The spatial scale of habitat selection by red deer

James A. Schaefer, Nicolas Morellet, Dominique Pépin, and Hélène Verheyden

Abstract: Accounting for spatial scale is essential for understanding habitat selection, but few studies have used spatial statistics to reveal the characteristic scale at which organisms respond to their environment. We studied habitat selection by GPS-tracked red deer (Cervus elaphus L., 1758) in the Pyrenees Mountains, France, by applying a geostatistical model that compares autocorrelation of a resource between used and available sites to uncover the scale at which animals assess habitat. Using an artificial landscape, we demonstrated that the model can handle discrete habitat classes. Based on conventional hierarchical analysis, deer selected for open habitat, especially meadow, and avoided coniferous forest, more strongly at the coarse level of the home range than GPS locations. Home ranges exhibited generally lower autocorrelation in elevation and meadow habitat than random locations within the population range, indicative of preference for high habitat heterogeneity. Mean maximum discrepancy in autocorrelation, which was more pronounced at the level of the home range than GPS locations, occurred at 830 m for meadow habitat and at 1511 m for elevation, suggesting that red deer responded to their environment at this scale. Our study demonstrates how spatial statistics can serve as an instructive complement to conventional approaches to habitat selection.

Résumé : L’étude de l’échelle spatiale est essentielle pour comprendre la sélection de l’habitat, mais peu d’études ont utilisé des statistiques spatiales pour révéler l’échelle caractéristique à laquelle un organisme répond à son environnement. Nous avons étudié la sélection de l’habitat par des cerfs rouges (Cervus elaphus L., 1758) suivis par GPS dans les montagnes pyrénéennes, en France, en appliquant un modèle géostatistique, qui compare l’autocorrélation d’une ressource entre les sites utilisés et disponibles pour découvrir l’échelle à laquelle les animaux évaluent leur habitat. À partir d’un paysage artificiel, nous démontrons que ce modèle peut être généralisé pour traiter des classes discrètes d’habitat. D’après une analyse hiérarchique conventionnelle, les cerfs sélectionnent un habitat ouvert, plus particulièrement les prairies, et évitent les forêts de conifères, de façon plus marquée au niveau plus grossier du domaine vital que celui des localisations GPS. Les domaines révèlent généralement une plus faible autocorrélation pour l’altitude et l’habitat prairie que les localisations aléatoires dans le domaine populationnel, révélateur d’une préférence pour une forte hétérogénéité d’habitats. L’écart moyen maximum d’autocorrélation, plus prononcé à l’échelle du domaine individuel que des localisations GPS, est de 830 m pour l’habitat prairie et de 1511 m pour l’altitude, ce qui laisse croire que le cerf réagit à son environnement à cette échelle. Notre étude démontre comment les statistiques spatiales peuvent servir de complément instructif aux approches conventionnelles de sélection de l’habitat.

Introduction

Spatial scale has become a prominent feature in the study of habitat selection (Johnson 1980; Senft et al. 1987; Boyce 2006). Because inferences about habitat selection are often sensitive to scale, investigations now commonly span several levels of analysis, between the grain of the individual animal location and the extent of a species range. The benefits of a multiscale framework are many — for example, by helping to overcome arbitrary notions of availability (Schaefer and Messier 1995), facilitating comparisons across species (Ihl and Klein 2001; Jenkins et al. 2007), and potentially revealing the most significant population limiting factors (Rettie and Messier 2000).

While a hierarchical approach is informative, determining the explicit scales at which animals select resources, in units of area or distance, is still desirable. The “characteristic scale” at which organisms react to their environment is essential for understanding patterns of species occupancy and responses to landscape change (Olden et al. 2004), and such scales may not be intuitive. Mule deer (Odocoileus hemionus (Rafinesque, 1817)), for instance, appear to assess their surroundings well beyond the home range when establishing a home range (Bowyer and Kie 2006).

Spatial statistics are the basis of a recent geostatistical model to detect these scales (Mayor et al. 2007; Schaefer and Mayor 2007). The premise of the model is that habitat selection may be regarded as a shift, often a reduction, in the variance of resources or conditions. By comparing the spatial structure of a resource at sites used by an organism and the general environment, the scale of perception is revealed — the point of maximum divergence in either semivariance or spatial autocorrelation. In studies of habitat selection, geostatistics have been applied to describe the


J.A. Schaefer,1 Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.

N. Morellet, D. Pépin, and H. Verheyden, Institut National de la Recherche Agronomique — Comportement et Ecologie de la Faune Sauvage, chemin de Borde Rouge-Auzeville, B.P. 52627, F 31326 Castanet-Tolosan CEDEX, France.

1Corresponding author (e-mail: jschaefer@trentu.ca).
distribution of resources within a study area (e.g., Meisel and Turner 1998; Boyce et al. 2003) but not to examine “used” vs. “available” sites. This is the key comparison that may reveal the extent of organism response to the environment (Schaefer and Mayor 2007).

The geostatistical model is appropriate when a resource is treated as a continuous variable. Although spatial statistics have been used to reveal the patterns of binary landscapes (Carpenter and Chaney 1983; Dale and Blundon 1990), it is unclear whether the model can accommodate discrete habitat classes, a common circumstance when habitats are mapped by remote-sensing (Table 1).

Here, we explored the application of this geostatistical model of habitat selection to GPS-tracked red deer (*Cervus elaphus* L., 1758) in the Pyrenees Mountains in southwestern France (Fig. 1). First, we tested the model using an artificial landscape categorized into discrete habitat types. We show that the model is capable of uncovering scales of selection when habitats are viewed under a binary classification. Second, we used the model to study habitat selection by red deer. From GPS tracking of 11 individuals, we analysed the patterns of habitat selection based on a conventional approach of use vs. availability (Thomas and Taylor 1990) at three hierarchical levels: population range, home ranges, and GPS locations. Then, using two habitat features (meadow and elevation), we used the geostatistical model to uncover the explicit scales at which these animals assess their montane environment.

**Materials and methods**

**Test of the model with discrete habitats**

We followed the general approach of Schaefer and Mayor (2007) to explore the suitability of the geostatistical model using strict binary habitat classes. First, we built a toroidal landscape of 500 sites with variable levels of a resource using the logistic equation with a stochastic variable ($\xi$) to set the resource abundance ($y$) at each site:

$$y_{i+1} = y_i e^{1-(y_i/K_i) + \xi}$$

where $y_{i+1}$ is the resource level in the adjacent cell, $y_i$ is the resource level in the $i$th site, $e$ is base of the natural loga-

---

**Table 1.** Habitat classes and characteristics in the study area in the Pyrenees Mountains, France.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Code</th>
<th>Floristic attributes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meadow</td>
<td>MEAD</td>
<td>Grasses and forbs</td>
</tr>
<tr>
<td>Birch margin</td>
<td>BIRCH</td>
<td><em>Betula pubescens</em>, myrtle blueberries (<em>Vaccinium myrtillus</em> L.), grasses</td>
</tr>
<tr>
<td>Juniper grassland</td>
<td>JUNIP</td>
<td>Grasses, <em>Juniperus communis</em>, <em>Calluna vulgaris</em>, <em>Vaccinium</em> spp.</td>
</tr>
<tr>
<td>Oak forest</td>
<td>OAK</td>
<td><em>Quercus</em> sp.</td>
</tr>
<tr>
<td>Other moorland</td>
<td>OTHER</td>
<td><em>Pteridium aquilinum</em>, <em>Rhododendron ferrugineum</em></td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>DECID</td>
<td><em>Quercus</em> sp., common hazel (<em>Corylus avellana</em> L.), sweet chestnut (<em>Castanea sativa</em> Mill.), <em>Fagus sylvatica</em></td>
</tr>
<tr>
<td>Heather moorland</td>
<td>HEATH</td>
<td><em>Calluna</em> spp., grasses, <em>Vaccinium</em> spp.</td>
</tr>
<tr>
<td>Mountain pasture</td>
<td>PAST</td>
<td>Grasses and forbs, <em>Calluna</em> spp., <em>Vaccinium</em> spp.</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>CONIF</td>
<td><em>Abies alba</em>, <em>Fagus sylvatica</em></td>
</tr>
</tbody>
</table>

---

**Fig. 1.** Population range (broken line) and home ranges (solid lines) for red deer (*Cervus elaphus*) in the Pyrenees Mountains (arrow in the inset map), France.
rithm, $r$ is the exponential rate of change, $K$ is the stable equilibrium point, and $\xi$ is a normally distributed random variate with a mean of 0 and a standard deviation of 0.2. We set $r$ to 0.1 and both $y_1$ and $K$ to 100.

We then populated this landscape with animals that selected sites based on the surrounding neighbourhood, i.e., the distance from that site to the most distant site of perception. The neighbourhood extended in both directions. A site was used if its resource abundance exceeded the neighbourhood mean. We ran the model with neighbourhoods of 5, 10, and 20 units. For each neighbourhood, the model was run 100 times on the same series of landscapes.

To fit this continuous landscape into a binary classification, we categorized the value at each site to either 0 or 1 based on whether its resource level was above or below the

**Table 2.** Characteristics of individual GPS-tracked red deer (*Cervus elaphus*) from the Pyrenees Mountains, France.

<table>
<thead>
<tr>
<th>Animal no. and name</th>
<th>Sex</th>
<th>No. of GPS locations</th>
<th>Size of home range (ha)*</th>
<th>Scale of selection (m)$^{\dagger}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Daniella</td>
<td>Female</td>
<td>199</td>
<td>113</td>
<td>875</td>
</tr>
<tr>
<td>2. Désirée</td>
<td>Female</td>
<td>2122</td>
<td>262</td>
<td>1875</td>
</tr>
<tr>
<td>3. Forsa</td>
<td>Female</td>
<td>98</td>
<td>292</td>
<td>375</td>
</tr>
<tr>
<td>4. Gelée</td>
<td>Female</td>
<td>451</td>
<td>418</td>
<td>625</td>
</tr>
<tr>
<td>5. Karine</td>
<td>Female</td>
<td>140</td>
<td>239</td>
<td>1125</td>
</tr>
<tr>
<td>6. Mémère</td>
<td>Female</td>
<td>688</td>
<td>266</td>
<td>1125</td>
</tr>
<tr>
<td>7. Pierrette</td>
<td>Female</td>
<td>880</td>
<td>229</td>
<td>1125</td>
</tr>
<tr>
<td>8. Tiente</td>
<td>Female</td>
<td>1174</td>
<td>591</td>
<td>375</td>
</tr>
<tr>
<td>9. Phil</td>
<td>Male</td>
<td>1266</td>
<td>4099</td>
<td>875</td>
</tr>
<tr>
<td>10. Seb</td>
<td>Male</td>
<td>464</td>
<td>459</td>
<td>125</td>
</tr>
<tr>
<td>11. Sébastien</td>
<td>Male</td>
<td>559</td>
<td>1111</td>
<td>625</td>
</tr>
</tbody>
</table>

*Size of the home range was estimated by 95% fixed kernels.

$^{\dagger}$Scale of selection was determined as point of maximum divergence in Moran’s $I$ between individual ranges and population range.

**Fig. 2.** Geostatistical model to detect the scale of habitat selection using binary (0 or 1) habitat categories on an artificial landscape. Extents of animal perception (neighbourhoods) were set at 5, 10, or 20 units.
mean across the entire landscape, i.e., $y_i = 0$ (if $y_i > \bar{y}$) or $y_i = 1$ (if $y_i < \bar{y}$). We also explored the effect of misclassification of the landscape by altering the classification criterion to four other values ($\bar{y} + 1\ SD$, $\bar{y} + 0.5\ SD$, $\bar{y} - 0.5\ SD$, and $\bar{y} - 1\ SD$). The neighbourhood was set at 10 units.

We constructed variograms (semivariance vs. lag distance) and correlograms (Moran’s $I$ vs. lag distance) between all possible pairs of sites, separately for the general environment (all sites) and used sites. The semivariance ($\gamma$) at some distance ($h$) is half the sum of the squared difference between pairs (Meisel and Turner 1998):

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{i=1}^{n} (y_i - y_{i+h})^2$$

where $y$ is the value of the variable at the $i$th and $(i+h)$th sites and $n(h)$ is the number of pairs of sampling locations separated by distance $h$. The value is divided by 2 because the summation from 1 to $n$ sampling locations considers each pair twice in the calculation.

Moran’s $I$ was computed for each distance class, $d$ (Legendre and Legendre 1998):

$$I(d) = \frac{\frac{1}{W} \sum_{h=1}^{n} \sum_{i=1}^{n} w_{hi}(y_h - \bar{y})(y_i - \bar{y})}{\frac{1}{2} \sum_{i=1}^{n} (y_i - \bar{y})^2}$$

where $w_{hi}$ is 1 when sites $h$ and $i$ are at the distance $d$ and $w_{hi}$ is 0 otherwise. $W$ is the sum of $w_{hi}$ for each distance class. Moran’s $I$ usually varies between +1 and −1; positive values denote positive autocorrelation and negative values represent negative autocorrelation.

**Habitat selection by red deer**

The field data were derived from a 180 km$^2$ study area in the Pyrenees Mountains, southwestern France. Elevation ranged between 800 and 2200 m above sea level. Vegetation consisted mostly of meadows in the bottom of the valley and, as elevation increased, grassland with common juniper.
from the Service d’Utilité Agricole Inter-chambres d’Agriculture Pyrénées, and a bear habitat map from the Office National de la Chasse et de la Faune Sauvage. We refined some broad habitat classes based on vegetation composition and physionomy. From field surveys, we constructed a “training map” of homogeneous habitat patches (forest on sunlight, forest on shadow, open on sunlight, open on shadow) of a trichromatic SPOT image covering the study area. The four classifications were done to disentangle similar trichromatic responses to some forest and green meadow patches and to shadow. The habitat map was validated using extended patches of the training map and up to 1000 records of vegetation biomass and cover from the field.

Eleven adult deer (8 females, 3 males) were fitted with GPS radio collars (Table 2), programmed to record locations every 3 h, with a precision of <30 m. These animals were treated under authorization certificate no. 31-265, in accordance with guidelines from the Canadian Council on Animal Care. Data were collected from November 2002 to April 2004. Elevation was determined from topographic maps.

Owing to transmitter malfunctions and mortality of four animals in February and March 2003, there was substantial individual variation in the duration of tracking (2–12 months) and the number of GPS locations (100 to >2100). Our sample size did not afford the opportunity to investigate variations owing to sex, time of day, or season, which can be appreciable for this species (Boyce et al. 2003; McCorquodale 2003).

We conducted analysis of habitat selection at two levels. Home ranges (minimum convex polygon (MCP) around each animal’s GPS locations) were compared with the population range (MCP surrounding all GPS locations from all individuals together; Fig. 1); GPS locations were compared with home ranges. For each habitat type (Table 1), we computed percent use minus percent available (Thomas and Taylor 1990), where availability was denoted as the adjacent, higher level in this hierarchy (Schaefer and Messier 1995). We also tested for selection of forest by combining treed habitats (birch margin, oak, deciduous, and coniferous forests) into one. We assessed significance with one sample t tests under the null hypothesis that the mean of percent use minus percent available was zero.

We applied the geostatistical model, using correlograms, on two variables (meadow and elevation), both of which are important to deer (Albon and Langvatn 1992; Mysterud et al. 2001, 2002). Meadow was treated as a binary variable (i.e., meadow = 1; all other habitats = 0). Plots of Moran’s I vs. distance were computed among all possible pairs of GPS locations, and compared with 5000 random points within the overall population range. Distance classes were set at 250 m intervals, to a maximum of 4000 m, the midpoints of which were used in subsequent analyses. Computations were conducted in SAM version 1.1 (Rangel et al. 2006) and STATISTICA version 7.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Test of the model with discrete habitats

In general, variograms and correlograms were effective in

![Fig. 4. Use and availability of nine habitat types by red deer (Cervus elaphus) in the Pyrenees Mountains. Availability was based on the adjacent, broader scale (i.e., GPS locations vs. home range, home ranges vs. population range). Each datum represents one animal. Means significantly different from zero are indicated by * (P < 0.05) or ** (P < 0.01). Habitat codes from Table 1.](image-url)
uncovering the scale of selection when the simulated landscape was viewed in a binary classification. In this artificial environment when neighbourhoods were set at 5, 10, and 20 units, variograms diverged most strongly at scales of 4, 9, and 16 units, whereas for correlograms it was 4, 10, and 18 units, respectively (Fig. 2).

The misclassification of habitat only slightly obscured the outcome of the model (Fig. 3). The neighbourhood of 10 units was faithfully displayed as the maximum discrepancy in variograms and correlograms when the classification criterion was close to the resource mean (i.e., ±0.5 SD). When the classification diverged even more strongly from the mean, (i.e., ±1 SD), the point of divergence became only slightly less accurate (range = 8–12 units), but the ability to discern the peak difference became somewhat more difficult (Fig. 3).

**Habitat selection by red deer**

Deer selected most strongly at the level of the home range (Fig. 4); they preferred some open habitats (meadow, birch margin, and juniper), whereas pasture and especially coniferous forests were avoided. GPS locations differed little from the composition of the home ranges, with the exception of modest avoidance of deciduous forests ($t_{10} = 2.27, P = 0.047$; Fig. 4). Similarly, when we combined forested habitats into one category, deer showed marginal avoidance of forests at the home range ($t_{10} = 2.05, P = 0.067$) but not at the level of GPS locations ($t_{10} = 1.42, P = 0.097$).

Moran’s $I$ was lower at sites used by deer than in the general environment (Figs. 5, 6) for both elevation and meadow, both at the home range and radiolocation level. This indicated greater habitat heterogeneity in sites used by red deer compared with their surroundings. Based on the point of maximum discrepancy in Moran’s $I$ between the home ranges and the population range, deer responded to their habitat at the scale of several hundred metres: 830 m (±146 SE) for meadow (Fig. 5) and 1511 m (±270 SE) for elevation (Fig. 6; Table 2). The scales of response to the environment, determined by the model, were not predictable from home-range size quantified using a 95% kernel estimator; there was no significant correlation between them (meadow: $r = -0.064, P = 0.852$; elevation: $r = -0.235, P = 0.487$).

The model was sensitive to the level of comparison. Based on the point of maximum discrepancy in Moran’s $I$ between GPS locations and population range, deer responded at a similar but slightly finer scale: 625 m (±126 SE) for meadow (Fig. 5) and 943 m (±143 SE) for elevation.
Fig. 6. Correlograms of elevation for 11 red deer (*Cervus elaphus*) in the Pyrenees Mountains at three levels: population range, home ranges, and GPS locations.

Discussion

Spatial scale is inherent to many ecological patterns and processes, like habitat selection. The power of spatial statistics, such as variograms and correlograms, rests in their capacity to detect how pattern changes across scales. Geostatistics, however, have not regularly been applied to studies of habitat selection (c.f., Meisel and Turner 1998; Morellet and Guibert 1999; Boyce et al. 2003). This is surprising because, as Levin (1992, p. 1947) has noted, the identification of pattern is “an entrée into the identification of scales”.

At the heart of the geostatistical model is the spatial structure of a resource, not just across the study area, but at sites used by animals — a comparison that may reveal the extent of organism response to the environment (Mayor et al. 2007; Schaefer and Mayor 2007). Our study demonstrates that this approach may be extended to categorical habitats (Figs. 2, 3), characteristic of most studies using remote sensing. Variation in the classification scheme appears to have minimal bearing on the outcome of the model, although it may obscure patterns if there is discordance in the habitat categorization and the resource to which animals respond.

Red deer exhibited more pronounced habitat selection, especially for meadow, at the scale of the home range (Fig. 4). In our study area, this community provided abundant graminaceous plants — the principal forages for red deer (Gebert and Verheyden-Tixier 2001). At the finer level of GPS radiolocations, however, these patterns largely disappeared, implying that a different set of factors may be more limiting within the home range (Rettie and Messier 2000). Indeed, there appears to be a strong diurnal pattern to habitat use by these deer. They used primarily open habitats like meadow at night, but forested habitats during the day (Adrados et al. 2008). This may represent a reaction to avoid
daytime human activities (Morgantini and Hudson 1979; Morellet et al. 1996).

This heterogeneity in habitat selection may have accounted for the consistent pattern in the correlograms — the lower than expected autocorrelation across both variables and nearly all scales (Figs. 5, 6). Thus, by choosing habitats, red deer experienced heightened variance in conditions compared with the general environment. Such a pattern is indicative of selection for complementary resources (Schaefer and Mayor 2007), a feature that would not have been readily evident without the geostatistical model. Indeed, a preference for high diversity in vegetation and topography is characteristic of red deer (also known as wapiti in North America) in montane environments (Albon and Langvatn 1992; Morellet and Guibert 1999; Mysterud et al. 2001; Boyce et al. 2003; Sawyer et al. 2007; Hebblewhite et al. 2008). Unfortunately, our data were insufficient to construct separate correlograms for daytime and nighttime GPS locations to explore patterns at a finer temporal resolution; we were also unable to explore sex-related differences that can be considerable in this dimorphic species (Clutton-Brock et al. 1987).

The correlograms, comparing the home ranges and population range, suggest rather consistent scales (830 m ±146 SE) for meadow and 1511 m ±270 SE) for elevation; Figs. 5, 6) at which red deer responded to their surroundings, despite some appreciable individual variation (Table 2). Schaefer and Mayor (2007) hypothesized that these scales may be indicative of an animal’s perceptual range. These results are remarkably similar to the movement patterns of wapiti in the Rocky Mountains of Alberta. Using first-passage time analysis, Frair et al. (2005) uncovered movement scales of 550–1650 m, non-linearly correlated to the patch size of cutover forest within the home range. Among other ungulates, moose (Alces alces (L., 1758)) appear to react to the environment over the scale of a few kilometres (Maier et al. 2005), whereas for migratory caribou the extent of response to winter food was approximately 13 km (Mayor et al. 2007). The biological basis for these variations is unclear. More comparisons across species and across environments will be needed before the underlying causes can be better understood.

The model is in need of further exploration. For example, it is not yet clear what set of observations (e.g., radio-locations, home ranges) represent an appropriate level of “use”. Indeed, when GPS locations (rather than home ranges) were compared with the population range, scales of selection by deer appeared somewhat finer (200–500 m less). We surmise that the hierarchical level where animals exhibit the most pronounced selection (in our study, the home range; Fig. 4) will be most informative. More simulations with the model would be informative — in particular, by manipulating the hierarchical levels at which resources are most strongly selected.

Scale now predominates in studies of habitat selection. Following Mayor et al. (2007), we suggest that it may be valuable to distinguish between two complementary notions of spatial scale: relative, organism-defined levels such as feeding patch, home range, or species range (Johnson 1980; Meyer and Thuiller 2006), and absolute, strictly spatial measures of distance or area. Levels such as home range, while offering a consistent entity to compare study areas and species, may vary dramatically in size. As noted by Bowyer and Kie (2006) and underscored by our study, there is no necessary link between the two. We believe increased attention to scaling may lead to a general theory of how organisms respond to their environment.

Acknowledgements

This study was supported by Fédérations Départementales et Régionale des chasseurs, Office National de la Chasse et de la Faune Sauvage, Office National des Forêts, and Centre Régional de la Propriété Forestière. The European Union and the Conseil Regional de Midi-Pyrénées gave financial support for this study. J.A.S. was assisted by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada; he is grateful for the hospitality from le Laboratoire Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, during his sabbatical visit.

References


