Importance of movement constraints in habitat selection studies

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ABSTRACT

The aim of this study is to empirically illustrate the importance of taking movement constraints into account when testing for habitat selection with telemetry data. Global Positioning System relocations of two Scandinavian brown bears were used to compare the results of two different tests of habitat selection by the bears within their home range. Both relied on the comparison of observed dataset with datasets simulated under the hypothesis of random habitat use. The first analysis did not take movement constraints into account (simulations were carried out by randomly distributing a set of points in the home range) whereas the second analysis accounted for these constraints (simulations were carried out by building random trajectories in the home range). The results for the two analyses showed contrasted results. Therefore, not accounting for movement constraints in analyses may result in a misleading biological interpretation. Autocorrelation between relocations is not undesirable: it contains information about ecological processes that should be integrated in habitat selection analyses.

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1. Introduction

During the last decade, the Global Positioning System (GPS) has been used increasingly by biologists to study the habitat selection by animals. The study of habitat selection with this kind of data implies a comparison between the habitat used by this animal and a null model describing the habitat that would have been used under the hypothesis that no habitat selection occurs (random habitat use, Boyce et al., 2002).

The simplest and the most widely used null model considers that, assuming random habitat use, the habitat used by the animal would be similar to the habitat composition of an area considered available to the animal (usually its home range, Aebischer et al., 1993). The use of this null model strongly relies on the assumption of independence between animal relocations which implies that the animal could be found anywhere within its home range at any time of the study period. In other words, this model supposes that patterns observed in the relocations of the animal (e.g. areas of higher relocations density) are only due to the animal's habitat choices. In many instances, this is often a reasonable assumption. However, this might not be the case in

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studies relying on GPS data. Due to automated positioning using GPS, these data are often characterized by short time intervals between relocations, which causes serial autocorrelation in the position of successive locations (Swihart and Slade, 1985). Thus, the position of an animal at time t is constrained by its movement capabilities between $t-1$ and t.

Ignoring this autocorrelation may result in misleading conclusions concerning the animal habitat selection. Several authors have noted that autocorrelation may result in an increased probability of type I errors (Legendre, 1993). It is therefore necessary to use an appropriate null model incorporating these movement constraints for the description of random habitat use. On the other hand, it is difficult to dissociate the effect of the movement constraints from that of habitat choice behaviour when building the null model under the hypothesis of habitat selection. We advocate that the null model used in habitat selection studies should depend both on the biological knowledge and on the available data for the studied individuals (species, sex, age, season of monitoring, study area, etc.). We therefore challenge the idea that some statistical methods can be used systematically to test for habitat selection, as no automatic method allows the design of such context specific null model. In this paper, we illustrate this approach by comparing the results of two "automatic" methods to test for habitat selection by two female brown bears (*Ursus arctos*) monitored using GPS. Our aim is not to draw conclusions about habitat selection by brown bears, but rather to illustrate the potential different conclusions regarding the strength of habitat selection depending on which approach is used. In the first analysis, we did not take movement constraints into account, and we assumed the spatial distribution of relocations to be explained exclusively by the habitat (i.e. a model without constraints, which is the simplest null model as described above). In the second analysis (i.e. a model with constraints), the null model accounted for patterns of the animal's trajectory to test the habitat selection: random habitat use was thus simulated preserving the shape of the observed trajectory.

2. Materials and methods

2.1. Data

We used GPS data from two Scandinavian female brown bears (ID numbers: W0208 and W0410) followed in central Sweden (Fig. 1): one female was alone whereas a second one was followed by cubs of the year. Relocations were collected every 30 min, from mid-April until the end of July 2006 (a total of 2309 and 2812 were available for the lone and the followed female bear, respectively).

We used raster maps of bear home ranges to describe the habitat, with a resolution of 200 m × 200 m. The maps included nine variables: elevation, slope, aspect, vegetation, distance to private and to public roads, distance to streams, distance to settlements and distance to houses. Each pixel of the resulting map thus contains geographic coordinates and the value for each variable. This environmental information is stored in a table **X** containing N rows (the N pixels of the home range) and P columns (the P environmental variables). This table has been centred and scaled, so that each habitat variable has a mean of 0 and a variance of 1. Each row of this table contains the coordinates of a point in the P-dimensional space defined by habitat variables (Fig. 2). The proportion of relocations in each pixel of the map is a utilization weight of the pixel (Fig. 2). The set of points in the available space for which the utilization weights are greater than 0 define the niche of the animal.

2.2. Habitat selection measurements

To study the strength of habitat selection, we used the concept of ecological niche formalized by Hutchinson (1957) (Fig. 2); a species niche is the hypervolume in the multidimensional space of environmental variables where the species can maintain a viable population. In this study, we extrapolated this definition to the third-order selection on Johnson's (1980) scale of selection, i.e. preferred habitat within the home range. We thus considered each home range, estimated by the Minimum
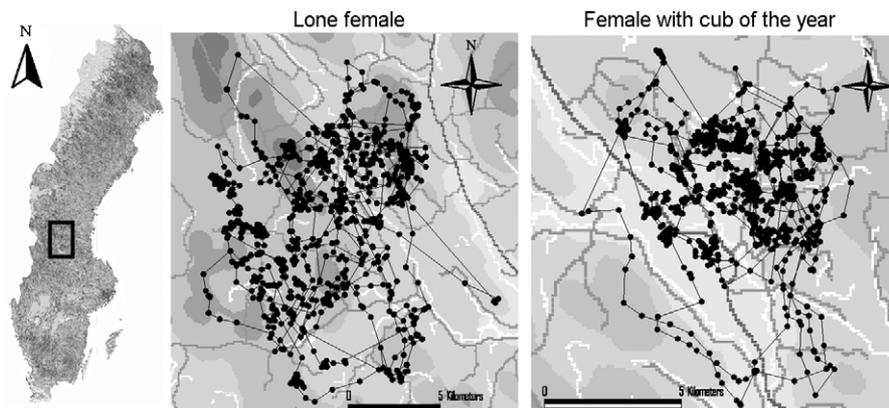

Fig. 1 – On the left: study area in central Sweden. On the right: trajectories (in black) of the two female brown bears on an elevation map. Grey lines are private roads and white lines are streams.
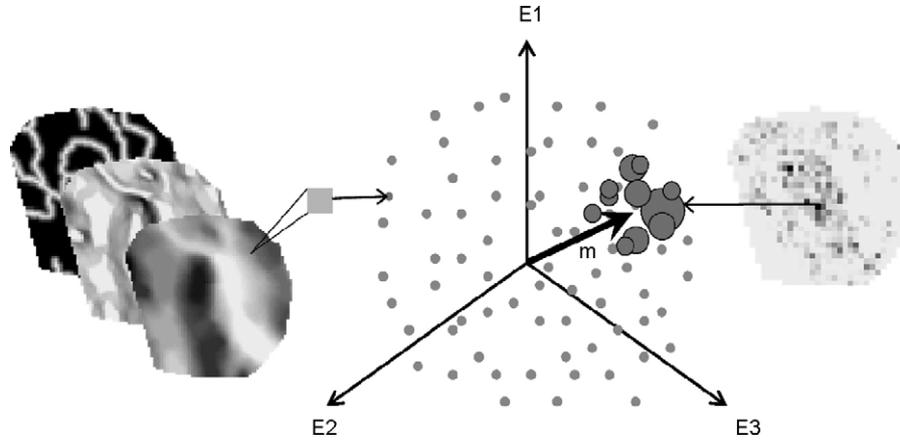
Fig. 2 – The use of the niche concept for study of habitat selection using GPS data. For a given animal, P maps of its home range are available (left). Each one of the P mapped variables defines one dimension in a multidimensional space, the ecological space (centre). Each pixel of the home range takes a value for each variable, so that each pixel corresponds to an available point in this space. On the other hand, the number of relocations of the animal in each pixel of the home range corresponds to a "utilization weight" (UW) of this pixel (right). These utilization weights are represented by grey circles in the middle figure (with a diameter proportional to the weight). The niche of the animal in the ecological space is defined by the set of points having an UW greater than 0. As the cloud of available points is centred (the origin of the space corresponds to the average available habitat conditions), the vector M, connecting the origin of the space and the average used habitat conditions, is the marginality vector.

Convex Polygon method (MCP; Mohr, 1947), as the available physical space.

Two complementary parameters can be used to characterize the niche: marginality (an index of the eccentricity of the niche relative to the average available habitat conditions) and tolerance (an index of the volume of the niche in the space of environmental variables) (Doledec et al., 2000; Hirzel et al., 2002). Marginality corresponds to the squared distance between the average habitat conditions used by the animal and those available to it:

$$m^2 = \sum_{j=1}^{P}(u_j - a_j)^2$$

with u_j the average use of the variable j and a_j the average availability of the variable j.

Tolerance is the sum, over all habitat variables, of the variances of the used pixels:

$$t^2 = \sum_{i=1}^{N}\sum_{j=1}^{P}p_i(x_{ij} - u_j)^2$$

with p_i the utilization weight of the pixel i and x_{ij} the value of the variable j in the pixel i. Note that the variables are centred and scaled, i.e.

$$\frac{1}{N}\sum_{i=1}^{N}(x_{ij} - a_j)^2 = 1$$

for all j.

These parameters have already been used by several authors to measure habitat selection (Doledec et al., 2000; Hirzel et al., 2002).

2.3. Habitat selection analysis

For each female, we tested the strength of selection behaviour using randomization tests of marginality and tolerance for the two models. In other words, we tested whether the marginality and the tolerance of their niche were significantly different from those obtained under the hypothesis of no selection, i.e. random use of the habitat, which we measured in two different ways.

In the model "without constraints", we distributed 1000 samples of N random points within the home range of each bear, N being the number of actual relocations of the corresponding bear. In this model, any pixel in the home range is considered to be available at any time, and each set of points corresponds to a simulation of random habitat use.

In the model "with constraints", we kept the shape of the animals' trajectory unchanged, to account for the autocorrelation between relocations. We performed 1000 rotations of the observed trajectory for each of the female around the centroid of the respective observed trajectories (Fig. 3). Each random rotation of the trajectory corresponded to a simulation of random habitat use by the animal taking into account the movement constraints on the trajectory.

For each model, marginality and tolerance were computed on simulated datasets. These values were then compared with observed values of marginality and tolerance to test for the strength of habitat selection in the two models.

Analyses were carried out using the package "adehabitat" (Calenge, 2006) for the R software (Ihaka and Gentleman, 1996).

3. Results

For each female, the range of simulated values of marginality and tolerance for the model "with constraints" was much
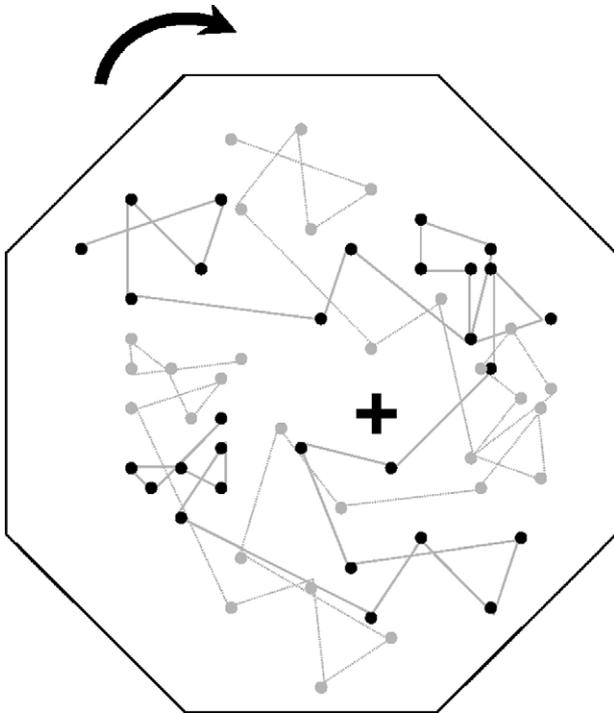
Fig. 3 – Trajectory simulation procedure for the model with constraints. The polygon represents the individual home range. Simulated trajectory (dashed grey line) were generated by a clockwise rotation (arrow) of the observed trajectory (black line) around its centroid (black cross).

broader than that for the model "without constraints" (Fig. 4). This result can be explained by the fact that habitat availability is restricted when simulating trajectories. Indeed, due to constraints of speed and orientation (turning angles between successive moves) the probability is higher for the next relocation to be located in a pixel close to the previous one. Therefore, the probability of remaining in a similar habitat type is high, resulting in a less homogeneous distribution of

these simulated "used" points in the home range. This results in larger differences between the simulated "used" pixels and the pixels of the whole home range, and therefore larger values of marginality.

Note that for the lone female, the observed habitat use (observed marginality and tolerance) is far from the distribution of simulated values obtained by randomly sampling points in the home range. This null model was therefore rejected, which suggested a strong habitat selection. On the other hand, the observed habitat use was located on the border of the distribution of values obtained by randomly rotating the trajectories. This other null model was accepted, which suggests a very weak habitat selection. We obtained the same results for the female with cubs, except that the observed used point is in the centre of the distribution of values estimated using simulated trajectories.

4. Discussion

We compared two extreme approaches to test for the habitat selection by two female brown bears monitored using GPS. For both bears, the results depended on the approach used to perform this test. When we tested habitat selection using a null model that did not account for movement constraints (the most common in the literature), we found a strong habitat selection by both bears. However, ignoring movement constraints might lead to an overestimation of the strength of this selection, because not considering these constraints artificially reduces the marginality and the tolerance under the assumption of random habitat use. Indeed, this model relies on the assumption that the individual not only has the capacity to move everywhere in its home range at any time, but also that it has no intrinsic constraints (due to feeding or resting requirements, restriction on movements because of cubs, etc.). When we tested for habitat selection accounting for movement constraints, using random rotations of the trajectories, we found no significant habitat selection for either bear. Actually, the shape of the trajectory, which is kept
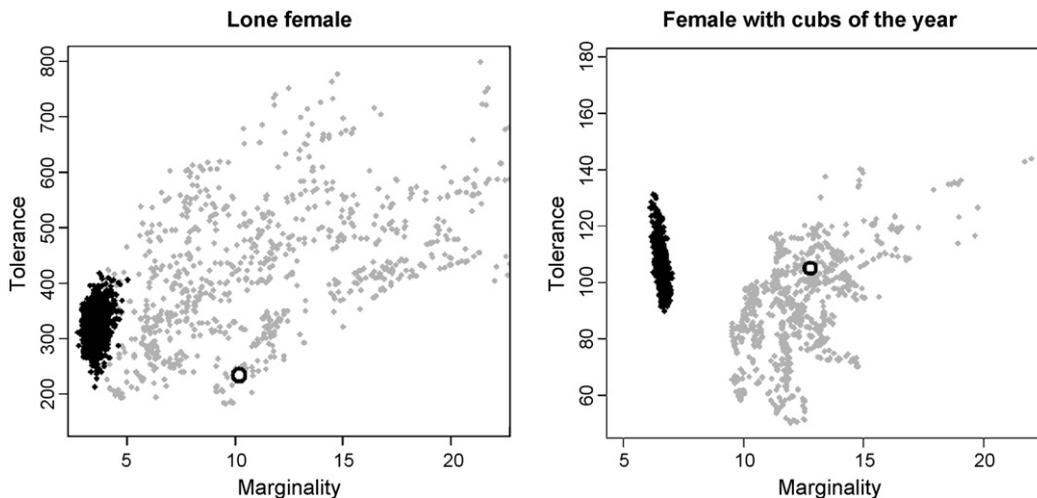

Fig. 4 – Joint distribution of the marginality and the tolerance for each female brown bear according to the two tested models of absence of habitat selection. Black points: simulations "without movement constraints" model; grey points: simulations "with movement constraints" model. The white point indicates observed data.

unchanged in our rotations, is also partly the result of habitat selection. For example, animals move less in some periods perhaps because they search intensively for food in specific habitat, indicating habitat selection. Keeping the shape of the trajectories unchanged in this test may have been too conservative and underestimated the strength of habitat selection. For the female with cubs, the difference between the simulations computed with random points and random trajectories was more pronounced than for the lone female. This can be explained by the difference in trajectories structure between the two females (see Fig. 1). The female with cubs was constrained to move in a more "patchy" way, probably because small cubs are not capable of large movements in spring, and the female may be avoiding potential infanticide (Bellemain et al., 2006). Thus, she was restricted to small areas that she used in a more intensive and homogeneous manner. It is important to stress that the observed distribution of an animal's positions is the result of several effects: (i) intrinsic constraints (depending on the status and activity rythm of the individual), (ii) extrinsic constraints (environmental or artificial barriers), and (iii) the actual habitat selection. However, most of habitat analyses inside home range ignore intrinsic and extrinsic constraints. A few biologists praise accounting for autocorrelation in their models (Arthur et al., 1996; Fortin et al., 2005; Rhodes et al., 2005), but the nature of the dependence between relocations within the whole trajectory is seldom analysed, as noted by Calenge (2005). Indeed, the so called design IV (Thomas and Taylor, 2006) is increasingly used to compare position of relocations at time t and $t-1$, but this procedure only considers trajectories as a first order Markovian process and deems the successive steps (displacement between two relocations) independent whereas they may be themselves autocorrelated. Indeed, when an animal changes its behaviour during the monitoring period, the mathematical properties of the steps (e.g. their length) may change accordingly (e.g. shorter step length when the animal forages than when it flees from a predator). This non-stationarity in the animal behaviour often results in autocorrelation of the trajectory property (Calenge et al., unpublished).

A possible solution to this problem would be to study the spatial structure of the trajectory to identify patterns of movement before relating these patterns to habitat structure. This is a similar approach to indirect ordination in community ecology (Okland, 1996) which has met a large success in relating the environmental variable to pattern of vegetation composition. Starting with identifying patterns in the data, and then relating them to the environment, is an approach that has been widely used in community ecology because of its strong efficiency. As noted by Morales (2002), *the main challenge of scaling up movement resides in the complexities of individual behaviour rather than in the spatial structure of the landscape.* Such an approach would allow identifying the role of both the environment and the animal behaviour on animal movements.

This knowledge would be essential in most fields of ecology, wildlife management, and conservation. In particular, the recent field of complex adaptive systems would benefit from this statistical approach. Indeed, more and more models in this framework presently tend to integrate movement behaviour to predict population dynamics (Railsback et al., 1999; Railsback, 2001). Such models are of the utmost inter-est to manage a population, as the framework to which they belong is used to predict emerging properties of population dynamic (population growth, survival, reproduction...) using computer programs simulating a biological population composed of interacting individuals with a behaviour defined by the modeller (Clark and Rose, 1997; Van Winkle et al., 1998; Breckling et al., 2005). These individual-based models heavily rely on the definition of the individual behaviour of the animals in relation to the environment. In particular, many of these models attempt to include the moving behaviour of the animals in relation with both the internal state of the animals (e.g. current energy reserves) and the environment (e.g. see Clark and Rose, 1997; Railsback, 2001). As noted by Railsback (2001), *movement rules are critical to realistic simulation of how individuals, and therefore population, respond to changes in habitat and population density.* Considering seriously autocorrelation in studies of GPS data will increase our knowledge into animal moving behaviour, and thereby allow a more efficient modelling of population dynamic.

Acknowledgements

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