

ANIMAL MOVEMENTS IN HETEROGENEOUS LANDSCAPES: IDENTIFYING PROFITABLE PLACES AND HOMOGENEOUS MOVEMENT BOUTS

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Abstract. Because of the heterogeneity of natural landscapes, animals have to move through various types of areas that are more or less suitable with respect to their current needs. The locations of the profitable places actually used, which may be only a subset of the whole set of suitable areas available, are usually unknown, but can be inferred from movement analysis by assuming that these places correspond to the limited areas where the animals spend more time than elsewhere. Identifying these intensively used areas makes it possible, through subsequent analyses, to address both how they are distributed with respect to key habitat features, and the underlying behavioral mechanisms used to find these areas and capitalize on such habitats. We critically reviewed the few previously published methods to detect changes in movement behavior likely to occur when an animal enters a profitable place. As all of them appeared to be too narrowly tuned to specific situations, we designed a new, easy-to-use method based on the time spent in the vicinity of successive path locations. We used computer simulations to show that our method is both quite general and robust to noisy data.

Key words: *area-concentrated search; area-restricted search; first passage time; movement analysis; residence time; segmentation; signal processing; state-space models.*

INTRODUCTION

Most animals have to move through heterogeneous landscapes, a mosaic of areas that are more or less convenient with respect to their specific needs. For example, they should forage at the most profitable food patches and rest at the most suitable places in terms of safety, temperature, or other critical factors. They usually cannot spend all their time in a single spatially limited and suitable area, both because their needs change in time (profitable foraging places are not necessarily the same as, nor adjacent to, those that are suitable for other activities or resting), and because most places that are initially profitable in terms of resource supply are progressively depleted during their exploitation.

Charnov (1976) and Parker and Stuart (1976) showed how animals can maximize their fitness by optimizing the time they spend in different areas. In these pioneering works, and numerous others that followed, this question was addressed in the somewhat idealized situation where the most profitable places are well-identified discrete patches. In a number of situations, however, profitable areas cannot be identified a priori (Arditi and Dacorogna 1988). The way animals allocate their time to the various areas available to them can be

studied by looking at how animals alternate between intensive (area-concentrated) and extensive (ranging and relocation) search modes, assumed to correspond to intrapatch and interpatch movements, respectively. This is clearly an adaptive behavior (Murdie and Hassel 1973, Knopien and Reddingius 1985, Benhamou 1992, 1994), which has been observed in various species for a long time (e.g., Banks 1957, Smith 1974, Thomas 1974, Nakamuta 1985, Mellgren and Roper 1986, Fielden et al. 1990). Although it is quite hard, in this context, to derive the optimal time allocation, especially when different needs are considered simultaneously, it can be assumed that local environmental profitability is directly related to actual intensity of space use, defined as the time spent per unit area.

Dividing a long, composite movement through heterogeneous landscapes into a series of homogeneous intrapatch and interpatch movement bouts presents a twofold interest. First, it makes it possible to identify the intensively used areas a posteriori and thereby to study their spatial distribution with respect to key habitat features. It also enables studies of behavioral mechanisms by which animals reach these profitable places and locally intensify their space use. When an animal enters a profitable place, it usually adopts a more tortuous path and/or reduces its speed (Benhamou and Bovet 1989). Only a few movement analysis methods that explicitly aim at identifying intensively used areas based on the detection of spatial and/or temporal changes in movement behavior have been published (Fauchald and Tveraa 2003, Morales et al. 2004, Jonsen et al. 2005, 2007, Gutenkunst et al. 2007, Tremblay et al. 2007). As

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all of them appeared to be fully operational only when particular conditions are fulfilled, we designed a new, easy-to-use method, based on the automatic segmentation of time spent in the vicinity of successive path locations. We tested our method using simulated model movements with well-defined characteristics, and showed that it is both applicable to various situations and robust to noisy data.

For the sake of clarity, let us recall some basic principles. All the methods cited below (as well as ours) are based on the assumption that a continuous animal movement in two-dimensional space can be reliably represented as a discrete, ordered set of locations and associated times (x_i, y_i, t_i) , with $0 \leq i \leq n$. In this context, any step \vec{l}_i with $1 \leq i \leq n$ is defined as the movement between two successive locations $(x_{i-1}, y_{i-1}, t_{i-1})$ and (x_i, y_i, t_i) , with length $l_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{0.5}$, orientation (i.e., moving direction) $\theta_i = \arctan[(y_i - y_{i-1})/(x_i - x_{i-1})] + a\pi$ radians, with $a = 0$ for $x_i > x_{i-1}$ and $a = \pm 1$ otherwise, and duration $d_i = t_i - t_{i-1}$, from which other series of variables can be obtained such as speeds $s_i = l_i/d_i$ and turning angles $\alpha_i = \theta_{i+1} - \theta_i$. Movements are often initially recorded at constant time intervals, that is, with a constant step duration d , but it may be useful, for analytical purposes, to rediscritize the paths through a linear interpolation to obtain movement representations (x'_i, y'_i, t'_i) based on a constant step length l instead of a constant step duration d (Bovet and Benhamou 1988, Benhamou 2004, 2006).

CRITICAL REVIEW OF PREVIOUS METHODS

Fauchald and Tveraa's first passage time method

The method developed by Fauchald and Tveraa (2003) is quite easy to use (see e.g., Pinaud and Weimerskirch 2005, 2007, Bailey and Thompson 2006). It focuses on the difference, hereafter referred to as the "first crossing duration,"

$$\Delta_R(i) = F_{1,R}(i) - B_{1,R}(i) \quad (1)$$

between the "forward first passage time" $F_{1,R}(i)$ and the "backward first passage time" $B_{1,R}(i)$ at the perimeter of a virtual circle with a given radius R centered on the i th path location occurring at time t_i (see Redner 2001 for an introduction to first passage times). In other terms, $F_{1,R}(i)$ is the first exit time after the i th location (the time at point 4 on Fig. 1) and $B_{1,R}(i)$ the last entrance time before the i th location (the time at point 3 on Fig. 1). The first crossing duration is therefore equal to the sum of the times required to exit the circle from its center in the forward direction [$F_{1,R}(i) - t_i$] and in the backward direction [$t_i - B_{1,R}(i)$]. Assuming that the profitable patches are circular areas of same diameter D , and that the animal increases space use within a patch only by using its perimeter as a reflecting boundary (the path tortuosity remains otherwise unchanged, and the speed remains strictly constant), the authors showed using computer simulations that the variance of the logarithm

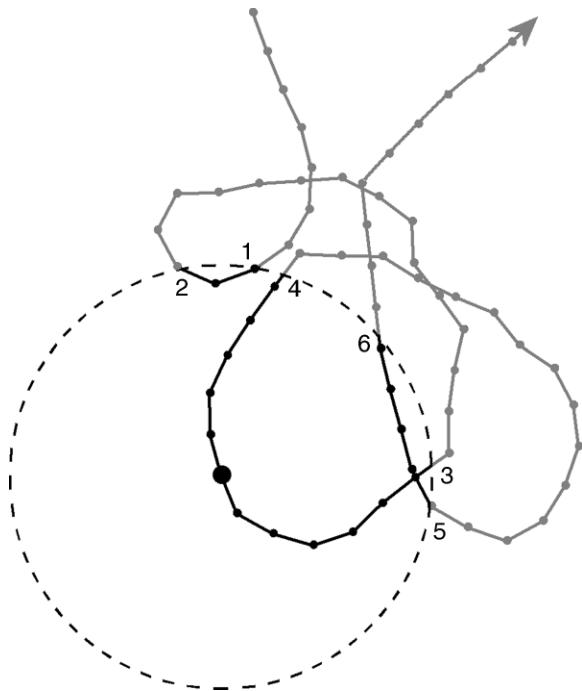


FIG. 1. Computation of the residence time, as the sum of the durations associated with the various portions of the path occurring within a virtual circle (dashed perimeter) with a fixed radius (5 step lengths here) centered on any given location i (large solid circle). In this example, the successive locations considered are equidistant in space (but not in time, as speed is not assumed to be constant). Depending on the movement analyzed, better results may be obtained with locations equidistant in time rather than in space (see *The residence time method: A new signal*, and discussions later in the article). The points at which the path intersects its perimeter are numbered from 1 to 6, with odd numbers corresponding to entrances and even numbers corresponding to exits. The corresponding passage times are computed by linear interpolation (1, backward third passage time; 2, backward second passage time; 3, backward first passage time; 4, forward first passage time; 5, forward second passage time; 6, forward third passage time). The time spent within the circle during the second (3–4) within-circle portion (black path) corresponds to the first crossing duration. Additional times spent within the circle during the first (1–2) and/or third (5–6) within-circle path portions will be taken into account only if the preceding (backward 3–2 and forward 4–5, respectively) outside-circle path portions (gray paths) are not larger than a given threshold.

of the first crossing duration, $\text{Var}[\log(\Delta_R)]$, is maximized by a radius $R^* = D$. The patch occurrences are then determined visually by examining the series of first crossing duration computed with an R^* -radius circle sliding along the path. Four criticisms can be addressed to this method.

1) When applied to a mere correlated random walk (CRW) in a homogenous environment (no patch), $\text{Var}[\log(\Delta_R)]$ increases progressively with R , provided R remains low with respect to the path net displacement. When R become relatively large, the circles set at successive path locations overlap to a large extent, so that even the Δ_R values measured at distant times along

the path remain autocorrelated, leading to an artefactual decrease in $\text{Var}[\log(\Delta_R)]$. This phenomenon hence misleadingly generates a peak for a radius R^* that is not related to any patch diameter. It is easy, however, to avoid this drawback by not considering radius larger than a given threshold (e.g., one-quarter of the net displacement).

2) The authors did not explain why R^* is equal to D , nor evaluate whether this equality holds true in other situations. Actually, R^* is the smallest radius allowing the virtual circle centered on any within-patch location to encompass the whole patch. Using computer simulations, we checked that, when patches are of close but different sizes, R^* is equal to the mean patch diameter. The first crossing duration measured at path locations within a patch with diameter $D > R^*$ then provides an unreliable signal as it alternates large and low values (the latter being similar to that obtained at unsuitable locations) depending on whether the whole patch is or is not included within the R^* -radius circle. We saw that R^* also depends closely on the scale at which some abrupt spatial change occurs. If, for example, the intensive mode rests on an Archimedean spiral covering the whole patch from its center, R^* is still equal to D . In contrast, if it rests on a series of repeated wave motifs ($\cup\cup\cup\cup\cup\cup$), R^* is equal to the size of a single motif (\cup), and if it consists only in slowing down in the profitable patches, R^* corresponds to the smallest radius: in both cases, R^* is much smaller than the mean patch size, and the first crossing duration measured with a R^* -radius circle provides an unreliable signal.

3) In a real, noisy world, the speed is likely to be submitted to random fluctuations in both the intensive and extensive modes. When the intensive mode rests on both patch reflecting boundaries and speed decrease, the variance is still maximized by a radius equal to D , and the speed decrease enhances the mean contrast between the two modes. For animals that are not expected to dramatically slow down when entering a profitable area, however, taking the speed into account can only increase the noise level. A cleaner signal is obtained by considering the “first crossing length” rather than the “first crossing duration.”

4) The last problem, but not the least. No statistical procedure was proposed to analyze the time series: the breakpoints in the signal provided by the first crossing duration obtained with a radius R^* are assumed to be just detected visually, which is a procedure likely to be affected by subjective biases. Consequently, one can guess that highlighting different types of areas will be easy and undisputable only if they are characterized by clearly dissimilar (i.e., highly different inter-areas means and low intra-area variances) first crossing durations or lengths.

The main problems of Fauchald and Tveraa's (2003) method are therefore the involvement of a purely visual and thereby subjective segmentation of the path, the failure of the procedure for selecting the size of the

virtual circle in a number of cases, and in general, the lack of a full statistical framework.

Hidden Markov and state space models

A far less subjective approach consists of modeling a hidden discrete variable (the movement mode) corresponding to a behavioral state related to the movement process. This type of approach seems extremely promising for modeling animal movements in heterogeneous environments (review in Patterson et al. 2008). It has been used by Morales et al. (2004) and Jonsen et al. (2005, 2007) to develop original path segmentation/clustering methods.

Morales et al. (2004) considered animal movements recorded as locations acquired at constant time intervals. The Hidden Markov Model (HMM) they developed consists in a composite CRW whose local mean step length (a proxy for the mean speed) and turn dispersion are indexed by a hidden movement mode. The speed and turn joint probability distributions expected in the various modes are used as templates for a Bayesian estimation, and the sequence of hidden movement modes (with the associated speed and turn parameters) is then revealed with a Monte-Carlo Markov Chain (MCMC) algorithm using the freely available WinBUGS software (Lunn et al. 2000). Using computer simulations, we checked that, when the movement corresponds to a composite CRW and the model speed and turn distributions (Weibull for speeds and wrapped Cauchy for turns) serving as templates are close to those we simulated (gamma for speeds and wrapped normal for turns), the estimated mode for any path location correctly converged toward its respective true mode. It is worth noting, however, that more clear-cut results should be obtained for actual movements by considering the speed and turn distributions obtained after discretization with a constant step length, even if the movements were initially recorded with a constant step duration. Indeed, when entering a favorable area, an animal often tends both to increase its path sinuosity and to slow down, and using a constant step duration (leading to shorter steps in favorable areas), tends to overshadow the increase in turn dispersion, which is positively related to the sinuosity but negatively related to the step length (Benhamou and Bovet 1989).

Jonsen et al.'s (2005, 2007) State Space Model (SSM) is, to a large extent, similar to the HMM model used by Morales et al. (2004), and is also fitted to the data using WinBUGS. A major difference is that the movement process is modeled in terms of differences in latitude and longitude between successive locations instead of step lengths and turning angles. A step is decomposed into a deterministic rotational component (rotation matrix applied to the vector of the previous differences in latitude and longitude) and a stochastic translational component (normal bivariate vector). A scalar parameter modulates the amplitude of the deterministic rotation with respect to the random translation. As in

Morales et al.'s framework, the movement parameters take their values in discrete sets and switches between them according to their preceding state (that is, they follow a Markov chain). The variability in latitude and longitude as well as the sequence of the hidden behavioral states are then estimated via Bayesian methods. However, this approach makes it more difficult to understand the biological significance of the parameters estimated, because they are expressed in an exocentric system of reference in terms of changes in latitude and longitude (or some other coordinates expressed in a fixed earth- or environment-bound frame) instead of in the animal's egocentric system of reference in terms of distances moved and angles turned. Contrary to Morales et al.'s approach, however, Jonsen et al.'s approach makes it possible to estimate the observational noise error. The latter approach should therefore be preferred when observational noise is large and the former when a biological interpretation of the movement parameters is required.

The major drawback of these two methods is that the movement model has to be specified a priori as a (possibly biased) CRW, with a hidden movement mode, either in the egocentric (Morales et al. 2004) or the exocentric (Jonsen et al. 2005, 2007) formulations. In a number of cases, however, modeling the underlying movement process as CRW or biased CRW (BCRW) appears to be very difficult. For example, let us consider that the intensive mode rests only on patch-reflecting boundaries, with the same specifications as those used by Fauchald and Tveraa (2003) in their computer simulations: outside the patches, the animal is assumed to perform a CRW with constant step length and duration (constant speed), whose turning angles are drawn from a wrapped normal distribution with a null mean and a standard deviation of 0.1 radian. Once it enters a patch, the animal is assumed to move in the same way, except that it bounces backward when encountering the patch boundary with a reflection probability of 0.9. The only available information about the presence of the animal within a patch then comes from a sporadic abrupt turn occurring at bouncing locations. We were not able to derive a correct template respecting the simulated step length structure for this case in Morales et al.'s (2004) framework, so that the Bayesian procedure did not converge, leaving the path nonsegmented. Of course, a correct model can still be obtained by discretizing the initial path with a larger step length equal to the mean patch diameter (so that the intrapatch path becomes an antipersistent CRW where the animal tends to reverse its moving direction after each step), but this requires knowing a priori the patch size, which should not vary too much. The same problem also occurs in Jonsen et al.'s (2005, 2007) framework. Furthermore, in most natural cases, it is quite difficult to have a guess about the potential shape of the movement model to be specified to serve as a

template toward which the procedure will be able to converge.

One additional limitation is worth noting. The SSMs and HMMs cited above often involve switching probabilities between behavioral states (the hidden variable follows a first-order Markov process). The switching probabilities can be constant, or with a specified dependency on the habitat type (e.g., see Morales et al. 2004). If one does not know which kind of link between habitat type and movement mode to specify, and hence assumes constant switching probabilities, then one also implicitly assumes a geometric distribution of the number of consecutive steps in a given behavioral mode (Picard 2005), which means that long segments are relatively scarce. If the actual movement process encompasses a number of segments that are larger than would be expected if the rate of transition between behavioral states were constant, then some of them are likely to be split.

SSMs and HMMs are thus certainly the most powerful models for segmenting a long movement through a heterogeneous landscape into homogeneous movement bouts when the possible types of behavioral changes occurring along the path in relation to the environment can be a priori anticipated and modeled in terms of CRW or BCRW. Otherwise, when such knowledge is lacking, and it is often the case, they become inadequate.

Other recent methods

A slightly different approach was proposed by Gutenkunst et al. (2007). They considered another, purely spatial variable, the local path straightness (i.e., the ratio between the beeline distance and the path length traveled) to segment the path, and another convergence procedure, based on an iterative trial-and-error feedback algorithm. The method they developed was, however, similar in its basic principle (the convergence toward expected speed and turn [and heading] joint distributions serving as templates) to that of Morales et al. (2004). Hence it intrinsically suffers from the same problems if the expected movement model is wrong or hard to specify. Nevertheless, the approach of Gutenkunst et al. (2007) is more flexible, as it does not assume switching probabilities. It appears to work fine in the particular case these authors considered. More effective results might be obtained in the general case by relying on a segmentation variable that integrates both spatial and temporal changes, as the intensive use of a profitable place is also often characterized by some slowing down. However, thanks to the WinBUGS software, most users will probably find Morales et al.'s (2004) method more adaptable to various ecological situations and easier to implement.

Tremblay et al. (2007) proposed to segment an animal path based on its local fractal dimension. They assumed that the expected difference between the path portions performed within and outside profitable areas is large

enough to result in a markedly bimodal frequency distribution, making it easy to visually sort and cluster the various path portions considered. To date, most actual animal paths have been better modeled as mixtures of CRW or BCRW, which may look superficially fractal, than as truly scale-free walks, such as fractional Brownian motion or Lévy walks (Turchin 1996, Benhamou 2004, 2007, Morales et al. 2004, Edwards et al. 2007). The apparent fractal dimension of a CRW directly reflects its sinuosity (Nams 2005), and nothing guarantees that the path sinuosity values obtained in the extensive and intensive modes are sufficiently contrasted for an irrefutable visual segmentation. If the behavioral change involves a simple change in path sinuosity, the best method available to identify the profitable places visited is that of Morales et al. (2004), with adequate intensive and extensive turn distributions serving as templates.

THE RESIDENCE TIME METHOD

Based on the above considerations, we sought to specify a new, robust, and effective method involving an automatic path segmentation procedure based on a rigorous statistical framework. It requires finding a relevant signal (i.e., a variable whose sequence over time or space conveys information about local space use), and a statistical procedure to process it.

A new signal

We designed a new signal by computing the “residence time,” which corresponds to the amount of time spent in the vicinity of any location. It can be seen as an extension of the first crossing duration, designed to provide a more integrative measure of space use with a clearer biological meaning, by taking additional forward and backward times spent within the circle into account. The residence time $\Psi_R(i)$ at any given location i is therefore computed by determining the various times at which the path intersects the perimeter of the circle centered on location i , both forward and backward, and then by summing the durations associated with the various portions of the path occurring within the circle (Fig. 1):

$$\Psi_R(i) = \Delta_R(i) + \sum_{v=1}^{V(i)} [F_{2v+1,R}(i) - F_{2v,R}(i)] + \sum_{w=1}^{W(i)} [B_{2w,R}(i) - B_{2w+1,R}(i)] \quad (2)$$

where $\Delta_R(i)$ is the first crossing duration as defined by Eq. 1, $F_{m,R}(i)$ and $B_{m,R}(i)$ are the m th passage times (computed by linear interpolation from the two closest path locations) in the forward and backward directions, respectively, at the perimeter of a circle with radius R centered on the i th path location. The differences $F_{2v+1,R}(i) - F_{2v,R}(i)$ and $B_{2w,R}(i) - B_{2w+1,R}(i)$ for increasing v and w indices so correspond to additional, increasingly distant, forward and backward times spent

within the circle, and $V(i)$ and $W(i)$ are the maximum values allowed for the iteration indices v and w at location i . This constraint is useful to prevent the residence time computation from incorporating irrelevant movement portions encompassed within the circle, as the animal may intersect its own path after having wandered off somewhere else for a long time, especially if it spatially restricts its movements within a home range. The possible additional forward and backward crossing durations are therefore merged with the first crossing duration only when the animal did not travel more than a given distance or time threshold outside the circle before reentering it. Eq. 2 is useful to formally define the residence time as the sum of the first crossing duration and additional forward and backward times spent within the circle. In practice, however, the residence time is computed in a simpler way by adding the increasingly distant forward and backward times spent within the circle until the animal traveled more than a maximum allowed step number outside the circle (i.e., without explicitly computing the first crossing duration and the values of $V(i)$ and $W(i)$; see the Pascal algorithm provided in the Supplement). Taking additional relevant times spent within the circle into account makes the residence time less sensitive than the first crossing duration to the radius R , and more liable to be statistically stationary for a given R value while the animal performed the same movement behavior, especially if the path bounced at some reflecting boundaries. (Note that one gets $\Psi_R(i) = \Delta_R(i)$ when the path is mainly straight.)

A residence time series is therefore obtained by considering the various movement portions encompassed within virtual circles with a constant radius R centered at successive locations along the animal's path. Although not strictly necessary, a constant step length or duration warrants a uniform movement sampling, either in space or in time, respectively. (The algorithm provided in the Supplement includes an optional movement rediscrretization with a constant step length or duration.) A clearer signal should be obtained with a constant step duration if the animal spent long periods of time within very small places (e.g., resting or feeding on highly concentrated prey items), and with a constant step length otherwise. The step length or duration should be short enough to get a detailed and faithful path representation at the smallest possible scale (see Benhamou 2004 for details). The choice of the circle radius should rest on biologically relevant considerations in terms of radius of perception, spatial cognition, and resource density, but such knowledge is often lacking. Ideally, to perform a detailed small-scale analysis, the (mean) step length used should be equal to a few body lengths for a slow-moving animal in a close environment (e.g., a forest deer) or to a few dozen body lengths for a fast-moving animal in an open environment (e.g., a sea bird; see Plate 1), and the circle radius should be equal to a few step lengths. In a number

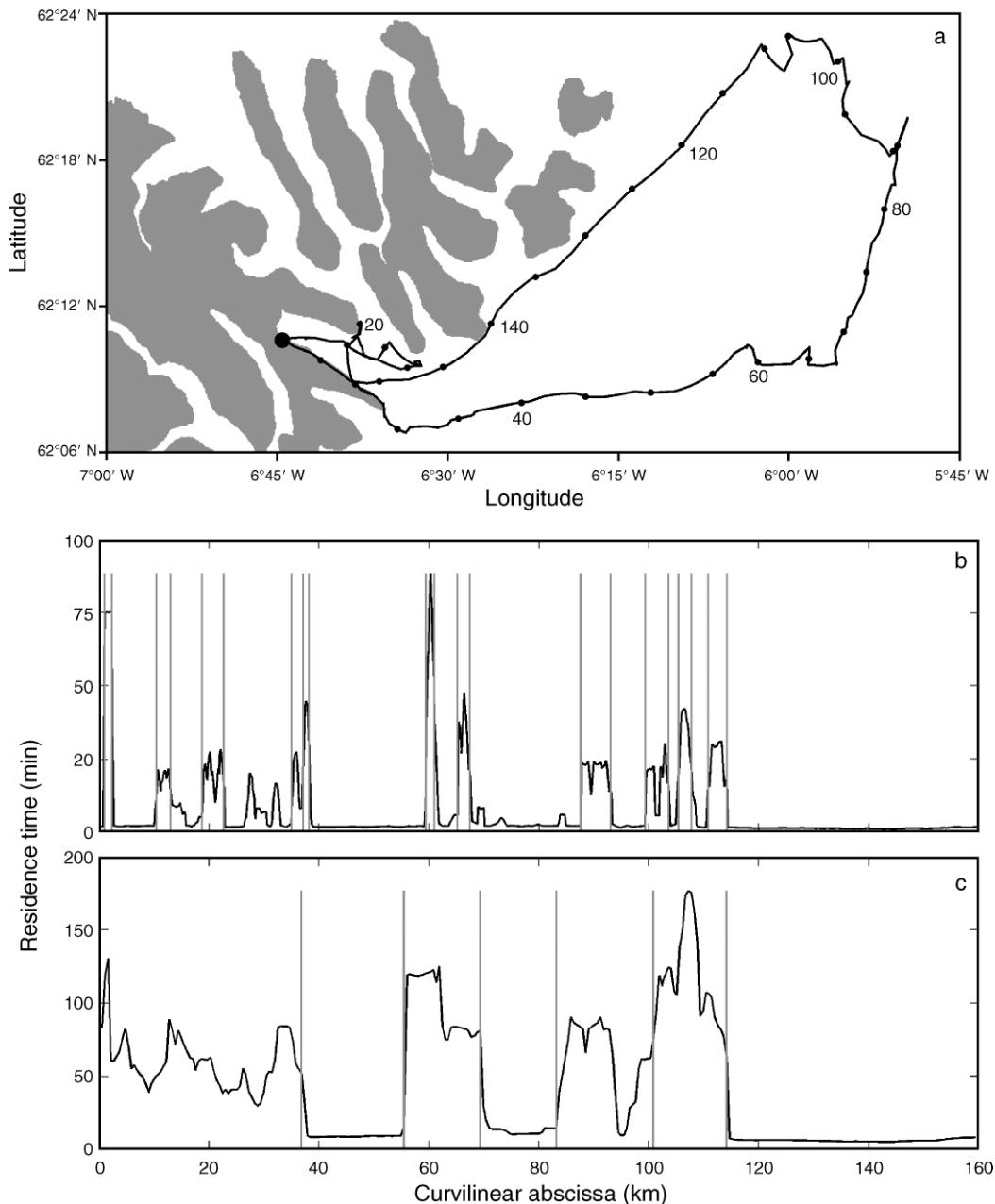


FIG. 2. Illustration of how the residence time method segments the foraging round trip of an Arctic Fulmar. (a) GPS-recorded path, drawn as a black line. The large solid circle indicates the nest location, and smaller circles indicate the bird's location every 5 km; in addition, the running path length (curvilinear abscissa, expressed in kilometers) is indicated every 20 km, for easy correspondence with parts (b) and (c). Gray areas indicate land (Faroe Islands); white areas are the sea. (b, c) Residence time computed at spatially equidistant locations, using a rediscritization step length of 100 m (b), or 500 m (c), with the radius of the virtual circle set to five steps and the maximum threshold distance allowed for leaving the circle before reentering it set to 25 steps. The most likely segmentation solution obtained in each case is indicated by the gray vertical bars.

of cases, however, the animal's raw locations have not been initially recorded with a sufficiently high frequency and accuracy (relatively to the animal size and speed) to obtain a small-scale path representation. As illustrated in Fig. 2, our method can easily be used to analyze larger scale path representations involving longer step lengths, but obviously, it will only highlight the areas intensively

used at the scale at which the movement has been initially recorded and at larger scales. At any scale, performing detailed analyses requires a relatively small radius (i.e., a few step lengths), but more contrasted results are likely to be obtained with a larger radius. Plots of the residence time series for various radii may help to choose the radius leading to the best trade-off

between accuracy and reliability. The analysis should also be performed several times with different radius values to check for consistency.

Signal processing

To segment a path based on the residence time series, we relied on Lavielle's (2005) model selection procedure, which aims at automatically finding the most likely locations of breakpoints in a signal when their number is unknown, and thereby to divide the signal considered into bouts that are homogeneous in terms of mean and/or variance. Indeed, the problem we face when trying to reliably segment a path based on a given series of an observed variable $\mathbf{z} = (z_1, \dots, z_p)$, thought to be a relevant signal, is known in statistics as the multiple change-point problem. Some changes are likely to occur in the signal (beyond the random fluctuations), and one wants to know where the signal properties are actually changing, that is where are the $K^* - 1$ breakpoints ($\tau_1^*, \dots, \tau_{K^*-1}^*$) located when the number of homogenous parts in the signal K^* , i.e., the number of segments, is a priori unknown. Lavielle's (2005) method answers these questions in two steps: (1) by finding the best segmentation $\hat{\tau} = (\hat{\tau}_1, \dots, \hat{\tau}_{K-1})$ for any fixed segment number K through minimizing a global contrast function $J(\tau, \mathbf{z})$ which is a measure of the distance between any proposed segmentation τ and the actual data set \mathbf{z} , and (2) by selecting the most likely segment number K^* through an adaptive procedure. The whole procedure is equivalent to minimize a penalized contrast $H(\tau, \mathbf{z}) = J(\tau, \mathbf{z}) + \beta \text{pen}(\tau)$, where $\text{pen}(\tau)$ is a penalty on the number of model parameters and β a weighting of that penalty. Readers familiar with model selection would probably find this approach similar to those based on Akaike's Information Criterion (AIC) or the Bayesian Information Criterion (BIC) (Burnham and Anderson 2002). Lavielle (2005) showed that using AIC or BIC strongly overestimates the number of breakpoints, thus creating the rationale for the use of another criterion. His method is more heuristic (it involves a tuning parameter) than its maximum likelihood counterparts (Picard 2005), and is also far more flexible, as it allows for autocorrelation in the data set (see Lavielle 1999). It is very easy to use thanks to Matlab programs freely provided by M. Lavielle. We strongly advise the readers interested in the workings of this segmentation method to consult the original paper directly, but we give an introductory summary in the Appendix.

Three parameters have to be specified in the segmentation procedure. The first sets the basis (mean, variance, or both) on which breakpoints have to be tracked. This choice changes the shape of the "local costs" used to compute the global contrast function. The residence time is only assumed to increase in mean within intensively used areas, but variance and mean are often positively related. A plot of the residence time series should help to determine whether there are changes in both the mean and the variance, or only in

the mean. The other two parameters (the minimum segment length and the maximum segment number) are used to limit any possible oversegmenting. The first one should be set to the ratio "diameter of the virtual circle/(mean) step length," which defines the maximal "resolving power" of our method, whereas the second one should be set to 2–4 times the expected segment number (as roughly estimated from the plot) to give the procedure some working room without excessively increasing the risk of oversegmenting the path. Note that the occurrences of a few very high residence times (e.g., due to resting) may result in excluding a number of suitable areas characterized by lower residence times from the "minimum contrast" solution. In such cases, the second or third likely solutions (i.e., with higher values of the global contrast function, optionally displayed by the segmentation procedure) usually provide more realistic path segmentations.

An illustrative example

The working of our method is illustrated on an actual foraging round trip performed by an Arctic Fulmar (*Fulmarus glacialis*) breeding in the Faroe Islands in summer 2007 (Fig. 2a). The movement was recorded by a GPS logger (GiPSy-2; Technosmart, Rome, Italy) programmed to acquire a location every two minutes. Such a high acquisition rate made it possible to analyze the path at a small scale, using a spatial rediscritization step length of 100 m (Fig. 2b). For movements recorded with a lower acquisition rate, such a small-scale analysis may not provide useful results, as the relevant information at this scale may be missing, but a similar analysis can be performed at a larger scale by using, for instance, a spatial rediscritization step length of 500 m (Fig. 2c). In both cases the radius of virtual circle was set to five steps, and the maximum allowed threshold distance flown outside the circle before reentering it was set to 25 steps, and the most likely segmentation solution was computed with the maximum segment number set to 40, the minimal segment size set to the circle diameter (1 and 5 km, respectively) and the tracking mode set to "mean only" (as the variance of the residence time did not appear to change dramatically along the path). There is no means, however, to ascertain to which extent the resultant path segmentation is correct in such an example, because the true underlying behavior is not known. Hence we quantified the segmentation effectiveness using composite random walk simulations with well-defined characteristics.

QUANTIFICATION OF SEGMENTATION EFFECTIVENESS

Behavioral changes considered

The animal was assumed to forage by alternating between extensive interpatch search (ranging and searching for patches) and intensive within-patch search (area-concentrated searching for prey items) modes. The extensive search mode corresponds to a nearly straight and fast movement through unsuitable areas (Benha-

mou 1992, Zollner and Lima 1999). Shifting to the intensive search mode involves spatial and/or temporal changes. The simplest spatial solution consists in increasing the path sinuosity in some way (Benhamou 2004). It is not very effective, however, because of a random drift that leads the animal to progressively search intensively outside the food patch. The number of items encountered is dramatically improved when the animal can use the patch edge as a reflecting boundary, or perform search loops around the remembered location of the last detected item (Benhamou 1994). At the temporal level, using a lower speed enables the animal to increase the probability of detecting encountered items (Gendron and Staddon 1983, Knoppin and Reddingius 1985), but this also results in a lower encounter rate, and thus does not greatly improve the detection rate (Benhamou 1992). Nevertheless, the speed should be lower in profitable food patches for many other reasons, as the animal needs some extra time to capture, handle, and ingest prey items. A lower speed is also likely to occur in areas that are suitable for other purposes (e.g., resting). In our simulations, we then considered three typical possibilities when the animal enters a patch. In the purely spatial case (PS), the animal was assumed to increase its sinuosity and to bounce at the patch boundary. In the purely temporal case (PT), it was just assumed to slow down. In the spatiotemporal (ST) case, it was assumed to do both.

Simulated walks

Any simulated walk was made of steps with a constant length l serving as unit distance. It was composed of 11 segments, six in the extensive mode, totaling a path length of $1000 l$, and five in the intensive mode, corresponding to the exploitation of five circular patches set at regular intervals, totaling a path length of at least $500 l$. In both the PS and ST cases, the five patches had diameters of 10, 15, 20, 25, and $30 l$, and the animal had to move through each of them five times before leaving (see the following paragraph), whereas in the PT case, the patch diameters were adjusted so as to obtain within-patch path lengths of 50, 75, 100, 125, and $150 l$.

The paths were simulated mainly as composite, behavioral-mode-dependent CRW. In both modes, turns were drawn from a wrapped normal distribution with a null mean and standard deviation σ , but in PS and ST cases, additional turns occurred in the intensive mode when the animal bounced at the patch boundary. Speeds were drawn from a log-normal distribution whose coefficient of variation (CV) took values 0.2, 0.4, 0.6, 0.8, and 1, in order to simulate five different noise levels. In the extensive mode (interpatch movement) of any of the three cases considered, turns had a standard deviation $\sigma_{\text{ext}} = 3^\circ$ and the mean speed was set to $1 l/t$ (t being an arbitrary unit time). In both PS and ST cases, the turn standard deviation in the intensive mode (within patch movement) was set to $\sigma_{\text{int}} = 30^\circ$, and the patch edge also acted as a reflecting boundary until

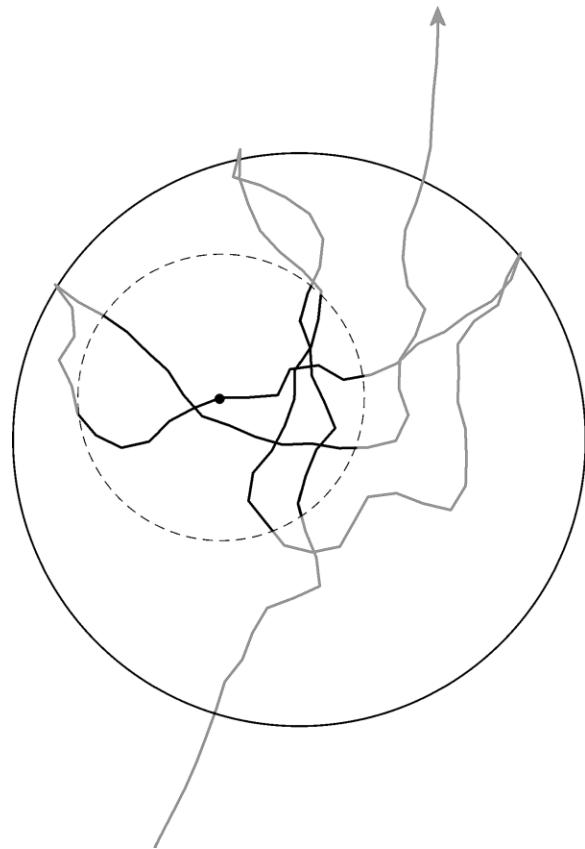


FIG. 3. Simulated path in spatial (or spatiotemporal) case. When moving within a patch (solid black perimeter), the animal adopts a higher sinuosity and uses the patch edges as reflecting boundaries. In this example, the patch diameter is equal to 20 step lengths, and the path length traveled within the patch is equal to 121 steps. The virtual circle (dashed black perimeter) with a radius of 5 step lengths used to compute the residence time is drawn for a single location (large black dot). The portions of the path taken into account in the residence time associated with this target location are black lines; other path portions are gray lines.

the animal had moved a path length larger than five times the patch diameter (Fig. 3). In PS, the mean speed remained equal to $1 l/t$ in both modes, whereas in ST, the animal also decreased its mean speed to $0.33 l/t$ in the intensive mode. In the PT case, the animal only slowed down to $0.33 l/t$ when entering any of the five patches ($\sigma_{\text{ext}} = \sigma_{\text{int}} = 3^\circ$). Ten walks were simulated in each of the 15 conditions (five noise levels \times three cases). An additional set of 10 single-mode $1500 l$ CRW (without area-concentrated searching) was used as a control: turns were drawn from a zero-centered wrapped normal distribution with a standard deviation $\sigma = 3^\circ$, and speeds were drawn from a lognormal distribution of mean $1 l/t$ with $\text{CV} = 0.6$.

Path segmentation

Residence time series were computed using a circle of radius of $5 l$ and a threshold path length for reentering

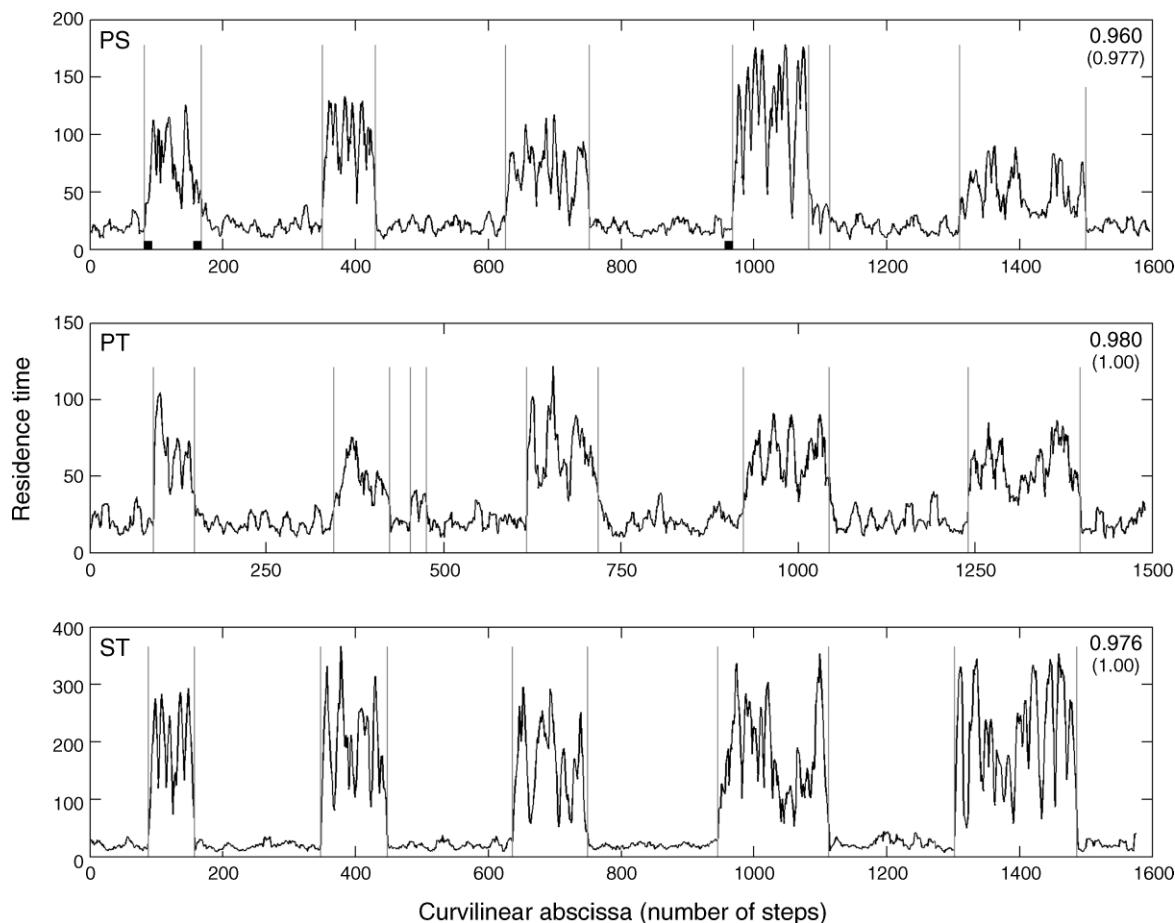


FIG. 4. Segmentation of paths simulated in the purely spatial (PS), purely temporal (PT), and spatiotemporal (ST) cases with the highest noise ($CV = 1$). The most likely segmentation solution is indicated by the gray vertical bars. Global percentages of path locations ascribed to the right mode are indicated at the top right corner of each panel. (The refined values, ignoring accuracy errors, are shown in brackets.) In the PS graph, there were three detection errors (involving a total of 37 locations), which are indicated by solid squares on the x -axis. There was none in either the PT or SP graphs. Note that in PT, where the residence time is simply equal to the first crossing duration, the signal contrast is relatively weak between intensively and extensively used areas; two additional breakpoints have been detected at locations where the animal remained in the extensive mode, but the mean residence time of the resulting pseudo-patch was low enough to allow the path locations involved to be correctly ascribed to the extensive mode. In PS and ST, where the intensive mode involves an increase in the path tortuosity, the residence time usually incorporates additional path portions, and the signal is more contrasted.

the circle set to 100 l . They were segmented using Lavielle's (2005) procedure with the minimum segment length set to 10 (circle diameter/step length), the maximum segment number set to 30, and the tracking mode set to "both mean and variance." Only the most likely solution was retained (Fig. 4). A clustering was then needed to attribute a movement status (intensive or extensive search mode) to each of the segments obtained. There exist automated clustering methods that can be applied easily to the simple two-mode case considered here (e.g., "single linkage" hierarchical clustering of the mean residence times obtained for each segment), but they are not error free. We think that such methods are likely to work poorly on actual movement data, for which we advocate the use of a clustering based on detailed path analysis (see *Discussion*).

For this reason we choose here to evaluate the segmentation effectiveness alone (rather than any given combination of segmentation/clustering, which will reflect in part the clustering errors) using the best clustering possible, as follows. The various segments were sorted into two groups (intensive and extensive) depending on whether their respective mean residence times are higher or lower than a given threshold. This threshold was systematically varied so as to consider the whole range of possible classifications, and the "segmentation-only" effectiveness was then computed as the maximum value obtained for the percentage of locations correctly ascribed to their true status. It is therefore worth keeping in mind that the final effectiveness obtained when analyzing actual movements will be somewhat lower, because clustering errors are then

TABLE 1. Effectiveness of the residence time method.

Noise	Purely spatial (%)	Purely temporal (%)	Spatiotemporal (%)
0.2	97.0 ± 0.4	97.6 ± 0.1	96.9 ± 0.3
	99.7 ± 0.4 (4)	100 ± 0 (0)	100 ± 0 (0)
0.4	96.8 ± 1.0	98.2 ± 0.4	97.1 ± 0.5
	99.1 ± 1.1 (5)	100 ± 0 (0)	99.9 ± 0.5 (2)
0.6	96.9 ± 1.1	98.3 ± 0.4	97.3 ± 0.3
	99.1 ± 1.3 (5)	100 ± 0 (0)	100 ± 0 (0)
0.8	96.5 ± 0.9	98.1 ± 0.6	97.3 ± 0.2
	99.1 ± 0.9 (7)	99.8 ± 0.5 (1)	100 ± 0 (0)
1.0	96.2 ± 1.5	97.8 ± 0.7	97.1 ± 0.9
	98.4 ± 1.5 (7)	99.6 ± 0.7 (3)	99.6 ± 1.0 (2)

Notes: In each case, the mean ± standard deviation of the percentage of locations ascribed to the correct mode (intensive or extensive) is given in the first row, and the value obtained when the accuracy errors are neglected is given in the second row. Values in parentheses are the number of simulated walks (out of 10) for which there was at least one detection error, i.e., a portion of 10 or more successive locations ascribed to the wrong mode. The noise level corresponds to the coefficient of variation of the intramode speed.

likely to occur in addition to segmentation errors. To refine the results obtained here, we distinguished two types of segmentation errors: detection errors, which occurred when long (≥ 10) series of locations were ascribed to the wrong mode, and accuracy errors, involving shorter error series, which occurred when a segment was globally ascribed to the right mode, but with a slight shift in the starting and/or ending locations.

RESULTS

In any of the three cases considered, the mean effectiveness, whatever the behavioral changes involved and the noise level considered, was beyond 96% including accuracy errors, and beyond 98.4% once accuracy errors had been filtered out (Table 1). Even with the strongest noise level ($CV = 1$), the mean effectiveness among all cases (PS, PT, ST) was of 99.2%, which means that, on average, <1% of the points were wrongly classified. The residence time series obtained for the 10 control paths (single-mode CRW) by construction provided a signal similar to the basal signal obtained for the extensive mode of the PS, PT, or ST cases. The segmentation of these control paths resulted in a single segment for half of them. For the other half where at least two segments were identified, the mean residence times were close to each other (0.75 to 1.25 time the overall mean, with intrasegment coefficients of variation of about 0.2), so that the various segments obtained could be merged into a single one when analyzed into details. Our method thus appears both quite effective and robust to the presence of noise in the movement process.

DISCUSSION

Identifying the profitable places actually used by animals living in heterogeneous landscapes from the changes in their movement behaviors needs both a

relevant signal and an effective procedure to process it. We have showed that applying Lavielle's (2005) segmentation procedure to the residence time measured at (spatially or temporally) equidistant path locations can constitute a reliable method to identify the intensively and extensively used areas. As animals are here only assumed to spend more time in profitable places, irrespective of the underlying changes in movement behavior, the residence time series should indeed provide a relevant and robust signal. The procedure we chose to segment this signal has been previously used to segment electroencephalograms (EEG) and financial time series (Lavielle 1999, 2005). Although, to our knowledge, it has not yet been used in ecology, it appeared to us the best statistical method currently available to segment the residence time series. The field of statistical segmentation, however, is evolving quite fast (Picard 2005), so that new, still more powerful segmentation procedures will certainly become available in the future.

Based on a purely visual segmentation of a sometimes irrelevant signal, the first crossing duration, Fauchald and Tveraa's (2003) method is too subjective to provide a reliable path segmentation except in trivial cases. On the other hand, methods based on state-space models (Jonsen et al. 2005, 2007), hidden Markov models (Morales et al. 2004), as well as other related methods (Gutenkunst et al. 2007), rest on effective but very constraining statistical frameworks, which makes them difficult to apply when the various movement modes an animal can use are a priori unknown, or hard to specify in an ad hoc way. These methods are effective parametric segmentation/clustering procedures, by which the estimated status of path locations converge to their respective true status, provided a number of specific assumptions about the area-concentrated searching mechanisms actually used are fulfilled. By relying on the (almost) assumption-free residence time, our method can be seen as an effective nonparametric segmentation procedure, by which the estimated status of the path locations converges to their respective residence time-based status, irrespective of the behavioral mechanisms actually used.

Our approach is therefore clearly advantageous when precise behavioral knowledge is lacking, but limited to the segmentation process. The characterization of the various, presumably homogenous, movement bouts obtained (i.e., the statistical problem of clustering) requires subsequent detailed analysis to determine the behavioral mechanisms involved in each of them. For movement bouts showing large mean residence times, assumed to occur within profitable places, special attention should be paid to the turn and speed distributions, as well as the possible occurrences of reflecting boundaries or search loops. For those showing low mean residence times, the major question to be addressed is whether these bouts correspond to a random search for profitable places with a high



PLATE 1. African Fish Eagle (*Haliaeetus vocifer*) preying on a catfish. In such a case the residence time method will highlight the sit-and-wait places used to scan the environment and those used to ingest prey items, rather than the prey catching locations. Photo credit: S. Benhamou.

directional persistence or to oriented paths (Benhamou 2006), thereby indicating an ability to perceive the profitable places at a distance or to memorize their locations. These types of detailed analyses have already been conducted on movements performed in environments where the profitable places can be determined a priori (Benhamou 1990, Girard et al. 2004). The automatic path segmentation based on the residence time therefore offers the possibility of conducting similar movement analyses when the precise locations of such profitable places are a priori unknown, as well as

studying their spatial distribution with respect to key landscape features. It is worth noting that strong random fluctuations within the signal might be falsely interpreted as breakpoints by the automatic segmentation procedure, leading to an oversegmentation of the path. Hence, two consecutive segments will be obviously merged if the subsequent detailed analyses show that they present similar movement characteristics.

One should also keep in mind that the profitable places highlighted with our method as the intensively used areas are likely to be only a subset of the whole

suitable areas available, and depend on the animals' current needs. For example, a tired animal coming upon a large area with ideal characteristics for resting will use only a very small fraction of it, whereas even a hungry animal may run in a straight line through a profitable food patch when attempting to escape a predator. Because we only assumed that the time spent in the vicinity of a given location is positively related to the local space use, our method appeared much more robust than the previous ones, which are more or less tuned to situations involving specific types of behavioral mechanisms. Although our simulation results were obtained in a foraging context, they are quite general, because they are transferable to all other contexts where the residence time increases with the local space use. In some special situations, however, e.g., a predator running after a zigzagging prey target, intensive space use may result in larger values in both path tortuosity and speed, making the residence time uninformative. The residence path length may then provide an alternative relevant signal.

Natural landscape patchiness may arise at two spatial scales only, when the resources items are aggregated in patches that are themselves distributed at random or regularly in space, or at multiple spatial scales, with some hierarchical structures such as clusters of patches (Wiens 1989, Beecham and Farnsworth 1998, Farnsworth and Beecham 1999, Fauchald 1999). Pinaud (2008) recently proposed to study the way an animal interacts with its environment at different scales using Fauchald and Tveraa's (2003) method, but as we showed, this method is not reliable. Some other authors suggested that such multiscaled interactions could be empirically studied by looking at how some space use estimates measured along the path depends on the scale through some arbitrary subsampling (Nams 2005, Wilson et al. 2007). This approach seems very useful to highlight which scales are the most relevant depending on the animal's locations, but it cannot reveal the behavioral mechanisms involved at these various scales. Although our method can also be applied at various arbitrary scales (Fig. 2b, c), it further provides the basis for studying such behavioral mechanisms because it can act as a nonarbitrary, behavior-based subsampling procedure. Indeed, once the profitable places at the lowest reachable scale have been identified (using the segmentation method and subsequent analyses), it becomes easy to obtain a biologically relevant movement representation at the immediately higher scale by simply considering the sequence of the profitable places visited (i.e., by taking interpatch movements as straight-line moves and neglecting intrapatch movements [Benhamou 1990, Turchin 1991]). In this way, it becomes possible to determine to which extent the characteristics of an animal's movements depend on the spatial scale considered and how the various scales are interrelated.

At the smallest scale, once the patches have been identified, intrapatch movement analysis will reveal the mechanisms used to gather the resource items (such as

slowing down, using a highly sinuous random search, bouncing at the patch perimeter, performing search loops around the last item detected, and so on), and interpatch movement analysis will reveal a ballistic process (target-directed behavior) if the patches can be detected at a distance or if their locations have been memorized, or a diffusive process if the animal encountered the patches by moving at random. At the largest scale, the movement will be reduced to the series of patches visited at the immediately lower scale, and hence will appear ballistic, diffusive, or highly subdiffusive, depending on whether the animal is migrating in a fixed direction, is erratic, or restricts its activity within a home range, respectively. What happens at intermediate scales, if any, is likely to depend largely on the environment structure. Our segmentation procedure can be repeatedly applied at increasingly higher scales, simply by considering the profitable places identified at a given scale as the elementary locations of an upper scale movement. This bottom-up approach hence opens very interesting perspectives in the study of the ways animals redistribute themselves at various spatial scales.

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APPENDIX

Lavielle's (2005) model selection procedure (*Ecological Archives* E089-191-A1).

SUPPLEMENT

Pascal program for computing the residence time (*Ecological Archives* E089-191-S1).