

## WATER AS A HABITAT CUE FOR BREEDING SWAMP AND SONG SPARROWS<sup>1</sup>

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**Abstract.** Habitat use by Song (*Melospiza melodia*) and Swamp (*M. georgiana*) sparrows was studied along 1.2 km of contact between the species in northwestern Pennsylvania. The two species had only narrowly overlapping territories (4 to 5%). Several lines of evidence suggest that the opposite response of territorial sparrows to the presence of surface water accounts for this spatial segregation. The presence or absence of water was a nearly perfect predictor of which species was defending a particular area (95% correct), whereas a step-wise discriminant function based on 10 vegetative variables categorized the territories by species with only 74% accuracy. An area drained of water by the destruction of a beaver dam changed from containing five Swamp Sparrow territories to supporting five partial Song Sparrow territories; local densities of the two species were otherwise similar. During record rainfall and flooding in June of the second year of the study, male Swamp Sparrows were opportunistically defending newly developed flooded areas. Aggression between the species was not common and males did not respond to playbacks of heterospecific songs. These observations suggest that major changes in habitat distribution can occur through a change in response to a single habitat cue. The later arriving Swamp Sparrows are smaller and socially subordinate to Song Sparrows. Song Sparrows settle on dry territories leaving the wetlands to the Swamp Sparrows.

**Key words:** *Habitat selection; Melospiza; marsh birds; Pennsylvania.*

### INTRODUCTION

Lack (1933, 1937, 1945) and Miller (1942) suggested that closely related species may occupy different habitats in sympatry based, in a proximate sense, on the response to one or a few reliable cues rather than overall characteristics of these habitats. It is an hypothesis that is difficult to test, however, and there are few studies that identify the importance of particular features for habitat selection in birds in the field (Morse 1985). Most studies of responses to specific cues have focused on animals in captivity (Klopfer 1965, Wiens 1970, Partridge 1974, Gluck 1984). However, the careful study of ecotones between closely related species may prove to be a fruitful place to examine the response of species to particular habitat variables in the wild.

Based on some preliminary observations, it appeared that although Song (*Melospiza melodia*) and Swamp (*M. georgiana*) sparrows occupy largely nonoverlapping territories, the vegetative cover of these territories is quite variable, ranging from pioneer woods and shrub thickets to open meadows. The precise interspecific bound-

aries appeared to be determined by the placement of territories with respect to surface water conditions. Surface water is an excellent potential cue to study for habitat selection because each point in a territory can be assigned unambiguously to a surface moisture class and because surface moisture can change much more rapidly than physiographic or vegetative features.

In this study, I examined the hypothesis that Song and Swamp sparrows have strong and opposite responses to the distribution of surface water by measuring the distribution of Swamp and Song sparrow territory boundaries with respect to: (1) a variety of vegetative and surface moisture-related variables, (2) changes in surface water conditions, and (3) prolonged within-season change in surface water conditions resulting from intense flooding.

### STUDY AREA

The research was conducted June to July 1985 and April to July 1986 in the Erie National Wildlife Refuge, primarily along a 1-km transect at a Swamp Sparrow-Song Sparrow ecotone near Kelly's Corner, 19 km NE of Meadville, Crawford County, Pennsylvania. An additional 200 m was studied at nearby Ferris Corners. The transects were routed so that every territory was

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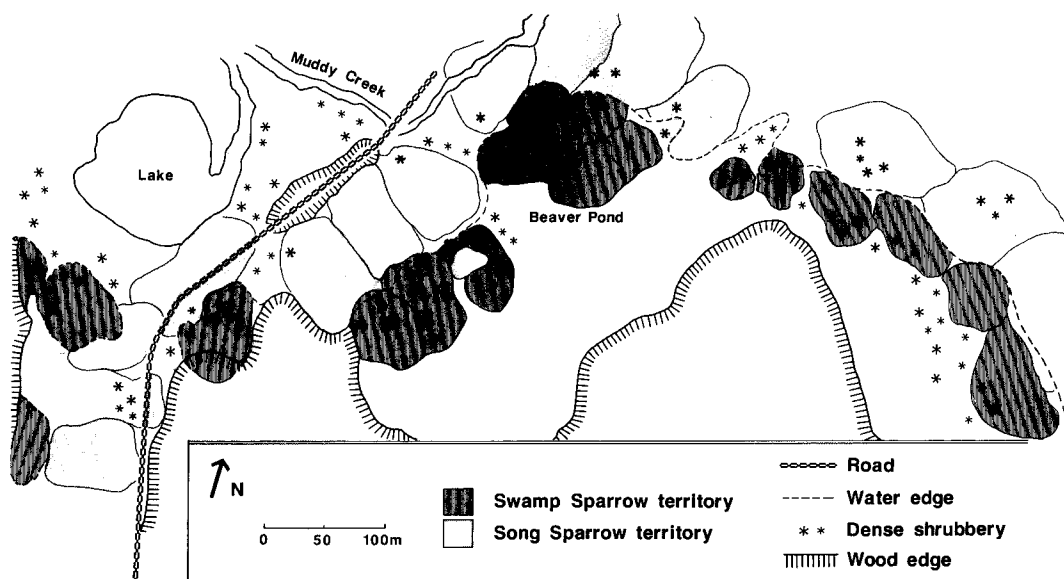


FIGURE 1. Map of territory distribution along Kelly's Corner transect in 1985.

adjacent to or overlapped the territory of at least one heterospecific. In addition, the study area is adjacent to Muddy Creek, which floods the area during spring melt-off and heavy summer rains. Information on flooding was provided by the Army Corps of Engineers, which operated a gauging station at Teepleville, 3 km downstream from Kelly's Corner. The transect runs through a variety of major macrohabitat types including oldfield, drained beaver lake, small extant beaver pond, young willow-alder woods, and marshland (see Fig. 1).

#### METHODS

Much of the field time was spent mapping the territories of singing male sparrows. In 1985 this was accomplished over a 3-week period by slowly moving along the transect, recording the location of males on maps with respect to coordinates of an established grid system. In 1986 the maps were made on a monthly basis based primarily on the resighting of color-marked sparrows. A total of 92 sparrows were marked, of which 62 were members of pairs resident on the transect; this includes all of the male Swamp Sparrows and 11/13 male Song Sparrows. The mapping I completed with color-marked birds produced similar results to the spot mapping of unmarked birds in 1985, and I am confident that

the spot mapping produced reliable territory maps.

To establish the relationships of the territories to the distribution of habitat features, I conducted a detailed survey of vegetation and surface moisture at 7-m intervals on a grid. In 1985 I surveyed an average of 71.1 points (46.5 SD) on 19 Song Sparrow and 61.8 (32.0 SD) points on 20 Swamp Sparrow territories during the June and July census periods. This period was selected for habitat analysis because the territorial array had achieved sufficient stability. Because most of the vegetation measurements are based on the distribution of perennial vegetation types, the analysis should also reflect what is available to birds earlier in the season. Since both species established territories prior to the growth of annual vegetation, it is not likely that this new growth could be used by sparrows for habitat selection. Rainfall during this period was normal and moisture conditions remained stable with only a small amount of drying and an absence of flooding during the period. In 1986 I only conducted habitat censuses in areas where the flooding by beaver dam construction had been reversed due to the trapping of the beaver.

For a 10-cm diameter circle at each sampling point, I recorded the presence or absence of the following types of ground cover: forb, grass (including small various graminiae, and sedges such

as *Eleocharis* sp., *Carex vulpenoidea*, *C. arenaea*, and *C. lurida*), rush (including *Juncus inflexus*, *Scirpus validus*, *Carex crinita*, and *C. folliculata*), and brambles (*Lonicera* sp., *Rosa palustris*, and *Rubus* sp.). If two or three types of ground cover were found at one point, I assigned each type an arbitrary value of 0.5 and 0.33, respectively. I measured the maximum height ground cover and classified the surface moisture conditions into one of the following three categories: water present (depth measured), including soil that exudes water when squeezed between fingers and appears to glisten, moist (soil smears into a paste between fingers), and dry (soil crumbles between fingers). I also recorded the number of stems of each shrub and tree species within a 1-m diameter circle. Trees were uncommon on the study plot and lumped into the shrub category. The three most common shrub species, *Spiraea alba*, *Cornus stolonifera*, and *Viburnum* spp., were analyzed separately as well as included in total shrub density.

To derive single values per territory, I summed the number of points covered with a particular ground cover type or categorized into a soil moisture class and divided by the total number of points sampled for that territory. I calculated the mean value per territory for the mensural and density characters. For vegetation height and water depth, values were only entered for sampling points where there was ground cover and water present, respectively. Because a small amount of drying occurred between sparrow settlement and the habitat analysis, I examined both the percentage water cover and the percentage water cover plus moist soil. These values should bracket the true distribution during the period of territorial settlement.

Each variable was compared between species using a Mann-Whitney *U*-test based on the values for each territory. A step-wise discriminant function analysis (DFA, SAS 1985) was used to determine the overall separation of habitats used by the two species with different combinations of variables. Because the DFA was used to explore differences in an existing data set, rather than to make inferences regarding the group membership of territories not used in the analysis, the use of proportional data is legitimate.

In May 1986 I conducted playback experiments of Song and Swamp sparrow songs (from the Cornell Laboratory Records) using a Uher 4000 tape recorder. For eight territories of each

species, I played the Song Sparrow song and the Swamp Sparrow song for 5 min each. I alternated trials at nonadjacent Swamp and Song sparrow territories. Within species I alternated the order of presentation. All experiments were conducted under calm wind conditions between 08:00 and 10:00 with the speaker placed approximately 10 m from a shared Swamp-Song boundary. I recorded any approaches by an individual of either species to the area described by a 5-m circle around the playback tape. My observations were made from a hidden position behind a shrub at least 10 m from the tape recorder.

## RESULTS

### TERRITORY DISTRIBUTION

In 1985, the territories of the Song and Swamp sparrows were largely nonoverlapping (Fig. 1). Based on the number of grid points that fell into the area of mapped overlap, I determined that the average Song Sparrow territory was overlapped 4% (4% SD) by Swamp Sparrows and the average Swamp Sparrow territory was overlapped 5% (4% SD) by Song Sparrows. It should be remembered that the study was restricted to Song and Swamp sparrow territories that abutted each other; overlap and habitat similarities were probably much lower for the population as a whole. The amount of territorial overlap between the species along the ecotone was essentially unchanged in 1986.

### THE PHENOLOGY OF SPARROW SETTLEMENT

Song Sparrows arrive in Crawford County, Pennsylvania in early March, whereas Swamp Sparrows arrive early to late April (D. Snyder, pers. comm.). When I visited the study site 12 April 1986, only two Swamp Sparrows were singing on territory. The complete array of territorial Song Sparrows was already present in mid-April. Although it was difficult to completely map territories during this period of poor weather, the location of all Song Sparrows was within the territories as mapped in May to July and none of the singing male Song Sparrows was in areas that were later defended by Swamp Sparrows. During April, small groups of apparently non-resident Song Sparrows were observed in the frozen marshy habitat. Between mid-April and mid-May Swamp Sparrows arrived and established territories in flooded areas. Although there was

TABLE 1. Comparison of Song and Swamp sparrow territories for single habitat variables ( $\bar{x}$  with SD in parentheses based on one value per territory).

Variable	Song Sparrow	Swamp Sparrow	Mann-Whitney <i>U</i> -test
<i>n</i>	19	20	
Grass cover (%)	22.8 (13.4)	30.4 (13.3)	ns
Forb cover (%)	59.4 (18.4)	34.4 (18.8)	<i>P</i> < 0.05
Rush cover (%)	7.1 (8.2)	25.0 (17.2)	<i>P</i> < 0.01
Total ground cover (%)	92.1 (11.0)	85.1 (22.3)	ns
Bramble cover (%)	2.7 (3.6)	0.1 (0.7)	<i>P</i> < 0.05
Ground cover height (m)	0.75 (0.18)	0.81 (0.3)	ns
<i>Viburnum</i> density <sup>a</sup>	0.09 (0.15)	0.03 (0.09)	ns
<i>Spiraea</i> density	0.12 (0.34)	0.27 (0.45)	ns
<i>Cornus</i> density	0.25 (0.23)	0.30 (0.33)	ns
Total shrub density	0.59 (0.46)	0.65 (0.41)	ns
Water depth <sup>b</sup> (m)	5.5 (8.2)	7.4 (8.4)	ns
Water cover (%)	13.2 (24.0)	92.2 (12.3)	<i>P</i> < 0.001
Water + moisture cover	15.9 (23.8)	97.0 (4.9)	<i>P</i> < 0.001

<sup>a</sup> Shrub density values are in stems/3.14 m<sup>2</sup>.  
<sup>b</sup> Water depth at points with water.

considerable turnover and movement of individuals during this period, most of the Swamp Sparrows were observed in or about these flooded areas.

HABITAT ANALYSIS

The habitat of Song and Swamp sparrow territories differed for several variables (Table 1). The largest difference was in the percentage water cover (92% vs. 13%); the distinction is even greater when a single Song Sparrow territory outlier is removed (92% vs. 8%). There was no significant difference in the average depth of water (at flooded points), which was quite variable for both species. Swamp Sparrow territories had significantly greater cover of rushes and large sedges. Song Sparrow territories had a greater cover of forbs. Average height of the ground cover, however, was similar for the two species.

The discriminant function derived based on all 13 variables listed in Table 1 was significant with an *R*<sup>2</sup> of 0.88 (*F*<sub>2,36</sub> = 134.7). The only variables entered into the function were total water + moisture cover (*r*<sup>2</sup> = 0.85) and total ground cover (*r*<sup>2</sup> = 0.20). A similar analysis run with only the 10 vegetation variables produced a discriminant function with an overall *R*<sup>2</sup> of 0.31 (*F*<sub>3,35</sub> = 5.37). This function included rush cover (*r*<sup>2</sup> = 0.21), *Spiraea* density (*r*<sup>2</sup> = 0.08) and *Viburnum* density (*r*<sup>2</sup> = 0.06). The first analysis, with the moisture variables included, produced an a posteriori classification error rate of 5% compared to 27% for the second analysis. When plots of factor scores and the total water + mois-

ture cover are compared (Fig. 2), it becomes clear that the separation of territories results almost entirely from a differential response to the presence of water.

These results probably underestimate the importance of water in determining the limits of the species. Because single values were entered for each territory to assure statistical independence, the degree of within-territory variance for

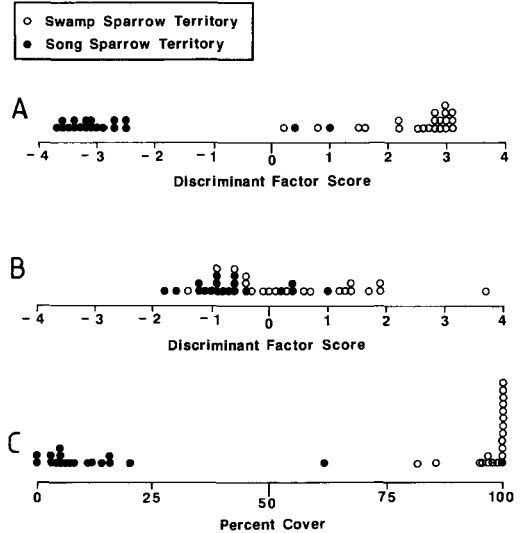


FIGURE 2. Plot of discriminant scores of Song and Swamp sparrows for (A) a function based on the initial entry of 13 variables and (B) a function based on 10 vegetation variables. (C) is a plot of values for water + moisture cover.

each variable has been masked. However, because the values for moisture cover cluster around 0% and 100%, the within-territory variance in this parameter is much smaller than for the vegetation variables. Whether a particular point was defended by a Song or Swamp sparrow could be predicted with 90% accuracy based solely on whether there was standing water or saturated soils.

#### THE DRAINING OF A BEAVER POND

By March 1985, due to the actions of local beaver trappers, a 1-ha portion of the transect that had been flooded ( $\bar{x}$  = 12.5 cm water) by an active beaver pond in 1984 was drained. The area had been defended by five Swamp Sparrows in 1985. In 1986 the area comprised a portion of five Song Sparrow territories and only a small area was still flooded and actively defended by a single color-banded Swamp Sparrow. This Swamp Sparrow did not settle until early May (many Swamp Sparrows arrived in mid- to late April). From 1 to 10 May the remaining flooded area decreased in area from 0.25 to 0.11 ha and the periphery of the area defended by a Swamp Sparrow contracted with the receding water. The vegetation in the area was sampled in early July and found to be similar in most respects to the vegetation sampled at the same time in 1985. All of the vegetation cover and shrub density values were within five percentage points except for forb cover which increased from 17 to 27% between years. Total moisture cover, however, changed from 98 to 12% found on the once flooded and now dried area. The change from Swamp to Song sparrow occupancy did not result from a fluctuation in overall relative density of the two species; I found similar numbers of pairs of each species along the rest of the 1-km transect at Kelly's Corner in both years (12 Swamp and 13 Song sparrows in 1985 vs. 12 Swamp and 15 Song sparrows in 1986). The two additional Song Sparrow territories in 1986 occurred in a section of transect away from the beaver pond that was also significantly drier in 1986 than in 1985.

#### THE RESPONSE TO UNUSUAL SUMMER FLOODING

The study area received unseasonably high rainfall during June 1986. This is supported by rainfall data from Meadville, Pennsylvania (12 km SW), which showed normal amounts of precip-

itation in April, May, and July, but record rainfall in June (25 cm, previous high of 20 and average of 10 cm). In general, flooding is a brief phenomenon, with waters receding to a base level within 24 hr. During June 1986, rains were heavy for a number of days (10 days with over 1.25 cm of rain in a period of 18 days). Flooded areas were more persistent than usual. Flooding occurred when Muddy Creek overflowed its banks and drained into the low-lying areas of the study plot. Such flooding, as indicated by the number of days when creek stage exceeded 1.6 m at the Teepleville gauging station, is regular in April with an average of 1.6 flood days per year. However, flooding is less common during the sparrow breeding season. Flooding occurred in April 84% of the 24 years of record, but only occurred in 47% of the years during May and June, and 27% of the Julys. In June 1986 there were more days with flood stages over 1.6 m than any other summer month (May to August) in the record.

During this period known male Swamp Sparrows moved 50 to 300 m into the Song Sparrow area and set up singing posts (Fig. 3). Seven such males were observed, all of which were observed to return frequently to their previously mapped territory. These incidents all occurred within a week of flooding which lasted at least 21 days. I located a new female and a new nest for one of these males; however, the male's original nest was destroyed by predators and his original female disappeared. Song Sparrows, on the other hand, were not observed to abandon territories during flooding.

#### RESPONSE TO SONG PLAYBACKS

Response to conspecific songs was strong, with males and occasionally females of both species approaching in 7/8 cases for Swamp Sparrows and 8/8 cases for Song Sparrows when played within their territories. Furthermore, Swamp Sparrows came into Song Sparrow territories on four occasions to approach a Swamp Sparrow playback. Approaches to the speaker were unambiguous, involving alarm chips, fly-overs, wing spreading, pileal erection, and other behaviors associated with a high degree of arousal. Conversely, heterospecific playbacks were never approached. On two occasions Swamp Sparrows that came into Song Sparrow territories were briefly chased. These chases did not end with the sparrows being chased from the Song Sparrow territory.

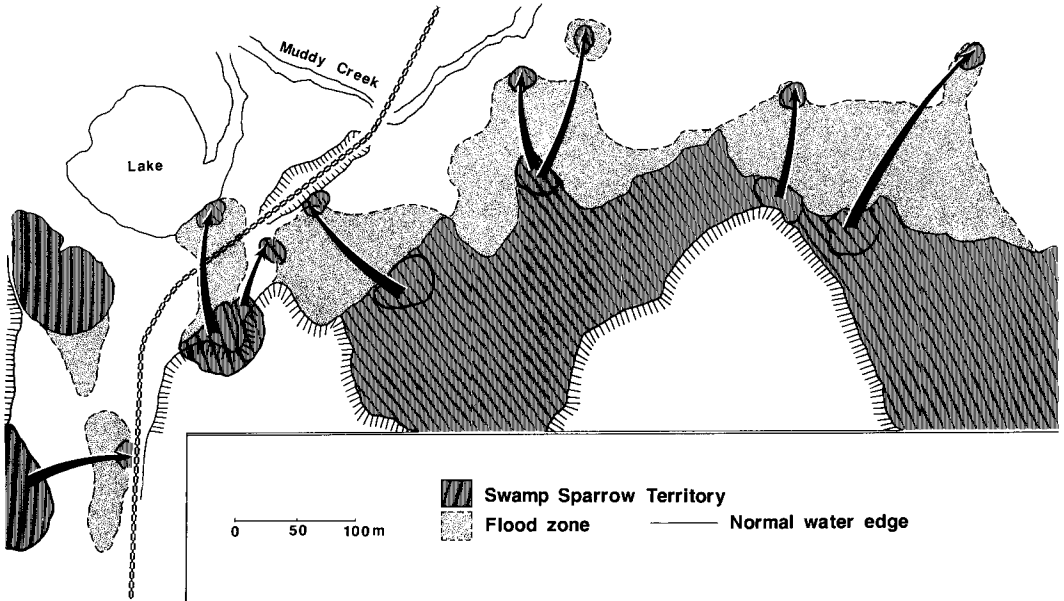


FIGURE 3. Map showing the location of flooding and the movement of male Swamp Sparrows to new song perches in 1986; also depicted is the Song-Swamp ecotone and the water line between flooding events, both of which were stable late May to July.

#### OBSERVATIONS OF INTERSPECIFIC AGGRESSION

Observations of interspecific aggression were uncommon. Most of the chases or supplantings occurred early in the season between nonterritorial birds. Song Sparrows chased Swamp Sparrows in 16 of the 20 instances in which the identity of the birds was identified unambiguously. I have found that the larger Song Sparrow is dominant to the Swamp Sparrow in winter flocks as well (Greenberg, unpubl.). Only 10 of the 16 chases resulted in a Swamp Sparrow leaving the territory of the Song Sparrow. Not only were chases observed rarely but they were far outnumbered by observations of Song and Swamp sparrows feeding or singing in close proximity without aggression. These observations were made in the narrow zone of territorial overlap.

#### DISCUSSION

Three lines of evidence suggest that the non-overlapping distribution of Song and Swamp sparrows on the study site results, in a proximate sense, from opposite responses to the presence of surface water. Other variables may differ on the average between territories of the two species, but the actual difference in habitat selection, in

a proximate sense, probably results largely, if not entirely, from the response to water: (1) the degree of accuracy with which the presence or absence of surface moisture predicts the ecotone between the two species; (2) the turnover of Swamp to Song territories in an area that was drained by the removal of a working beaver; and (3) the establishment of outlying singing posts by male Swamp Sparrows on temporarily flooded areas during the mid-breeding season. The lack of response by Song Sparrows during this period may result from the fact that territory abandonment is unlikely during the middle of the breeding cycle even under deteriorating conditions.

The sharpness of habitat differences between the species, as well as the difference in response to surface water, is not found in nonbreeding Song and Swamp sparrows. Nor is it found in nonresident sparrows, or family or dispersing juveniles during the breeding season. This suggests that the response to water in a proximate sense may be governed by hormonal changes associated with breeding activity. Such a mechanism has been suggested for habitat preference based on experiments with captive Dark-eyed Juncos (*Junco hyemalis*, Roberts and Weigl 1984).

One possible cause of habitat selection is differences in the ability to forage in areas of stand-

ing water. To forage at the surface of a typical Swamp Sparrow territory requires that a sparrow hang on to shrub vegetation while leaning to reach the water surface or wading in the water. For brief periods in April, when no leaves were on the shrubbery, I was able to observe foraging of both Song and Swamp sparrows. All 12 Swamp Sparrows I observed moved agilely through the bases of *Cornus* and *Spiraea*. Ten Song Sparrows, in the same area, attempted to land on small bits of flotsam or dirt clods breaking through the water surface. They appeared unable to move through the vegetation and search for food on the water surface. In addition, I have observed Swamp Sparrows foraging for long periods while wading in shallow water (see also Witherbee 1968). This behavior, which I have not observed in Song Sparrows, may be facilitated by the relatively long legs of Swamp Sparrows (Witherbee 1968).

An alternative explanation for such completely nonoverlapping territories is interspecific territoriality, which has often been found in marsh-nesting birds (Orians and Willson 1968, Catchpole 1972). Although I observed some chasing of Swamp Sparrows by Song Sparrows early in the season during feeding, I observed almost no interactions between singing territorial birds, even when Swamp Sparrow males established singing posts within Song Sparrow territories. In addition, the small number of experiments I performed, and the greater number performed by others (Peters et al. 1980, Searcy et al. 1981), indicate little if any response by birds of either species to the song of the heterospecific played in their territory.

Cases of interspecific territoriality found in other species pairs often consist of late arriving marsh species displacing an earlier arriving species. This has been well-documented in Yellow-headed (*Xanthocephalus xanthocephalus*) and Red-winged (*Agelaius phoeniceus*) blackbirds (Orians and Willson 1968), Tricolored (*A. tricolor*) and Red-winged blackbirds (Orians and Collier 1963), Reed (*Acrocephalus scirpaceus*) and Sedge (*A. schoenobaenus*) warblers (Catchpole 1972, 1973), Reed and Marsh (*A. palustris*) warblers, and Great Reed (*A. arundinaceus*) and Reed warblers (Catchpole and Leisler 1986). In contrast to these well-known examples, in this study, the later arriving species is subordinate to the earlier arriving species. The dominant Song Sparrow does not appear to attempt to occupy the marsh habitat, leaving it open for coloniza-

tion by the smaller species. I suggest that territorial system and resource use are the driving forces behind the difference between these sparrow and other species pairs. Unlike the blackbirds and warblers, the sparrows defend all-purpose territories supporting most or all of the foraging as well as nesting. Foraging in marsh habitats appears to demand exploitative ability that is facilitated by small size; only the small Swamp Sparrow can easily move through dense foliage and maneuver agilely.

Later arrival of the marsh-dwelling Swamp Sparrow may be due to temporal differences in the suitability of wet and dry habitats. Water may affect the phenology of a site. Wet sites usually thaw later and may experience colder soil temperatures until later in the spring; I found soil temperatures to remain 2 to 4°C cooler on flooded vs. unflooded areas on the study site (unpubl. data). In addition, April is a period of regular annual flooding on this site. It may be dangerous for birds that build their nests on or near the ground to attempt breeding in lowland sites early in the season (I observed several sparrow nests destroyed in the June 1986 flooding). Song Sparrows may use lack of surface moisture (or ice) as a cue for the availability of territories that are safe and productive early in the year.

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