Examining the social landscapes of alternative reproductive strategies

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Abstract

Social environments are inherently dynamic, often changing depending on the frequency and outcomes of conspecific interactions – they can be simultaneously the targets and agents of selection. Understanding how organisms settle in heterogeneous social environments and the effects this has on reproductive success is vital to our understanding of the selective forces at work in wild populations. From an intensive behavioural and ecological study of territoriality in the polymorphic white-throated sparrow (*Zonotrichia albicollis*), we demonstrate that males of the two morphs inhabit social niches that correspond to their respective alternative reproductive strategies. By integrating molecular ecology and Geographic Information Systems, we generated continuous, socio-spatial models of local conspecific density and cuckoldry risk. Our results suggest that the morphs segregate their territories based on socio-spatial variables, creating a heterogeneous social landscape that matches each behavioural phenotype with a favourable social environment. Specifically, the monogamous tan males tended to settle in low-density areas that were also low for cuckoldry risk, while the opposite was true for the promiscuous white males. This pattern of socio-spatial heterogeneity, combined with the social niche partitioning we observed, might act as a *social* niche polymorphism, and play an important role in maintenance of the alternative reproductive strategies of the white-throated sparrow. Socio-spatial factors, similar to those observed in the white-throated sparrow, may play important roles in the evolution of mating systems in other species, even those with more continuous or cryptic variation.

Introduction

The maintenance of phenotypic variation in the face of selection remains a fundamental focus in evolutionary biology (Byers, 2005; Hedrick, 2006). How alternative strategies and tactics are maintained has been of particular interest (Maynard Smith, 1982; Gross, 1996; Shuster & Wade, 2003) because if the average fitness of each alternative were unequal, selection should cause the extinction of the strategy with the lower fitness (Thompson *et al.*, 1993; Brockmann, 2001). Several

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evolutionary processes are thought to play a primary role in the maintenance of alternative phenotypes (Maynard Smith, 1982; Endler, 1986; Charnov, 1993; Gross, 1996); these include frequency- and density-dependent selection, context-dependent switching, and spatial and temporal heterogeneity of the environment (Brockmann, 2001). Most empirical work examining the maintenance of alternative strategies has focused on frequency- and density-dependent selection (e.g. Gross, 1991; Sinervo *et al.*, 2000, 2001; Svensson & Sinervo, 2000; Bleay *et al.*, 2007; Vercken *et al.*, 2007); relatively fewer studies have investigated the importance of multiple niche polymorphism and environmental heterogeneity (however, see Shine *et al.*, 2005; Svensson & Sinervo, 2004; Koseki & Fleming, 2006; Gosden & Svensson, 2008). Although the theoretical conditions for the maintenance of diversity via ecological heterogeneity

are specific (Prout, 1968; Hedrick *et al.*, 1976; Maynard Smith & Hoekstra, 1980; Hedrick, 1986; De Meeus & Goudet, 2000; Ravigne *et al.*, 2004), varying environments have been shown to be an important force in some systems (for review and examples see Hedrick, 2006).

The study of natural polymorphisms has helped reveal the role of environmental heterogeneity in the maintenance of phenotypic diversity. Several species that exhibit colour polymorphisms also exhibit habitat segregation and intraspecific niche partitioning. The ultimate and proximate causes of habitat segregation vary between these systems, although differential predation is often a common theme. Several species of terrestrial snails (including the well-studied *Cepaea* genus) exhibit intraspecific colour morph segregation among habitats or across environmental gradients, and both the absorption of solar radiation and differential predation have been cited as plausible mechanisms contributing to partitioning in these systems (e.g. *Theba pisana*: Hazel & Johnson, 1990; *Cepea*: Jones, 1982; Ozgo, 2005; and reviewed in Cook, 1998; *Littorina obtusata*: Phifer-Rixey *et al.*, 2008). In the walking stick genus *Timema*, the different colour morphs segregate among plant host species. There is strong evidence that divergent selection on colour pattern by avian predators contributes to reproductive isolation between the morphs and has led to differential host (habitat) preferences (Sandoval, 1994; Nosil, 2004; Sandoval & Nosil, 2005). Occasionally the colour–morph habitat segregation is observed in the predator itself, as is the case in the red-tailed hawk (*Buteo jamaicensis*), where the darker morph tends to be found in darker perching sites than their lighter counterparts (Preston, 1980).

The majority of the above examples have examined ecological factors that contribute to the maintenance of the niche partitioning behaviour and possibly the maintenance of the colour polymorphism. However, recent advances in quantitative genetic and selection theory suggest that heterogeneity in the *social environment* (i.e. the environment created by interactions with conspecifics) may also be important in phenotypic evolution (Moore *et al.*, 1997; Wolf, 2003) and the maintenance of heritable genetic diversity (Gosden & Svensson, 2008; Harris *et al.*, 2008). The social environment can generate 'social selection' (Wolf *et al.*, 1999), which occurs when the phenotypes of social partners affect the fitness of focal individuals (West-Eberhard, 1979, 1983; Wolf *et al.*, 1999; Sinervo *et al.*, 2001). Social selection theory is vital to our understanding of selective processes because it allows researchers to quantify the effects social interactions have on total selection (Moore *et al.*, 1997; Wolf *et al.*, 1999). This perspective emphasizes that the social environment affects both the form of selection and the evolutionary response to it (Wolf *et al.*, 1998).

Heterogeneity in the social environment may generate stable, nonrandom groups, or 'social niches' (Formica *et al.*, 2004). Just as with ecological niches, the behav-

iours that result in the occupation of social niches can be innate or plastic, and can be the product of past selection regimes, current selective processes, learned behaviours or phenotypic plasticity. The phenotypic covariance necessary for social selection could be generated if individuals segregate among social niches based upon their own phenotypes. This phenomenon would be similar to intraspecific, ecological niche partitioning, where conspecifics segregate to avoid competition for resources (Skulason & Smith, 1995; Smith & Skulason, 1996; e.g. Butler *et al.*, 2000; Adams, 1996; Perry, 1996; Schoener & Schoener, 1982). Similar to habitat partitioning, social niche partitioning could occur if there are nonrandom associations of phenotypes among particular social environments (*sensu* Jones, 2001).

As with other behavioural processes, it may be difficult (or impossible) to differentiate whether social niche partitioning is an emergent property of interactions with other conspecifics, the result of active choices by individuals, or simply the result of past selection. If this phenotypic segregation covaries with differences in fitness (e.g. individuals found outside of their social niche experience a reduction in fitness), we hypothesize that social niches could operate in a fashion similar to multiple niche polymorphism models involving ecological niches (Levene, 1953; Levins, 1968; Hedrick *et al.*, 1976; Hedrick, 1986, 2006), thereby contributing substantially to the maintenance of phenotypic and genotypic diversity. Examples in which social niche partitioning could play an important role in generating selection regimes include conspecific competition (Brown & Orians, 1970; Brown, 1975; Møller, 1991; Westneat & Mays, 2005), mate dispersion (Shuster & Wade, 2003), information dissemination (e.g. social foraging; Giraldeau & Caraco, 2000), systems with intra- and inter-population variance in morph frequencies (Svensson *et al.*, 2001; Gosden & Svensson, 2008), dominance hierarchies (Ficken *et al.*, 1990; Moore *et al.*, 2002), food caching (Dally *et al.*, 2005) and territoriality (Brown & Orians, 1970; Trivers, 1972; Davies & Houston, 1984).

Quantifying social heterogeneity is not intuitive, and social environments are defined in a variety of ways, some of which may be better suited than others for defining social niches. Typically, social environments are either described qualitatively, characterized by population-level measures (e.g. population density: Shilova & Orlenev, 2004; Saeki *et al.*, 2005; Svensson & Sinervo, 2000; Hirschenhauser *et al.*, 2003; or morph frequency: Sinervo *et al.*, 2001; Svensson *et al.*, 2001), sex ratio (e.g. Carroll & Corneli, 1995; Sadowski *et al.*, 2002; Saeki *et al.*, 2005), defined by membership in groups (e.g. Kaiser *et al.*, 2003; Moore & Moore, 2003; Croft *et al.*, 2004; Moretz *et al.*, 2007) or social environments are measured by quantifying individual interactions between conspecifics (Moore *et al.*, 1997; e.g. Wilson *et al.*, 2009; McGraw *et al.*, 2003; DeVries, 2002). Ecological (abiotic)

environments, however, are often quantified by measuring specific variables over spatial and temporal ranges. Therefore, we suggest that a useful way to quantify social environments and their phenotypic and fitness effects is to approach them as landscapes by measuring social and behavioural variables across a spatial coordinate system. By generating social landscape models researchers can easily quantify and visualize social heterogeneity, correlate social and ecological variables, and predict how individuals' social experiences change as they move across space and time. To accomplish this goal, we conducted a spatial exploration of the social landscape that included territorial settlement choices, local density, realized reproductive success, and predicted cuckoldry risk as measures of the social landscape in the white-throated sparrow (*Zonotrichia albicollis*). White-throated sparrows are particularly useful for examining the social environment through the lens of quantitative genetics because they are one of a few species with two morphs that exhibit fixed, genetic, alternative life-history strategies (Tuttle, 2003) and so a high level of covariance between genotype and phenotype has already been established.

Our first aim was to determine if the settlement choices of the males of each morph generated heterogeneity in local density, a social-landscape variable. Our second aim was to determine if the previously proposed partitioning of social niches in this species (Formica et al., 2004) translated into differences in regions of varying cuckoldry risk across the landscape. Such a finding would suggest that spatial settlement patterns are an important component of the alternative reproductive strategies of the males. Finally, we wanted to combine these analyses to examine if our spatially continuous measure of local density covaried with a spatial model of predicted cuckoldry risk across the entire landscape.

Methods

Study species

The white-throated sparrow is a socially monogamous territorial songbird that exhibits a stable genetic polymorphism caused by a complex rearrangement of the second chromosome (Thorneycroft, 1966, 1975; Thomas et al., 2008; Romanov et al. 2009). The presence or absence of the rearrangement corresponds to two distinct plumage morphs, white and tan, that are found in both sexes. White morphs are heterozygous, whereas tan morphs are homozygous and do not carry the rearrangement (Thorneycroft, 1966, 1975); very few individuals have been identified as homozygous for the rearrangement, suggesting lethality. In addition to plumage (Lowther, 1961; Lowther & Falls, 1968), morphology, behaviour and life-history characteristics all appear to have a genetic basis, as they are also correlated with

morph (Ficken *et al.*, 1978; Knapton & Falls, 1983; Knapton *et al.*, 1984; Piper & Wiley, 1989; Tuttle, 1993, 2003; Falls & Kopachena, 1994). White and tan birds mate disassortatively (i.e. tan males typically mate with white females and white males with tan females); this mating pattern, in combination with the Mendelian inheritance of the chromosomal rearrangement, results in the stability of the polymorphism across the species range (Thorneycroft, 1966, 1975). All pairs examined in this analysis followed this mating pattern, so that all males were mated to females of the opposite morph. White and tan males attempt to maximize their reproductive success by pursuing alternative reproductive strategies (Tuttle, 1993, 2003). White males are more aggressive, sing more, intrude frequently, and are promiscuous (pursue extra-pair copulations or EPC). Tan males guard their mates more, do not pursue EPC (Tuttle, 1993, 2003), and invest more effort in parental care (Knapton & Falls, 1983). White males are no more likely to win antagonistic interactions than tan males (Piper & Wiley, 1989). In our population, we find no evidence that one morph arrives earlier than, or has spatial dominance over, the other. The male morphs tend to segregate according to social environment, with the majority of the promiscuous, white males settling in high density bog areas and the majority of monogamous, tan males settling in low-density, neighbour-restrictive pond habitats (Formica et al., 2004). We hypothesize that habitats of varying density provide different social niches, thereby creating socio-spatial heterogeneity. We acknowledge that territory settlement patterns may be influenced by female behaviours, but the majority of behaviours that we use to define territory boundaries (singing, expelling intruders, etc.) are expressed almost exclusively by males (personal observation) and so we consider the territories as extended phenotypes of the males.

Field

We studied a population of white-throated sparrows located 2.4-km east of Cranberry Lake Biological Station in the Adirondack Mountains of St. Lawrence County, New York (44.15°N, 74.78°W). The study site is approximately 2 km^2 and supports between 20 and 60 breeding pairs. We consider this a closed population with few to no additional pairs interacting with the marked individuals. The area surrounding this population is mostly contiguous forest with few locations for additional pairs to settle. Individuals spend the majority of their time within the territorial boundaries; however, individuals have been observed in forays across the study site, suggesting that individuals are free to move within the entire study area (E. M. Tuttle, unpublished data). Although this population has been studied since 1988, in this paper, we report results of an intensive analysis of 28 territorial pairs conducted in 2000, and 34 territorial pairs in 2004. These

2 years were chosen because they were sufficiently separated temporally as to have little overlap in individual composition; only four adult territorial males were present in both years. In addition, they are the only two years for which we have complete parentage for nests across a continuous spatial range. The geographical information systems (GIS) methods we employed for modelling cuckoldry risk are sensitive to spatial areas where there is incomplete information. Since we do not have complete parentage data for the 2001–2003 breeding seasons because of high predation, only data from 2000 to 2004 could be employed for this analysis. Coincidently these two years also represent a lower (2000) and an average (2004) population density; although this allows us to anecdotally compare the two, we are hesitant to draw any general conclusions about the effect of population density with a sample size of two years. Additionally, these breeding seasons represented years that were most similar in genotype frequencies. All birds at the study site, including hatchlings surviving to six days post-hatch, are uniquely colour-banded (U.S. Fish & Wildlife Service Master Banding Permit #22297 to E. M. Tuttle).

Breeding pairs were observed for an average of 80 h throughout both breeding seasons. Nests were found by observing the females during nest building, egg laying and incubation. Every observation of a territorial resident and each nest 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). After post-differential correction, these locations are accurate to approximately 3 m. The data were corrected using CMT PC-GPS v3.7 software (CMT 2001) with correction data from the Syracuse Hancock International Airport base station (43.10°N, 76.08°W) in 2000 and the Paul Smiths College (44.43°N, 74.25°W) base station in 2004 in the National Geodetic Survey base station network. All data were reprojected into Universal TransMercator 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 (Hooge & Eichenlaub, 1997; Fig. 1b) following the methodology presented in Formica et al. (2004).

Once nests were found, they were checked every day and the number of eggs and/or chicks was recorded. After six days post-hatching the chicks were banded and ~80 µL of blood was taken from the brachial wing vein. Adults were captured either by passive mist netting throughout the breeding season or during banding of their nestlings, and ~200 µL of blood was taken from the brachial vein. Hematocrit was stored in Longmire's solution (Longmire et al., 1992) at 4 °C until DNA extraction.

Molecular parentage

DNA was extracted from preserved hematocrit using the Promega DNA IQ® magnetic extraction kit (Promega, Madison, WI, USA). Five polymorphic microsatellite primer sets (Gf01 and Gf12, Petren, 1998; MME1, Jeffery et al., 2001; DPµ01 and DPµ03, Dawson, 1997), originally designed for use in other species, were optimized for white-throated sparrows. All microsatellites showed a high number of alleles (14–30 per locus) and a low number of null alleles. We used the polymerase chain reaction (PCR) protocol outlined in the above listed literature with the exception of the thermal cycle for both DPµ primers; for those we used a thermal cycle of 94 °C for 3 min, then 30 cycles of 94 °C for 30 s, 49 °C for 30 s and 72 °C for 30 s. Amplified samples were kept at 4 °C until analysed on an ABI 310 Genetic Analyzer® (Applied Biosystems, Foster City, CA, USA).

We analysed paternity in a two-step process (*sensu* Webster et al., 2004; Stutchbury et al., 2005). We began our parentage assignment using data generated from four of the microsatellite markers (Gf01, Gf12, MME1 and DPµ03) in the program CERVUS 2.0 (Marshall et al., 1998), which uses a likelihood approach to rank all possible biological parents for each chick by calculating a likelihood score (the LOD score) and totalling the mismatched alleles between possible parent and chick. Egg dumping is rare in white-throated sparrows (Tuttle, 2003); therefore, we assumed that if the social mother had zero mismatched alleles, she was the biological mother of the chicks. We then compared, by hand, the genotypes of all males with 0–1 mismatched alleles, as well the social father of the chicks. For each paternity assignment, we used a 'total evidence' approach to determine whether the CERVUS assignment based on LOD was reasonable (see Prodöhl et al., 1998). In most cases, we accepted the CERVUS assignment. In the rare case ($n = 9$) that two males had similar LOD scores, and no mismatched alleles with a particular chick, we used a fifth microsatellite (DPµ01) to assist in making final decisions on parentage. In all cases the fifth microsatellite resolved any parentage discrepancies.

Geographical information systems

Raster data analysis is a type of GIS analysis that divides the study site into a continuous grid, assigning values (i.e. digital numbers) to each cell. Raster analysis is typically used for modelling continuous variables across a landscape, such as elevation, land use classifications or vegetation distribution (DeMers, 2002). The territory polygons described above were converted to 10 m × 10 m raster grid layers (i.e. rasterized). Ten meters was chosen as the grid cell size because it was the largest cell size that did not distort the shape of the territories. A
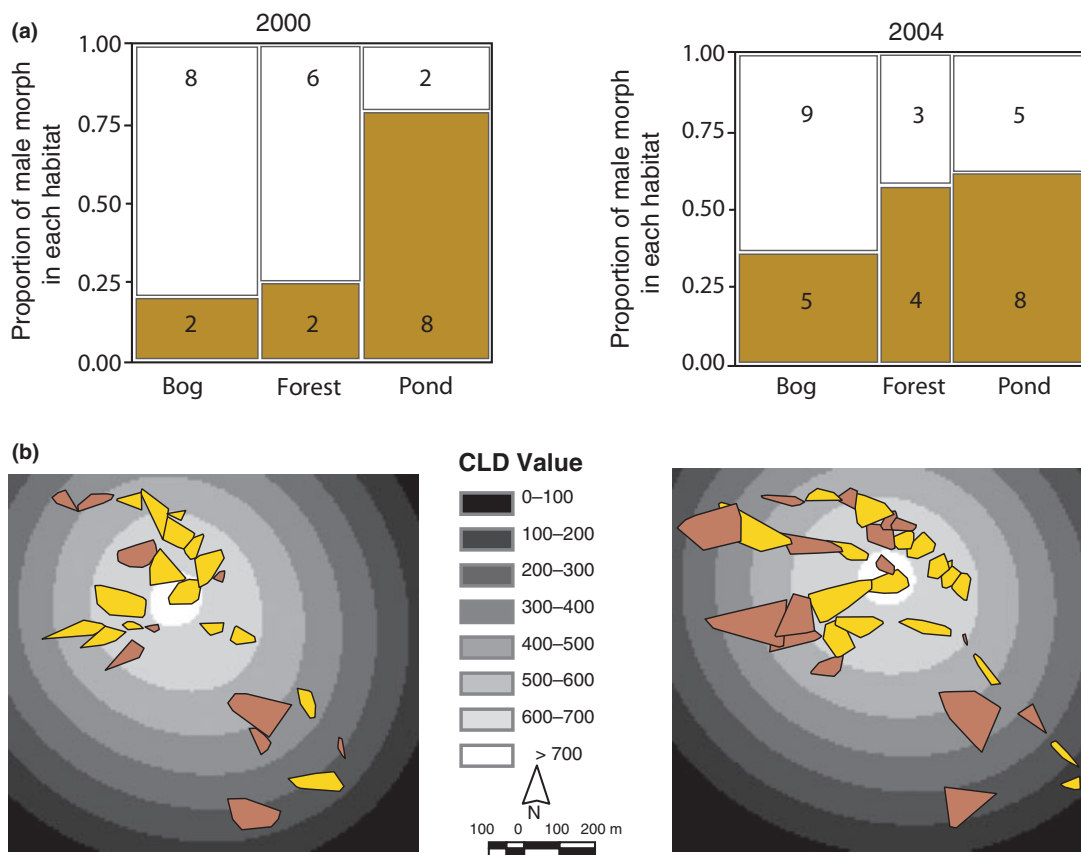
Fig. 1 Territory settlement patterns for 2000 and 2004. (a) Habitat distribution for both morphs during 2000 and 2004. Dark bars represent tan male × white female (T×W) territories; white bars represent W×T territories. Width of the columns indicates the proportion of the total territories each habitat encompasses. A significant difference in settlement pattern between the two pair types was detected in 2000, but not in 2004. (b) Continuous local density (CLD) surfaces overlaid with territories. The dark polygons represent tan male × white female (T×W) territories and the lighter polygons represent white male × tan female (W×T) territories. The darker areas contain the lowest CLD values and the lighter areas contain the highest CLD values. A subset of these pixels was used for the analysis (see Methods for description of pixel sub-sampling).

larger cell size would have left out large amounts of occupied space from the analysis; a smaller cell size may have implied greater resolution in our generated raster data (Jensen, 2005). This 10 m × 10 m cell size was used for the rest of the generated raster data sets to facilitate data overlay; however, researchers wishing to replicate this type of analysis for future studies should choose a grid cell size that best fits the spatial scale of their system.

Continuous local density
Individuals within a population may feel the effects of population-level density differently, especially in species where the dispersion of individuals is not uniform and clumping can occur. White-throated sparrows may be segregating their territories based on the amount of social interaction they receive at various areas across the study site (Formica *et al.*, 2004), and the amounts of social interaction may be dependent on the local conspecific

density in a particular area. To analyse the effects of local density on individuals throughout the study site, we needed a measure of conspecific density that took into account the overall population density, dispersion of the population, and was continuous over the entire landscape. To create a measure of continuous local density (CLD), we summed the distances of each of the grid cells to the closest edge of every territory polygon; this value was then divided by the number of territories to obtain an average distance to all territories. Generated values were inversely related to local density; therefore, to easily discuss CLD as a measure of local density, all numbers were subtracted from 1000. A CLD *value* refers to the single value of a grid point, and a CLD *layer* refers a GIS raster layer of grid cells covering the entire study site. The final grid layer was 132 × 208 cells. All other grid layers that were generated in this study used these same size parameters and alignment to insure congruence during overlay analysis. Both years, 2000 and 2004, were

produced independently, generating two CLD layers (one for each year; Fig. 1b).

Interpolated risk surface

Cuckoldry risk itself is not usually thought of as a spatial variable, and yet organisms have evolved a host of implicitly spatial tactics and strategies to cope with this risk. Mate guarding, for example, occurs when a male limits the physical distance between himself and his mate, preventing her from copulating with another male (Møller & Birkhead, 1991; Birkhead, 1998a,b). Territoriality has also been hypothesized to have evolved as a paternity guard (Møller, 1990, 1992). By creating a buffer or protective zone that he defends from other males, the resident is essentially creating a spatial area of reduced cuckoldry risk.

Our goal was to generate a spatial model (surface) that accurately described the social environment an individual would experience at any given location across the study site. To this end we used the end product of those behavioural strategies, realized reproductive success, to inform our geographic analysis of cuckoldry risk. To generate this surface, we employed inverse distance weighted (IDW) interpolation (Johnston *et al.*, 2001; DeMers, 2002; Jensen, 2005), a method that is often used to produce continuous elevation layers from surveyed sampling points. IDW interpolation uses a spatial 3D point layer (longitude, X; latitude, Y; and a third 'Z value', commonly 'meters above sea level') to estimate the values of the continuous space between the sampling points. This method also generates a raster grid layer with the entire study site divided into equal-sized (i.e. $10 \text{ m} \times 10 \text{ m}$) cells and the Z-value of each cell is calculated from the values of the sampling points, and is forced through the original sampling points (nests). As the name implies, the IDW algorithm presents greater weight to the sampling points that are closest to the focal cell. In other words, sampling points that are farther from the focal cell have less influence on its final value. The method does not take into account any other variables and assumes that the space between the sampling points changes in the Z-value in a smooth and even way.

We applied IDW interpolation to extra-pair paternity (EPP) risk by using the results of each nest as a sampling point of promiscuity across the landscape. The proportion of chicks in each nest to survive to day 6 that were not sired by the social father (proportion of chicks excluded) was used as the Z-value of each nest. In the GIS software the power of the IDW interpolation was set at two, which is often the default for geography interpolation analysis and assumes high spatial autocorrelation (Johnston *et al.*, 2001). For both 2000 and 2004 the IDW interpolation was generated using all nests for which the parentage data for all chicks were known. Without having knowledge of the exact variables, spatial and otherwise, that lead to EPP, we used this nonbiased method to estimate the level of EPP risk across the entire landscape. As the

IDW interpolation was based on the resulting EPP in existing nests, the gridded surface represented a summation of ecological and social variables that affect EPP risk and was the product of the behaviour of the female, the extra-pair male, and the resident pair-bonded mate, as well as other variables such as female reproductive state and sperm competition. This methodology allowed us to convert the results of reproductive behaviour to a spatial variable. We termed the grid layers resulting from the IDW interpolation 'risk surfaces' (Fig. 2); we consider these two surfaces (one for each year) a spatial model of reproductive behaviour rather than an actual predictive model of EPP in unsampled nests. Using this method we compared risk surfaces between years, and looked for stability or consistency of risk across years, morphs and habitat types.

We clipped the $1320 \text{ m} \times 2080 \text{ m}$ rectangular grid themes (both CLD and risk surfaces) to space that was currently occupied by a territorial male in the 2 years that were studied. The study site at Cranberry Lake can be categorized according to one of three habitat types described in Formica *et al.* (2004) bog, forest, or pond – which correspond to areas of varying conspecific density. Territories in the years 2000 and 2004 were then classified according to one of these three habitat types.

The overlay of the above data layers resulted in a grid data layer for each year of 3520 cells, where each $10 \text{ m} \times 10 \text{ m}$ grid cell contained the following information: (1) a CLD value; (2) a risk value (proportion of chicks predicted to be excluded had a nest been present); (3) a habitat classification of bog, pond, or forest; (4) a classification of whether the cell was occupied during the focal year by either a tan male or a white male; and (5) the ID of the resident male. Statistical analyses involve comparisons between corresponding values at the same spatial location (i.e. the same grid cell).

Statistics

All statistical tests except for the 2×3 Fisher exact tests were completed using JMP version 4.1 (SAS Institute, 2007); the 2×3 Fisher exact tests were completed using the VASSERSTATS program (Lowry, 2006).

The spatial surfaces that were generated with the GIS (CLD and risk) are continuous space-filling surfaces, which cover the entire landscape; however, we are only interested in including space utilized by white-throated sparrows in our statistical analyses. To this end, we only included pixels that were within the territories of white-throated sparrows ($n = 3520$ pixels).

Both the CLD and risk interpolation surfaces were generated using spatial data from the entire population (i.e. all of the territories in the population). As most individuals spend the majority of their time on or near their breeding territory, our methods (e.g. IDW interpolation) assume that the influence of a particular individual decreases with distance from the space that individual
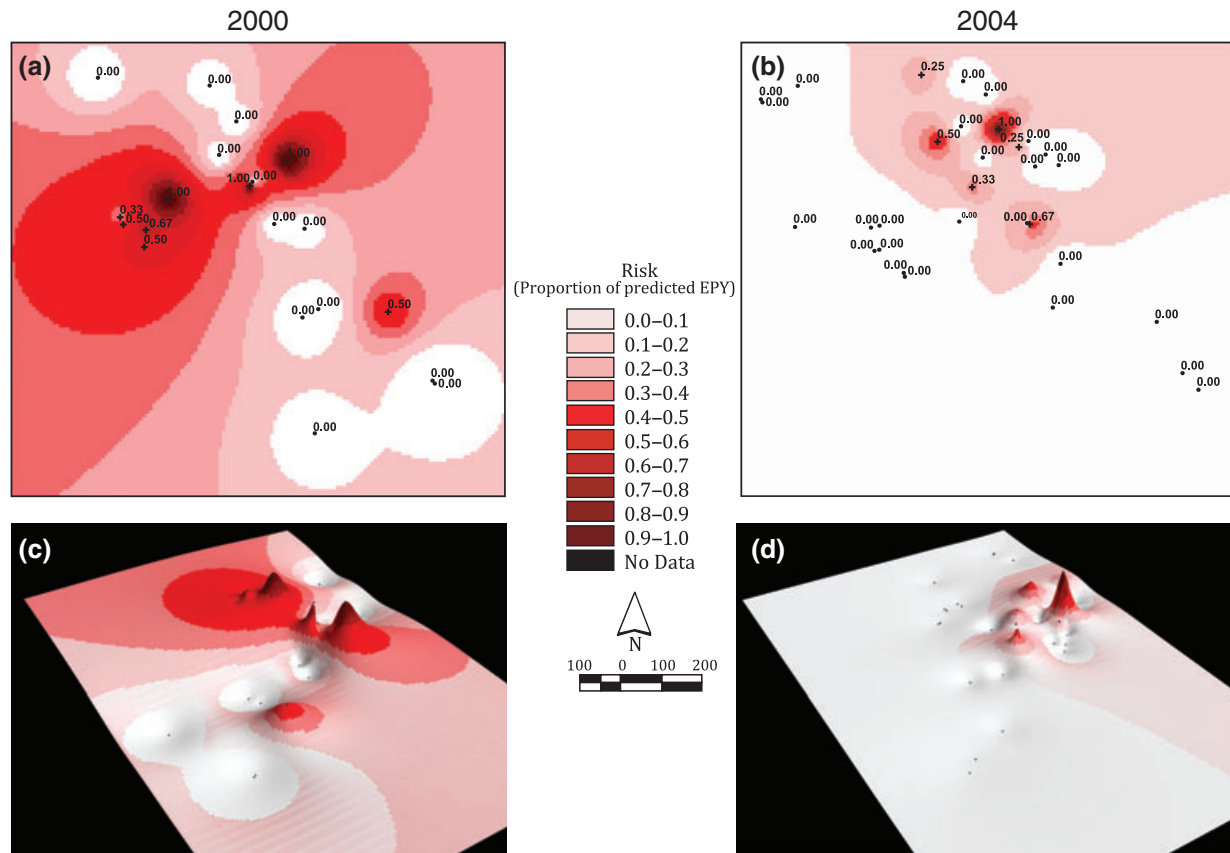
Fig. 2 Interpolated risk surfaces for 2000 and 2004. (a, b) Two-dimensional maps of the interpolated risk surface from 2000 and 2004 respectively. (c, d) Three-dimensional perspective designed to show relief in the risk surfaces.

utilizes. These assumptions are akin to the first law of geography, spatial autocorrelation (Tobler, 1970). The two layers in our analyses are predictive surfaces that describe the potential for social interactions; therefore, our results and the conclusions we draw concern the scale of the entire landscape, and we are careful not to make claims about individuals nests or territories.

Standard least squares (LS) REstricted Maximum Likelihood (REML) models were run for both CLD and risk as dependent across both years. These models allow us to visualize and examine the social landscape from a spatial perspective but are conservative with degrees of freedom, because the effects of individual territorial males can be statistically controlled as a random effect. For the CLD model, year, morph, and habitat were included as fixed effects. Year × morph was included as a fixed interaction term because there were differing morph frequencies between the years (Fig. 1); habitat × morph was also included as a fixed interaction term because the morphs were previously shown to segregate by habitats (Formica *et al.*, 2004). Individual male ID were included as random effects. The risk model was identical to the above description except that CLD was also included as a fixed effect. Means for significant tests

are reported and graphed as LS mean values, which have been adjusted by the REML model, controlling for other effects that were included in the model. All *post hoc* tests [Tukey high significant difference (HSD)] were conducted on the LS mean values.

Results

Local density and habitat segregation

Population density (i.e. number of territorial pairs) differed in 2000 and 2004. The year 2000 was low-density as compared with other breeding seasons observed at Cranberry Lake (Tuttle, 1993, 2003) with only with 0.48 pairs per hectare, 28 total pairs; 16 white male × tan female (W×T) pairs and 12 tan male × white female (T×W) pairs; and so territories were located further from each other and some historical territory locations were left unoccupied (unpublished data). Typically, densities are between 0.56 and 0.63 pairs per hectare (mean = 56.6 ± 0.06 SE). In 2004, there were 0.56 pairs per hectare (34 total pairs; 17 white male × tan female and 17 tan male × white female). The difference in population density was primarily driven by an

increase in the number of T×W pairs. There were also differences in settlement patterns of white and tan males; in 2000 there was significant habitat segregation between the morphs (Fisher's exact test $P_{d.f.=2} = 0.009$, $n = 29$), whereas in 2004, habitat segregation was not detected (Fisher's exact test $P_{d.f.=2} = 0.627$, $n = 34$; Fig. 1a). A three-way contingency test reveals that this difference in segregation pattern between the years is significant ($G^2 = 11.24$, d.f. = 4, $P = 0.024$).

Year, morph, and the morph × year interaction did not yield significant results in the CLD REML model. Habitat and the morph × habitat interaction, however, were significant (Figure 3; $R^2 = 0.962$, $n = 3520$ pixels; see Table 1 for effect details). A *post hoc* Tukey HSD test on the LS mean values revealed that all habitats were significantly different from each other in CLD (bog = 580.92 ± 18.5 SE, forest 557.54 ± 18.4 SE, pond = 542.74 ± 18.3 SE). Further *post hoc* tests on the interaction terms demonstrate that, for tan males, CLD was significantly lower in the pond and the forest than in the bog, and for white males, territories in the bog were significantly higher in their CLD than those in the forest or pond (Table 2).

Paternity

Extra-pair paternity differed between the years and habitats. In 2000 (the low-density year), 35.0% of the nests sampled contained at least one extra-pair chick, and 27.4% of the chicks sampled across all nests showed EPP

Table 1 Continuous local density restricted maximum likelihood model results for fixed effects.

Fixed effects	d.f.	Denominator d.f.	F ratio	P value
Year	1	51.78	0.3981	0.5308
Morph	1	51.72	2.3011	0.1354
Morph × year	1	51.78	0.0316	0.8596
Habitat	2	3504	26.674	< 0.0001
Habitat × morph	2	3504	5.4112	0.0045

Table 2 Continuous local density (CLD; least squares) mean values from restricted maximum likelihood model for both male morphs across habitats.

Morph	Habitat	CLD (LS means)	SE	Post hoc significant differences*		
Tan	Bog	564.331	27.59	A		C
Tan	Forest	520.941	27.31		B	
Tan	Pond	513.266	26.82		B	
White	Bog	597.514	24.75	A	B	
White	Forest	594.146	24.77	A	B	
White	Pond	572.229	24.90			C

Post hoc results are reported from a Tukey high significant difference test.

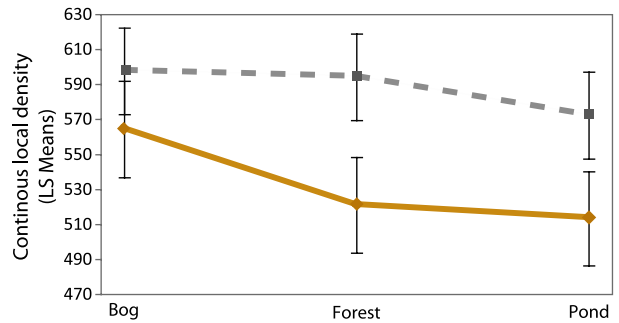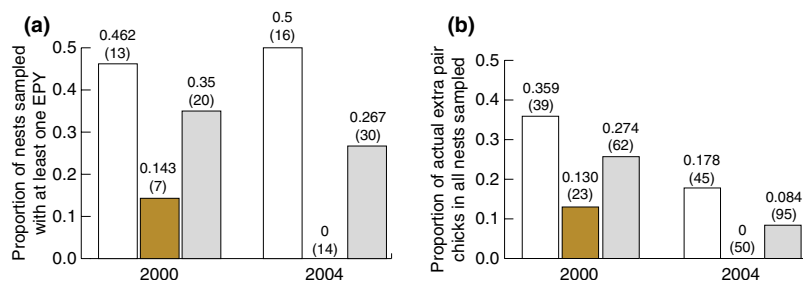*Levels not connected by the same letter are significantly different.

Fig. 3 Morph by habitat interaction for local density. Continuous local density (CLD) least squared mean values from the CLD restricted maximum likelihood model for both morphs across habitat. See Table 2 for *post hoc* significance tests among the points. The dashed line represents data for white males and the solid line represents tan males.

(Fig. 4). Surprisingly, in 2004 (the higher-density year) there was a lower amount of EPP: 26.7% of the nests sampled contained at least one extra-pair chick but only 8.4% of chicks were the result of EPP (Fig. 4). This difference in percent EPP between the years was primarily because of more EPP in tan male nests during the low-density year; however, EPP in tan male nests was nonexistent during the average-density year.

The analysis of EPP by pair type by year is difficult because of smaller sample sizes once data are partitioned; nonetheless, it is important to report these traditional types of analyses before progressing to our interpolated risk surface. There are several interesting factors that indicate that territory location plays a role in the reproductive success of resident males. In 2000, the distribution of EPP differed across habitat types for W×T broods: 80% of those nests located in the bog contained at least one extra-pair chick, vs. 20% in the forest and 0% in the pond ($\chi^2 = 5.89$, d.f. = 2, $P = 0.05$). In fact, the only white males to which we could attribute EPP success all had territories in the bog; two of five white males in the bog were identified as successfully securing EPP. Tan males were never observed to obtain EPP. In 2004, the distribution of EPP in W×T broods did not differ according to habitat ($\chi^2 = 1.31$, d.f. = 2, $P = 0.52$). Finally, in 2000 white males tended to have higher total success (within-pair + EPP) when they established territories in high-density bog habitats than in low-density forest and pond habitats ($F = 3.35$, d.f. = 2, 12, $P = 0.08$). Although the sample size of tan males establishing territories in the high-density bog was low, total success of tan males was higher when they established territories in low-density pond habitats ($F = 17.28$, d.f. = 1, 9, $P = 0.009$); this is primarily driven by one tan male with a territory in the bog who lost all his parentage to a neighbouring white male. However, in 2004 total success was the same across all habitats for both white males ($F = 0.19$, d.f. = 2, 16, $P = 0.83$) and tan males ($F = 0.86$, d.f. = 2, 16, $P = 0.45$).

Fig. 4 Results from parentage analysis for 2000 and 2004. White bars represent white male × tan female (W × T pairs), dark bars represent T × W pairs, and grey bars represent totals. (a) Proportion of nests sampled that contained at least one extra-pair young (EPY). Values in parenthesis represent the total sample size of each group. (b) Proportion of chicks sampled that were EPY.

Total success did not differ between W×T and T×W pairs in high-density habitats [W×T total success = 2.27 ± 0.33 (SE) chicks/nesting attempt; T×W total success = 2.50 ± 0.81 (SE) chicks/nesting attempt; $t = -0.30$, d.f. = 29, $P = 0.76$], but in low-density habitats, T×W total success was significantly greater than that of W×T pairs [W×T total success = 2.00 ± 0.73 (SE) chicks/nesting attempt; T×W total success = 3.36 ± 0.29 (SE) chicks/nesting attempt; $t = -2.11$, d.f. = 18, $P = 0.05$]. Of the nine extra-pair young (EPY) for which we could absolutely assign the extra-pair father, all nine were sired by white males from bog territories (2000 $n = 5$, 2004 $n = 4$).

Cuckoldry risk

Year, CLD, habitat and the morph × habitat interaction were significant in the REML model for cuckoldry risk, whereas morph and the morph × year interaction effects were not ($R^2 = 0.7302$, $n = 3520$ pixels; see Table 3 for fixed effect details). The year 2000 (low-population density) had higher risk (predicted proportion of EPY) than 2004 (2000 = 0.297 ± 0.031 SE, 2004 = 0.090 ± 0.026 SE), and yet local density (CLD) was still positively correlated with risk.

Overall, the pond habitat had significantly lower risk than the bog, and the forest had intermediate levels of risk but could not be statistically separated from the other two habitats in a *post hoc* test (bog = 0.227 ± 0.027, forest = 0.188 ± 0.026, pond = 0.166 ± 0.025). Tan males had significantly higher risk of cuckoldry when in the bog than when in the forest or pond (as indicated by the morph × habitat interaction and *post hoc* test). The

post hoc test also revealed that white male territories do not have significantly different risks across habitats (Fig. 5; Table 4).

Local density and cuckoldry risk

To compliment the above analysis of the interpolated risk surface and to examine the effect of CLD on the actual EPP in the nests, we compared the CLD pixel value at each nest for which we had parentage data. In 2000,

Table 4 Risk (least squares) mean values from restricted maximum likelihood model for both male morphs across habitats.

Morph	Habitat	Risk (LS mean values)	SE	Post hoc significant differences*
Tan	Bog	0.270	0.042	A
Tan	Forest	0.146	0.040	B
Tan	Pond	0.145	0.035	B
White	Bog	0.184	0.033	A B
White	Forest	0.229	0.033	A B
White	Pond	0.187	0.034	A B

Post hoc results are reported from a Tukey high significant difference test.

*Levels not connected by the same letter are significantly different.

Table 3 Risk restricted maximum likelihood model results for fixed effects.

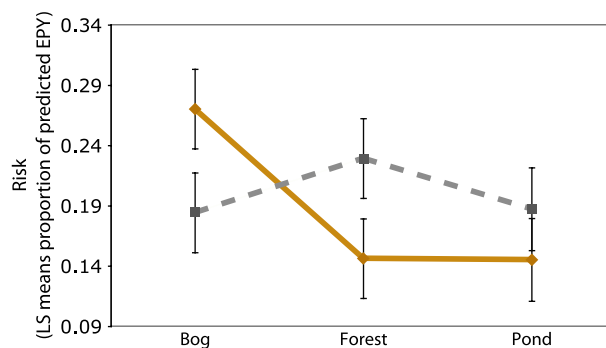| Fixed effects	d.f.	Denominator d.f.	F ratio	P value
Year	1	52.97	37.00	< 0.0001
Morph	1	52.41	0.077	0.783
Morph × year	1	52.93	0.887	0.351
1000-CLD	1	1993	8.373	0.004
Habitat	2	2136	4.670	0.010
Habitat × morph	2	1965	7.141	0.001

CLD, continuous local density.

Fig. 5 Morph by habitat interaction for cuckoldry risk. Predicted cuckoldry risk least squared mean values from the risk restricted maximum likelihood model for both morphs across the three habitats. See Table 4 for *post hoc* significance tests among the points. The dashed line represents data for white males and the solid line represents tan males.

nests with at least one extra-pair chick were not significantly different in their CLD value than those without any EPY (logistic fit, $P = 0.4281$, $\chi^2 = 0.628$, d.f. = 1,18), and the percent extra-pair chicks in the nest did not correlate with CLD value ($P = 0.200$; $n = 20$, $r_s = -0.299$). However, in 2004, nests with at least one extra-pair chick were significantly higher in their CLD value than those without any EPY ($P = 0.0017$, $\chi^2 = 9.84$, d.f. = 1, 28), and percent EPP significantly correlated with CLD values at the nest ($P = 0.0090$; $n = 30$, $r_s = 0.469$).

Discussion

Various behavioural 'decisions' modify the social landscape, affecting the social niches of others in the population. As an individual settles in a particular area, a feedback system is created in which its presence changes the nature of the entire landscape; this, in turn, affects the individual's own reproductive choices and the future settlement of others. In other words, the socio-spatial environment affects the individual and the individual affects the socio-spatial environment simultaneously. The interacting phenotypes that form the social landscape are both the targets and the agents of selection (*sensu* Moore *et al.*, 1997; Wolf *et al.*, 1999).

Our results suggest that male white-throated sparrows exist within a social landscape that results from their respective alternative life-history strategies. Although the male morphs do not differ in their overall mean cuckoldry risk, the level of risk does differ for the two morphs across the landscape (among the different habitats). Furthermore, there is a detectable pattern of habitat segregation between the morphs across the years. Finally, these settlement 'decisions' seem to have very real consequences for fitness. Monogamous tan males tend to settle in low-density pond areas, thereby occupying space that is relatively low in cuckoldry risk; this strategy reduces their encounters with white males seeking EPP and, accordingly, tan male reproductive success is the highest when they settle in these low-density areas. Tan males do not themselves pursue EPP; rather, they guard their social mates from white males seeking EPP. Tan males settling in areas of high cuckoldry risk will have direct fitness costs with none of the benefits gained through EPP. However, for males who pursue EPP, risk is only one side of the behavioural strategy 'coin'. Promiscuous white males settling in high-density bog areas maximize their encounters with fertile females and, as a result, create areas of high cuckoldry risk. Although white males experience similar levels of cuckoldry risk across the landscape, only white males with territories in the bog gain reproductive success through EPC. Interestingly, all EPY for whom we could assign parentage were sired by white males from the high-density bog. Therefore, living in an area of high risk seems to benefit promiscuous white males. In the white-

throated sparrow, matching with the appropriate social environment may enhance the success of an individual's behavioural strategy.

As with other behavioural phenomena such as habitat selection or optimal foraging, social niche partitioning can be an emergent property of past selection or the result of current phenotypic plasticity. Likewise, in our system it may be impossible to differentiate the proximate causes of the observed pattern of segregation between the pair types, as it may be an emergent property of unobserved competition or an unknown environmental variable. Regardless of the underlying causes, the combined evidence from traditional molecular parentage analysis, morph segregation patterns, local density measurements, and the cuckoldry risk surface demonstrates that the pair types are experiencing differences in social environment across the landscape based on their settlement. Furthermore, the direct comparison of realized reproductive success suggests these differences in social environments are generating variance in reproductive success.

Conspecific density is a vital component of any socio-spatial phenotype, for the simple reason that in dense areas conspecifics should encounter each other more often and therefore interact at higher rates. Extra EPC should be similarly effected (Morton *et al.*, 1990; Birkhead & Møller, 1992); however, the exact effect density has on EPP frequency is far from understood (Westneat & Sherman, 1997; Griffith *et al.*, 2002). Some species show a positive relationship between population density and EPP (e.g. Gowaty & Bridges, 1991; Bjornstad & Lifjeld, 1997), others show a negative relationship (e.g. Hasselquist *et al.*, 1995; Hoi-Leitner *et al.*, 1999), while still others show no relationship at all (e.g. Bollinger & Gavin, 1991; Dunn *et al.*, 1994; Sundberg & Dixon, 1996; Tarof *et al.*, 1998; Chaung *et al.*, 1999, Moore *et al.*, 1999; for a comprehensive review of correlates with EPC/EPP frequency see Griffith *et al.*, 2002). Interactions between EPP frequency and density may be even more complex than previously thought. For example, our analyses revealed that cuckoldry risk was highest during the year with the lowest population density. Yet our measure of local density (CLD) positively correlated with interpolated cuckoldry risk for both years. The pattern was consistent even when we restricted our spatial analysis to the nest area, suggesting that individuals may not directly experience differences in overall population density, but instead, are more likely to feel the effects of the density in their local neighbourhoods – it is this factor that actually contributes to the overall amount of EPP. Overall population density may not accurately describe the rate of conspecific interactions that individuals are experiencing, especially if some individuals are able to alter their selective regime by settling in neighbour-restrictive or isolated regions; however, it will be necessary to compare the results from several years of varying population densities before we can draw broader conclusions.

Differences in population density may affect individuals pursuing alternative life history strategies in unique ways. We hypothesize that during low-density years, monogamous tan males successfully use local density to make spatial settlement decisions and construct social niches by settling in areas that are low in cuckoldry risk (i.e. relocational niche construction; *sensu* Odling-Smee *et al.*, 2003). However, during higher-density years, especially those with higher numbers of tan males, the finite number of pond habitats may become occupied quickly, forcing some tan males to settle in areas with higher local density (with high CLD values). During a 5-year study of territory settlement in this population we never observed more than 12 territories in the pond habitats (mean = 11.8). In 2004 the population increased by five tan males and one white male (an increase of ~21% in total population and an increase of ~42% in the number of tan males), resulting in an increase in the number of tan males only in the forest and bog habitats (Fig. 1).

Conclusions

Geographical information systems methods such as raster analysis and spatial interpolation are powerful tools evolutionary biologists can use to model and visualize social environments that are the products of complex behavioural processes. Social environments are inherently dynamic and can change from moment to moment depending on the frequency and outcomes of conspecific interactions. By modelling the social landscape across space and time, we have shown how the dynamics of social interactions might alter the pattern and, possibly, the opportunity for selection. In territorial species, the variance in reproductive success translates into heterogeneity in the social landscape, causing some individuals to be located in areas with increased social interactions and others to be located in areas of decreased interactions. These 'social niches' may act like ecological niches, providing refuges for polymorphism. Socio-spatial heterogeneity combined with social niche partitioning may create multiple *social* niche polymorphisms, having wide-ranging effects on the maintenance of genetic diversity in general. Socio-spatial factors, similar to those seen in the polymorphic white-throated sparrow, may also play important roles in the evolution of mating systems in species with more continuous genotypic, morphological and behavioural differences.

Acknowledgments

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