males. Some males show high site fidelity from year-to-year while others do not, and some so-called “floaters” do not even set up territories. Of those setting up territories late in the season, only 57% of song sparrows in some populations actually set up territories in completely unoccupied spots, while 37% of males will invade another male’s territory while that male is preoccupied with feeding his young. The remainder are floaters that encroach upon the territories of males not actively

feeding young (Hughes and Hyman 2011). This shows that some song sparrows do use a form of social information in territory selection. However, in the case of Hughes and Hyman (2011), the social information used was the presence of a male too preoccupied with feeding and caring for his young to invest heavily in defending his territory. This social information indicates reproductive success, and thus differs from the cues provided by my experiment, which just indicated the presence of a male.

In summary, while my results initially showed a strong difference between the experimental and control territories, there was ultimately not a difference between the likelihood that an experimental territory was settled over a control. Previous work has shown that social information can be more important than an individual's assessment of a habitat. However, these were only in cases where habitat varied very little or predictably from year-to-year (Danchin et al. 1998, Doligez et al. 2003, Betts et al. 2008). Given the variability in habitat at the field site, the density of the population, the long windows for breeding and territoriality, and the variability in song sparrow territorial behavior, there simply may not be enough consistency from year-to-year for social information to play a large role. Using a field site with a less dense population and more quantifiable habitat would allow for more consistent experimental and control territories, which along with a larger sample size could potentially provide different results. Likewise, playing song for a longer period of time in the experimental territories and continuing observations through the end of summer the following year could also possibly result in a different outcome.

Understanding the influence of social behavior in habitat choice can be important, as successful conservation depends on a sufficient knowledge of the behavior and

processes behind territory and habitat selection. In one seabird conservation effort, arctic tern (*Sterna paradisaea*) decoys and calls were used to attract arctic terns back to Eastern Egg Rock, Maine where populations had been reduced due to predation by increasing gull populations. After the first year of setting out decoys with speakers that played arctic tern calls, the sighting rate of terns on the island had doubled. In the following years, breeding pairs of common terns (*Sterna hirundo*), arctic terns, and roseate terns (*Sterna dougallii*) continued to increase (Kress 1983). So, in cases where the native habitat is still viable, song may potentially be used to help rebuild bird populations by attracting breeding birds into their native habitat. Furthermore, many species are able to adapt quickly and survive in nonnative habitats (Thomas et al. 2001), so song could also potentially be used to draw birds into nonnative habitats if their native habitat has been lost or otherwise altered.

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