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SPATIAL DYNAMICS OF ALTERNATIVE REPRODUCTIVE STRATEGIES: THE ROLE OF NEIGHBORS

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Abstract. In territorial species, the reproductive success of a male is dependent on the quality of his territory. One important component of territory quality is spatial location. High-quality territories not only should be located in areas of high food abundance and low predation, but also should be located in areas that offer optimal amounts of social interaction. Such optima might be different for individuals according to their sex, dominance, or genotype. We studied territory quality (size, vegetation structure, and placement) in a socially monogamous, polymorphic passerine, the White-throated Sparrow (*Zonotrichia albicollis*), in order to determine how spatial attributes contribute to selection intensity on two genotypes. In this species, plumage (white and tan), behavior, and life-history characteristics have a genetic basis and are correlated with the presence or absence of a chromosomal inversion. Using remote sensing and Geographic Information Systems (GIS), we found that the territories of white and tan males do not differ in size or vegetation structure, suggesting that these factors are not of primary importance to males when deciding where to establish a territory. Instead, we suggest that the placement of white and tan territories depends on the number of neighbors (particularly, white male neighbors). Tan males settle in low-density, neighbor-restrictive habitats where intruder pressure from white males seeking extra-pair copulations is reduced. In contrast, white males tend to settle in high-density areas where the probability of encountering neighboring fertile females is greatest. This segregation has led to intraspecific niche partitioning in the two disassortative pair types so that each male morph can best exploit its respective reproductive strategies. These factors may, in turn, contribute to the maintenance of this unusual mating system and, ultimately, the stability of the polymorphism in this species. Similar forces may be operating in other species without distinct morphological markers; we suggest that researchers keep social factors in mind when examining habitat selection.

Key words   alternative strategies; neighbor effects; niche overlap; polymorphism; remote sensing; reproductive success; social niche; spatial dynamics; territoriality; White-throated Sparrow; Zonotrichia albicollis.

Introduction

The spatial distribution of individuals strongly influences evolutionary change in populations, species, and ecosystems by influencing factors that contribute to selection. Territoriality can alter the spatial distribution of organisms by limiting breeding densities, thereby skewing the reproductive success of individuals (Brown 1964, 1969, Brown and Orians 1970). Suitable breeding habitat is sometimes limited and males able to secure sole access to these habitats are able to attract one or more mates. Those unable to do so are often unable to breed. Such bachelor or floater males are a common phenomenon in territorial species; these males rarely, if ever, accrue reproductive success (Krebs 1971, Brooke 1979, Seastedt and MacLean 1979, Ewald et al. 1980, Arcese and Smith 1988).

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Further variance in reproductive success exists if males secure territories that differ in quality (Andersson 1994). The quality of a male's territory influences his reproductive success by influencing the number and quality of females that he is able to attract (Brown 1975), as well as the survivorship of his offspring (Lack 1954). Factors influencing territory quality commonly include ecological attributes such as food abundance and the amount of cover or nesting habitat. Territory quality can also be influenced by other biotic factors such as the number and type of predators, parasites, or interspecific competitors (Robertson 1972, Robinson et al. 1999). Finally, conspecifics also can alter the quality of a territory if increased densities lead to higher predation rates, greater risk of infection from disease, increased intruder pressure, or an increased probability of cuckoldry (MacLean and Seastedt 1979, Muller et al. 1997). Given all of the possible effects on territory quality, males should attempt to establish territories in only the best habitats. However, their ability to do so will depend on their own capabilities, status, and motivation. Furthermore, a high-quality area for one in-

PLATE 1. (Left) High-density ''bog'' habitat and (middle) low-density ''pond'' habitat, both showing the low shrubs and grass tussocks in which White-throated Sparrows (*Zonotrichia albicollis*) nest. (Right) A female White-throated Sparrow (*Z. albicollis*). Her bright and high-contrast plumage identifies her as a white morph. Photo credit: V. A. Formica.

dividual may be a low-quality area for another individual; the ''value'' of a given area is not constant across all individuals.

We investigated territoriality in the White-throated Sparrow (*Zonotrichia albicollis*; see Plate 1), a bird with a known genetic polymorphism that correlates with morphological, behavioral, physiological, and ecological differences (for a review, see Falls and Kopachena 1994). There are two male morphs that invest differentially in reproductive activities (Tuttle 2003). Although both morphs are socially monogamous, one morph invests heavily in advertisement via song (Falls 1988) and the pursuit of extra-pair copulations (EPCs, or matings with individuals other than the social, pair-bonded mate), whereas the other morph invests heavily in mate-guarding (Tuttle 2003) and parental-care activities (Knapton and Falls 1983, Whillans and Falls 1990, Kopachena and Falls 1993). EPCs increase the variance in white male reproductive success, thereby resulting in an increase in the intensity of selection on white males (Tuttle 2003). The existence of alternative reproductive strategies implies that the male morphs might invest differently in other territorial behaviors (e.g., patrolling, aggressive defense, etc.) and, as a result, might occupy territories of varying quality. Because the ecological attributes of territories contribute substantially to the reproductive success of each male strategy, the study of territoriality in White-throated Sparrows will allow us to directly assess how ecology affects the evolution of genotypes.

Previous work on this species suggests that male morphs might partition habitats (Rising and Shields 1980) and establish territories in areas that differ in ''openness'' (Knapton and Falls 1982). Preliminary study of our population in the Adirondack Park of New York, USA, suggests that such segregation does not exist (Tuttle 1993). We therefore conducted in-depth analyses of territory size and vegetation structure to determine whether such patterns were, indeed, ubiquitous. We attempted to correlate vegetation structure with apparent reproductive success (i.e., the number of chicks in a nest). Furthermore, we analyzed the spatial

distribution of territories via Geographic Information Systems (GIS) to reveal differential patterns of landscape use in the morphs. We predicted that white males would have larger and/or better quality (as indicated by vegetation structure) territories than tan males because they invest more time in territorial defense via song (Falls 1988) and they are more aggressive (Ficken et al. 1978, Knapton and Falls 1983). White males also attempt polygyny (Knapton et al. 1984, Tuttle 2003), a strategy that often requires an increase in territory size to attract a secondary female (MacLean and Seastedt 1979). Finally, because there is commonly a trade-off between territorial and parental care activities or defense of a female (MacLean and Seastedt 1979, Studd and Robertson 1988) and because tan males invest more in parental care (Knapton and Falls 1983, Whillans and Falls 1990), we expected them to occupy smaller and/or lower quality territories. Our objectives were to correlate spatial factors with indicators of fitness, to examine how these factors contribute to the maintenance of polymorphism in this species, and to determine how the spatial distribution of individuals within a population might contribute to the maintenance of genetic diversity in general.

METHODS

Study species

The White-throated Sparrow (*Zonotrichia albicollis*; see Plate 1) is a socially monogamous passerine found breeding in the northern United States and Canada (Falls and Kopachena 1994). White-throated Sparrows exhibit a stable genetic polymorphism caused by a chromosomal inversion of the second autosome (Thorneycroft 1966, 1975). Genotype is absolutely correlated with crown plumage color, and both males and females can be separated into two distinct morphs (i.e., white or tan; Lowther 1961, Vardy 1971, Atkinson and Ralph 1980, Piper and Wiley 1989b). White morphs are heterozygous for the chromosomal inversion, whereas tan morphs are homozygous and do not carry the inversion (Thorneycroft 1966, 1975). The morphs

mate disassortatively with respect to this polymorphism (Lowther 1961, Thorneycroft 1975, Tuttle 1993, Falls and Kopachena 1994), and >97% of mating pairs consist of white males × tan females and tan males × white females (E. M. Tuttle, *unpublished data*). White and tan birds are found in relatively equal proportions throughout the species range. Because these morph ratios have remained stable for >125 years, it is reasonable to assume that the polymorphism has attained equilibrium (Lowther 1961, Falls and Kopachena 1994).

We studied a population of White-throated Sparrows located 1.5 miles (2.4 km) east of the Cranberry Lake Biological Station in the Adirondack Mountains of St. Lawrence County, New York (44°15′ N, 74°78′ W). Although this population has been studied since 1988, in this paper we report results of an intensive analysis of 29 territorial pairs conducted in 2000. All birds at this site are uniquely color-banded (U.S. Fish and Wildlife Service master banding permit number 22297 to E. M. Tuttle). We monitored breeding behavior and reproductive success throughout the breeding season, which ran from late April to early August. Female White-throated Sparrows nest on or near the ground in small shrubs or grass tussocks. Nests were found by random search or by observing the behavior of individuals involved in nest building, incubating, or feeding of chicks. Once nests were located, they were checked every other day and any surviving chicks were banded 5–8 days after hatching (median = day 7). In this study, we define observed reproductive success as the number of chicks in the nest at banding. If chicks survived to this time, they commonly survived to fledging.

Territory size and placement

Our conceptual definition of territory is the area of defended space utilized by a pair during the breeding season (Emlen 1957, Brown 1969). As suggested by Maher and Lott (1995) and outlined by Wittenberger (1981), we used the three-criteria definition of territory: (1) most activity of each pair was confined to these areas, (2) the presence of all males was advertised through spontaneous song throughout the day and dawn chorus, and (3) resident males maintained nearly exclusive use of all parts of these areas. Pair members associated closely and used contact calls during foraging.

Male White-throated Sparrows arrive before the females, compete, and settle in historical territory locations. Therefore, we assumed that territory selection was determined by the male. Territory locations and boundaries are relatively stable from year to year and seem to be based on physical structures (e.g., streams, large fallen trees). The boundaries of a given territory were distinct and they rarely overlapped neighboring territorial areas. During intrusion, which was almost always performed by neighboring white territorial

males (Tuttle 2003), territories were defended mostly by the resident male and sometimes by the resident pair. Male territorial defense usually consisted of interactive song bouts between the resident and the intruder. Early in the season during territory establishment, these interactions often would escalate into physical fights in which males would attempt to knock each other off song perches.

At our study site, White-throated Sparrow territories are located along a brook in forest edge, in a bog, and around ponds (see Plate 1). These are all-purpose, Type A territories (Nice 1941). After successful fledging, parents tending fledglings often travel outside territorial boundaries. These additional areas were not defended and were commonly utilized by other pairs with fledglings. We therefore considered these areas to be home ranges rather than territories, and have chosen to exclude these external areas from our analyses.

The studied population consisted of 29 focal pairs (16 white male × tan female; 13 tan male × white female), all of which mated dissassortatively. Two territories of tan males were excluded from this analysis due to unique circumstances. The first male never obtained a mate and the second male disappeared from his territory during the course of the study. All included pairs were observed for a minimum of 80 hours each over the entire breeding season. To delineate territory boundaries, every observation of a resident was flagged; at the end of the breeding season, all of the locations of the flags were recorded using a CMT MC-5 resource grade global positioning system (GPS; Corvallis Micro Technologies, Corvallis, Oregon, USA). The data were corrected using CMT PC-GPS v3.7 software (CMT 2001) with correction data from the Syracuse Hancock International Airport (43°10′ N, 76°08′ W) base station in the National Geodetic Survey base station network. All data were reprojected into Universal TransMercator (UTM) zone 18, NAD83, and were exported to ESRI (Environmental Systems Research Institute, Redlands, California, USA) ArcView (ESRI 1999) in shapefile format. Using the Animal Movement Extension of ArcView, we generated territorial boundaries and locations using minimal convex polygons, MCP (Hooge and Eichenlaub 1997; see Fig. 1A, B). The area represented by each polygon (i.e., territory size) was determined using ArcView. Because the MCP method of polygon construction can give biased results due to sampling effort (Powell 2000), we controlled for sampling effort in our statistical analyses.

In White-throated Sparrows, intruding birds are usually territorial white males occupying adjacent territories (Tuttle 2003). We determined the number of neighbors that a pair had because we felt that this would give an indirect estimate of intrusion pressure. In order to determine the number of neighbors, each territory polygon was given a 10-m external buffer. We chose 10 m because it was the median distance of overlap in

border disputes between neighbors (E. M. Tuttle, *unpublished data*). Any territory intersected by this buffer was operationally defined as a neighbor.

Vegetation structure

White-throated Sparrows are found throughout the northern United States and in eastern and western Canada (Falls and Kopachena 1994). Because the species range is so large, we assumed that White-throated Sparrow territories across this range would vary in vegetation composition, and that the distribution of this bird was not dependent on the presence and abundance of particular plant species. Based on these assumptions, we chose to classify vegetation according to structure instead of species. Our goal was to devise a method that would allow us to use GIS to quantify the structural attributes of territories at a scale that was still meaningful to a nesting passerine.

To analyze vegetation structure, we obtained infrared Digital Ortho-photo Quarter-Quads (DOQQs) of the study site and used remote sensing analysis to determine territory quality. These data are aerial photographs with a resolution of 1 m²/pixel; different vegetation types (often different species) have distinct reflectance values and are portrayed as discrete colors on the digital map. Using ESRI (1999) ArcView Erdas Image Analyst Extension (Image Analyst), we categorized the reflectance spectrum of the vegetation into 14 clearly defined structural classes using isodata clustering. The determination and validation of these structural classifications followed several steps. First, key locations of known vegetation types were spatially located using GPS ($n = 22$ locations). Second, we used GIS to choose 10 random locations to validate our remote sensing data with actual vegetation categories found in the field. Of these 10 points, seven accurately predicted the natural vegetation. We were unable to differentiate between wet grass and wet shrub, or between alders (*Alnus rugosa*) and other small deciduous trees, and we therefore collapsed these types into two categories (wet shrub and alders, respectively). The final 12 structural classifications were: mixed deciduous, wet shrub, medium conifer, large conifer, dead wood, maple, alders, larch (*Larix laricina*), medium deciduous, dry shrub, understory, and no vegetation (Fig. 1B). One of these (e.g., larch) was a single-species category, whereas the others contained more than one species (e.g., mixed deciduous and dry shrub). Third, using these 12 structural categories, we again validated our methodology and were able to accurately classify 100% of the random points that we later measured ($n = 15$ random points).

To determine the vegetation structure, we assigned one of the 12 structural classifications to every square meter in the study site, which provided us with nearly continuous structural measures for all settled and unsettled areas. Using the territory polygons drawn via MCP, we cut the categorized image data for each territory (Fig. 1B) and calculated the proportions of all structural classes for each territory using Image Analyst (ESRI 1999).

A previous study reported differences in the proportion of open habitat in white and tan male territories, using standard aerial photography to delineate open areas (Knapton and Falls 1982). We attempted to compare our results by collapsing our vegetation classes into "open" and "closed" habitat types. Open habitat included the no vegetation, wet shrub, dead wood, understory, and dry shrub classes. All other categories were classified as closed habitat. By using remote sensing techniques, we should have been able to identify open areas that are difficult to distinguish with traditional aerial photography.

In order to compare the amount of potential nesting habitat between the male morphs, we used five of the 12 vegetation classes where White-throated Sparrow nests have been previously found (1999 and 2000 nests; $n = 55$ nests). These classes include: wet shrub, dead wood, alders, larch (*Larix laricina*), and medium deciduous.

Habitat classifications

Based on visual assessment, we categorized territories at Cranberry Lake into three major habitat types: pond, forest, and bog. These categories differ according to the relative amount of unusable land (i.e., not suitable for nesting) on their boundaries. "Pond" territories are adjacent to small bodies of water (i.e., typical ponds). In addition, we categorized territories as "pond" if they were next to a large open area, such as a meadow of short grass that was not suitable as nesting habitat. We chose to also call these areas "pond" because both types of territories are adjacent to large, unusable tracts of land that may limit territory density. Territories labeled "forest" fall in the transitional zone from the older forest to the brook edge and usually contain both heavily wooded areas and dry meadows. Territory density is partially limited in theses areas because nesting habitat occurs only along either side of a brook. "Bog" territories are open areas highly inundated with water and rotten trees, both fallen and standing, and usually have large areas of usable land. Overall, there were 10 "bog" territories, 7 "forest" territories, and 10 "pond" territories.

Statistical analyses

When necessary, data were transformed to normality using a $\log_{10}$ transformation. All statistical tests were completed using JMP version 4.1 (SAS Institute 2001). In order to evaluate whether sampling effort affected MCP size and, thus, differences in territory size in our comparisons, we fitted a smoothing spline ($\lambda = 1000$; $R^2 = 0.38$) of the number of observations and territory size, and saved the residuals. All tests on territory size were performed using these residuals. Territory size was compared between the morphs and habitats using

FIG. 1. GIS map of the territories of white (white polygons) and tan (black polygons) male White-throated Sparrows. (A) A false color aerial photograph (DOQQ) shows the spatial distribution of territory polygons. Black areas are bodies of water (e.g., pond, stream); shades of salmon are different types of vegetation. (B) An example of two territory polygons (white and tan) showing isodata vegetation categories. For example, dark green represents wet shrub, and teal represents medium conifer.

a standard t test and ANOVA, respectively. Fisher's exact test was used to examine habitat segregation between the morphs. We used chi-square tests to compare the proportions of available territory types with those actually occupied by a morph. Comparisons between habitat and morph across the 12 vegetation categories were tested using MANOVA. The amounts of nesting habitat and open habitat were both analyzed via ANOVA.

Prior to these analyses, all proportional data (i.e., all vegetation classes, the proportion of nesting habitat, the proportion of open habitat) were normalized using an arcsine square-root transformation. All analyses involving the number of neighbors, the number of white neighbors, and reproductive success (the number of chicks) were performed with nonparametric statistics (Spearman's ρ, Kruskal-Wallis) because the data contained many zero values and did not respond to transformation. Significance was further tested using nonparametric post hoc tests (Zar 1998). To examine niche overlap, we calculated Pianka's measure of overlap (Pianka 1974, Krebs 1999) and the percentage of niche overlap (Schoener 1970, Krebs 1999). In order to determine whether morphs segregated into particular habitats, we calculated Manly's α (Manly et al. 1972, Chesson 1978, Krebs 1999). Manly's α and niche overlap indices were completed using Programs for Ecological Methodology, version 6.1 (Kenney and Krebs 2001).

Results

Ecological factors

White and tan males did not occupy territories of different size (tan male territories, 5461 $\pm$ 1785 m^2; white male territories, 5827 $\pm$ 875 m^2; $t = -0.21$; df $= 25$; $P = 0.83$). Territory size did not differ across habitat types (bog, 5637 $\pm$ 1029 m^2; forest, 4930 $\pm$ 1757 m^2; pond, 6242 $\pm$ 1835 m^2; $F = 0.15$; df $= 2$, 26, $P = 0.86$). Finally, territory size did not vary with vegetation openness ($r^2 = 0.01$, df $= 25$, $P = 0.61$).

There was no significant difference in the vegetation structure of white and tan male territories ($F_{morph} = 0.44$, df $= 1$, 21, $P = 0.55$; Fig. 2A), nor was there a difference in vegetation structure across habitat type ($F_{habitat} = 2.42$, df $= 2$, 21, $P = 0.11$; Fig. 2B). There was no interaction between morph and habitat ($F = 2.19$, df $= 2$, 21, $P = 0.14$). Because White-throated Sparrows nest in vegetation of specific structure (e.g., wet shrub, dead wood, alders, larch, and medium deciduous), we examined the proportion of these vegetation types in territories. There was no significant difference in the proportion of potential nesting habitat in white and tan male territories ($t = -1.45$, df $= 25$, $P = 0.16$).

To examine the structural requirements of vegetation in white and tan male territories, we calculated niche overlap between the two male morphs using the mean proportions of vegetation categories. Because the assumptions differed for each, we used three separate indices of niche overlap (Krebs 1999). Overlap according to Pianka's measure of overlap (corrected; Pianka 1974, Krebs 1999) was 0.864. Structural composition of white and tan male territories overlapped by 80.7%. If we take into account the relative abundance of vegetation types in the entire study site, and use Hurlbert's (1978) measure of niche overlap, the morphs overlap by 98.4%.

When we considered the proportion of open area in territories, there was no significant difference in territories occupied by the two morphs (tan, 0.45 $\pm$ 0.049; white, 0.44 $\pm$ 0.041; $F_{morph} = 0.1$, df $= 1$, 26, $P = 0.94$; Fig. 3) or between habitat types (bog, 0.53 $\pm$ 0.046; forest, 0.34 $\pm$ 0.055; pond, 0.43 $\pm$ 0.046; $F_{habitat} = 2.83$, df $= 2$, 26, $P = 0.08$). Furthermore, there was no significant interaction between morph and habitat ($F = 2.06$, df $= 2$, 26, $P = 0.15$).

Although there were no differences in the structural composition of territories across habitat or morph, the Fisher's exact test reveals that the morphs are segregated into different habitat types ($P = 0.0069$; $n = 27$ territories; Table 1, Fig. 4). Based on our data for 1988 through 2002, we used the proportion of available territories (i.e., areas that were at some point occupied by a territorial male) in each habitat as an indicator of the amount of resource potentially available in the environment. We used these values to calculate white and tan male ''preferences'' (Table 1) for habitat type (i.e., selection index; Manly et al. 1993). Tan males are found predominately in the pond habitat ($n = 8$; Fig. 4) and Manly's α reflects this ''preference'' (Manly et al. 1972; see Table 1). White males are most plentiful in the bog ($n = 8$ territories; Fig. 4), but are also found in large numbers in the forest ($n = 6$). A within-morph analysis using proportions of available habitat shows that tan males are found more often in the pond habitat than in the forest or bog ($\chi^2 = 7.74$, df $= 2$, $P = 0.02$; Table 1). However, the same analysis shows that white males are not found more often in any one habitat ($\chi^2 = 2.45$, df $= 2$, $P = 0.29$; Table 1). Therefore, habitat segregation appears to be driven by tan males. Although we acknowledge that we cannot differentiate whether observed patterns represent the actual habitat preferences of males or whether they exist because one morph is excluded from a habitat, the calculation of these indices further reveals the strength of segregation.

Social factors

White males have more neighbors (1.88 $\pm$ 0.32 neighbors) than tan males (1.00 $\pm$ 0.14 neighbors; Kruskal-Wallis $\chi^2 = 3.92$, df $= 1$, $P = 0.05$). Because the reproductive strategy of the white (aggressive) males is to seek EPCs with neighboring females, we had an a priori reason to examine the effect of the number of white neighbors as well. When we analyze the morph of the neighbors separately, white males also have significantly more white neighbors (1.3 $\pm$ 0.21 white neighbors) than do tan males (0.36 $\pm$ 0.26 white neighbors; Kruskal-Wallis $\chi^2 = 6.79$, df $= 1$; $P = 0.01$). Given that a white male owner has at least one neighbor, there is a 0.75 probability that this neighbor will be white. By contrast, given that a tan male owner has at least one neighbor, it is equally probable that neighbor will be white (probability $= 0.46$) or tan (probability $= 0.54$).
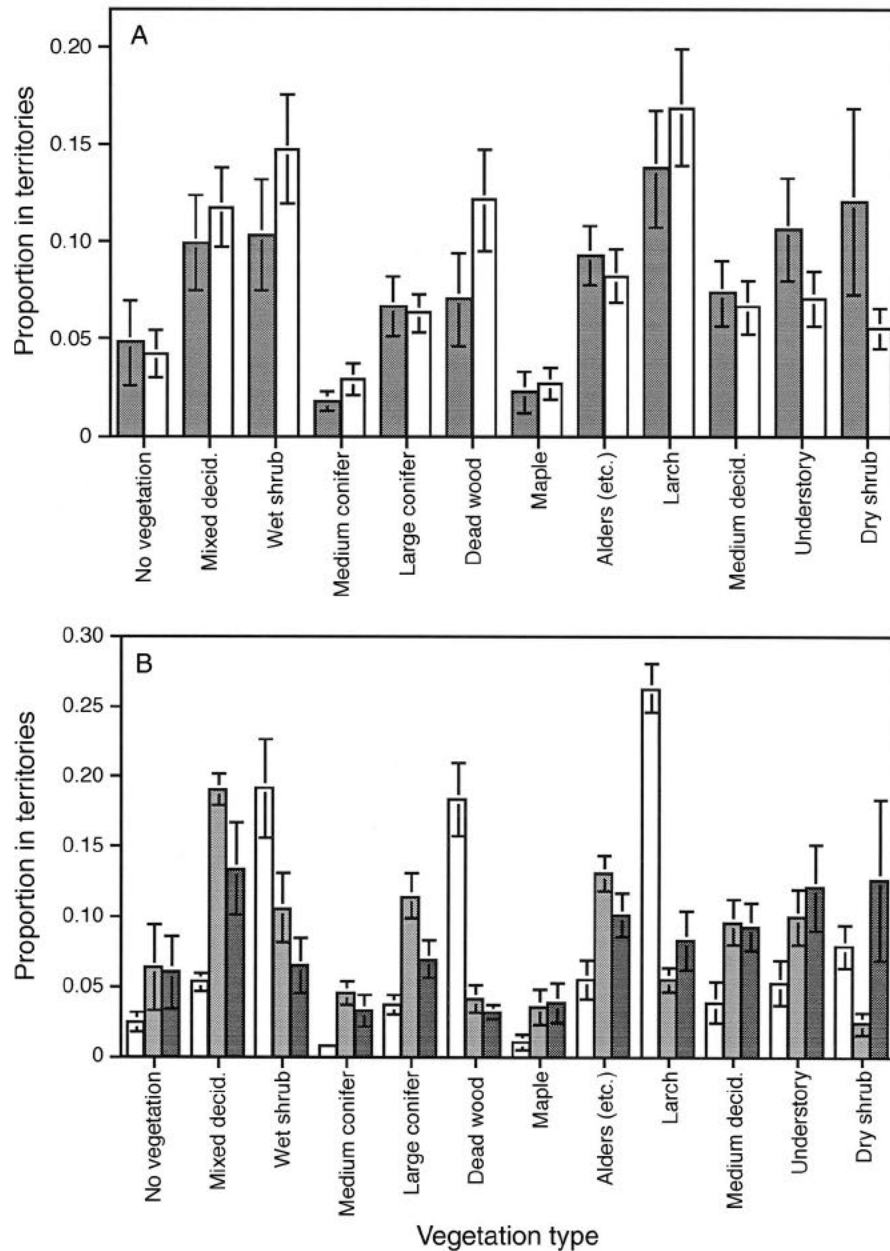
FIG. 2. Vegetation structure in White-throated Sparrow territories. (A) A comparison of proportions (mean ± 1 SE) of each vegetation class in white territories (open bars) and tan territories (gray bars). (B) Vegetation structure of White-throated Sparrow territories in each of the three habitats. Open bars represent bog, light gray bars represent forest, and dark gray bars represent pond habitats; shown are mean proportions ± 1 SE.

The number of neighbors differed significantly in bog, forest, and pond (bog, 2.3 ± 0.28 neighbors; forest, 1.4 ± 0.34 neighbors; pond, 0.80 ± 0.28 neighbors; Kruskal-Wallis χ^2 = 9.59, df = 2, P = 0.01). Significance is due to the difference between the pond and bog habitats (bog vs. forest Q = 1.59, P > 0.05; forest vs. pond Q = 1.10, P > 0.05; pond vs. bog Q = 2.96, P < 0.05). The number of white neighbors differed across habitat type (bog, 1.8 ± 0.21 white neighbors; forest, 1.0 ± 0.25 white neighbors; pond, 0.1 ± 0.21

white neighbors; Kruskal-Wallis χ^2 = 16.36, df = 2, P = 0.0003). Significance was mainly due to a difference in pond and bog habitats (bog vs. forest Q = 1.46, P > 0.05; forest vs. pond Q = 2.00, P > 0.05; pond vs. bog Q = 3.82, P < 0.05).

Increased intruder pressure should cause territories to be smaller (MacLean and Seastadt 1979); therefore, we analyzed whether the number of neighbors would affect territory size in white and tan males. We found that territory size was not affected by the number of
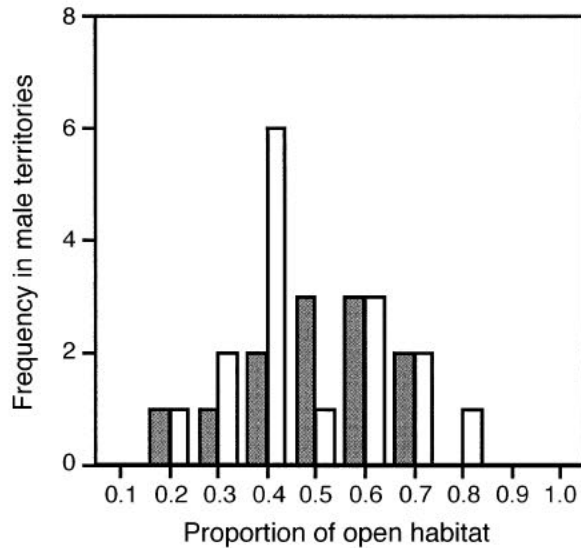
FIG. 3. Proportion of open habitat in white and tan male territories. The two morphs show almost complete overlap, contrary to the results reported by Knapton and Falls (1982) for Algonquin Park, Canada. Open bars represent white male territories, and gray bars represent tan male territories.

TABLE 1. Habitat segregation and "preference" values (Manly et al. 1972) for white and tan male morphs of the White-throated Sparrow, *Zonotrichia albicollis*.

Habitat	Proportion of territories (n)	"Preference" ratio†	Manly's α‡
White males			
Bog	0.50 (8)	1.36	0.45
Forest	0.38 (6)	1.26	0.42
Pond	0.12 (2)	0.38	0.13
Tan males			
Bog	0.18 (2)	0.49	0.17
Forest	0.09 (1)	0.30	0.10
Pond	0.73 (8)	2.18	0.73

† "Preference" ratios above 1.0 indicate preference; values less than 1.0 indicate avoidance.

‡ For Manly's α, values above 0.33 indicate relative preference, whereas values below this indicate relative avoidance.

For all males, reproductive success did not vary in territories with 0, 1, 2, and 3 neighbors ($\rho = -0.04$, $n = 27$, $P = 0.85$). When the morphs were considered separately, again, observed reproductive success did not differ as the number of neighbors increased (for white, $\rho = 0.19$, $n = 16$, $P = 0.47$; for tan, $\rho = -0.05$, $n = 11$, $P = 0.12$). In short, none of the factors measured was correlated with observed reproductive success.

DISCUSSION

If territories or habitats occupied by the two male morphs differ in some aspect of quality, such as food abundance or the availability of nest sites (Brown 1975), we should have detected differences in territory size or vegetation structure. We found no such differences, suggesting that male morphs (or more properly,

neighbors (Spearman's $\rho = 0.02$, $n = 27$ territories, $P = 0.91$), nor was it affected by the number of white male neighbors (Spearman's $\rho = -0.13$, $n = 27$ territories, $P = 0.52$).

We predicted that the value of a territory might differ according to the number of neighbors on its borders. Therefore, we used territory areas with 0, 1, 2, and 3 neighbors as a resource and calculated niche overlap between white and tan males. Territorial "niches" of white and tan males overlapped 24.4%, and Pianka's corrected measure of overlap (Pianka 1974, Krebs 1999) equaled 0.21.

Reproductive success

Observed reproductive success (i.e., the number of chicks to fledge), was not significantly different for the two disassortative pair types ($\chi^2 = 0.54$, df = 1, $P = 0.81$). White males (and tan females) produced 2.72 ± 0.75 chicks, whereas tan males (and white females) produced 2.50 ± 0.63 chicks.

For all males, there was no effect of territory size on reproductive success (Spearman's $\rho = 0.18$, $n = 27$, $P = 0.38$). When each morph was considered separately, reproductive success also did not differ with size of the territory (for tan males, $\rho < 0.001$, $n = 11$, $P = 0.84$; for white males, $\rho = 0.29$, $n = 16$, $P = 0.28$). Reproductive success did not differ in the three types of habitats (Kruskal-Wallis $\chi^2 = 1.40$, df = 2, $P = 0.86$). Strong habitat segregation prevented a within-morph analysis of reproductive success across habitats because sample sizes were small (e.g., there were only two tan males in the bog).
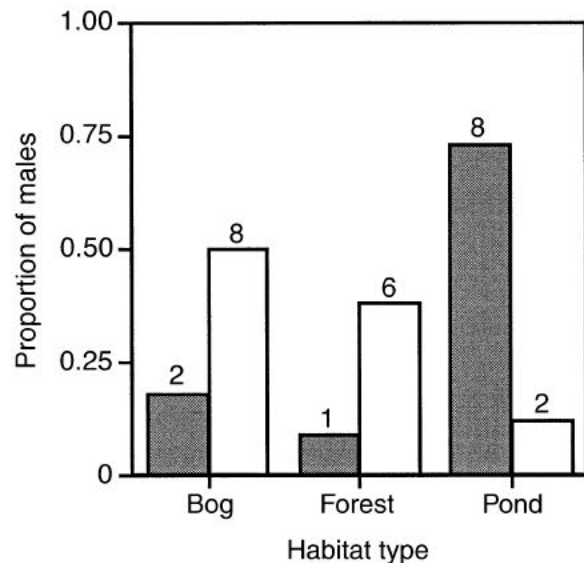

FIG. 4. Segregation of white (open bars) and tan (gray bars) males into the three habitats, with sample sizes shown above the bars.

disassortative pair types) might have similar ecological requirements and, as a result, require no differences in the quality of their territories. Several other pieces of evidence support this conclusion. (1) Although we did not measure "quality" via insect abundance in this study, preliminary analyses indicate that the amount of food does not differ in white and tan male territories (E. M. Tuttle, *unpublished data*). (2) Higher quality males should be able to defend higher quality territories (Hildén 1965, Muller et al. 1997) and an analysis of observed reproductive rates should reflect male and/or territory quality (Brooke 1979, Enoksson and Nilsson 1983, Arcese and Smith 1988, but see MacLean and Seastedt 1979). We found no differences in the number of chicks that the disassortative pair types were able to fledge. (3) In an analysis of the amount of nesting habitat, we detected no difference across morphs. (4) At Cranberry Lake, territories are not historically occupied by white or tan males and ownership can change from year to year (Tuttle 1993). All of these factors tend to further support the premise that the two disassortative pair types probably do not have different resource requirements.

Although the power of our analyses of vegetation structure and openness was relatively low, we did observe nearly significant effects of habitat, and interactions between habitat and morph. These trends can be accounted for by our most striking finding, habitat segregation by morph. Tan males (and white females) are found predominately in the pond, whereas white males (and tan females) are found predominately in the bog. White-throated Sparrows are a generalist species and live in a variety of habitats (Bull 1976); however, white and tan males appear to be specialists that actually use a small subset of the population's resource distribution (sensu Bolnick et al. 2002). Given that the territories of white and tan males are so similar in size and composition, what accounts for such strong segregation in White-throated Sparrows?

Habitat differences between the two pair types previously have been interpreted as evidence of ecological niche separation. Rising and Shields (1980) first suggested that differences in male morphometrics could cause the morphs to behave as two ecological "species" that occupy different habitats. Tan males were found to have smaller flying apparatus that would, theoretically, allow them to maneuver through areas of dense vegetation. White males, on the other hand, seemed better adapted for more open areas. Similarly, Knapton and Falls (1982) suggested that white males occupy territories that are relatively open, whereas tan males occupy territories with a greater range of openness. Utilizing aerial photography as well, our analysis of vegetation openness revealed no such relationship; territories of tan and white males included approximately the same amount of openness and the variance in openness was not greater for tan males. Thus our analyses of ecological requirements do not support the hypothesis of ecological niche separation.

Using different methods that allowed for a high-resolution analysis of select areas in each territory (i.e., transects), Knapton and Falls (1982) reported that herbaceous species differed in white and tan male territories, as well as in their four study areas in Algonquin Park, Ontario. However, tree species did not differ in the same way, suggesting that their two measures of composition differed in scale (Orians and Wittenberger 1991). We did not measure actual species composition, but instead categorized species into 12 classes according to structural characteristics and used remote sensing and GIS to map entire territories at a resolution of 1 m^2. This methodology could be used to analyze territory quality in White-throated Sparrows throughout their distribution because this species nests in a variety of edge habitats (Bull 1976). By categorizing vegetation by structure, we control for differences in plant species composition and vegetation scale that might vary throughout the White-throated Sparrow range. Our remote sensing analysis suggests that, at this scale, there is no difference between vegetation structure in tan and white male territories. We suggest that the differences in species composition observed are not important to territory quality.

We cannot presently determine whether males are choosing to settle in particular habitats or whether they are being excluded from certain areas. Segregation into optimal/suboptimal habitats by dominance interactions is relatively common in other species (Krebs 1971, Robertson 1972) and could, in fact, be operating in White-throated Sparrows. If one morph were dominant to the other, it could secure territories in preferred habitats, thereby forcing males of the opposite morph into suboptimal habitat. Although white birds are more aggressive than tan birds (Hailman 1975, Ficken et al. 1978, Watt et al. 1984, Kopachena and Falls 1993; E. M. Tuttle, *unpublished data*) and they initiate more aggressive attacks (Ficken et al. 1978, Kopachena and Falls 1993), both morphs are equiprobable recipients of aggression (Ficken et al. 1978). It is unclear if aggression translates into dominance, because white birds are not always dominant to tan (Watt et al. 1984, Piper and Wiley 1989*a*, 1991). Knapton et al. (1984) found that tan males × white females paired earlier than white males × tan females. Such evidence suggests that the former pair type might, in turn, have the opportunity to preferentially establish territories in high-quality habitats. So far, we are unable to discern such a pattern in our study population because settlement is obscured by the prior experience of breeding pairs (Tuttle 1993). Despite our inability to determine settlement in this species, if habitat segregation were due to differences in quality between habitat types, we should have seen differences in observed reproductive success between individuals occupying bog, forest, and pond territories.

TABLE 2. A comparison of observed densities of white and tan male territories in Adirondack Park (this study) and Algonquin Park (Knapton and Falls 1982).

Area	Density (no. pairs/ha)			Proportion of tan males
	Tan male	White male	Total	
Adirondack Park				
Bog	0.21	0.82	1.03	0.20
Forest	0.10	0.58	0.68	0.14
Pond	0.43	0.11	0.53	0.80
Algonquin Park				
Pioneer Logging Exhibit	0.37	0.92	1.30	0.29
Camp Road	0.34	0.34	0.69	0.50

We suggest that males segregate their territories for social reasons rather than ecological reasons, and that the distributions of white and tan male territories are determined by the relative locations of conspecifics. The quality or ''value'' of a territory to its owner is probably determined by the presence or absence of neighboring territorial males. This value could change depending on two factors: (1) the morph of the territory owner, and (2) the morph(s) of neighbor(s). White and tan males have adopted alternative reproductive strategies (the pursuit of EPCs vs. monogamy, respectively; Tuttle 2003) whereby the success of their behavioral strategies depends on the proximity to neighboring pairs. White males pursuing extra-pair paternity will be more successful at gaining fertilizations if their territories are located near other fertile females. Therefore, white males might do best by establishing territories in high-density areas, such as the bog in our study site. Tan males, on the other hand, do not pursue extra-pair paternity, but instead guard their females from intruding neighboring males seeking copulation. These males might do better by establishing territories in low-density areas (e.g., ponds) where intrusion pressures from neighboring males are reduced. For tan males occupying territories in the forest and bog, intrusion rates were higher than for their white counterparts (Tuttle 1993, 2003). Our results also suggest that all neighbors are not equally detrimental. Intrusion pressure and the risk of cuckoldry will both be higher when a neighbor is white; accordingly, tan males appear to occupy territories with fewer white male neighbors. Such patterns imply that, in some species, social factors, rather than ecological factors, primarily influence spatial distribution.

Lack (1968) posited that one of the main functions of territoriality was to isolate a breeding female from competing males. Møller (1990, 1992) expanded this idea to include the isolation of fertile females from males seeking extra-pair copulation. He suggested that the combination of defense of a large territory and mate guarding was a more efficient paternity guard than mate guarding alone (Møller 1992). Finally, Eason (1992) suggested that certain territory shapes were optimal, not because they aided in foraging, but because they provided increased intruder detectability and therefore reduced defense costs. We further expand these ideas by hypothesizing that, in some species, territory placement, rather than territory size, can be used to isolate fertile females from EPC-seeking conspecifics.

We believe that our results can be generalized to explain territory distribution throughout this species' range. For the morphs to maximize their respective reproductive strategies, all that is required is that the densities of intruding neighbors be variable; this can be accomplished by variations in the physical landscape. In the Adirondack Park, tan males are most prevalent in the pond habitats, where overall male and, in particular, white male densities are the lowest (Table 2). Our results suggest that this pattern has nothing to do with the ponds per se, but instead reflects the fact that these habitats are neighbor restrictive. We were able to use data reported in Knapton and Falls (1982) for an analysis of two sites in Algonquin Park. A similar pattern emerges in which tan males are most prevalent in the area of low overall male and white male densities (Table 2). We predict that the landscape structure of this area (Camp Road) probably also serves to limit the number of neighbors. Validation of this hypothesis will require a large survey of the territory distributions in populations of white and tan males throughout the species range.

We suggest that white and tan males are able to ''tip the evolutionary scales'' in their favor by settling in habitats of high and low density, respectively, thereby altering the effects of selection. In order to determine whether these spatial trends are truly part of each morph's reproductive strategy we first need to determine realized reproductive success via microsatellite analyses of parentage. Because the reproductive strategy of white males involves the pursuit of extra-pair paternity, this analysis is necessary to determine whether males are fathering chicks in neighboring nests and whether reproductive success changes with density. Second, we need to use analyses such as habitat isodars (Morris 1996*a*, *b*) to recast fitness–density curves and to test for quantitative (Rosenzweig 1979, 1981) as well as qualitative differences in habitat preference (Morris 1988). Both analyses are currently underway and should provide insight into the evolution of polymor-

phism in this species, and the maintenance of biological diversity in general.

Alternative reproductive strategies lead to differences in the social ''requirements'' of the two male morphs, resulting in the segregation into different ''social niches.'' Social niches, like ecological niches, can be temporally or spatially based. Regardless of the cause, habitat segregation of white and tan males normally should have led to niche partitioning and, perhaps, to speciation. However, disassortative mating ensures that both morphs are maintained in the population. Therefore, much like ecological niche partitioning in the sexes, the evolutionary fate of the two morphs is intertwined.

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