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Short communication

Beyond the Utilization Distribution: Identifying home range areas that are intensively exploited or repeatedly visited

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ABSTRACT

The Utilization Distribution (UD) provides a useful global but static (time-integrated) representation of space use patterns of animals that perform home range behavior. To promote a more dynamic approach, we show how areas of particular interest in terms of exploitation intensity (mean residence time per visit) or in terms of path recursions (visit frequency) can easily be identified by combining and extending two procedures that were initially published to compute the residence time on the one hand and the movement-based UD on the other hand. Identifying the areas of a home range that are intensively exploited and/or repeatedly visited opens interesting perspectives in the study of the processes by which home range owners adapt their movement behavior to the dynamics of the resources they feed on.

1. Introduction

A common procedure to assess space use within a home range is to compute the Utilization Distribution (UD) with a kernel method. The usefulness of classic location-based kernel density estimation (LKDE; Silverman, 1986; Worton, 1989), which considers locations as a set of independent points, can however be questioned when recorded locations are to a large extent serially correlated (Kie et al., 2010). A number of improvements or alternative approaches have been recently developed (Getz et al., 2007; Horne et al., 2007; Keating and Cherry, 2009). Movement-based kernel density estimation (MKDE; Benhamou, 2011; Benhamou and Cornélis, 2010) constitutes a significant progress. It makes it possible, within a sound theoretical framework, to compute active UDs by explicitly incorporating movement information and activity status (as provided by sensors or, for species that have to move when being active, through a distance threshold between successive relocations). Habitat selection analyses can then be made separately for activity and resting periods by considering active UDs on the one hand and resting locations on the other hand (e.g. Cornélis et al., 2011).

Home range owners restrict their movement, at least for some time, to a set of areas that is far smaller than expected from their sole locomotion capacities (Börger et al., 2008; Van Moorter et al., 2009) and therefore repeatedly visit each of these areas with various frequencies (Bar-David et al., 2009; Li et al., in press). Some areas, in particular those that are more profitable, tend to be exploited more intensively during a given visit, involving a longer residence time. An initially profitable area may be avoided for a while once depleted if the resources it encompasses renew very slowly, but should tend to be revisited quite often otherwise, or if it is depleted only partially at each visit. It therefore appears to be useful, when investigating space use and habitat selection, to split an active UD in its two basic components, the mean residence time per visit and the number of visits. The purpose of this short paper is to show how this can be done easily by slightly altering and combining existing procedures, so as to compute the Intensity Distribution (ID), corresponding to the spatial distribution of the mean residence time per visit, and the Recursion Distribution (RD), corresponding to the spatial distribution of the number of visits, in addition to the active UD.

2. Materials and methods

2.1. Computing the residence time and the number of visits

The residence time $\Psi(i)$ at any path location $\mathbf{Z}_i = (X_i, Y_i)$ can be computed as the sum of the durations associated to the portions of

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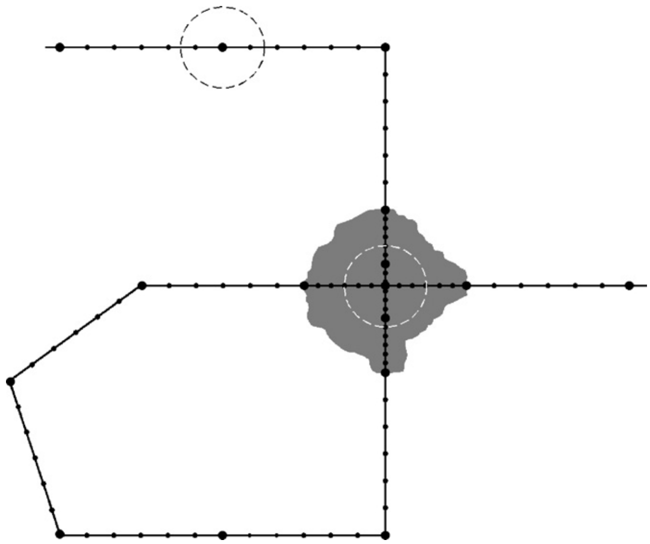

Fig. 1. Idealized movement example. The animal is assumed to move at a constant speed, except when entering the gray area. The animal visits this particular area twice, and adopts a reduced speed to exploit it more intensively, two times lower than its current speed on one occurrence, and three times lower on the other. Big dots correspond to locations recorded every 30 min, and small dots to in-between locations interpolated at 5-min intervals. The virtual circle used to compute the residence time and the number of visits is represented twice: one time centered on a location outside the gray area (drawn in black), and one time centered on the crossing point at the heart of the gray area (drawn in white). In analyses of actual data, it will be centered successively on every (interpolated or recorded) location.

the path occurring within a virtual circle with a constant radius R centered on this location (and so acting as a buffer of proximity), provided the times spent outside the circle before re-entering it are smaller than a given threshold T_C (expressed by the maximum iteration indices $M_f(i)$ and $M_b(i)$):

$$\psi(i) = F_1(i) - B_1(i) + \sum_{f=1}^{M_f(i)} [F_{2f+1}(i) - F_{2f}(i)] + \sum_{b=1}^{M_b(i)} [B_{2b}(i) - B_{2b+1}(i)] \quad (1)$$

where $F_m(i)$ and $B_m(i)$ are the forward and backward, respectively, mth passage times through the circle perimeter, computed by linear interpolation from the two closest path locations. They correspond to the crossing times of the circle perimeter occurring after (forward) and before (backward) the occurrence of the location on which the circle is centered (see Fig. 1 in Barraquand and Benhamou, 2008 for a conceptual diagram). An inside forward time $F_{2f+1} - F_{2f}$ will be taken into account in the residence time computation only if all preceding outside forward times, $F_{2n} - F_{2n-1}$ for any n in $[1,f]$, are less than T_C, and an inside backward time, $B_{2b} - B_{2b+1}$ will be taken into account only if all following outside backward times, $B_{2n-1} - B_{2n}$ for any n in $[1,b]$, are less than T_C. This extension of the first passage duration $F_1(i) - B_1(i)$ clearly improves the assessment of the exploitation intensity of areas where animals perform area-concentrated search through some alteration of the path structure (e.g. search looping; Barraquand and Benhamou, 2008).

It is quite easy to slightly alter the residence time computation procedure to also make it count the number of visits to any given path location. A new forward revisit is counted each time an even forward passage time F_{2f}, with $f \geq 1$, occurs after a delay larger than T_C since the preceding odd passage time F_{2f-1} (i.e. $F_{2f} - F_{2f-1} > T_C$). Similarly, a new backward revisit is counted each time an odd backward passage time B_{2b-1} occurs after a delay larger than T_C since the preceding even passage time B_{2b} (i.e. $B_{2b-1} - B_{2b} > T_C$). Then, the number of visits within the circle centered on path location $\mathbf{Z}_i$ is simply computed as $\zeta(i) = 1 + \phi(i) + \beta(i)$, where $\phi(i)$ and $\beta(i)$ are the number of forward and backward revisits, respectively. New passages into the circle centered on a given path location will therefore be taken into account only in terms of residence time if all preceding (for forward passages) or following (for backward passages) times spent outside the circle are lower than T_C, and only in terms of number of revisits if the immediately preceding (for forward passage) or following (for backward passages) time spent outside the circle is larger than T_C. Beyond the improvement of the assessment of the local exploitation intensity, using a relatively high threshold T_C will also avoid to artefactually increase the number of visits attributed to areas where the animal performs convoluted paths (i.e. areas where the animal is likely to quickly exit and re-enter the virtual circle centered on a given path location without really leaving the whole area exploited).

The residence time and the number of visits are computed all along the path through a pseudo-continuous sliding of the circle along the path from its starting to its ending point. For this purpose, the circle is centered on successive locations set along the path with an inter-location distance low enough to enable the circle to encompass at least the previous and next locations. Initially (Barraquand and Benhamou, 2008), it was proposed to rediscretize the movement either spatially or temporally, depending on the type of movement behavior (in particular whether the animal considered could be active without moving for a long time or tended to move to some extent when being active). Rediscretization is a special linear interpolation procedure that replaces the original recorded locations by new ones that are warranted to be equidistant in space or in time. It is not mandatory (and even not necessary for species tracked with a high constant frequency) when one simply aims at computing the residence time. In the present context, however, to be consistent with the MKDE-based UD computation procedure (see Section 2.2), the movement must undergo a classic interpolation based on the activity time (i.e. the total time spent between any two successive relocations multiplied by the proportion of activity during this period): the original recorded locations are all kept, and additional locations are linearly interpolated between them so that the activity time interval between any two successive locations is almost constant. This mandatory interpolation aims at generating a density of locations that is proportional to the activity time (a prerequisite for computing MKDE-based UDs). It is however applied only to couples of successive relocations that are sufficiently close in time to warrant that the straight line segment linking them constitutes a reliable representation of the movement actually performed (track segments longer in time, e.g. because of missing recorded locations, are ignored).

It is worth noting that the residence time is a measure of space use intensity that is localized both in space and time. Thus, when an animal is within a given area at time t_i and returns within this area at time $t_j > T_C + t_i$, with path locations $\mathbf{Z}_i$ and $\mathbf{Z}_j$ being close in space (at a distance less than the radius R of the virtual circle used to compute the residence time and the number of visits), the value of residence time attributed to location $\mathbf{Z}_j$ may be quite different from the value attributed to location $\mathbf{Z}_i$. In contrast, the UD integrates residence times over the whole period considered, and therefore provides space use estimates that are localized in space but not in time. Finally, the number of visits has a mixed status: as the residence time, it is localized both in space and time (i.e. a number of visit is attributed to every location along the animal path) but it shows a high spatial consistency, and therefore is almost time-independent: when two path locations $\mathbf{Z}_i$ and $\mathbf{Z}_j$ are very close in space but distant in time, they will be attributed similar numbers of visits.