Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors

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Testing for aggregation or regularity in point patterns is difficult in the presence of spatial variation in abundance due to environmental heterogeneity. Using a recently developed method generalizing Ripley's K function for non homogeneous point patterns, we test the aggregation of the nests in two species of birds (little owl and Montagu's harrier) exhibiting heterogeneous distributions in response to landscape structure. We compare the results obtained under different null models accounting for environmental heterogeneity at large and/or small spatial scales.
Whereas both species were initially found to form clusters at some scale, taking spatial heterogeneity into account revealed that 1) territorial little owls showed no clustering of territories when habitat availability was considered; 2) semi-colonial harriers still formed significant clusters, but part of the aggregation in this species could be explained by landscape structure alone. Our results highlight that it is feasible and highly recommended to account for non-stationarity when testing for aggregation. Further, provided that sufficient knowledge of the study system is available, this approach helps to identify behavioural and environmental components of spatial variation in abundance. Additionally, we demonstrate that accounting for large or small-scale heterogeneity affects the perception of spacing behaviours differently, so that both need to be considered.

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The aggregative response of individuals in patchy environments is central to population dynamics and behavioural ecology (e.g. Sutherland 1996). However, local aggregation may involve multiple processes, such as habitat selection (Boyce and McDonald 1999), or social aspects such as conspecific attraction (Danchin et al. 1998). Therefore, a comprehensive understanding of the aggregative response requires addressing the interplay between the response to environmental heterogeneity and the spatial interactions between individuals (Stamps 1988, Muller et al. 1997, Reich et al. 2004).

Conspecific attraction or repulsion occur commonly and influence the distribution of individuals (Stamps 1988), though in a scale-dependent way (Lima and Zollner 1996, Gordon 1997, Muller et al. 1997). For instance, Atlantic gannets *Sula bassana* are evenly spaced at a very fine scale inside the colony by maintaining fixed inter-individual distances using their wings and bills, but they are clumped within dense colonies at a medium scale, and at larger scales colony distribution exhibits regular spacing (Furness and Birkhead 1984, Nelson 2002).

The spatial distribution of items (individuals, nests, colonies) is conveniently analyzed using point process statistics. An acknowledged method, the K(r) function (Ripley 1977), can be used to detect interactions (aggregation or inhibition) in a point pattern (data consisting simply of point locations within a defined

area, e.g. the distribution of individual trees in a forest). While this function has been widely used in epidemiology and plant ecology (e.g. Diggle and Chetwynd 1991, Pélissier and Goreaud 2001, Freeman and Ford 2002), the less powerful nearest neighbour-based statistics (Clark and Evans 1954) are still the commonest methods in animal ecology and behaviour (Newton et al. 1977, Campbell 1995, Kraus et al. 2003), despite early examples given by Ripley (1981) involving bird nest data.

Spatial point patterns are subject to both first- and second-order effects. First-order effects refer to systematic variations in intensity over space or, in biological terms, variations in abundance resulting from ''environmental'' heterogeneity (e.g. soil properties or prey availability). By contrast, second-order effects refer to interactions between points, which involve any biological mechanism promoting active spacing or clustering behaviour, such as competition or social behaviour. The K(r) function is designed to detect second-order effects, and makes the assumption that the processes are first-order stationary, i.e. that the intensity of the points is spatially homogeneous (expected values are constant over the area studied). However, both types of effects may lead to aggregation at some scale (Moller and Waagepetersen 2002), and may be confounded.

Disentangling first- and second-order processes is difficult since they involve, respectively, methods for quantitative variables such as regression, and point pattern analysis (Cressie 1993). However, practical approaches have been proposed, that fit both spatial variations in point density with covariates and interpoint interactions (Berman and Turner 1992, Baddeley and Turner 2000, Baddeley et al. 2000). So far, these methods have been largely overlooked in ecological research, including reviews in this field (Perry et al. 2002, Wiegand and Moloney 2004, but see Reich et al. 2004 for an example of joint modeling of habitat features and spatial inhibition).

Our aims are three fold: first, using two contrasted study species, we show that methods for non homogeneous point patterns can more generally apply to both inhibitive and aggregative processes. We then propose that the ''social'' component of aggregation may be identified as the clustering detected among birds after accounting for environmental heterogeneity. Finally, we demonstrate that the results and their biological interpretation can be very sensitive to the way environmental effects are taken into account. In particular, large and small-scale heterogeneity may affect the perception of spacing behaviours differently. In this study, we analyze the spacing of bird nests or territories (second-order interactions), taking into account first-order effects by modeling the response of bird densities to the environment. Environment in our study system is composed of an homogeneous habitat matrix (an intensive agro-ecosystem), dotted by villages and built up areas that create localized and strong heterogeneities in landscape structure. We compare the effects of village distribution on spacing behaviour in two raptor species exhibiting different responses to this particular landscape element. The little owl *Athene noctua*, is a territorial, resident, philopatric and monogamous nocturnal raptor (Génot and van Nieuwenhuyse 2002), usually inhabiting open habitats (van Nieuwenhuyse et al. 2001). In our study area, cultivated areas between villages can be used by foraging owls, but they are unavailable for nesting due to the absence of potential nest sites (e.g. tree holes, rock crevices). Therefore, little owls are found only in the villages, where they can find cavities for nesting (Bretagnolle et al. 2001). The second species, the Montagu's harrier *Circus pygargus*, is a diurnal raptor that breeds and hunts in open areas, and for which built up areas are repulsive. It nests in intensive cereal crops in our research site, where it is abundant and easy to locate. Both species show (presumably social) aggregative behaviour: although the little owl is territorial, it is known to form clusters (Bretagnolle et al. 2001), whereas Montagu's harrier is semi-colonial (Arroyo 1995).

Methods

Study area

This study was carried out in central-western France, in the south of Département des Deux Sèvres (46°11′N, 0°28′W). The study area covers 340 km^2 of intensive agricultural landscape, and is dominated by a system of intensive cereals, colza and spring-sown crops (maize, sunflower and pea). Built-up areas were mapped into a Geographic Information System using aerial photographs and field data. They are typically clustered as villages, with very few isolated buildings (Fig. 1). The intensification of agricultural practices since the 1950s has led to an increase of parcel sizes (mean surface of 3 ha, with 50% of parcels accounting for 82% of the cultivated area). Some old hedgerows are still present but are confined to the vicinity of villages and farms.

Study models and species census

Little owl

Owl censuses were conducted in 2001 and 2002. We used the playback method to record the presence of the little owl (Bretagnolle et al. 2001). A total of 174 playback stations were located systematically in order to sample every built-up area (see Fig. 1). Playback stations were situated at the fringe of the villages, at least 500 m apart from each other. One playback consisted of 1 min listening, 1 min playing little owl hoots, and then 3 min
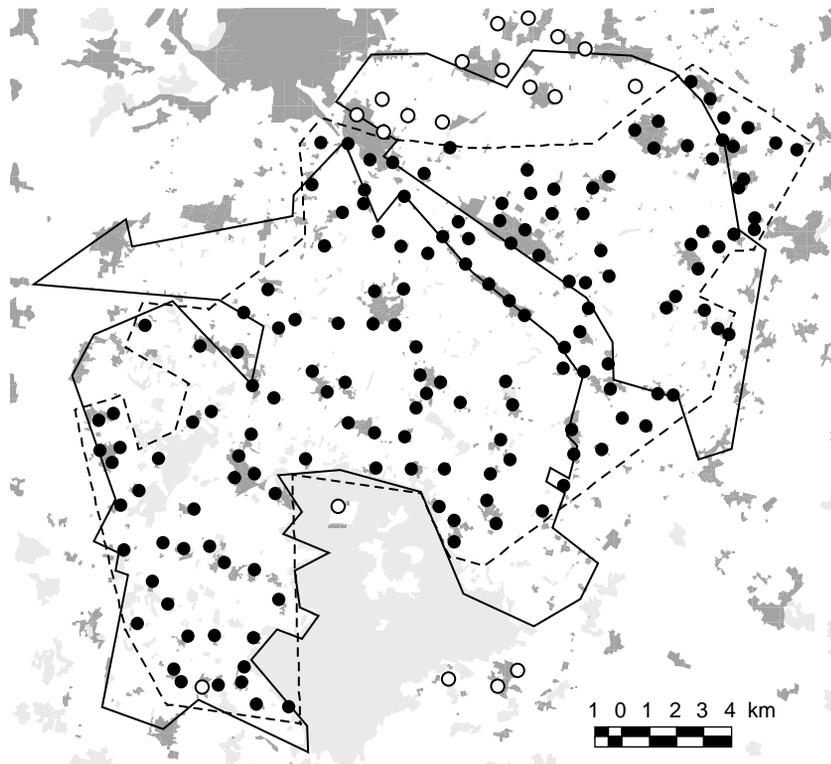
listening again (Bretagnolle et al. 2001). Each station was visited twice during the breeding season, once in March and once in May. A special protocol based on a sample of known established pairs in the area gave a probability of response of 0.88 in March and 0.75 in May, resulting in a probability of 0.97 over the breeding season if response probabilities in March and May are assumed to be independent.

For each owl contact, call type and the estimated location of the calling bird were reported on detailed maps (1:25000). The statistical units ("bird points") refer to territory holders rather than, strictly speaking, breeding pairs. They were obtained as follows. Each isolated contact was considered as from a territory holder and produced one bird point. N simultaneous hooting individuals heard from a single playback station were considered as N different points whatever the distance between them. However, two territorial responses from two neighbouring playback stations were considered two different territories if >500 m apart (otherwise, they could be produced by the same, moving bird, and only the midway point was conserved). This 500 m threshold value was derived from published little owl home ranges (Génot and van Nieuwenhuyse 2002).

Four playback points were isolated in the south of the main study area (Fig. 1) and were not considered for the analysis. Additionally, we removed a portion in the north from which owls were absent in both years, resulting in a final 305 km^2 area (Fig. 1).

Montagu's harrier

The Montagu's harrier is a conspicuous raptor, whose nests are easily located by observing the adults during the pre-laying (aerial displays by males), incubating and chick rearing stages (food provisioning by the male). We systematically searched for nests over the 340 km^2 of the study area in 2001 and 2002 (Fig. 1), and assume that no successful breeding pair remains undetected at the end of the breeding season (Millon et al. 2002). Nest locations were plotted as precisely as possible (usually within ca 50 m) into the GIS.

Non-stationarity in point pattern analysis: a background

Ripley's K function is aimed at testing for point process departure from randomness towards aggregation or regularity (Ripley 1977, 1981). Let λ be the intensity of a point process (in practice, the intensity is estimated by the density of the points), then λK(r) is the expected number of neighbours within a radius r of any point of the process. Expected value of K(r) under randomness is πr^2. Values of K over πr^2 indicate a departure towards clustering, whereas inferior values indicate regular spacing.

One of the most critical and often ignored assumptions of Ripley's function is that the point process has to be homogeneous (i.e. stationary) (Ripley 1981). Failing to account for heterogeneity can lead to spurious results (Pélissier and Goreaud 2001). Real point processes often show first-order heterogeneities due to endogenous or

exogenous factors (Baddeley et al. 2000, Pélissier and Goreaud 2001, Wiegand and Moloney 2004), but few studies have addressed this issue so far. One method consists in delimitating homogeneous sub-areas where the analyses can be conducted separately (Pélissier and Goreaud 2001, Wiegand and Moloney 2004). However, homogeneous sub-areas rely to some extent on arbitrary delimitations, and may not actually exist, e.g. in the case of gradients. Another method (Diggle and Chetwynd 1991) compares the L function (a linearized form of the K function) of observed epidemiological cases to that of the underlying (clustered) control population (Nekola and Kraft 2002, Jolles et al. 2002, Kraft et al. 2002, Lancaster and Downes 2004). However, this "case-control" method is not a convenient framework when no control population is available. Other approaches to deal with first-order heterogeneities involve estimating local intensity using either kernel density estimates (Baddeley et al. 2000, Pélissier and Goreaud 2001) or moving windows with a radius chosen ad-hoc (Wiegand and Moloney 2004). Then, heterogeneous poisson null models are generated that can be compared with the observed pattern (Wiegand and Moloney 2004). However, these non-parametric methods are unable to distinguish between spatial variations in density caused by first-order processes (e.g. habitat selection), or by second-order processes (repulsive or attractive spatial interactions). Additionally, this approach accounts for heterogeneity by correcting the null hypothesis, but fails to do so with the test statistics.

Recently, new methods have been proposed to estimate parametric models of spatial variations in point intensity, and simulate non homogeneous point processes with or without interactions, using standard Generalized Linear Models (GLMs) (Berman and Turner 1992, Baddeley and Turner 2000, Reich et al. 2004). Additionally, Baddeley et al. (2000) provided an extension to the K function for non homogeneous point patterns (K_{inhom}) which shares the same properties as K. Their methods solve the above-mentioned problems, by allowing the modeling of most heterogeneities using relevant covariates, and by facilitating the simulation of heterogeneous point patterns which provide null models. Finally, the K_{inhom} statistics explicitly include spatial heterogeneity in the calculation of K, so that the traditional stationarity assumption is not needed.

Outline of our approach
We compared the results obtained when using Ripley's functions while accounting for small- and large-scale heterogeneities in territory/nest density. To account for heterogeneity, the observed pattern must be compared to realistic null models (Wiegand and Moloney 2004). We estimated models of intensity (expected density of territory holders or nests) in relation to relevant covariates (Fig. 2, step I), using generalized linear
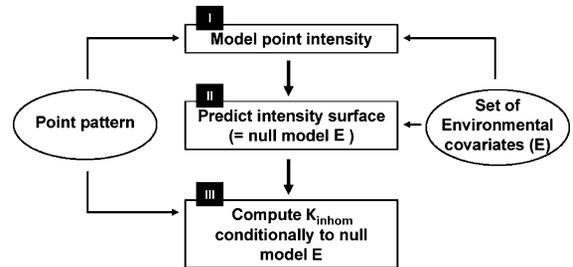

Fig. 2. Diagram of the analysis approach. Ellipses represent the observed data; the rectangles indicate the three steps of the analysis. The steps I–III are repeated for each set of environmental covariates (E) chosen. I this paper, we explore E_1) constant environment; E_2) large-scale heterogeneity (trends); E_3) small-scale heterogeneity (due to villages); E_4) combination of large- and small-scale heterogeneity.

models (Berman and Turner 1992, Baddeley and Turner 2000). From these functions, we derived intensity surfaces by calculating the predicted value at each locality in the study area, which will serve as null models of first-order heterogeneity (Fig. 2, step II). Finally, we computed the K_{inhom} function (Baddeley et al. 2000), which accounts for local differences in intensity as previously modeled (Fig. 2, step III).

Modeling heterogeneity in bird density
All the models were fitted as heterogeneous Poisson models (spatial variations in intensity, but no interaction between points), where the log(intensity) is a linear function of covariates (Berman and Turner 1992, Baddeley and Turner 2000). The intensity of points was estimated by their density (number of points per unit area) over a digital approximation of the study area (grid), using the procedure developed by Berman and Turner (1992) and Baddeley and Turner (2000). The size of the grid cells (ca 350×350 m) was automatically calculated by the functions provided by Baddeley and Turner 2005. Covariates (X and Y coordinates, and distance to the nearest building) were calculated using a GIS on a more precise grid (125×125 m cells), which offered acceptable spatial resolution and computation time.

We took a step-by-step approach to explore the effects of using four successive null models of first-order variation in the intensity of the points (Fig. 2): E_1) constant intensity (homogeneous environment case); E_2) large-scale trends in intensity (e.g. environmental gradient); E_3) small-scale heterogeneity due to the presence of villages; E_4) combined (additive) effect of E_2 and E_3. Since our purpose was not to select an overall best model, we only considered a limited number of covariates and combinations for each null model. Additionally, we did not consider the possible effect of cereal crop availability for the Montagu's harrier since this habitat is very common in our study area (ca 50% of land use: for instance, when digitizing the study area into a grid of 125 m units, cereals are present in 75% of the cells) and

does not constitute a spatial constraint at the scales of interest (i.e. from a few hundreds of meters to a few kilometers). Models were compared on the basis of their AIC, and their significance was checked using the Likelihood-ratio test (Crawley 2003).

Trend surfaces (polynomials of X and Y coordinates) were used to model gradients or large scale spatial structure in the density of points (Ripley 1981). Increasing the polynomial's order typically enhances the local fit to the data, and also increases the risk of inadvertently fitting second-order interactions. Such trade-offs are common to time series and other spatial analyses, and have no unique solution (Cressie 1993, p. 162). Since we were also interested in small scale patterns, we did not investigate further than quadratic trend surfaces, to allow the detection of second-order neighbourhood interactions and small scale first-order processes such as the village effect.

Second, we accounted for small-scale heterogeneity by modeling the effect of distance to buildings. Because we suspected distance to villages to affect bird behaviour only up to a threshold value, we used a piecewise regression procedure. We assumed that the distance effect on owl densities was constant up to this threshold and (log-) linear after this, while the opposite was assumed with the harriers (i.e. (log-) linear effect up to a given distance and no more effect thereafter). The optimal threshold was estimated by using an array of values with 10 m increments, and selecting the value that maximized the likelihood of the model.

Non homogeneous K-functions
We computed K_{inhom} using (eq. 1), that calculates the number of extra points within a given distance of an arbitrary point of the pattern, corrected by the local intensities,

$$\widehat{K}_{inhom}(t) = \frac{1}{|W|} \sum_{y_i \in Y \cap W} \sum_{y_j \in Y \cap W \setminus \{y_j\}} \frac{w_{y_i, y_j} 1(\|y_i - y_j\| \leq t)}{\lambda(y_i)\lambda(y_j)}$$

(1)

where t is the distance, $|W|$ is the area of the observation window W, Y is the point process, w_{y_i, y_j} is the edge-correction factor, and $\lambda(y_i)$ and $\lambda(y_j)$ are the estimated intensities at the points y_i and y_j, according to the intensity surface model of interest (see Baddeley et al. 2000 for a more detailed account).

In practice, we use the linearized form $L_{inhom}(r) - r =$ sqrt($K_{inhom}(r)/\pi$) $- r$ which is more convenient to interpret since it equals zero for any r under randomness (Cressie 1993). For simplification, $L_{inhom}(r) - r$ will be termed "L_{inhom}" thereafter. To correct for edge effects, the border method (Ripley 1981) was used. In the case of an homogeneous point pattern (our first null model), the intensity surface is constant, and L_{inhom} simply reduces to the ordinary L function.

Testing for departures from randomness
We used Monte-Carlo simulations to compare the L_{inhom} values for the actual data to those obtained with our null models. For each data set and null model, we generated 1000 random point patterns conditional to the respective heterogeneous Poisson process (the intensity surfaces previously fitted to the data). Simulations were generated by independent random thinning (point deletion) of Poisson processes by the intensity surface (Cressie 1993) (see also Baddeley et al. 2000). L_{inhom} was computed for each simulation and the 95% critical intervals were derived from the 2.5 and 97.5 percentiles of the simulations for each distance class (Cressie 1993). Note that this provides a local (i.e. true for any r) rather than a global test of significance at the 5% level. Here, our first model assuming homogeneity just reduces to the classical testing against the null hypothesis of CSR (Complete Spatial Randomness), represented by a homogeneous Poisson process.

Statistical analyses were performed using R 1.9.1 (Anon. 2003). Additional R libraries were used for bootstrapping the median distance to built-up areas ("boot" by A. Canty and B. D. Ripley). All the spatial analyses and models were done using functions of the "spatstat 1.4.3" library by A. Baddeley and R. Turner (Baddeley and Turner 2005).

Results

Habitat selection: effect of villages

The effect of distance to built-up areas was assessed for both species by comparing the distances to villages for territories/nests to those distances for points generated at random. The distribution of little owl territories in our study area was, as expected, limited to built-up areas. Using 1000 bootstrap resamplings, the median distance ($\pm$SD) to built-up areas was 280 m ($\pm$3 m, n = 20 000 points) for random points, compared to 4 m ($\pm$4 m, n = 162 territories) for little owl territory holders. Only one individual heard >450 m apart from a built-up area was contacted (750 m, year 2001), and this outlier was removed from subsequent analyses. In contrast to little owls, Montagu's harriers strongly avoided built-up areas: bootstrapped (1000 resamplings) median distance to villages was 379 m ($\pm$3 m, n = 20 000 points) for random points, whereas it was 735 m ($\pm$36 m, n = 98 breeding pairs) for harrier's nests.

Point pattern analysis assuming homogeneity

When assuming an homogeneous Poisson process as the null hypothesis, little owls showed regular spacing (negative values) at small scales, from 0 to 150 m in years 2001 and 2002 (Fig. 3E_1). In 2001, an aggregation

peak (positive values) was found at 750 m, and at 350 m in 2002 (Fig. 3E$_1$). Ripley's L values at larger scales (from 1000 to 4000 m) lay inside the confidence interval, suggesting a random distribution at these scales. A similar analysis was performed on harriers, and showed that in both years, harriers were clustered at intermediate to large scales, from 200 to 3000 m (Fig. 4E$_1$).

Point pattern analysis with spatial variations in abundance

We accounted for large scale heterogeneity (first order variations) within the study area by fitting trend surfaces. In little owls, a quadratic rather than a linear trend surface best fitted the data in 2001, but this was only marginally significant in 2002 (Table 1). However trends in the two years showed similar tendencies, with fewer birds in the southern part and the northern fringe (see the maps in Fig. 3E$_2$). In this species, incorporating large scale spatial trends (model E$_2$) in the calculation of the L$_{inhom}$ function had little effect on the results, as compared to the homogeneous L function (model E$_1$, compare Fig. 3E$_2$ and E$_1$, and see Table 2). There was a general shift towards more regular spacing that resulted in marginally significant aggregation (Fig. 3E$_2$). Small scale regular spacing (0–150 m) was unaffected.

At a more local scale, we found a highly significant effect of distance to built-up areas on owl densities in both years (Table 1). No threshold value could be found in the effect of distance to villages as the fit of the models decreased regularly when distance threshold values increased, and thus we retained the raw distance variable. In comparison with the homogeneous and large-scale heterogeneous L functions (models E$_1$ and E$_2$), a very different picture emerged after introducing small-scale heterogeneity due to the distribution of villages (model E$_3$, see Fig. 3E$_3$, and Table 2). In particular, although little owls were still found regularly spaced at small scales, aggregation between 300 and 1000 m totally disappeared, as emphasized by arrows on Fig. 3.

Finally, the best models for 2001 and 2002 were obtained by adding the trend and distance terms in each year (model E$_4$, Table 1). The corresponding L$_{inhom}$ functions (Fig. 3E$_4$), were very similar to that obtained after models using only the distance to villages, indicating that small-scale heterogeneity influenced the results more than large-scale variations for the owl data sets (Table 2).

A similar procedure was performed for Montagu's harrier. Quadratic trend surfaces were highly significant and performed better than linear ones (Table 1), indicating a consistently higher nest density in the northeast of the study area (illustrated in Fig. 4E$_2$). As compared to the homogeneous L functions (model E$_1$), the L$_{inhom}$ function conditional to trend surfaces (model E$_2$) indicated less clustering at very short distances
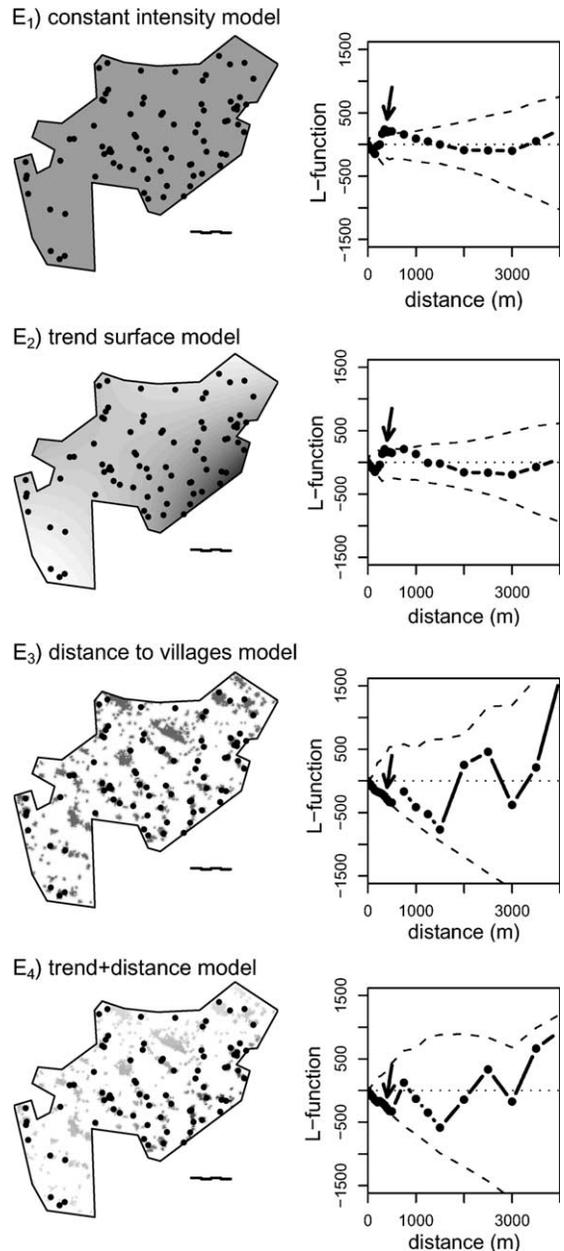

Fig. 3. Modeled intensity surface of little owl locations in 2002 facing the corresponding L functions. Similar results were obtained in 2001 (figure not presented). Grey levels in the background of maps represent the fitted null model of process intensity on a relative colour scale, overlaid with actual bird locations (points). Bold lines and dots represent the L values for the observations. Dashed lines correspond to the 95% critical interval for the null hypothesis tested. Null models were E$_1$) Poisson distribution with constant intensity; E$_2$) Poisson distribution with intensity following a second order trend surface; E$_3$) Poisson distribution with a log-linear decrease in intensity with distance to built-up areas; E$_4$) Poisson distribution with a second order trend surface intensity combined to a decrease with distance to built-up areas. Scales in the lower right of maps represent 4 km. Arrows point to distances where major changes in L$_{inhom}$ occur within a data set, across null models.
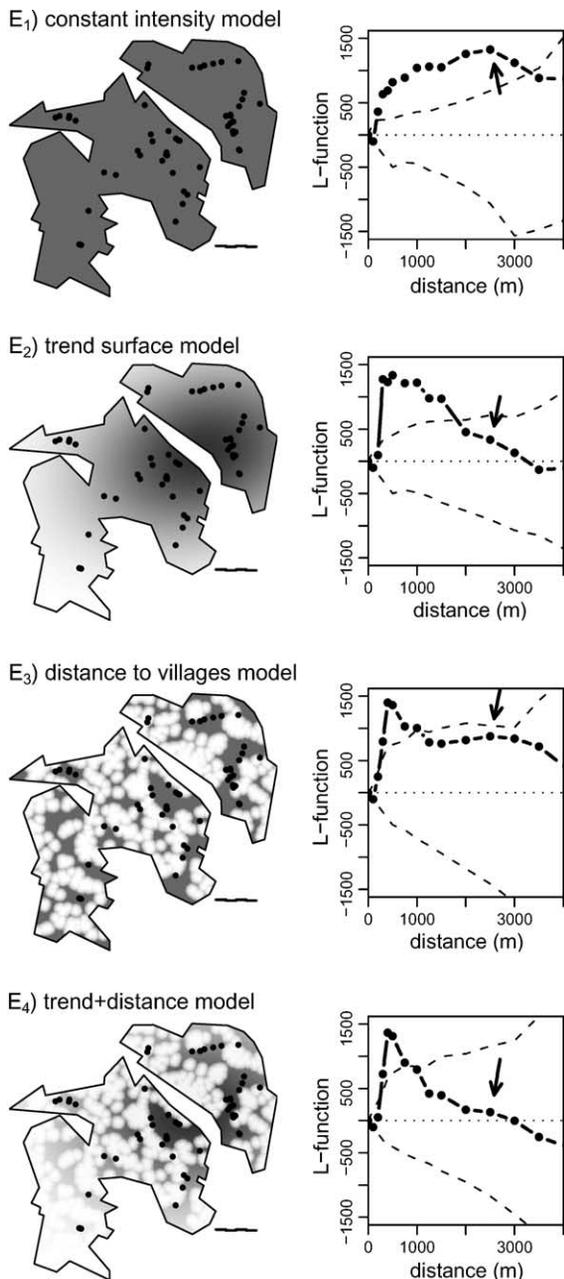
Fig. 4. Modeled intensity surface of Montagu's harrier nests in 2002 facing the corresponding L functions. Generally similar results were obtained in 2001 (figure not presented). Null models were E_1) Poisson distribution with constant intensity; E_2) Poisson distribution with intensity following a second order trend surface; E_3) Poisson model with log-linear increase with distance to built-up areas, up to 640 m (constant after the threshold); E_4) additive model of the two previous ones. See Fig. 3 for other symbols.

(0–300 m), and a strong decline in aggregation values at largest scales (2000–2500 m), which became non-significant in both years (see arrows on Fig. $4E_2$). At intermediate scales (ca 300–750 m), aggregation levels

remained virtually unchanged (compare Fig. $4E_2$, and E_1, and see Table 2 for a summary).

The quadratic trend surfaces only accounted for a fraction of the spatial heterogeneity. GLMs also confirmed the local, strong repulsive effect of built-up areas on harriers, as expressed by the distance to nearest buildings (Table 1). We tried a range of possible distance thresholds to model the effect of distance to villages for the Montagu's harrier. In 2001, the fit of the models showed a clear maximum around the 720 m value, whereas this was found at 640 m in 2002 (Table 1). The 720 m (or 640 m in 2002) upper-bounded distance model, assuming a log-linear effect of distance between 0 and 720 m (640 m), and a constant intensity after 720 m (640 m), fitted the data better than raw distance (Table 1). Adding the repulsive effect of buildings in the model induced a high patchiness in potential harrier habitat within the study area (Fig. $4E_3$). After accounting for this small-scale heterogeneity (model E_3), the L_{inhom} values and confidence intervals differed from the respective homogeneous L functions (model E_1, compare Fig. $4E_3$ and E_1) but were similar to the L_{inhom} with large trends (model E_2, compare Fig. $4E_3$ and E_2, and see Table 2).

A final additive model, including a quadratic trend surface and a function of distance to buildings, was fitted (model E_4, Table 1). From the corresponding L_{inhom} values, aggregation at small scales (up to 400 m), became less, or not significant (Fig. $4E_4$). Maximum aggregation values converged in the two years at distances of ca 500 m.

Discussion

The little owl and Montagu's harrier both showed large- and small-scale spatial variations in abundance and accounting for this heterogeneity at one or both scales had different effects on the perceived aggregation patterns of each species. The actual effects changed with the spatial scale of heterogeneity considered, differed between the two species and, more importantly, these effects could hardly have been predicted a priori.

First-order spatial patterns: broad and local heterogeneity

Although generally thought of as large-scale phenomena (Wiegand and Moloney 2004), first-order spatial variations result from the heterogeneity in some exogenous factors and may occur at any spatial scale. In contrast, second-order processes (i.e. attraction, inhibition) are most likely to occur at small scale, within the neighbourhood of an individual. Separating first and second order variations appears critical as they correspond to very different biological processes (Cressie 1993, Pélissier and

Table 1. AIC and Likelihood ratio tests for the intensity models in the little owl and Montagu's harrier.

Data set	(#)	Model	AIC	p-value
Little owl 2001	(1)	Constant	2617.2	–
	(2)	Trend1	2613.8	$0.024^{(2\ vs\ 1)}$
	(3)	Trend2	2610.9	$0.032^{(3\ vs\ 2)}$
	(4)	Distance	2453.7	$<0.0001^{(4\ vs\ 1)}$
	(5)	Trend2+Distance	2439.8	$<0.0001^{(5\ vs\ 4)}$
Little owl 2002	(1)	Constant	2586.9	–
	(2)	Trend1	2586.3	$0.098^{(2\ vs\ 1)}$
	(3)	Trend2	2586.0	$0.054^{(3\ vs\ 1)}$
	(4)	Distance	2412.5	$<0.0001^{(4\ vs\ 1)}$
	(5)	Trend2+Distance	2404.1	$0.0025^{(5\ vs\ 4)}$
Montagu's harrier 2001	(1)	Constant	1548.1	–
	(2)	Trend1	1544.8	$0.026^{(2\ vs\ 1)}$
	(3)	Trend2	1540.3	$0.015^{(3\ vs\ 2)}$
	(4)	Distance	1499.4	$<0.0001^{(4\ vs\ 1)}$
	(5)	Distance720	1477.4	$<0.0001^{(5\ vs\ 4)}$
	(6)	Trend2+Distance720	1476.0	$0.045^{(6\ vs\ 5)}$
Montagu's harrier 2002	(1)	Constant	1737.0	–
	(2)	Trend1	1729.8	$0.0036^{(2\ vs\ 1)}$
	(3)	Trend2	1726.4	$0.024^{(3\ vs\ 2)}$
	(4)	Distance	1710.2	$<0.0001^{(4\ vs\ 1)}$
	(5)	Distance640	1703.7	$0.0035^{(5\ vs\ 4)}$
	(6)	Trend2+Distance640	1694.9	$0.0021^{(6\ vs\ 5)}$

The "p-value" results from pairwise comparisons of the models by the Likelihood Ratio Test; the models compared are given in parentheses with reference to the model number (#). "Trend1" and "Trend2" are first- and second order polynomials of the geographic coordinates of the points, respectively. "Distance" is for distance to nearest building, and "DistanceX" a transform of "Distance" with an upper bound at X m (see text). All the models include a constant term (not shown for clarity, except for models including the constant only).

Goreaud 2001, Wiegand and Moloney 2004). However, first- and second-order spatial processes both result in point aggregations (Ripley 1981) and cannot be distinguished from each other without incorporating additional biological information in the statistical models.

Trend surfaces were used to model large scale variations in territory/nest density from unidentified environmental sources. For both species, very consistent trends were found between years 2001 and 2002, suggesting stable large scale patterns in distribution, even though the individual locations of nests and territories varied locally between years. Possible causes for large scale variations in owl density could involve dispersal and colonization processes, or response to spatial variations in habitat quality, such as the degree

of urbanization (van Nieuwenhuyse et al. 2001), which were not explicitly tested here. Harrier spatial patterns of abundance were consistent with trends in food availability (Cornulier et al. unpubl.).

Variations in territory/nest densities were also detected at small scales. We were able to model the strong association between the little owl and villages in our study area (Bretagnolle et al. 2001). One might hypothesize that the first-order village effect is an artifact of locating the playback stations around the villages. Nevertheless, our station network also covered most of the un-built areas (Fig. 1), and the absence of contacts away from villages provides good support for our assertions. A positive effect of sparse or rural built-up areas has already been reported for that species at

Table 2. Influence of null models on the results of point pattern analyses at different spatial scales. "Small scale" refers to ca 0–400 m; "Medium" to ca 400–1000 m; "Large" to 1500 m or more. "I" refers to "Inhibited" (regularity in spacing), "R" to "not different from Random", "A" to "Aggregated" and "A+" to "strongly Aggregated". Slash-separated letters indicate a succession of patterns at a given scale. Bold letters point to differences from the reference model with homogeneous (constant) intensity over space.

Species	Null model	2001			2002		
		Small scale	Medium scale	Large scale	Small scale	Medium scale	Large scale
Little owl	(E₁) Constant	I	A	R	I	A	R
	(E₂) Broad Trend	I	A	R	I	A	R
	(E₃) Distance to villages	I	**R**	R	I	**R**	R
	(E₄) Trend+Distance	I	**R**	R	I	**R**	R
Montagu's harrier	(E₁) Constant	A	A+	A+	I/R	A+	A+
	(E₂) Broad Trend	A	A+	**A/R**	I/R	A+	**R**
	(E₃) Distance to villages	A	A+	A+	I/R	A+	**R**
	(E₄) Trend+Distance	A	A+	**A/R**	I/R	A+	**R**

different scales (Martinez and Zuberogoitia 2004, van Nieuwenhuyse et al. 2004), though human settlements at higher densities have a negative impact (van Nieuwenhuyse et al. 2001). Suitable nesting cavities are very scarce in open intensive agro-ecosystems and are often restricted to buildings and trees in the proximity of the villages (Bretagnolle et al. 2001). Furthermore, the surroundings of the villages combine features known to be very favorable to the species, such as farms, pasture lands, cattle breeding, gardens and traditional orchards, hedgerows and hollow trees (van Nieuwenhuyse et al. 2001, Génot and van Nieuwenhuyse 2002). In contrast, Montagu's harrier frequently breeds in intensive, open agricultural landscapes. Our data indicate an avoidance of village neighbourhoods for nest settlement. Although avoidance of human settlements by breeding raptors has been traditionally explained by intense persecution several decades ago (Newton and Gammie 1979), such avoidance has not been reported previously in this species. However, an alternative hypothesis suggests that breeding in the vicinity of villages may decrease the availability of nearby feeding areas (Cornulier et al. unpubl.).

Second-order processes: aggregation patterns

Preliminary spatial analyses assuming homogeneity can be useful for providing a crude description of the distribution patterns without any underlying assumption. In the little owl, previous studies using NND led to conflicting results: in northern Belgium and the Netherlands, little owl calling males were found to be randomly distributed, with a tendency to regular spacing consistent with territoriality (van Nieuwenhuyse et al. 2001). However, using similar methods, Bretagnolle et al. (2001) found a significant tendency to clustering in our study area, a result interpreted as conspecific attraction. In our study, when assuming homogeneity, owls maintained some regular spacing at small scales (ca 150 m), as expected from a territorial species, whereas territories were clustered at medium scales, between 500 and 1000 m (Table 2). Consequently, opposite patterns can be found in a single dataset at different scales, highlighting an important limitation of classical NND methods that generally fail to detect the scales and nestedness of spatial structures (Campbell 1995).

Furthermore, most spatial analysis methods, such as the K or L functions, are sensitive to non-stationarity in the processes they depict. In this study, we found little difference between L_{inhom} assuming a constant intensity (the standard L function) and L_{inhom} after accounting for large scale trends in little owl abundance. Therefore in this example, large scale trends had little effect on the statistics and hence on the patterns of regularity and aggregation detected (Table 2). While regular spacing can result from territorial behaviour, aggregation of

territories at larger scales is less easy to explain. For instance, aggregation of territories has been observed in lekking species (Höglund and Alatalo 1995), as well as in non-lekking ones (hidden lek hypothesis, Wagner 1997). However, aggregation can be induced by heterogeneity in environmental quality (e.g. Gordon 1997, Boyce and McDonald 1999), thus inducing variations in density rather than true clustering behaviour. Accounting for patchiness of suitable habitat (villages and their surroundings) decreased the value of the L_{inhom} function and suppressed the clustering pattern in the little owl (Table 2), therefore suggesting that the distribution of suitable habitat patches was sufficient to explain the clustering of owl territories. Imprecision in the location of owls by ear may affect our results. A study by Freeman and Ford (2002) suggests that location imprecision may lead to moderate underestimation of the intensity and range of regularity in spacing (territoriality).

In harriers, preliminary analyses assuming homogeneity reported clustering over a wide range of scales. However, accounting for heterogeneities in nest intensity according to absolute location (trend surfaces) and distance to villages affected the L_{inhom} functions, and led to a decrease in the range and magnitude of large-scale aggregation. In this species, considering large-scale trends or small-scale heterogeneity led to similar results, suggesting a possible correlation between these two features in our study area. However, using both effects improved the fit of the models, and the distance to buildings seemed to be the most influential in the final shape of the L_{inhom} functions. Aggregation peaks were consistently found around 400–750 m across models and years, in agreement with the scale previously found using NND in an other population (ca 600 m, Arroyo 1995). However, as for little owl, analyses accounting for spatial heterogeneity suggested that habitat preferences were responsible for larger-scale aggregates in 2002, and to a lesser extent in 2001.

A possible concern in this study involves the effect that the non-detection of harrier's nests or owl territories could have on our results. However, a property of Ripley's function is that it is invariant under spatially independent thinning (independent random retention of points in the point process) (Baddeley et al. 2000, Moller and Waagepetersen 2002). Consequently, the method is robust to missing data, provided that these are not spatially biased.

Conclusions

Whereas both species were initially found to form clusters at some spatial scale, accounting for spatial heterogeneity using the L_{inhom} function revealed that 1) territorial, village dwelling little owls showed no clustering of territories when habitat availability was considered; 2) semi-colonial harriers still formed significant clusters, but

part of the aggregation in this species could be explained by landscape structure alone. In contrast with standard K or L functions assuming stationarity, new statistics such as L_{inhom} can therefore deal explicitly with environmental heterogeneity at several spatial scales, allowing the analysis of a wide range of ecological situations. Further, these methods provide new insights into ecological processes shaping the distribution of organisms, by distinguishing between environmentally-induced aggregation and active spacing behaviours (repulsion or agregation). However, as generally noticed in spatial ecology, our conclusions rely closely on the biological knowledge of the system (Real and McElhany 1996, Jolles et al. 2002, Keitt et al. 2002). In particular, it is essential to identify correctly the environmental variables determining bird abundance at different spatial scales.

In this respect, estimating trends in abundance directly from the pattern (i.e. without biologically relevant information) with non-parametric smoothers or polynomials (Wiegand and Moloney 2004) may be acceptable for the larger spatial scales. At smaller scales however, our results with the little owl example indicate that the interpoint interactions of interest can be confounded with spatial heterogeneity occurring at similar scale. In such circumstances, first- and second-order effects are not separable without additional information, and smoothing methods may produce unreliable results. This is particularly of concern when using high-order polynomials of geographic coordinates, local kernel density estimators (e.g. Baddeley et al. 2000, Pélissier and Goreaud 2001), or the related moving-window estimate (Wiegand and Moloney 2004) with small radii. Therefore, we advocate model-based approaches (Berman and Turner 1992, Baddeley et al. 2000, Reich et al. 2004) using relevant covariates to model spatial heterogeneity. Coupling these models with the powerful L_{inhom} function allows testing for spacing behaviours in heterogeneous environments, with biologically sensible null hypotheses.

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