

Disentangling habitat and social drivers of nesting patterns in songbirds

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Received: 30 March 2008 / Accepted: 24 January 2009 / Published online: 8 February 2009
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Abstract Nest locations of breeding birds are often spatially clustered. This tendency to nest together has generally been related to a patchy distribution of nesting habitat in landscape studies, but behavioral studies of species with clustered breeding patterns draw attention to the importance of social and biotic factors. Indeed, it is becoming increasingly apparent that the breeding system of many territorial, migrant birds may be semi-colonial. The reasons for, and

extent of, spatial clustering in their breeding systems are not well understood. Our goal was to tease apart the influence of habitat availability and social drivers of clustered breeding in a neotropical migrant species, the hooded warbler (*Wilsonia citrina*). To test alternative hypotheses related to clustered habitat or conspecific attraction, we combined a habitat classification based on remote sensing with point pattern analysis of nesting sites. Nest locations ($n = 150$, 1999–2004), collected in a 1213 ha forested area of Southern Ontario (Canada), were analyzed at multiple spatial scales. Ripley's K and pair-correlation functions g (uni- and bivariate) were used to test whether nests were clustered merely because potential nesting habitat was also clustered, or whether nests were additionally clustered with respect to conspecifics. Nest locations tended to be significantly clustered at intermediate distances (particularly between 240 and 420 m). Nests were randomly distributed within available habitat at larger distance scales, up to 1500 m. A reasonable hypothesis to explain the detected additional clustering, and one that is consistent with the results of several behavioral studies, is that females pack their nests more tightly than the available habitat requires to be situated closer to their neighbors' mates. Linking spatially explicit, point pattern analysis with strong inference based on Monte Carlo tests may bring us closer to understanding the generality and reasons behind conspecific attraction at different spatial scales.

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Keywords Point pattern analysis · Spatial aggregation · *Wilsonia citrina* · Conspecific attraction · Pair-correlation function

Introduction

Many territorial bird and animal species have clustered distributions of breeding individuals (Kiester and Slatkin 1974; Lima and Zollner 1996; Muller et al. 1997; Etersson 2003; Tarof and Ratcliffe 2004; Bourque and Desrochers 2006). As animals are limited by required resources (or assumed to be), the primary hypothesis to explain spatial clustering is that the required resources are also spatially clustered (Kiester and Slatkin 1974; Tarof and Ratcliffe 2004). When resources are abundant and the species of interest is absent, it becomes apparent that behavior or other biotic factors (e.g. dispersal) may be influencing occupancy and breeding patterns, assuming all abiotic requirements have been identified. An explicit treatment of how individuals are distributed in space at multiple scales is needed in order to reveal aspects of behavior and the biotic environment that influence spatial clustering and the distribution of individuals.

Behavioral studies of territorial species show that individuals preferentially settle near conspecifics (e.g. Allee 1931). Several hypotheses have been suggested to explain observed territorial groupings. For example, birds may gather information about mate or habitat quality from conspecifics in the vicinity (Etersson 2003; Danchin et al. 2004; Stamps and Krishnan 2005), or individuals may cluster as an anti-predator strategy (Hamilton 1971; Perry and Andersen 2003). Alternatively, sexual selection pressures could influence whether or not birds settle into dense territorial clusters (Tarof and Ratcliffe 2004). Wagner's (1993, 1998) 'hidden lek' hypothesis relates aggregations of territorial birds to sexual selection pressures resulting from extra-pair copulations (EPCs). Leks are clustered groupings of males that are visited by females seeking to mate with the most central or dominant male (Wagner 1993; Tarof and Ratcliffe 2004). The selective pressures for males and females are deemed similar in 'hidden leks', which are 'hidden' in species with larger territories because the aggregations are less obvious at larger scales (Fletcher and Miller 2006). The word 'hidden' also seems appropriate for species that are socially

monogamous yet genetically non-monogamous. Extra-pair copulations are a key component of the mating system of many birds, and extra-pair fertilizations (EPFs) tend to involve immediate neighbours (Stutchbury et al. 1994 and references therein; Neudorf 2004 for review; Tarof et al. 2005 for example).

Fletcher and Miller (2006) developed a set of explicit predictions based on different evolutionary models of hidden lekking behavior; these models emphasize male quality (hotshot males), female choice (appraisal and accessibility of aggregated males for selective EPCs), male aggregations over resources used by females (hotspots of activity), or kin selection (dominant males with support from subordinates). Yet, all of these processes—from restricted resources, information gathering, and predator avoidance to sexual selection pressure—lead to clustered breeding distributions that positively affect individual fitness in non-exclusive ways. In order to show that sexual selection pressures, for example, compel individuals to cluster breeding sites, one would first have to show that the level of clustering is higher than expected given the distribution of resources. Then, alternative explanations for conspecific attraction would have to be ruled out, or more specific correlates of the sexual selection hypothesis would need to be verified.

Point pattern analysis (PPA) can be used to statistically indicate which of the processes under investigation are consistent with observed spatial patterns at multiple scales (Wiegand and Moloney 2004; Fortin and Dale 2005). Point pattern analysis of spatial structure has been used extensively in the field of vegetation science (e.g. Condit et al. 2000). In animal ecology, mobile species can be studied using PPA by converting nests or breeding locations to point data. PPA has recently undergone rapid development to correct for problems with edge effects, irregular study areas, and a lack of homogeneity (Haase 1995; Goreaud and Pélissier 2003; Wiegand and Moloney 2004; Schiffrers et al. 2008). When coupled with appropriate randomization procedures, point pattern analysis can be used to test alternative hypotheses about the underlying processes that generate spatial patterns (Wiegand and Moloney 2004). Null-model processes can be used heuristically to investigate how individuals would be distributed in the absence of behavioral processes (Lancaster and Downes 2004). These models help to elucidate what processes are theoretically possible at a given scale.

To test whether social processes are an underlying reason for spatial clustering of a territorial species, we used uni- and bivariate point pattern analysis and data on the nesting distribution of hooded warblers (*Wilsonia citrina*), located over a period of 6 years (1999–2004). Hooded warblers are territorial neotropical migrant birds that feed predominately on insects and breed in the eastern deciduous forests of North America. With less than approximately 500 breeding pairs north of the Canada–US border, and because of high habitat fragmentation in their northern breeding range, the species is currently listed as threatened in Canada (Friesen et al. 2000). Field data often indicate that some forested areas are preferred because they are inhabited by high densities of *W. citrina* whereas nearby and seemingly identical forested habitats are left almost vacant. Indeed, the species may even be semi-colonial (Friesen et al. 2000). Given that the species forms pair bonds for the breeding season, yet is genetically non-monogamous, some level of sociality is implicit in their mating system (Stutchbury et al. 1994; Tarof et al. 1998). Hence, the species is an interesting case study for investigations into conspecific attraction in territorial neotropical migrants. This study investigated spatial clustering in *W. citrina* nesting sites in relation to the pattern of available nesting habitat and the territory locations of mated and unmated males.

Methods

Study Area, avian surveys and nest searching

The largest known population of *W. citrina* in Canada occurs in St. Williams' Conservation Reserve, Norfolk County, Southern Ontario (hereafter St. Williams' Forest, 1213 ha; 42°42'N, 80°28'W). The history and ecology of the area have been described by Whittam et al. (2002). Bird Studies Canada, in collaboration with the hooded warbler/academic flycatcher (*Emidonax virescens*) recovery team initiated a long-term study of *W. citrina* in 1999 in St. Williams' Forest to examine nesting ecology, site fidelity, and survival rates, permitting easily identifiable nesting habitat preferences in Canada (Whittam et al. 2002; Pasher et al. 2007).

In May (1999–2004), the locations of territorial males in St. Williams' Forest were marked with

flagging tape to the nearest trail, and the UTM position was georeferenced with a global positioning system (GPS) unit; a 12-channel Garmin, Etrex, with a horizontal accuracy of 15 m was used. The position of each male was located on a paper map and the territory was confirmed on repeated visits, but the UTM was generally not re-recorded, unless there were large shifts in the distribution of birds. Only birds that were heard singing in the same area throughout the breeding season were considered to be holding a territory. The location where a male was first heard singing was therefore considered to be the 'center' of his territory. Each territory was visited at least weekly from May to August, and the area was thoroughly searched to find nesting females and to establish mating status. When a nest was located within a male's territory, the fixed UTM location of the nest replaced the UTM for the male's territory in the associated database records.

W. citrina nest sites are found in dense understory shrubbery characteristic of small temperate forest canopy openings (gaps) that vary in size between 5 and 1,178 m², with a median gap size between 40 and 200 m² in Canada (Whittam et al. 2002). These small forest gaps can be identified using remotely sensed imagery at spatial resolutions of 1 m (Melles 2007; Pasher et al. 2007). Male *W. citrina* arrive at breeding areas 1–2 weeks prior to the arrival of females, and they compete for and defend breeding territories. The size of an average male's territory was 3.1 ha (range: 1–7.3 ha, D. Badzinski, unpublished data, 2004).

Second and third nesting attempts for a given female are often located in close proximity to first nesting attempts during the breeding season (D. Badzinski, unpublished data, 2004). Accordingly, known second and third nesting attempts of banded females were discarded for the purpose of our analyzes. All first nests ($N_1 = 66$) and nests where the attempt number was unknown ($N_U = 84$) were included in the analyzes (Table 1). The locations of *W. citrina* nesting territories are also likely to be correlated among years (Howlett and Stutchbury 2003). To control for this temporal correlation, we used each of the 6 years of available nest data separately and averaged the results, creating a joint PPA statistic over all years in tests for hypotheses about habitat and social drivers of nest point patterns (see below).

Table 1 Numbers of nests and unmated territorial males found in St. Williams' Forest (1999–2004)

Year	1999	2000	2001	2002	2003	2004	Total
Nests							
N_U^a	15	14	23	10	4	18	84
N_1^a	4	8	7	13	23	11	66
Year total	19	22	30	23	27	29	150
Unmated males	9	4 ^b	6	12	11	10	48

^a N_U , N_1 -indicates nesting attempt number (unknown or first)

^b UTM's of unmated territorial males and bird pairs were either not recorded or were unavailable for the year 2000

Habitat classification

Fine spatial resolution Ikonos imagery (red, near infrared, and panchromatic bands, 1–4 m resolution) were used to classify nesting habitat in St Williams' Forest. The multi-banded Ikonos image was classified using an unsupervised classification procedure to create a number of unique spectral classes by Iterative Self-Organizing Data Analysis (Lillesand et al. 2004). Identified spectral classes were compared with nest reference data to determine their information utility by selecting the spectral class that encompassed the most nest gap locations within the smallest search neighborhood. The selected spectral class was then compared with canopy gaps that were visually evident on the Ikonos image, and the class that matched gap openings was identified as canopy gap habitat.

In related work, Melles (2007) tested the classification accuracy of such canopy gap classifications from a larger region surrounding St. Williams' Forest by ground checking the images using independently collected field data from surrounding forest patches. Results were very promising. Overall classification accuracy was 93% (127/136) for canopy gap habitat. The error of omission (gaps present, but not detected by the classification) was 3% (4/131), and the commission error (gaps identified, but not observed on ground checks) rate was 4% (5/132).

For the purpose of matching the resolution of the habitat map with the accuracy of our GPS records for further PPA, we changed the resolution of the classified gap habitat map from 1 to 30 m. The resolution of the habitat map was decreased by aggregating 1 m² habitat squares up to a 30 m resolution. An analysis resolution

of 30 m represents a compromise between the excessive detail that is apparent at fine spatial resolutions and a more coarse resolution imposed by software limitations when the data are analyzed at the extent of the entire forest. As the UTM location of nest sites had associated horizontal errors of up to 15 m, it was considered appropriate to assign nest points to the centroid of cells at a 30 m resolution for ease of analysis. Habitat points were created from the habitat map by converting all 30 m × 30 m cells occupied by habitat to a point pattern, with a minimum inter-point distance of 30 m.

Point pattern analysis

Ripley's K -function is a second-order statistic that counts the number of points in increasing search areas to detect either the presence of spatial clustering or over-dispersion of points (Ripley 1976). Ripley's function assumes a complete census of the study area, and the statistic also assumes that the process is both stationary and isotropic (Fortin and Dale 2005). Given a completely random point pattern, the expected number of points within distance r of an arbitrary point is proportional to the area of a circle (πr^2) times the density of points over the area under investigation. A weighting factor is generally applied to the K -function to correct for edge effects when only part of the circle lies within the study area, but see Lancaster and Downes (2004) for a discussion of potential problems with edge corrections and the debatable ecological implications of weighting these points. The K -function is generally transformed into a linear version, $L(r)$, which is easier to interpret because the expected value of $L(r)$ under a random spatial process is zero, and this function has stable variance properties (Besag 1977; Ripley 1981).

Though Ripley's K -function is widely recognized, the cumulative character of this statistic often hampers the detection of scale-dependent patterns (e.g. Condit et al. 2000; Schurr et al. 2004). If clumping occurs on a relatively small scale, the point density at larger scales will be above average as well because increasing circular scales are cumulative. Consequently, we also used a related statistic, the pair-correlation function $g(r)$ (Ripley 1981; Stoyan and Stoyan 1994), which can be interpreted as the expected density of points within a given *ring* radius of an arbitrary point, divided by the mean density of

the pattern i.e. the intensity λ (Getzin et al. 2006). The $g(r)$ statistic is one under complete spatial randomness, whereas values above one indicate clustering, and values below one indicate regularity or—in the case of evenly spaced animal locations—territoriality. This statistic is considered more powerful in detecting spatial patterns across scales by using rings instead of circles (Wiegand and Moloney 2004; Getzin et al. 2006, 2008). Ripley's K was also included in our results as the more well-known reference statistic for comparison purposes.

Univariate forms of these statistics, $L_{11}(r)$ and $g_{11}(r)$, for a single point pattern can be extended to bivariate analysis in order to test the relationship between two point patterns (Lotwick and Silverman 1982). In the bivariate case, only neighbors of the opposite point pattern are counted within a radius or ring of an arbitrary point. The reader is referred to Wiegand and Moloney (2004) for K -, L -, and pair-correlation function $g(r)$ equations. All point pattern analyses were performed using the freely available software Programita.

Generation of alternative null distributions

To investigate which process(es) influence(s) nest spatial clustering, we tested the null and alternative hypotheses shown in Table 2, where a null hypothesis refers to random spatial pattern formation with respect to the available forest ($\text{null}_{(0, \text{RANDOM})}$), potential nesting habitat ($\text{null}_{(1, \text{HABITAT})}$), or the presence of conspecific birds ($\text{null}_{(2, \text{SOCIAL})}$). Nests may be randomly distributed within the forested

study area ($\text{null}_{(0, \text{RANDOM})}$), even though the availability of potential nesting habitat is limited or unequally distributed throughout the area. However, it is more plausible that the pattern of nest locations matches the level of clustering in available nesting habitat ($\text{null}_{(1, \text{HABITAT})}$). If nests are spatially clustered at levels that exceed expectations given a patchy distribution of nesting habitat then this would indicate that alternative explanations for clustered breeding are required ($\text{alternative}_{(1A, \text{CLUSTERED})}$).

Three of the evolutionary models to explain hidden lek behavior might apply in this case (female preference, hotshot, and kin selection, Fletcher and Miller 2006). We can rule out the hotspot model immediately as it predicts that females have large and overlapping home ranges and well-defined travel routes, which is not the case for *W. citrina* females. The hotshot model predicts only that the most dominant male is centralized and that subordinate males aggregate near hotshots to increase mating opportunities. Albeit if more than one dominant male is centralized, some amount of packing would be implicit in their spatial distribution, unless dominants are well-spaced out and only surrounded by clusters of females (and subordinate males). Kin selection also predicts that subordinates cluster around dominant males, but differs from the hotshot model in that subordinates preferentially settle near their relatives, implying high levels of male natal philopatry.

If we assume that subordinate males tend to be the unmated peripheral birds that typically settle after the dominants (e.g. Wagner 1998; Fletcher and Miller 2006), then a significant positive correlation between

Table 2 Summary of null and alternative hypotheses tested

Hypothesis	Explanation
$\text{Null}_{(0, \text{RANDOM})}$	Female nests—randomly distributed in the forested area
$\text{Null}_{(1, \text{HABITAT})}$	Female nests—randomly distributed in available nesting habitat
$\text{Alternative}_{(1A, \text{CLUSTERED})}$	Female nests—clustered beyond availability of underlying nesting habitat
$\text{Null}_{(2, \text{SOCIAL})}$	Female nests—uncorrelated with (unmated) male territories
$\text{Alternative}_{(2A, \text{KIN LEKING})}$	Unmated (assumed subordinate) males more correlated with nest sites than expected given average aggregation of both nests and males
$\text{Alternative}_{(2B, \text{HOTSHOT LEKING})}$	Unmated (assumed subordinate) males more correlated with nest sites than expected given average aggregation of both nests and males
$\text{Alternative}_{(2C, \text{FEM LEKING})}$	Unmated (assumed subordinate) males more clustered at some scales (i.e. larger scales) than nests are clustered at those scales, conditional on structure of overall clustering in the joined pattern

the pattern of unmated males and the pattern of female nest sites would provide some support for either the hotshot or the kin selection model, alternatives (2A, KIN LEKKING, OR 2B, HOTSHOT). This result would indicate that unmated (assumed subordinate) males are more densely distributed around female nests and their associated (assumed dominant) mates than expected, but without genetic data we would not be able to distinguish between these two models. Lastly, we test whether the data are in accordance with the female preference model, alternative_(2C, FEM LEKKING), which predicts both that all males (dominant and subordinate) aggregate together with conspecifics and that females preferentially settle in aggregations (Fletcher and Miller 2006). We proceed with the following caveat: explanations for hidden lekking are predicated on EPC behaviour, which creates selective pressures on birds to aggregate. The suggestion that pairing success is related to which birds (dominant or subordinate males) acquire EPCs seems a reasonable, though as yet unsupported assumption.

Null_(0, RANDOM) and Null_(1, HABITAT) were tested using univariate PPA, whereas null_(2, SOCIAL) was tested using bivariate PPA to examine whether female *W. citrina* nesting sites were correlated with the distribution of (unmated) territorial males in the area, given the combined level of clustering between the two point patterns. Unfortunately, it was not possible to test directly for nest clustering in relation to the location of *mated* males because of the way that UTM records were kept (as described above). In all randomization tests using the *L*- or pair-correlation function, simulation envelopes were created using the highest and lowest of 99 simulations as suggested by Bailey and Gatrell (1995), e.g. Getzin et al. 2006. Statistics for nest point patterns in each year were combined into an overall mean function and compared with the combined simulation limits for all years under investigation (Diggle et al. 1991; Diggle 2003; Wiegand 2004; Riginos et al. 2005). The mean function was a weighted average, with weights defined by the relative number of points per year in relation to all years (Diggle 2003). We computed the *L*- and pair-correlation function for scales up to 1500 m. Very large radii, relative to the size of the study area, were avoided to minimize additional problems with edge effects that cannot be adequately corrected with a weighting factor.

The ring width (90 m) for *g*(*r*) was selected as a compromise between minimizing pattern smoothing,

which occurs when rings are too wide, and avoiding jagged plots that result when rings are too narrow and too few points are included in the analysis (Wiegand and Moloney 2004). Moving window or kernel methods are used in the computation of *L*- and *g* statistics resulting in overlapping rings for neighboring distance bands. Therefore, statistics are computed at all scales with intervals equal to the minimum inter-point distance (i.e. 30 m in this study).

Several approaches can be used to control for the effects of an underlying heterogeneous environment (Wiegand and Moloney 2004). We used a univariate, random-labelling approach, which assumes that the spatial pattern of nest points is simply a random subsample of the joined pattern of nest and habitat points. During the randomization procedure, nest points for each year were shuffled between both the available habitat point locations and the existing nest locations. A random-labelling method was the most appropriate choice because it provides a strict randomization of nesting points within available habitat. In addition, nest-site selection is an event that occurs after the potential habitat was formed, and a random-labelling process is more appropriate under conditions where a distribution of *a posteriori* events is under investigation (Goreaud and Pélissier 2003). Univariate random-labelling methods should be used only if there are many more control points (i.e. habitat points) than there are cases (i.e. nest points as was the case here).

A clustered spatial pattern of habitat can mask the spatial pattern of nests at smaller scales. For example, nest-nest avoidance at small scales may be offset by habitat clustering at those same distance scales such that the overall pattern appears random when habitat is not considered. Thus, it is necessary to test for significant repulsion or clustering at all distance scales. Indeed, even if a point pattern appears to be random within a study area, it is still important to further test for significant levels of clustering or repulsion if the underlying habitat resources vary non-uniformly across the study area.

If null_(1, HABITAT) was rejected at any scale of examination, we accept the alternative_(1A, CLUSTERING) at that scale. We then further tested whether or not the pattern of nests was uncorrelated with the locations of *unmated* males (null_(2, SOCIAL)) using bivariate random-labelling *g*₁₂(*r*). Bivariate random-labelling assumes the same process was involved in creating the two patterns of points, a reasonable

assumption if unmated males arrive later than mated males, and if unmated males shift their territories in relation to the later arrival and settlement patterns of females.

We also tested for departures from random-labelling by assessing the significance of pairwise differences between g functions. Each pairwise difference (e.g. $g_{22}-g_{11}$) evaluates different biological effects and these tests are a powerful means to assess the predictions of carefully crafted alternative hypotheses (Wiegand 2004; Getzin et al. 2006, e.g. those hypotheses discussed by Fletcher and Miller 2006). We assessed whether the difference in univariate clustering amongst unmated males alone or amongst nest sites alone was probable given the overall clustering of the joined pattern. The difference $g_{22}-g_{11}$ does not evaluate the correlation between nests and unmated males directly (as above with g_{12}), but evaluates whether unmated males are more clustered than nests at a given scale, conditional on the structure of the joined patterns (Wiegand 2004). Therefore, it evaluates whether the given difference in the univariate clustering of either nests and unmated males is probable under the overall clustering of the joined pattern.

Results

W. citrina tended to nest in the north and southwest areas of St. Williams' Forest, or relatively close to forest edges that bordered roads and trails if adequate shrub cover existed in these areas. The south central forested area was occupied more sparsely (Fig. 1a). Almost 15% (17 out of 116) of all year-to-year pairs of nests over the 6 years of data were temporally correlated and located within a 30 m radius of nests found in the previous year.

For the test of $\text{null}_{(0, \text{RANDOM})}$, points were restricted to fall anywhere within the irregularly shaped study region. The L function for observed data (Fig. 1b, inset) showed that for scales between 360 and 900 m, nests were significantly clustered, whereas above and below these scales nests were randomly distributed within St. Williams' Forest. The pair-correlation function indicated that this clustering of nest sites occurred specifically at scales between 360 and 480 m; there was also evidence for significant clustering just above the 99% simulation envelope at the 240 m scale. Hence, the hypothesis

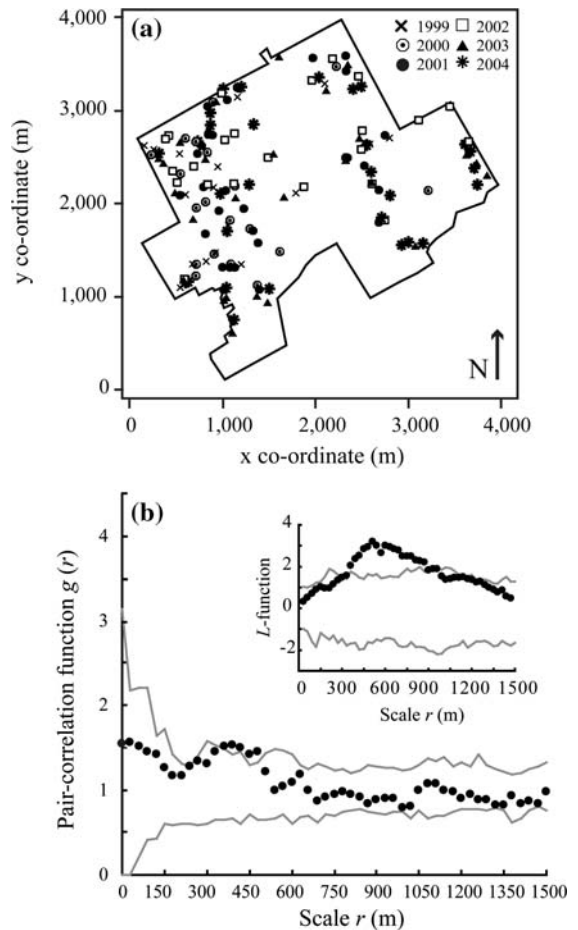


Fig. 1 Univariate analysis of the point pattern of *W. citrina* nesting locations in St. Williams' Crown Forest, Southern Ontario, Canada (1999–2004). **a** Nest locations ($n = 150$) for different years (symbols) within the search boundary (black solid line) of the study area. **b** Estimated L -function (inset) and the pair-correlation function $g(r)$ for nest locations (black dots) and the 99% simulation envelope (grey lines) for the null hypothesis of complete spatial randomness within the study area

that females locate their nests at random within the forested area was rejected at intermediate scales as female *W. citrina* clustered their nests at scales $r = 360$ – 480 m, Fig. 1b).

St. Williams' Forest is not uniform and potential nesting habitat for *W. citrina* was unevenly distributed over the study area (Fig. 2a, Melles 2007). Potential nesting habitat as identified by remotely sensed imagery was particularly concentrated in the northwest, south-central, and southwest sections of St. Williams' Forest. Nest locations may be clustered simply because nesting habitat is clustered.

Interestingly, repulsion between nest locations at the 30 m scale became evident when available nesting habitat was taken into account (Fig. 2b). When habitat was ignored, some of the gaps in the distribution of nests were actually related to the absence of habitat at both small and large distance scales (Fig. 1a). Only when the distribution of nesting habitat was taken into account, did the regularity of the pattern of nests at smaller scales become evident.

Nest sites were significantly clustered beyond that of potential nesting habitat at several scales identified by the pair-correlation function analysis (chiefly at scales between 240 and 420 m, Fig. 2b). As the width

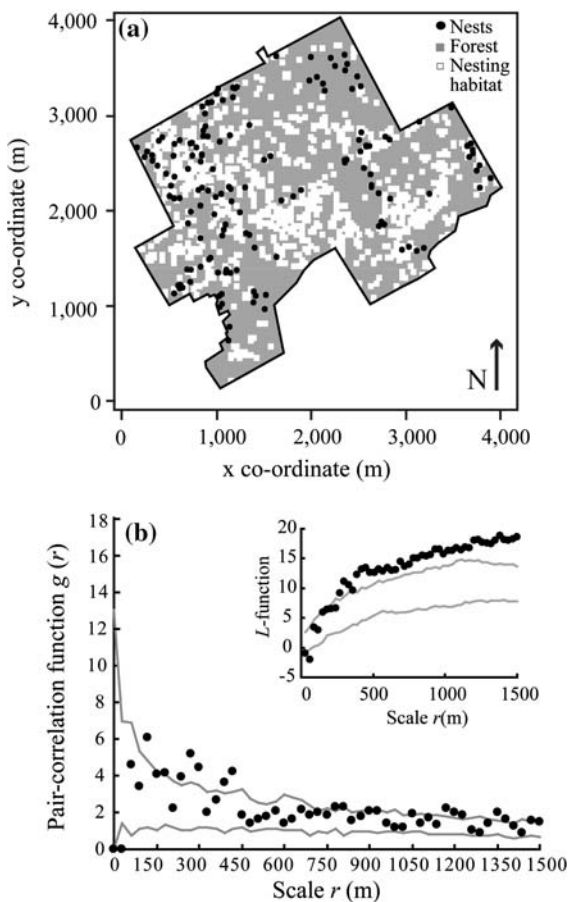


Fig. 2 Univariate analysis of the point pattern of *W. citrina* nesting locations in St. Williams' Crown Forest, Southern Ontario, Canada (1999–2004). **a** Nest locations ($n = 150$) and the distribution of nesting habitat as defined by remotely sensed image classification (*white squares*). **b** Estimated L -function (*inset*) and the pair-correlation function $g(r)$ for nest locations (*black dots*) and the 99% simulation envelope (*grey lines*) for the null hypothesis of randomness within available nesting habitat

of the simulation envelopes depends in part on the number of permutations, care must be taken when interpreting the reliability of marginally significant values (e.g. at larger scales). However, our results do suggest that we can reject $\text{null}_{(1, \text{HABITAT})}$ and accept the alternative $(1A, \text{CLUSTERED})$ that females clustered nesting sites at several scales, beyond patchiness associated with the underlying nesting habitat availability.

$\text{Null}_{(2, \text{SOCIAL})}$ tested for a lack of correlation between the two point patterns, nest locations and unmated males. If unmated males were more correlated with nest sites than expected under the combined aggregation of the joined pattern, the values of L_{12} and g_{12} would stray above the upper simulation limit, and such a result would provide some support for the HOTSPOT or KIN LEKKING alternative explanations for clustered nest sites. However, the distribution of females and unmated males was no more correlated than expected at all scales examined, given the combined pattern (Fig. 3b). Unmated males were not more densely distributed around female nest sites than other female nests and their associated mates. Hence, we have established that females cluster their nesting sites, but this additional level of clustering was not related to a significant interaction with the distribution of unmated males.

Regardless of whether or not unmated males are subordinate or dominant, the female preference model for 'hidden lek' behavior predicts that all males should aggregate their territories in relation to conspecifics in order to increase their likelihood of acquiring a mate or EPCs when females preferentially settle in aggregations. Therefore, the distribution of unmated males should be clustered at some scales, presumably larger ones if unmated males are indeed subordinate. Moreover, the distribution of female nests with their associated mates is also expected to be clustered under this model. The difference between these two univariate patterns (unmated males and nests, g functions g_{22} – g_{11}) is shown in Fig. 3c. What we see is that at and just below the 900 m distance scale unmated males were more clustered than were mated males (i.e. those with females nesting on their territories). Though this difference in the pairwise correlation functions is slight at these scales, these results provide some evidence that unmated males do cluster their territories, albeit at larger scales than do mated males.

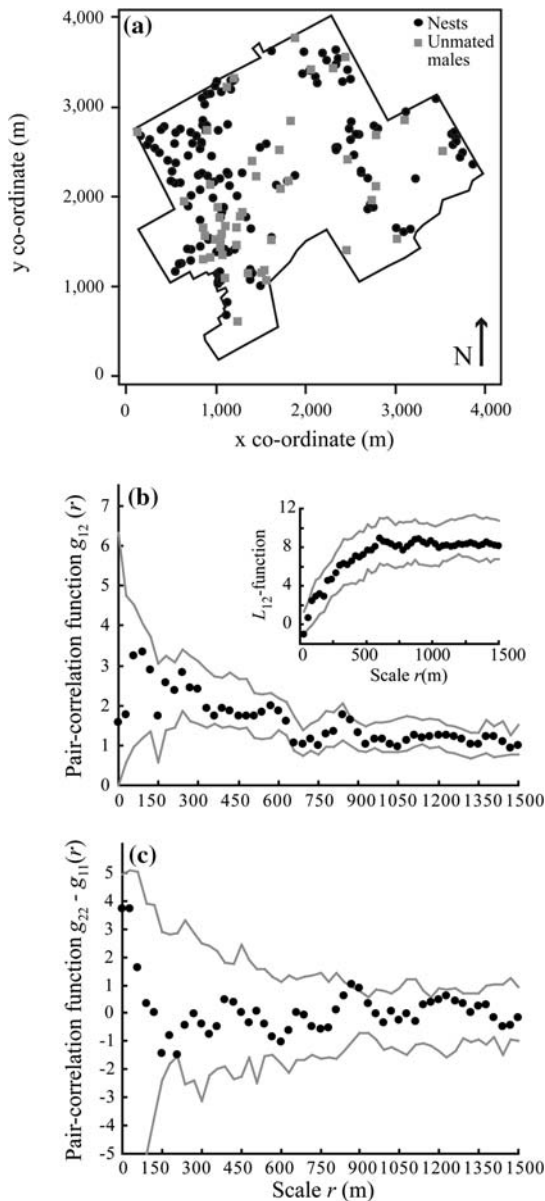


Fig. 3 Bivariate analysis of *W. citrina* nest locations and the distribution of unmated territorial males in St. Williams' Crown Forest, Southern Ontario Canada (1999–2004). **a** Nest locations (black dots, $n = 150$) and unmated territorial males (grey squares, $n = 48$). **b** Estimated bivariate L_{12} -function (inset) and the bivariate pair-correlation function $g_{12}(r)$ for nests and unmated males (black dots) as well as the 99% simulation envelope (grey lines) for the null hypothesis of no correlation between nests and unmated males beyond the average correlation of the joined pattern; or, **c** difference in univariate pair-correlation function $g_{22} - g_{11}(r)$ for unmated males and nests (black dots) with simulation limits as above for the null hypothesis that both patterns of points (nests and unmated males) are equally aggregated or dispersed at all scales

Discussion

Female *W. citrina* build their nests within the non-overlapping territories of their mates. Therefore some amount of spacing was anticipated at scales below the average size of a male's territory, and initially we were not entirely surprised that there was some evidence to suggest nest-nest avoidance at the 30 m scale. Nevertheless, we do not wish to over-interpret this finding because the minimum distance between nests was also 30 m given our methodology, and therefore it is not possible to resolve scales at or below 30 m. A nearest neighbour (NN) analysis may provide further insight; however there are issues with NN significance testing in areas with irregular study boundaries so we did not pursue this direction.

Females nested randomly within available habitat at scales approximately equal to the size of a male's territory (i.e. between 60 and 240 m, but see clustering at 120 m, Fig 2b). Support for the habitat hypothesis at these scales was a reasonable and intuitive result given that males defend territories with plenty of potential nesting habitat for females to select from. At intermediate scales, however, nests were significantly clustered; and at larger scales, the distribution of nests was effectively random again.

Conspecific attraction and potential explanations

Muller et al. (1997) provided empirical support for the hypothesis that territorial songbirds prefer to settle near conspecifics, showing that male House Wrens (*Troglodytes aedon*) preferentially selected territories next to previous residents over isolated territories of equivalent quality. More recently, Ward and Schlossberg (2004) used playback songs of territorial Black-capped Vireos (*Vireo atricapillus*) in an attempt to attract members of this endangered species to high-quality, unoccupied habitats. They were not only successful in attracting a significant number of vireos to their experimental sites with these vocalizations, but the vireos also bred successfully and returned the following year. Although other researchers have tried similar experiments in different areas and failed to permanently attract birds to suitable habitat using playbacks (Mills et al. 2006), these kinds of studies have major implications for avian population biology, conservation, and evolution (Muller et al. 1997; Fletcher 2007). For example,

social ‘hotspots’ that support high population densities may become self-perpetuating across generations, even if these areas are not consistently high-quality habitats, simply because conspecifics attract other individuals of the same species to settle and breed (Muller et al. 1997).

Our results showed that between 240 and 420 m, *W. citrina* nests were clustered in relation to conspecifics, beyond the degree of clustering expected given the restricted distribution of nesting habitat. Bourque and Desrochers (2006) also found that almost half the territorial bird species they investigated were significantly clustered after controlling for preferred habitat variables using regression with residual analysis. Indeed, more and more research suggests that territorial clustering may be widespread among songbird species (Muller et al. 1997; Ward and Schlossberg 2004; Bourque and Desrochers 2006). A reasonable explanation for these trends is that females select nest sites closer to other nesting females and their associated mates to secure extra-pair copulations from successfully mated neighboring males (Neudorf et al. 1997). Other research has shown that *W. citrina* often make extra-territory forays into neighboring territories of birds, and the majority of extra-pair copulations take place between immediate neighbors, a trend that is consistent with the ‘hidden lek’ hypothesis (Stutchbury et al. 1994; Neudorf et al. 1997; Tarof et al. 1998; Norris and Stutchbury 2001).

The distribution of nests, however, was uncorrelated with the location of *unmated* males at all scales examined. This result is consistent with several hypotheses explaining conspecific attraction, including sexual selection. For instance, females may use the presence of nesting conspecific females as an indicator of mate quality (sexual selection and the hidden lek hypothesis, Wagner 1993). Alternatively, females may gain information from other females about the distribution of high quality habitat (Doligez et al. 2002; Pärt and Doligez 2003; Etterson 2003). These two hypotheses are not mutually exclusive because high quality mates may be able to secure better quality habitats. Female nests may be clustered because the highest ranking males have restricted their options. Certainly, the finding that unmated males were clustered at larger scales than were females (and their associated mates) lends support to the suggestion that females preferentially settle in

compact aggregations, limiting lower ranking males to cluster at peripheral scales, i.e. to increase their prospects of acquiring EPCs in the ‘hidden lek’ (Wagner 1993, 1998; Tarof et al. 2005; Fletcher and Miller 2006).

Nonetheless, several authors have been unable to conclusively demonstrate support for hypotheses related to mate choice or mate quality. Stutchbury et al. (1997) found that morphological indicators of male quality (i.e. size and age) were not correlated with extra-pair fertilization success (Stutchbury et al. 1994). Tarof et al. (1998) examined whether breeding density covaried with extra-pair fertilization success in an attempt to test the hidden lek hypothesis, but they found that nearest neighbour distance and the number of adjacent neighbours within 300 m was not related to extra-pair paternity. However, older female *W. citrina* produce fewer extra-pair young, which is consistent with the hypothesis that more experienced females obtain higher-quality social mates (Stutchbury et al. 1997). Thus, it would be interesting to investigate aspects of male quality further using PPA to examine whether the distribution of older males influences female settlement patterns. We did not have complete data on the age of all males in this population to perform this test. Albeit, there was little indication in this study that the territories of unmated males were of lower quality in terms of nesting habitat because both mated and unmated males had similar amounts of potential nesting habitat within 150 m of their territory centers (*data not shown*).

Another possible explanation for clustering of nests is that there could be anti-predator benefits to clustering that are related to earlier detections of predators and joint nest defense strategies (Perry and Andersen 2003). There is no empirical evidence to indicate that *W. citrina* engage in joint nest defense strategies, but a lack of observational evidence does not rule out the possibility of such a strategy. If birds cluster their nests to avoid predators, then predation rates in the nesting stage should be lower when birds are more tightly grouped. In a related study, egg and nestling predation pressures were similar in smaller forest woodlots surrounding St. Williams’ Forest in 2004 and 2005. These surrounding forest patches had lower densities of nesting *W. citrina* (Melles 2007), though patch size can be confounded with density, the smallest occupied patch was 7.6 ha in size. Thus, even as the nest predation data to date fail to support

the prediction that clustering leads to anti-predator benefits, Perry and Andersen (2003) showed that clustering is related to anti-predator behavior in adult Least Flycatchers (*Empidonax minimus*). Consequently, it would be imprudent to draw conclusions about anti-predator benefits until more research can shed light on the relationship between nest predation and density (or clustering) in territorial songbird species (e.g. Tarof and Ratcliffe 2004).

The above discussion features two approaches, experiments in behavioral ecology and pattern analysis of animal distributions at multiple spatial scales, which are conceivably quite complementary. Only by doing experimental manipulations can ecologists rigorously determine the behavioral processes of attraction that influence settlement patterns in particular areas (e.g. Ward and Schlossberg 2004; Mills et al. 2006; Nocera et al. 2006; Fletcher 2007). However, such experiments are necessarily limited to the study of individuals at fine spatial scales and small extents because of the intensive amounts of field work involved. With spatial pattern analysis, the outcome of different behavioral processes can be evaluated by examining patterns generated under ensuant, restricted null, or neutral models of behavior; and these techniques can be employed at a variety of scales to study both empirical (data dependent) and prototypical (data generated) environments. Therefore complementary experiments in behavioral animal ecology and investigations of spatial patterns in landscape ecology would be particularly beneficial for generalizing the findings and theoretical foundations of (behavioral) landscape ecology.

Limitations

Although it is interesting to find evidence for significant clustering in this species, we reject the habitat hypothesis at intermediate scales with some caution. It is difficult to eliminate the possibility that there could be some other unmeasured aspect of habitat that may be driving the observed pattern of nest clustering. Our habitat classification had errors of both omissions where habitat was present though undetected in the classification, and commission where habitat was predicted present yet was undetected on ground checks (Melles 2007). In the north-east portion of the habitat map (Fig. 2a) for instance, there were areas with nests that fell outside areas of

potential habitat as defined by our image classification at the 30 m resolution. These errors should have little impact on our test of the habitat null-model because nests were randomized between the joined pattern of habitat and nest points. Both types of locations were equally likely to have a nest 'label' in the random-labelling shuffling process. We cannot, however, rule out the possibility that other important aspects of *W. citrina*'s nesting habitat were not captured in the binary habitat classification.

It is likely that habitat varies more continuously and does not easily fit within the categories suitable or unsuitable (Dennis et al. 2003). The distribution of feeding resources may have differed; or there may have been differences in vegetation characteristics, such as the size and height of surrounding canopy trees, that were not captured by the image classification. Indeed, the nesting habitat class simply indicated where the Ikonos image matched canopy openings in terms of spectral (i.e. reflectivity of vegetation) and textural properties (i.e. variations in tonal details resulting from shading). Additionally, the analysis resolution (30 m × 30 m) was coarser than the median forest gap size used by *W. citrina*, which entails a loss of information at small scales. Although habitat was detected at finer resolutions and aggregated to coarser resolutions, this meant that we were unable to resolve the spatial pattern below a 30 m resolution.

The limitations of PPA are that the method relies on detailed point location data and assumes the entire area has been thoroughly searched. As the extent of a study area gets increasingly large in fragmented landscapes, this type of data is difficult and expensive to acquire. Avian point count data could be used for studies at larger spatial extents, but the layout of points would need to be designed in such a way as to survey entire patches and areas. It is important to note, however, that PPA assumes complete detections, which is seldom the case when using point counts of relative abundance. Territory mapping, which involves repeated visits to an area to map the locations of breeding birds, may be more suited to this methodology.

Conclusions

Conspecific attraction in territorial songbirds is beginning to receive more and more attention in empirical research. Given the need to identify how

behavioral tendencies influence the distribution of species occurrence patterns at larger spatial scales, a variety of methods to detect conspecific attraction are beginning to be employed. For example, spatially autocorrelated residuals of species-habitat regression models have been used as evidence for conspecific attraction (Bourque and Desrochers 2006). Alternatively, conspecific attraction has been studied using nearest neighbour distances (Etterson 2003). However, animals and birds can be territorial at fine scales, clustered at other scales, and randomly distributed at still further scales, so methods that quantify spatial patterns and resolve their probable causes are needed at multiple spatial scales. By linking point pattern analysis with strong inference based on Monte Carlo tests of null models about individual settlement patterns, we will be closer to understanding the generality and reasons behind conspecific attraction at different landscape scales. Patchy distributions of resources underpin many models of species distributions, but often it is the remaining unexplained levels of aggregation that require further understanding. Point pattern analysis can be used to study the processes of inter-specific and intra-specific competition, environmental heterogeneity, and dispersal limitations. However, this technique is currently underutilized. Indeed, this research may represent one of the first applications with developed tests of alternative hypotheses in the field of avian ecology. Analysis of breeding point patterns has great potential to integrate studies of behavioral and landscape ecology. A productive union between these two types of studies is needed if we are to understand how behavioral factors influence habitat selection in human modified and fragmented systems.

Acknowledgments We thank all of the field assistants (Jody Allair, Jessie Antoniak, Jennifer Carson, Peter Carson, Rhonda Donley, Rosalind Ford, Christian Friis, Mary Gartshore, Audrey Heagy, Tara Innes, Brad McLeod, Stuart Mackenzie, David Okines, Ross Wood and Becky Whittam). Funding was provided by Environment Canada and Bird Studies Canada through the Hooded warbler/Acadian flycatcher Recovery Team, with support from: Environment Canada–Ontario Region’s Species at Risk program; a PREA Award and an NSERC research grant to M.-J. Fortin; and the Frederick Ide Graduate Award and an Ontario Graduate Scholarship to S. J. Melles. We also thank all anonymous referees for their very valuable suggestions and we are grateful to Thorsten Wiegand and Stephan Getzin for their analysis advice.

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