



# Using remote sensing image texture to study habitat use patterns: a case study using the polymorphic white-throated sparrow (*Zonotrichia albicollis*)

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## ABSTRACT

**Aim** Ecological factors that vary along spatial scales can greatly influence the outcome of evolution. However, often it is difficult for researchers to identify significant ecological variables that might be associated with the geographical distribution of phenotypes and genotypes in nature. In this paper, we use remote sensing image texture analyses to investigate breeding territories of the white-throated sparrow (*Zonotrichia albicollis*), a polymorphic passerine species that has been shown to segregate spatially according to morph. Our aim was to examine how an integrative measure of landscape feature, such as image texture, could be used to distinguish subtle differences in habitat use and, presumably, habitat selection.

**Location** A population of white-throated sparrows located 1.5 miles east of the Cranberry Lake Biological Station in the Adirondack Mountains of St Lawrence County, New York, was used in this study; the study site itself was approximately 1 km<sup>2</sup>.

**Methods** We analysed 27 territories (16 white males; 11 tan males) to determine if image texture can be used to distinguish differences in vegetation and structure in territories of the two colour morphs. First (variance)- and second (homogeneity)-order image texture measurements with three different window sizes were derived using the green, red, and near infrared bands of Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) data. Texture was then placed into *t*-tests to determine statistical differences between the territories of the two male morphs.

**Results** Significant differences between the territories of the two morphs were found in both variance and homogeneity texture measures in the red and green ASTER bands in all three window sizes. There were no differences with any near infrared texture measures.

**Main conclusions** Examination of first- and second-order statistical measures indicated that the territories of tan males have significantly more spectral variance than the territories of white males, while white males' territories are significantly more homogeneous. These findings are consistent with the previous finding of the morphs settling in 'high' and 'low' neighbour density habitats that differ with respect to the amount of useable area on their borders. Previous study has also suggested that white and tan male territories differ according to overall landscape structure, not vegetation composition. Therefore, we suggest that red and green spectra may be more useful when examining differences in territory structure and possibly territory quality of similar edge-type species. Our results suggest that image texture is a useful tool for ecological and evolutionary modelling of the distributions of phenotypes/genotypes across landscapes.

## Keywords

ASTER, habitat use, image texture, landscape patterns, polymorphism, remote sensing, spatial patterns, territory quality.

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## INTRODUCTION

Quantitative research methods that elucidate spatial patterns are necessary elements for fully understanding evolutionary and ecological processes (Turner & Gardner, 1991). Advancements in landscape ecology and biogeography have emphasized the importance of space and spatial dynamics in examining environmental issues; however, the investigation of the role of these factors in evolutionary ecology is still in its infancy. An increased attention to spatial dynamics in ecology and evolution also underscores the need for methodologies that are capable of integrating multiple factors which can, in turn, be used to develop robust landscape models (Turner & Gardner, 1990; Tucker *et al.*, 1997). Remote sensing is one such methodology that can provide integrated geospatial information about complex landscape features (Roughgarden *et al.*, 1991). Remote sensing techniques, data, and the models they generate will provide an accurate way for landscape ecologists and evolutionary biologists to assess the health and diversity of fauna and flora within entire ecosystems. The ability to map spatial patterns, model landscape structure, and relate this information to ultimate processes will grow in importance as wild lands continue to shrink. Therefore, the integration of these factors promises to be a vibrant area of study for years to come.

The study of habitat selection and use is a prime example where the integration of microevolutionary processes, ecological patterns and remote sensing may yield robust landscape-level models that can help generate novel biogeographical hypotheses. Habitats vary in space and/or time and animals should be selected to differentiate between suitable and non-suitable patches (Wiens, 1976) as fitness (i.e. survival and reproduction) is intimately linked to habitat quality (Hildén, 1965). Habitat selection involves the interpretation of various environmental cues associated with expected fitness returns (Wiens, 1989; Reed, 2004). For example, several species have been shown to establish territories and home ranges based on environmental cues indicating suitable nesting areas (Wiens, 1989; Marshall & Cooper, 2004), ample resource abundance (Jaenike & Papaj, 1992; Marshall & Cooper, 2004), and the presence (or absence) of conspecifics (Stamps, 1988, 1991; Mönkkönen & Forsman, 2002; Thomson *et al.*, 2003; Parejo *et al.*, 2005). Cues used in breeding site selection might differ between the sexes or by age, condition, or stage (Reed, 2004). Similarly, in species where there are alternative reproductive strategies (Gross, 1996), relevant cues might differ according to the strategy of a particular individual. In other words, as individual phenotypes can vary greatly in nature, the selection of 'suitable' habitats will require individual assessment of the particular costs and benefits associated with the fit of an organism to its environment.

As scientists, we often attempt to identify the relevant cues organisms use to determine settlement by examining the correlation of a single habitat feature with individual abundances. However, it is likely that organisms visually interpret the entire landscape, taking into account context, edges, habitat structure, and subtle variation in vegetation features. Therefore, when developing a landscape-level model for a particular organism, it

might be more appropriate to consider an integrative measure of landscape features, one in which multiple measures at several scales are assessed simultaneously. Remote sensing offers such opportunities, as image texture algorithms have been developed to calculate neighbourhood information that do not rely on a single pixel. These methodologies, which analyse the brightness of digital pictorial data, allow us to interpret obvious and subtle structural landscape patterns simultaneously (Musick & Grover, 1990).

The following study builds on the work of Formica *et al.* (2004) by spatially analysing the territory composition of a passerine bird, the white-throated sparrow (*Zonotrichia albicollis*), using texture measurements derived from satellite remote sensing data. This study specifically investigates the potential of first- and second-order texture measurements to distinguish territories of competing individuals (i.e. morphs).

### The study species

The white-throated sparrow (*Zonotrichia albicollis*) is a socially monogamous passerine that breeds in edge habitat of the boreal forests throughout the north-eastern United States and Canada. This species is polymorphic, and both sexes can be separated into tan and white morphs based on the colour of the median crown stripe (Lowther, 1961; Vardy, 1971; Atkinson & Ralph, 1980; Watt, 1986; Piper & Wiley, 1989a). The plumage polymorphism correlates with a chromosomal polymorphism resulting from a pericentric inversion of the second chromosome (Thornycroft, 1966, 1975). White-throated sparrows are unusual in that they mate disassortatively with respect to the polymorphism, so that white almost always mates with tan (Lowther, 1961; Thornycroft, 1975; Tuttle, 1993, 2003).

The polymorphism is also correlated with behavioural differences. White birds are more aggressive than tan birds (Hailman, 1975; Ficken *et al.*, 1978; Watt *et al.*, 1984; Kopachena & Falls, 1993a), yet white birds are not always dominant to tan (Watt *et al.*, 1984; Piper & Wiley, 1989b). White and tan morphs employ alternative reproductive strategies based on the trade-offs between current and future reproduction (Tuttle, 1993, 2003, 2005). Behavioural and ecological differences associated with these reproductive trade-offs are striking. White males invest heavily in securing matings through song, territorial intrusion, bigamy and the pursuit of extra-pair copulations (EPCs) at the apparent expense of mate-guarding and paternal care (Knapton & Falls, 1983; Kopachena & Falls, 1993b; Tuttle, 1993, 2003, 2005). Tan males invest heavily in monogamy (Tuttle, 1993, 2003, 2005) and their current brood through high levels of parental care (Knapton & Falls, 1983; Kopachena & Falls, 1993b). Behavioural and genetic data show that only white males are pursuing EPCs; however, white males are also losing a higher proportion of their paternity to extra-pair fertilizations than tan males.

Using intensive behavioural observation, geographical information systems (GIS) and remote sensing, Formica *et al.* (2004) compared the vegetation structure contained within, and placement of, white and tan male territories. They suggested that

because white males seek extra-pair copulations (EPCs) with neighbouring territorial females (Tuttle, 2003), the relative success of the white male reproductive strategy should increase with the increasing density of breeding pairs (see also Westneat & Sherman, 1997). Similarly, the success of the tan male reproductive strategy (i.e. monogamy and mate-guarding) should depend on the density of EPC-seeking white male neighbours. In accordance with this hypothesis, Formica *et al.* (2004) found that white and tan males tended to segregate their territories. Whereas white males tended to settle in high-density neighbour-rich areas, tan males tended to settle in low-density neighbour-restrictive areas. This segregation was not correlated with ecological factors (i.e. vegetation structure), as the amounts of suitable vegetation (e.g. dry shrub, which is preferred for nesting) did not differ between white and tan male territories. Rather, Formica *et al.* (2004) postulated that this segregation was for the social reasons listed above. In this paper we have expanded the analysis of Formica *et al.* (2004) to include image texture. Our goal was to assess territory composition further in order to determine appropriate remote sensing measures that would help distinguish factors influencing the spatial distribution of phenotypes and genotypes. Such informative measures can be used to build spatially implicit ecological and evolutionary models.

## METHODS

### Study area

A population of white-throated sparrows located 1.5 miles east of Cranberry Lake Biological Station in the Adirondack Mountains of St Lawrence County, New York (44.15° N, 74.78° W), was studied for this project. This population has been monitored since 1988. Our analysis used 27 nonoverlapping white-throated sparrow territories (16 white males and 11 tan males) established in 2000 and described in Formica *et al.* (2004). Breeding pairs were observed for a minimum of 80 h each over the entire breeding season. Every observation of a territorial resident was marked (i.e. flagged), and 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 Inc, Corvallis, OR, USA). The data were corrected using CMT PC-GPS version 3.7 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, CA, USA) ArcView (ESRI, 1999) in shapefile format. We generated territorial boundaries by using the Animal Movement Extension of ArcView to delineate minimal convex polygons (MCP) (Hooge & Eichenlaub, 1997). These vector data (territory polygons) are the same data used in the analyses performed by Formica *et al.* (2004); however, the remote sensing data and the texture analysis are unique to this study.

### Remote sensing data

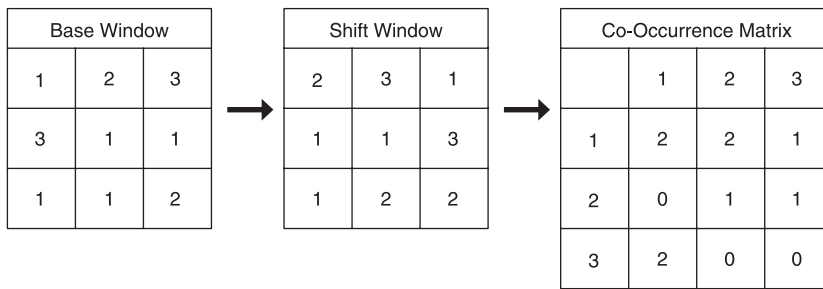
Data from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) sensor were used to provide complete coverage of the study area. ASTER is a relatively new space-borne sensor that is similar in spectral resolution to Landsat Thematic Mapper data, but is collected at a spatial resolution of 15 m vs. the 30-m resolution of Thematic Mapper. An ASTER image of the study area acquired in July 2001 was used for this study. The image was geometrically corrected using a United States Geological Survey Digital Orthophoto Quarter Quadrangle image.

ASTER data are collected in several wavelengths, often referred to as bands. This study employed bands 1, 2 and 3, measuring the green, red and near-infrared (NIR) segments of the electromagnetic spectrum (520–600 nm, 630–690 nm and 790–860 nm, respectively). ASTER data have been found to be useful in other remote sensing studies (e.g. Jensen *et al.*, 2003).

### Image texture

When humans interpret remotely sensed imagery visually, they account intuitively for context, edges, and tonal variation of colour. The result is a complete analysis of the image that allows informed decisions to be made. It is likely that many animals, particularly vertebrates, use similar analyses. Conversely, most remote sensing processing algorithms are based only on image spectral information (e.g. brightness values or 'digital numbers'). To remedy this, many image texture algorithms have been developed that allow computer software to examine other aspects of the image that may influence the way a given pixel or area is classified (Jensen, 2000). These algorithms often generate what is known as image texture. Image texture refers to the pattern of brightness variations or grey-levels within an image or region within an image (Musick & Grover, 1990; Carr, 1999). It is often termed as the tonal change on an image. Texture is produced by an aggregation of unit features that may be too small to be discerned separately on the image (Lillesand & Kiefer, 2000). Texture classification and texture algorithms are different from traditional statistical methods because they rely on statistical properties of a neighbourhood of pixels (Chen, 1998). For example, local (neighbourhood) intensity variance or other statistics derived from individual pixel attributes are sometimes used as statistical texture measures (Musick & Grover, 1992). Conversely, statistical classifiers, such as maximum likelihood, neglect neighbourhood information (Schaale *et al.*, 2000). Put simply, when a small area of an image (e.g. a 3 × 3 pixel area) has little tonal variation, the dominant property of that area is grey shade. However, when a small area has large tonal variation, the dominant property of that area is texture (Jensen & Gatrell, 2005).

We used texture analyses to examine habitat use patterns (i.e. territoriality) in a natural population of white-throated sparrows. Because white-throated sparrows are edge species (Lowther & Falls, 1968; Knapton & Falls, 1982; Tuttle, 1993, 2003) that defend territories in the transition zones between habitats, we focused on texture variance and homogeneity to



**Figure 1** Number of occurrences of the relationship between a pixel and its specified neighbour (e.g. the co-occurrence matrix shown was produced using each pixel and its horizontal neighbour (shift values X = 1 and Y = 0) for a 3 × 3 pixel window).

look for differences in habitat use. Texture variance is a first-order measure that shows the overall diversity of pixel values in a territory. Texture homogeneity is a second-order measure that takes into account the spatial orientation and direction of pixels, thereby allowing detection of the magnitude of change within a territory.

*First-order neighbourhood texture*

First-order texture properties are usually derived through first-order statistics of local areas such as variance. In this study, variance was chosen as a texture measure to account for the variability of spectral responses in white and tan male territories. Moving pixel windows are used to calculate texture for each pixel based on it and its surrounding pixels. Variance was calculated in several different moving window sizes (7 × 7, 5 × 5, and 3 × 3) with the following equation:

$$Variance = \frac{\sum(x_{ij} - M)^2}{n - 1},$$

where  $x_{ij}$  is the digital number (brightness value) of pixel  $(i,j)$ ,  $n$  is the number of pixels in the moving window and  $M$  is the mean in the moving window (ERDAS, 1997).

*Second-order grey level co-occurrence matrix*

A second-order set of image texture measures was proposed by Haralick (1979, 1986) based on spectral value spatial dependency grey level co-occurrence matrices (GLCM). GLCMs contain information about spectral intensities of pixels and their neighbours at fixed distances and orientations. The GLCM is a matrix of relative frequencies with which pixel values occur in two processing windows specified by direction and distance. It shows the number of occurrences of the relationship between a pixel and its specified neighbour. For example, the co-occurrence matrix shown in Fig. 1 was produced using each pixel and its horizontal neighbour (shift values X = 1 and Y = 0) for a 3 × 3 pixel window.

Matrices can be formed for any direction and distance. It is assumed that all textural information is contained in the spectral value spatial-dependency matrices for angles of 0, 45, 90, and 135 degrees. Haralick (1979, 1986) proposed a number of measures to extract useful textural information from the matrices. One commonly used measure is homogeneity. Large changes in spectral values will result in very small homogeneity values.

Conversely, small changes in spectral values will result in larger homogeneity values. Homogeneity was calculated using the following equation:

$$Homogeneity = \sum_{i=0}^{quant_k} \sum_{j=0}^{quant_k} \frac{1}{1 + (i - j)^2} * h_c(i, j),$$

where  $quant_k$  is quantization level of band  $k$  (e.g. 28 = 0–255) and  $h_c(i,j)$  is the  $(i,j)$ th entry in one of the angular brightness value co-occurrence matrix (Jensen, 2005). In more general terms, homogeneous areas should be characterized by perceived and arithmetic ‘smoothness’, whereas heterogeneity should produce more coarse outcomes.

**Moving windows**

Moving window analysis is a technique in remote sensing where values for a new raster file are created by using the values of surrounding pixels within a designated area (e.g. a window size of 3 × 3 has 9 pixels) to calculate the new value of the central pixel. After each computation for the central pixel, the window then ‘moves’ over one unit (i.e. column or row) and repeats the process for every pixel over the entire area of interest. In this study, every pixel within each territory had a variance and homogeneity texture value calculated by a window that was moved in both the row and column dimensions, one pixel at a time. To test the robustness of our analysis and to avoid possible spurious results from analysis conducted at one particular scale, multiple window sizes were used. Because large window sizes (e.g. 7 × 7) integrate larger areas than those that are integrated using small window sizes (e.g. 3 × 3), such an analysis allows us to determine the most appropriate scale for our study species. Our window sizes were chosen considering both the resolution of the ASTER data as well as the average size of white-throated sparrow territories in this study population. There were no territories that were smaller than the moving window sizes.

**Spectral response**

Basic spectral responses (green, red, near-infrared) were extracted from the territories to be certain that texture measurements are more useful than basic spectral characteristics to differentiate between white and tan male territories.

**Table 1** Descriptive statistics for variance texture measures. Also shown are one-tailed *P*-values; values in bold type are significant at the 0.05 level

Band		Window size								
		3 × 3			5 × 5			7 × 7		
		Mean	SD	<i>P</i>	Mean	SD	<i>P</i>	Mean	SD	<i>P</i>
Green	W	3.93	2.79	<b>0.006</b>	6.61	3.93	<b>0.008</b>	9.27	4.24	<b>0.011</b>
	T	9.11	5.39		14.62	8.96		18.40	11.00	
Red	W	3.24	1.91	<b>0.008</b>	5.78	3.40	<b>0.010</b>	8.25	4.53	<b>0.010</b>
	T	8.89	6.31		14.60	10.40		18.50	12.00	
NIR	W	65.00	63.80	0.250	106.00	108.00	0.240	137.00	129.00	0.24
	T	84.20	77.10		143.00	142.00		185.00	187.00	

**Table 2** Descriptive statistics for homogeneity texture measures. Also shown are one-tailed *P*-values; values in bold type are significant at the 0.05 level

Band	Morph	Window size								
		3 × 3			5 × 5			7 × 7		
		Mean	SD	<i>P</i>	Mean	SD	<i>P</i>	Mean	SD	<i>P</i>
Green	W	0.794	0.077	<b>0.008</b>	0.785	0.071	<b>0.009</b>	0.775	0.068	<b>0.018</b>
	T	0.715	0.076		0.711	0.074		0.715	0.069	
Red	W	0.746	0.074	<b>0.024</b>	0.739	0.064	<b>0.029</b>	0.737	0.059	<b>0.029</b>
	T	0.673	0.096		0.679	0.083		0.686	0.068	
NIR	W	0.372	0.143	0.330	0.374	0.137	0.330	0.375	0.133	0.440
	T	0.351	0.095		0.357	0.060		0.370	0.059	

### Statistical comparison

After the texture measures were computed, territory polygons were used to extract the average texture values for each territory. These texture measure values were then placed into simple *t*-tests to determine differences between white and tan white-throated sparrow habitats. Spectral responses were also statistically compared using simple *t*-tests.

### RESULTS

Image texture was useful in detecting differences in habitat use in the white-throated sparrow. Significant differences were found in first-order neighbourhood texture (i.e. variance) between white and tan male territories in all moving window sizes in the green and red spectral bands (Table 1). The same results were also observed for second-order grey-level co-occurrence matrix (i.e. homogeneity; Table 1). Specifically, tan male territories had significantly greater variance texture values and lower homogeneity

values in both green and red bands than white male territories for all window sizes (Fig. 1). However, textures derived from near-infrared data were not significantly different for white and tan male territories. Although the differences in the near infrared bands were not significant, the trend was still the same with tan males having greater variance texture values and lower homogeneity values. These results were surprising because the near-infrared radiant flux is usually the best indicator of vegetation differences (ASTER Spectral Library, 1999). However, in this study the near infrared spectral bands resulted in much higher texture values with higher standard deviations (Tables 1 and 2). The non-significant differences in the NIR texture could be due to the high variability of the texture measures (Tables 1 and 2).

To complement the image texture analysis we had completed, we also analysed basic spectral responses gathered from territories. In no case was there a significant difference in spectral response between white and tan male territories (Table 3). Such results suggest that image texture may be more useful in differentiating between the territories of the two morphs.

**Table 3** Descriptive statistics for basic spectral responses. Also shown are one-tailed *P*-values

Band	Morph	Mean	SD	<i>P</i>
Green	W	46.12	4.37	0.23
	T	47.44	4.59	
Red	W	23.51	3.66	0.27
	T	24.44	4.01	
NIR	W	77.05	5.46	0.16
	T	80.24	9.22	

## DISCUSSION AND CONCLUSIONS

Assuming that the distribution of an organism reflects a hierarchical selection process, how individuals assess multiple cues that vary both temporally and spatially, yet reveal accurately the relative qualities of patches, remains unclear (Williams & Nichols, 1984; Hutto, 1985; Jones, 2001). When making decisions about habitat selection, organisms may or may not be assessing the abundance of a particular environmental factor; instead, it is likely that they simultaneously take into account multiple factors about habitat including context, edges, transitions, structure and vegetation composition. Determining the cues or parameters that are biologically relevant is difficult at best and, if lucky, we can find one environmental factor that covaries with the presence or absence of a species. To complicate matters further, there exists intraspecific variability in which different phenotypes and/or genotypes use various combinations of cues to determine where best they should reside. In order to develop landscape-level models that accurately describe animal distributions, we need complex measures of landscape features that represent the integration of information gathered from several scales. Our results indicate that remote sensing texture analysis is one such measure that is capable of distinguishing subtle features of the landscape associated with the habitat use of particular groups of individuals; this is not always possible with conventional GIS analysis.

Using red and green spectra we are able to detect significant differences in the image texture of the breeding territories of white and tan morphs of the white-throated sparrow. Examination of first- and second-order statistical measures indicates that tan male territories have significantly more spectral variance than white male territories, while white male territories are significantly more homogeneous. Our findings are robust, regardless of window size, suggesting that the methods we use and the results we present are similarly robust. These results are consistent with a previously published study, which found that tan males tended to establish territories primarily in low-density peripheral habitats that were adjacent to large 'uninhabitable' areas (e.g. ponds and meadows; Formica *et al.*, 2004). By establishing territories that border unusable areas, tan males are able

to limit the number of neighbours capable of competing for the parentage of their chicks. Conversely, white males exhibit a behavioural strategy that involves the pursuit of extra-pair matings (i.e. EPCs; Tuttle 1993, 2003, 2005) and, accordingly, they tend to establish territories in high-density contiguous habitats such as bogs (Formica *et al.*, 2004). High- and low-density habitats differ in the amount and type of structure and edge of which they are composed (Formica *et al.*, 2004; E. M. Tuttle, unpublished data) and so it is reasonable that our analyses show a difference when using red spectra, which is more indicative of structural landscape differences (ASTER Spectral Library, 1999). Structure and edge serve to limit the number of neighbouring males that can settle adjacently, thereby creating low-density habitats with fewer social interactions. High- and low-density habitats also differ in their vegetation composition, as certain species of plants tend to dominate their respective habitats (Formica *et al.*, 2004; E. M. Tuttle, unpublished data). Because green spectra tend to indicate differences in photosynthetic rates (ASTER Spectral Library, 1999), it is not surprising that analyses using this band are also significantly different for white and tan male territories. Together these results suggest that red and green spectra are perhaps the best wavelengths to use when examining differences in territory composition of similarly distributed 'edge' species. In addition, the strength of the evidence in any statistical test is contained in the *P*-value. To this end, *P*-values for the variance texture measurements were lower than the corresponding homogeneity *P*-values. This may indicate that texture variance is a better predictor of white and tan male territories. Also, *P*-values increased with increasing moving window sizes indicating that 3 × 3 windows may be best to identify territorial differences.

What is surprising, however, is that near infrared (NIR) reflectance did not resolve any textural differences in the territories of tan and white males. NIR data primarily indicate vegetation and are more sensitive to habitat changes (ASTER Spectral Library, 1999). Typically, white-throated sparrows occupy the transition zones between forest and more open habitat; they often establish territories along the edges of gaps, beaver meadows, streams, ponds and bogs (Lowther & Falls, 1968; Knapton & Falls, 1982; Tuttle, 1993, 2003). Because territories commonly include two or more habitat types, they necessarily exhibit high variances. In these cases, NIR may be far too sensitive to use for determining the differences between tan and white male territories. In addition, NIR is not necessarily the best band to examine if there are areas containing water (ASTER Spectral Library, 1999). As white-throated sparrow territories commonly encompass some sort of water (e.g. pond, stream or standing water associated with a bog), it is not unexpected that we detected no differences in the NIR. In sum, the NIR band may not be suitable for texture analyses in such a generalist habitat species as the white-throated sparrow.

The results we present in this study further suggest that the physical environment as assessed through texture analysis is somehow a factor in, or result of, the 'social segregation' of the two morphs. The fact that remote sensing image texture detects subtle differences in the habitat use patterns of two genotypes (i.e. white and tan) is an exciting prospect for ecological and evolutionary biology research. Our findings suggest that organisms

may use integrative cues from the physical landscape to find areas that fulfil not only their ecological requirements, but their social requirements as well. Whether similar results hold for other species with alternative reproductive strategies or with other intraspecific comparisons remains to be seen. However, once such information about habitat use is found, it can be used to generate explicit landscape-level models that incorporate both proximate and ultimate processes. For example, recently evolutionary biologists have begun to use cellular automata (CA) models, in which simple rules about how individuals interact are simulated on two-dimensional grids (Molofsky & Bever 2002, 2004; Molofsky *et al.*, 2001, 2002); such models could now be fashioned to incorporate information such as remote sensing image texture. Ecologists are often concerned with forest heterogeneity and the amounts of sharp and gradual boundary within an area (St-Louis *et al.*, 2004), yet by incorporating image texture into their models, all edges, regardless of whether they are hard or soft, are taken into account as an integrative measure of texture. Finally, conservation issues can be addressed via image texture because by understanding the use of habitat by edge species (Reis *et al.*, 2004), such as the white-throated sparrow, we gain insight into the preservation of important and threatened ecosystems such as the boreal forests of the North America (Hannon & Schmiegelow, 2002).

Researchers have often used vegetation characteristics to delineate animal territories and home ranges. However, observable differences are often not apparent (Formica *et al.*, 2004; Parejo *et al.*, 2005), leaving scientists to wonder about contributing factors. Such a situation does not necessarily mean that animals are not using some unknown attribute of vegetation to determine settlement; instead, it could indicate that researchers do not have the means to assess habitat differences in the same way animals do. Remote sensing data and techniques offer a viable alternative that is beginning to be used more frequently in ecological and evolutionary research (Haslett 1990, Roughgarden *et al.*, 1991). This is probably due to the synoptic coverage that remote sensing data provide over entire landscapes and regions. Further, remote sensing data can be acquired at multiple scales and at multiple times, thereby allowing analyses of ecological phenomena from local to global scales through time (Quattrochi & Pelletier, 1991). The method presented in this paper may provide a way to more accurately map and model habitat selection and use in a wide variety of animals. In particular, remote sensing image texture derived from the green and red portions of the electromagnetic spectrum may help to determine how habitat generalists, such as the white-throated sparrow, use various environments.

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