

ON THE USE OF TELEMETRY IN HABITAT SELECTION STUDIES

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ABSTRACT

Understanding the relationships between organisms and their habitat is a central question in ecology. The study of habitat selection often refers to the *static* description of the pattern resulting from the selection process. However the very nature of this habitat selection process is *dynamic*, as it relies on individual movements, which are affected by both internal components (i.e. related to the animal itself, such as its behavior; foraging, resting, etc.) and external components (i.e. related to the composition of the environment). Coupling habitat selection and movement analyses should thus provide new insights into the proximal mechanisms and evolutionary causes of animals' space use.

To achieve this, the introduction of GPS technology in the early 1990s showed great promise, as it facilitates tracking of animals with high fix frequency over long time periods. From a statistical point of view, this led to an increased temporal *autocorrelation* in the positions of successive locations. Whereas classic approaches of habitat selection often relied on the assumption of statistical independence between relocations, the

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development of newer methods has made possible the use of autocorrelation for more dynamic approaches. As several statistical tools are now available for researchers, autocorrelation can be incorporated successfully into the analysis, instead of being removed or even ignored. We emphasize the need to integrate individual behavioral mechanisms in habitat selection studies.

The use of GPS technology in wildlife management issues is, however, often motivated by its technological advantage to produce large amounts of data, rather than biological questions. We warn users of GPS devices about the statistical and conceptual changes induced by this technology used for studying habitat selection. We encourage a solid biological reflection about the ecological characteristics of studied species and spatial and temporal scales considered, before deciding on which sampling protocol and which telemetry technology to use in accordance with the biological question of interest.

INTRODUCTION

Understanding the relationships between organisms and their habitat is a central question in ecology. The habitat defines the available range of resources and living conditions for a species (Hall et al., 1997). Thus, the habitat potentially has an important impact on vital rates, such as survival and reproduction, which are directly related to population dynamics and evolution (Caswell, 2000). It is therefore crucial to study the mechanisms of habitat selection, i.e. the process by which animals actually choose specific habitat components within their environment. This process is recognized to be highly scale dependent; habitat selection at a given scale can be seen as the result of individual behavioral processes at finer scales (like movements), while at the same time it will be constrained by larger scale processes (like the geographical range of a species). In order to clarify the study of habitat selection, Johnson (1980) distinguished four levels or orders of selection, from the species' geographical range to the selection of food items, through individual home range establishment and patch selection within the home range. The higher levels, like the species' range, are governed mainly by population processes, whereas at lower levels individual choices are more important. To understand animal space use, ecologists have to investigate these multiple scales, often simultaneously (Johnson, 2002).

It has been recognized that both spatial and temporal scales are positively correlated (Holling, 1992). For example, distributional ranges of populations are necessarily defined at large spatial scales and the study of factors affecting large scale distribution of a given population requires knowledge of long-term population dynamics at large temporal scales. On the contrary, individual movement processes at fine spatial scales (e.g. within a home range) are considerably faster than population processes, and therefore need to be studied at much finer temporal resolutions.

Although “habitat selection” has been defined as a process, the study of habitat selection often refers to the *static* description of the pattern resulting from this process, i.e. “space occupancy”. For example, many individual-level studies dealt with the characteristics of the environment within home ranges (e.g. Mc Loughlin 2002 and 2004; Mitchell and Powell 2007). However, the very nature of the habitat selection process is *dynamic*, as it relies on individual movements, which are affected by internal and external components (such as individual state or vegetation types). Hence, habitat selection and movement processes are intimately related, because movement partly is driven by habitat selection, whereas habitat

selection is a consequence of movements. Coupling habitat selection and movement analyses should thus provide new insights into the proximal mechanisms and evolutionary causes of animals' space use.

To study the mechanistic aspects of individual habitat selection, it is therefore advisable to obtain and use detailed information on movements of individuals, based on a high frequency of relocations. The transition from a static to a more dynamic approach to habitat selection therefore can be achieved by increasing serial (or temporal) *autocorrelation* in the positions of successive locations (Swihart and Slade, 1985). The level of serial autocorrelation in datasets describes the importance of temporal structure in individual movements. In a dynamic approach of habitat selection, the spatio-temporal structure of relocations arising from more or less complex movements should be considered and studied (Frair et al. 2005), whereas in the static approach all relocations are considered to be temporally independent (Otis and White 1999). The choice to analyze habitat selection from a static or a dynamic point of view should be motivated by the biological questions of interest. Commonly, when studying habitat selection in a static way, autocorrelation is considered a nuisance that should be overcome (Morrison et al. 1998). The use of autocorrelation in habitat selection studies reflects a shift from the more classic static approach to a dynamic approach of habitat selection.

To study mechanisms of individual habitat selection, one possibility is to record movements by directly observing animals in their environment (e.g. Shine et al. 2004; Klaassen et al. 2006). However, this method of tracking animals requires many hours spent in the field, and cannot be done for elusive species, which are difficult to observe in their natural environment. Since its appearance in the early 1960s (Figure 1), VHF technology facilitated tracking of wildlife by providing researchers with a new tool to remotely detect individuals and then directly measure their location (consisting of a set of coordinates in the form of latitude x , longitude y , and time t) by homing or triangulation. This technology has been used successfully on elusive species. However, using this technology to estimate individual small-scale movements still requires a great deal of field effort (in terms of field work) to allow the collection of frequent relocations, and therefore often results in short-duration tracking (e.g. 1 location every 10 minutes for a couple of days, Nicholls and Racey 2006).

The introduction of GPS technology in the early 1990s, and its generalization at the turn of the century (Figure 1), showed great promise for studying processes of habitat selection. Thousands of relocations can now be stored on-board or even directly transmitted to the user, without relying on much human intervention after an animal is equipped with the tracking device. GPS technology, therefore, facilitates fine-scale tracking (relocations can be delivered up to every second, Fritz et al. 2003) of animals over longer time periods (e.g. 1 location every 3 hours for a whole year, Johnson et al. 2002). Although the accuracy of individual relocations obtained by GPS does not equal direct observations and measurements in the field, the accuracy obtained with recent GPS remains acceptable for most research purposes (around 20 meters). Hence, GPS technology facilitates the study of animal movement both at small and large spatial scales during long periods.

The purpose of this chapter is twofold. The first part is dedicated to the role of autocorrelation in habitat selection studies from the past till now. We demonstrate that, whereas temporal autocorrelation was first considered as a problem when studying habitat selection in a static way, the progressive combination of habitat selection and movement concepts have led to an increased use and interest in autocorrelation.

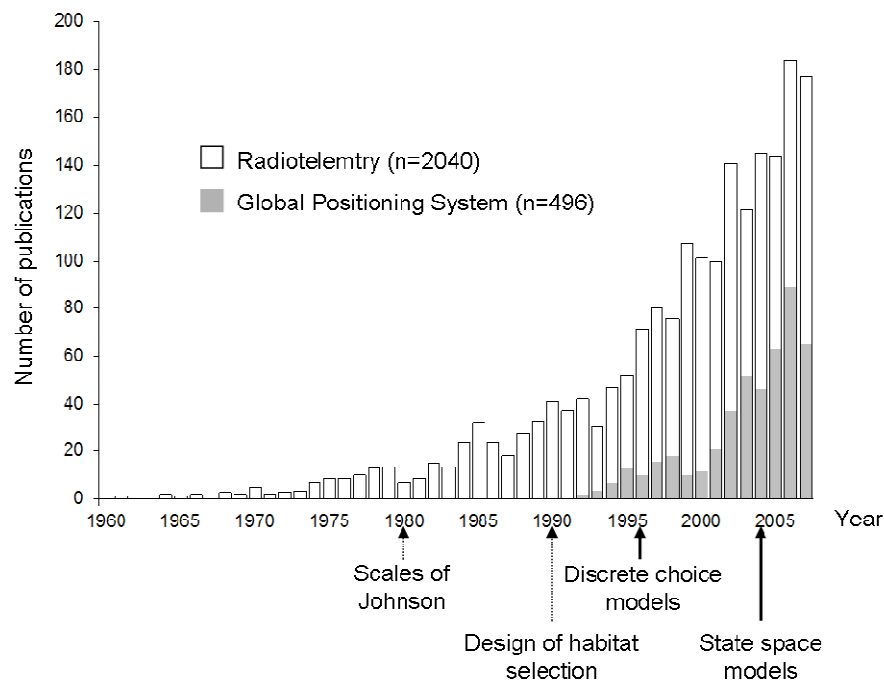


Figure 1. Trend in the number of publication including « radio telemetry » and « global positioning system ». The review was performed using the ISI Web of Knowledge with all data bases and was restricted to zoology, biodiversity and conservation, evolutionary biology and behavioral sciences. Dashed arrows represent the appearance of important concepts in habitat selection studies and black arrows the appearance of analytical methods.

As several statistical tools are now available for researchers, autocorrelation can be incorporated successfully in the analysis, instead of being removed or even ignored. We emphasize the need to integrate individual behavioral mechanisms into habitat selection studies. In the second part, we stress the importance of thorough reflections about biological questions before heading out into the field to deploy GPS collars. We provide some guidelines for the choice of monitoring technology in the context of habitat selection, regarding considerations of biological questions, spatio-temporal scales, and research costs.

1. TOWARDS THE USE OF AUTOCORRELATION IN INDIVIDUAL HABITAT SELECTION STUDIES

Johnson (1980) defined the selection of a habitat component as “*the process in which an animal actually chooses that component*”. Thus, tests of nonrandom habitat selection by individual animals usually compare used habitat components (the relocations of individuals, i.e. their actual habitat choice) with a null model describing the habitat components that could have been used alternatively by the individuals under the hypothesis of absence of habitat selection (i.e. random habitat use; Pendleton 1998, Millspaugh and Marzluff 2001, Boyce et

al. 2002). The latter components are called “available” components (Manly 2002). Rejection of this null model for the observed pattern allows the conclusion that a nonrandom process generated the observed data. At the scale of individual habitat selection, it is therefore crucial to define precisely what is available to animals, because the null model will depend directly on it.

Availability can be defined differently depending on whether the animals are identified or not (see Thomas and Taylor 1990, 2006, for an overview of the different study designs). In the case of identified animals (typically the case with telemetry), availability can be related to the selection order of concern: for second-order selection availability is defined at a population level, whereas for third-order selection availability is defined at an individual level (Aebischer et al. 1993). Several other factors may further affect availability. For example, movement capacity of animals is a factor that can restrict availability (Martin et al. 2008). The behavioral state of an animal is also a potential factor that can limit access to a particular area (e.g. resting animals). These factors therefore should be taken into account when determining which habitat components are available for use.

Classic statistical methods used to test habitat selection (e.g. logistic regression, log-linear regression, χ^2) assume independence between locations of a given individual (Johnson 1980, Thomas and Taylor 1990, Swihart and Slade 1997, Aebischer et al 1993, Alldredge and Ratti 1992, Pendleton et al 1998). In other words, individual relocations must not be spatially or temporally correlated. Dependency between relocations produces more similar values than expected by chance; as such, positive autocorrelation should result in underestimating the true variance. This induces an increased probability of type I error by inflating the number of degrees of freedom (Legendre 1993, Lennon 1999, Diniz-Filho et al. 2003, Martin et al. 2008), i.e. the null hypothesis (random habitat use) is rejected too frequently. The independence between relocations is often ensured by adopting a sufficiently large time lag between successive relocations, which circumvents the problem of autocorrelation. However, the growing use of GPS technology has led to a decrease in time intervals, and resulted in an increased serial autocorrelation.

1.1. From the Past. The Null Model as Random Locations: Autocorrelation as a Problem

Few statistical tools have been developed for individual data analyses; most of them being adapted from methods developed for second-order selection by unidentified individuals (Calenge 2005). For example, Manly et al. (2002) recommended estimating a Resource Selection Function (RSF) for each animal and then combining the results to infer conclusions at the population level. Means and variances for each individual are therefore estimated without considering autocorrelation between relocations and then averaged across animals to estimate population level selection parameters (Thomas and Taylor 2006). As a matter of fact, several authors considered autocorrelation not to be a concern if the statistical unit is the animal and not the animal's relocations (Alldredge and Ratti 1992, Aebischer 1993, Otis and White 1999). Indeed, there are several ways to deal with pseudo-replication when pooling a collection of relocations from several animals in analyses. However, temporal autocorrelation between individual relocations still remains a problem. When using relocations as sampling units, autocorrelation in the data makes variances and hypothesis tests no longer valid.

Therefore, tools that have been developed to test habitat selection at the population level still assume independence between relocations, i.e. a comparison of independent use points and independent available points (that is, randomly sampled in the study area; Figure 4a).

This problem is critically important in third-order selection, where the null model commonly is built using points randomly sampled within what is considered to be available. This will result, when important autocorrelation exists in the animal's relocations, in the comparison of used locations containing this autocorrelation structure with random available locations lacking such structure. Therefore, comparing autocorrelated data with uncorrelated data is not valid (Martin et al. 2008). An empirical demonstration of the effects of not considering autocorrelation in habitat selection studies has been conducted by Martin et al. (2008) on brown bears (*Ursus arctos*). They compared two extreme approaches to test third-order selection by individuals with autocorrelated data. Both approaches relied on the comparison of two datasets; an observed dataset of habitat used by individuals (through individual trajectories) and a simulated dataset (with the same number of relocations as the observed dataset) under the hypothesis of random habitat use. For each dataset, they estimated marginality (an index of the eccentricity of the used environmental conditions relative to the average available environmental conditions) and tolerance (an index of the range of used environmental condition compared to the range of available conditions), two measures of the strength of habitat selection (Doledec et al. 2000). In the first approach, simulated datasets did not take into account movement constraints affecting individuals, i.e. random relocations where points are randomly and independently sampled in the home range (corresponding to the classic approach). In the second approach, simulated datasets accounted for the observed shape of individual trajectories, i.e. simulations were carried out by randomly rotating the observed trajectories within the home range. The results obtained from the two approaches differed dramatically (Figure 2). The second approach (with unchanged trajectory shape) led to the conclusion that bears showed no selection of the variables considered in the analysis (i.e. the marginality of the observed dataset was not different from marginalities estimated from simulated datasets). On the contrary, the classic approach concluded that there was strong habitat selection (i.e. marginality of the observed dataset was significantly different from marginalities estimated using random locations from the home range) (see Figure 2). However, as noted by the authors, both approaches have their limitations, because neither of them took into account the nature of the autocorrelation between relocations. Indeed, the first one did not take any movement constraints into account and the second one kept the shape of the trajectory unchanged; in this later case both movement constraints and some actual habitat selection were included in the null model, which results in a too conservative testing of habitat selection. Therefore, this study highlights the risk of not accounting for autocorrelation in animal relocations by comparing them with an inappropriate null model.

As autocorrelation affects our ability to perform standard statistical procedures (Legendre 1993), it has often been advised to avoid autocorrelation in individual relocations (Morrison et al. 1998). Swihart and Slade (1985) developed a framework for analyzing independence between successive relocations in order to determine the time interval necessary to achieve statistical independence. They proposed using Schoener's (1981) ratio statistic (t^2/r^2 ; where t is the average distance between successive observations and r the average distance to the center of activity) to estimate the Time To Independence (TTI), i.e. the smallest time lag necessary to consider successive relocations as independent.

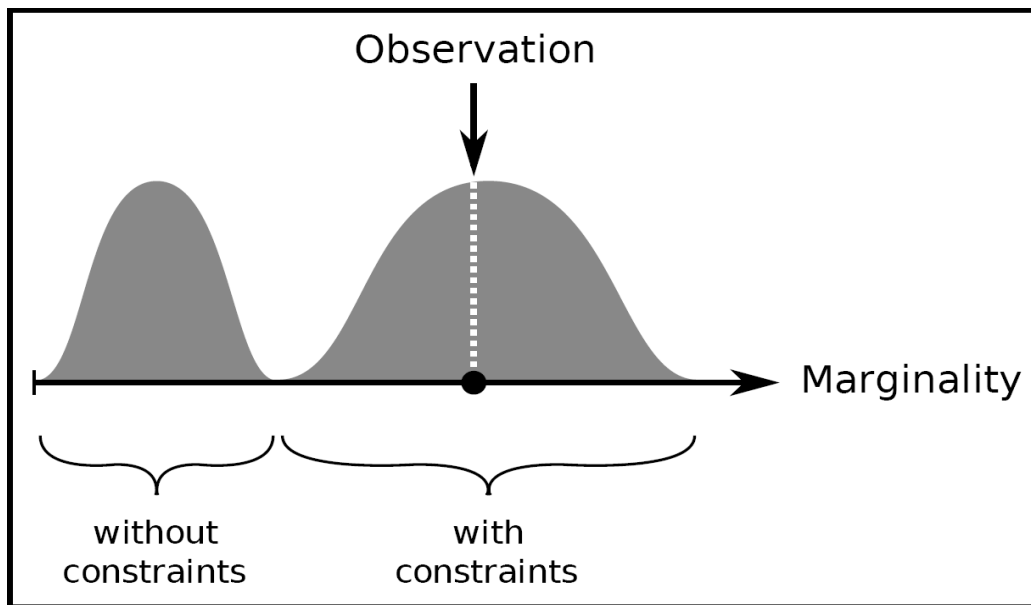


Figure 2. Martin et al. (2008) tested the marginality (deviation from the average conditions in the area) in habitat selection of female brown bears, following two tests. Both relied on the comparison of the observed dataset with datasets simulated under the hypothesis of random habitat use. The first 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 within the home range). In the first case, the observation is out of the range of the simulations and would be considered significant, whereas it is not the case while taking into account constraints (after Martin et al. 2008).

Often, the TTI between consecutive fixes is considered as the time lag required by an animal to cross its entire home range (Swihart and Slade 1985, White and Garrot 1990). The problem of autocorrelation can then be effectively circumvented by sub-sampling data (Boyce et al. 2002) or adopting a sampling regime that uses the TTI as a criterion for independence between relocations. Unfortunately, subsampling data (which is not a problem in itself, because it only removes redundancy) inherently brings with it the loss of data which are, as every field biologist knows, expensive to collect. Moreover, several authors have shown that attempting to obtain independent data is not always possible and can lead to a loss of biological meaning (Rooney et al. 1998, De Solla et al. 1999).

Serial autocorrelation is linked intimately with the definition of availability for individuals. Hence, independence between individual relocations assumes that animals are free to move between two relocations across the area that the researcher considered available, meaning that this whole area (often the home range) is available at each step. But even if the time lag between two relocations is long enough for the animal to cross this area, behavioral constraints (e.g. need for rest, need for foraging, movement constraints) result in the fact that animals are not free to move everywhere every time in this area. An extreme example illustrates this; an animal never wakes up at the other side of its home range! Therefore, even if we statistically reach the TTI, we seldom reach the biological independence between relocations with telemetry data. Moreover, when there is no stable home range, there is no TTI, or the TTI might become very large, in which case subsampling will not provide a

solution to the problem. There is thus a need to create a statistical framework that allows taking into account spatio-temporal structures of individual relocations, i.e. explicitly incorporating autocorrelation into models (Legendre 1993). Today, with the increased use of intensive sampling protocols, we can no longer consider fixes as independent relocations, but instead should consider them as trajectories. Analyses of animal movements are therefore needed in order to proceed with habitat selection.

1.2. The Present. The Null Model is a Random Walk: Accounting for Serial Autocorrelation

1.2.1. Analyses of Animal Movement

An animal's movement is a continuous path in space and time, but a discrete representation of the path facilitates its analysis (Figure 3a; Turchin 1998). Often, relocations are recorded with a fixed time interval and the straight-line moves between consecutive fixes are referred to as steps. The sequence of steps then provides the basic units for further analysis of the path (Turchin 1998). Several descriptors then can be used to describe the step series; most frequently used are step lengths and turning angles (see Figure 3b) and their distributions can be used to characterize animal movement paths. Accordingly, movement types can be identified based on these distributions. For example, intensive search movements can be characterized by short steps and low directionality of the turning angles, whereas exploratory movement steps will be long and have a high directionality in their turning angles.

The statistical framework for animal movement path analyses is based on the comparison of empirical data with a theoretical null model. Several theoretical movement models have been developed that could be used as reference. Each of these models has different statistical properties, and often different assumptions about the independence (i.e. absence of serial autocorrelation) of specific movement descriptors (like step length or relative turning angles). The observed movement characteristics are then compared with the theoretical ones and departure from these models allows inference of biological conclusions about animal behavior (Franke et al. 2004, see below). The mere random walk (RW) is the simplest null model of movement which can be used to model animal movement through a homogeneous environment (Turchin 1998; Figure 4b). It relies on the independence of all descriptors, and thus it assumes the absence of serial correlation between successive steps. Therefore a random walk does not take into account the natural tendency of animals to go forward and is therefore not very accurate to represent most of animal movement, especially at short time intervals (Turchin, 1998; Bovet and Benhamou, 1988). Today, the most widely used theoretical model is the correlated random walk (CRW), which differs from the RW in that absolute angles are generally dependent, whereas the relative or turning angles are assumed to be independent (Turchin 1998; Bovet and Benhamou, 1988). The distribution of turning angles is centered on 0, resulting in a forward persistence in the direction of movements. The direction of the previous step thus influences the direction of the following step.

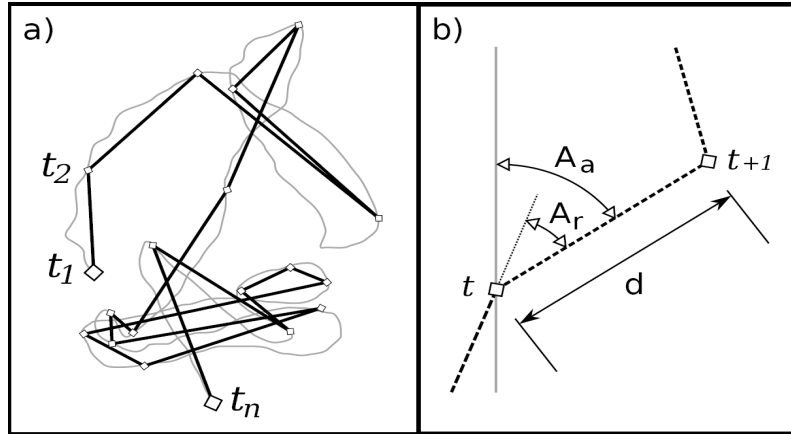


Figure 3: a) Representation of a movement path. In gray: actual path; in black: discrete representation of the path. A movement path is defined by a set of successive relocations, characterized by their position (generally latitude and longitude). Each movement between two successive relocations (i.e. between time t and $t+1$) describes steps. b) Examples of movement path descriptors: d is the distance between 2 relocations; A_r is the turning angle (or relative angle), i.e. the angle between the direction of the previous step (small dashed line) and the actual one; A_a is the absolute angle, i.e. the angle between a given direction (gray line) and the direction of the actual step.

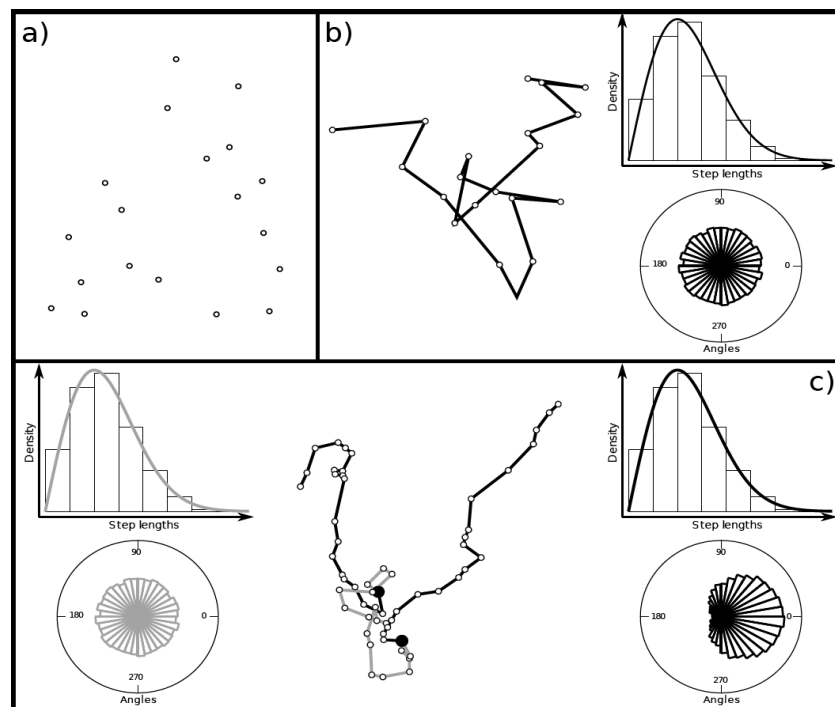


Figure 4: a) The null model as a set of locations randomly sampled in the study area; b) The null model as a random walk, where the whole trajectory can be characterized by step length distribution (top right) and turning angle distribution (lower right); c) The null model as a mixture of two random walks. In gray, a mere random walk, characterized by a uniform distribution of turning angles and normally distributed step lengths; in black a correlated random walk characterized by a distribution of turning angles centered around 0 (forward persistence) and normally distributed step length.

1.2.2. Discrete-Choice Models

Some authors have started to take serial autocorrelation into account by defining habitat availability separately for each relocation in the so-called “discrete-choice models” framework (Arthur et al. 1996, Hjernmann 2000, Fortin et al. 2005, Rhodes et al. 2005). The test for nonrandom habitat selection is derived from a comparison of random locations from this fix-specific availability with the actual chosen locations. In this case, the null model consists of random locations with serial autocorrelation, similar to the class of random walk models. Different authors have used different methods to determine availability, corresponding to different types of random walks. The simplest approach involves determining a circle around a fix of available locations (e.g. the availability radius of Arthur 1996); in this case there is no directional persistence. Alternatively, the observed distributions of step lengths and turning angles have been used to define availability. Even more complex relationships are possible with a dependence of availability on the time interval between fixes or habitat characteristics (Hjernmann 2000).

It is therefore assumed that for a given time lag between two relocations, the animal has access only to areas close to the current position, and not to its complete home range (Arthur et al. 1996). In the same perspective, Cooper and Millsaugh (1999) adopted a statistical technique derived from the field of economics that allows researchers to define availability separately for each animal observation. At each relocation, a unique set of habitat or resources is available, called the “choice set”. Fortin et al. (2005) also developed a simple statistical approach that incorporates movement into a logistic regression framework. This method, called Step Selection Function, considers steps (displacement between two relocations) as sampling units, each of them being contrasted with n random steps, which are defined using the observed distributions of step lengths and turning angles.

This approach partially resolves the statistical and biological issues of serial autocorrelation of relocation data. Indeed, this procedure only considers first-order autocorrelation, i.e. dependence between relocations at time t and $t-1$ only, and deems the successive steps as independent (Martin et al. 2008). However, the nature of the dependence between all the relocations making up the whole trajectory is seldom analyzed, as noted by Calenge (2005). Martin et al. (2008) stressed that positions of individuals are the results of three effects: (i) intrinsic constraints (e.g. movement capacity, activity patterns, internal state), (ii) extrinsic constraints (e.g. environmental or artificial barrier) and (iii) habitat selection behavior (the animal is in a particular habitat because it is “suitable” for it at this moment). Therefore, testing differences between used and available points suppose knowledge of the processes that generate data without any habitat selection, i.e. null model under the hypothesis of no habitat selection, by taking into account the internal constraints of animals that partly shape the trajectory. However, habitat selection analyses rarely take into account intrinsic and extrinsic constraints (Martin et al. 2008; see Matthiopoulos (2003) for an example accounting for movement and extrinsic constraints). In general, researchers aggregate data from different behavioral states and, therefore, their conclusions on habitat selection result from the joint selection of both activity and habitat components (Cooper and Millsaugh 2001). As habitat selection and animal behavior are closely related, there is need for a statistical approach that includes spatio-temporal aspects of individual behavior (Thomas and Taylor 2006, Martin et al. 2008).

1.3. Into the Future. The Null Model is a Mixture of Random Walks: Autocorrelation as a Paradigm

1.3.1. Nonstationarity, an Interesting Property of Many Animal Trajectories

As movements and activities are closely related, movement processes tend to be different according to the animal's behavioral state. For instance, during foraging activity an animal may have shorter and more sinuous movements than during transitions between patches of resources, where it should have directed and faster movements. As an illustration, consider a bee foraging on a patch of flowers. Movements between flowers will be short and sinuous compared with movement between patches of flowers or between the patch and the hive. Franke et al. (2004) used differences in movement characteristics to differentiate behavioral states of woodland caribou; they distinguished bedding, feeding and displacements. Indeed, for given spatial and temporal scales, we can consider most animal trajectories as a succession of different types of movement corresponding to specific activities, each of them being characterized by its own statistical properties (Figure 4c). However, trajectories can remain unchanged for different activities defined at very fine temporal scales (animals can switch quickly between foraging and vigilance while keeping the same type of movement). But at longer temporal scales, major activities, such as foraging, exploring, or resting, often correspond to specific movement types.

A statistical process is said to be nonstationary if the statistical properties of the process generating the trajectory change over time. Therefore, a trajectory composed of different movement types may be considered to have been generated by a nonstationary process. This implies that the definition of availability should be different according to the state of the individual. Indeed, an animal that is foraging or resting does not have the same available habitat as when it is searching for mates or patrolling its territory. Therefore, this nonstationarity is of major interest, because it provides information on animal behavior and activities. This nonstationarity of the process is often the cause of the autocorrelation in the data.

1.3.2. Building Movement Models as Mixtures of Random Walks

Each movement type trajectory potentially can be represented by a different theoretical model based on its properties. The trajectory can then be modeled as a succession of these movement models (Figure 4c). It is therefore important to partition the whole trajectory into different pieces of stationary paths, with stable mathematical properties. Typically, each of these stationary paths corresponds to a certain type of behavior. To date, several methods have been developed and used for this partitioning of trajectories, for instance First Passage Time (Fauchald and Tveraa 2003), fractal dimension (Nams and Bourgeois 2004), and State Space Modeling (Patterson et al., 2007). First Passage Time, for instance, has been used as a method to detect Area-Restricted Search (ARS) behaviors, which can occur when an animal encounters a food-rich resource patch. More recently, state-space models based on hidden Markov models have become more popular for extraction of behavioral states from movement paths (reviewed by Patterson et al. 2007). For example, Morales et al. (2004) employed state-space models to highlight a biphasic movement for elk (*Cervus elaphus*); the

“encamped” movement with small movements and sharp turns and the “exploratory” movements with longer directed movements. They modeled elk movement by fitting a mixture of random walk models with different properties, each model corresponding to a different behavioral state. However, these approaches often assume a constant probability of animal behavior changes (“switching probability”), or at least assume prior knowledge of factors that could potentially affect this switching probability (e.g. constraints on hourly activity patterns or environmental features, Morales et al. 2004). Such methods therefore require prior exploratory analyses of factors potentially influencing the shape structure of the trajectory.

1.3.3. Some Recommendations

In order to test third-order habitat selection with highly autocorrelated data, we stress that an in-depth analysis of the characteristics of individual trajectories is an important step towards a more accurate analysis of habitat selection process. Autocorrelation between relocations should not be removed or avoided, but rather integrated into a statistical framework. Discrete-choice models are a first step toward this integration, but only consider the first degree of autocorrelation to create the null model. Therefore, they do not take into account the behavioral state of individuals, which potentially may affect habitat selection behavior. We emphasize the need to analyze the rules of animal movement using partitioning methods based on the division of the whole trajectory into homogeneous movement bouts. Each of these movement bouts can then be characterized by a probability distribution for each descriptor (e.g. step length, turning angles). Then, for each relocation belonging to a particular behavioral state, availability can be estimated more precisely using the corresponding movement characteristics for this state. These state-movement analyses are required to build more realistic null models of random habitat selection that take into account behavioral constraints.

2. GPS TECHNOLOGY: A DOUBLE-EDGED SWORD

The appearance of new technologies has resulted in important advances in many scientific fields, as it offers new opportunities to answer more questions. Since the early 1990s, GPS technology has facilitated the measure of fine-scale movements of elusive animals in their natural environments over long time periods. Especially, it aids in our understanding of the link between fine-scale behavioral movement mechanisms and the actual distributions of animals. However, scientists, wildlife managers, and conservationists should be careful before adopting this technology. Even though GPS technology is appealing, the choice of the monitoring tool should be the consequence of a well-defined biological question. Such careful planning could aid the avoidance of mismatches between the question of interest and the type of data collected using a particular tool. Compared to older technologies (especially VHF) the use of GPS technology offers many advantages, but also induces different constraints and is not necessarily the adequate tool for every question about animal movements or distributions. Above all, the choice of the appropriate tool to record an

animal's locations should be directly dependent on the sampling protocol defined itself by the question of interest. Irrespective of the biological question or sampling protocol, it is an accepted fact that the number of equipped individuals should be as large as possible in order to increase the generality of the findings. Two other parameters can then vary according to the question of interest: the time lag between relocations and the study period. In the following, we will discuss the relationships between biological question, sampling protocols, and choice of the adequate tool to record animal locations.

2.1. Individual Variability

The ecological characteristics of the focus species and especially the ratio of inter/intra-individual variability in habitat selection can help determine the best sampling protocol and therefore the right tool to track animals in their environment. Girard et al. (2006) showed in their study that the number of animals is more important to assess habitat selection than is the number of fixes per animal. They obtained accurate habitat selection by moose with fix frequencies of only 1-7 per week, whereas often more than 15 individuals were needed to generalize the findings over the population. This suggests that, for generalist species with high inter-individual variability, it is important to obtain data from many individuals to assess habitat selection. On the contrary, if there is a strong intra-individual variability, the number of relocations obtained for each individual can become as important as the number of tracked individuals. Thus, knowledge about the biology of the species will influence the choice of sampling protocol (number of samples per individual versus number of sampled individuals) and, by consequence, the monitoring technology.

2.2. A Matter of Scale

The fix frequency of a telemetry protocol and the study period are generally a direct consequence of the scale of the study: questions regarding small-scale movements require high fix frequency (e.g. 1 point every second for a fractal analysis of albatrosses' movements, Fritz et al. 2003). In the beginning of this chapter we discussed the interest to combine fine-scale movement analyses with habitat selection studies. In this context, increased fix frequency may facilitate a more profound investigation of animal behavior. Moreover, the study duration may be long enough to explore the link between fine-scale behaviors and habitat selection at longer time scales.

However, many questions in ecology do not rely directly on fine-scale behaviors of animals. Large-scale distributional questions can be answered with a lower fix frequency (e.g. 1 point every 3 weeks for an analysis of home range composition and habitat use, McLoughlin et al. 2005). Important in the context of conservation and population dynamics in general is the linkage between habitat and animal performance (McLoughlin et al. 2005), for example to identify critical habitats for population viability in conservation biology (e.g. Akçakaya 1995). Mere occurrence has been shown to be misleading in some situations. For instance, an attractive sink is a habitat that is selected despite the lower performance experienced by the animals occupying it (Delibes et al. 2001). It can, therefore, be argued that to assess the existence of such attractive sinks, the measurement of performance is critical.

Performance of animals, e.g. lifetime reproductive success, however is defined over quite long time scales and often is related to large-scale distribution patterns (e.g. habitat use, Conradt et al. 1999, home range composition, McLoughling et al. 2007). These measures of space occupancy do not require fine-scale measures of animals' movements. Instead, a high number of individuals is often needed to highlight relationships between their performance and habitat. In this context it might be more interesting to invest less in fix frequency and more in number of tracked individuals.

2.3. Main Costs and Benefits of GPS Technologies

Tools and sampling protocols are intimately related, they often involve trade-offs between costs and perfect match. Prior to the selection of a telemetry technology, researchers should think about the associated costs and benefits (in terms of correspondence with the defined protocol) of the use of different tools within the biological context of the question. In theory, any study using VHF tracking by triangulation could be done with GPS tracking instead. That is, GPS collars potentially can deliver the exact same data (regarding frequency and time-lag) as VHF collars, whereas the reverse is not necessarily true over a long period. That being said, a study using telemetry will cover three main budget compartments; capture, equipment, and operation costs. We will consider only the case of nonlimiting captures, as it potentially involves limiting equipment and operating costs directly related to the monitoring technology to be chosen.

The cost of equipment to monitor one animal is considerably higher with GPS technology than with VHF technology; GPS-tracking devices are approximately 10 times more expensive than VHF devices. However, with GPS devices the collection of data is automated, whereas VHF devices require human intervention to be effective; relocations are usually collected by triangulation of the signal, which implies a relatively high time and financial investment in the field. This results in limited operation costs of GPS technology (even with the use of a GSM device to download the data) as compared to VHF technology, especially for high fix frequencies. At a fixed cost, GPS technology, therefore, leads to an increase in sampling intensity compared to VHF technology. However, when the budget of the study is limited, this is often at the cost of lower numbers of individuals monitored (Figure 5). It is thus important to take into account these considerations of costs before deciding upon the adequate tool to choose for the sampling protocol.

2.4. Some Recommendations

When a large number of relocations per animal must be collected, GPS technology can provide adequate data, thanks to the automation of the process. This technology is particularly useful when fine-scale movements of animals need to be recorded, especially over long periods of time. This tool is, therefore, most appropriate to study dynamic aspects of habitat selection, as reported in this chapter. However, when the number of individuals is critical (as for generalist species, see above), and no intensive tracking is required, other tools can be more appropriate (e.g. VHF). For example, when ecologists must link habitat selection and animal performance on long time scales, it is better to invest in more individuals, tracking

duration, and field personnel to obtain the essential animal performance measures (source of mortality, breeding, litter size, etc.). The GPS technology does not seem to be the best tool for this task and VHF tools combined with direct observations can provide sufficient locations per animals to estimate their habitat selection at a large spatio-temporal scale. In this case, the savings made on equipment can be used to increase the number of tracked individuals. In general, at constant costs, what is gained in sampling intensity with GPS technology, on one hand is lost in generality on the other hand.

It should be noted, however, that the increased fix frequency obtained by using GPS-tracking might prove useful in determining animal performance using their movement patterns. GPS-tracking can be used to assess foraging success in particular cases. For instance, it is now commonly used to determine kill sites by large predators (e.g. cougar (*Felis concolor*), Anderson and Lindzey 2003; wolf (*Canis lupus*), Sand et al. 2005). These applications require previous calibration and validation of the models on the field. These examples are likely only the top of the proverbial iceberg of potential applications; we can expect more applications with our increasing knowledge of how movement patterns change with specific factors, like the presence of offspring etc.

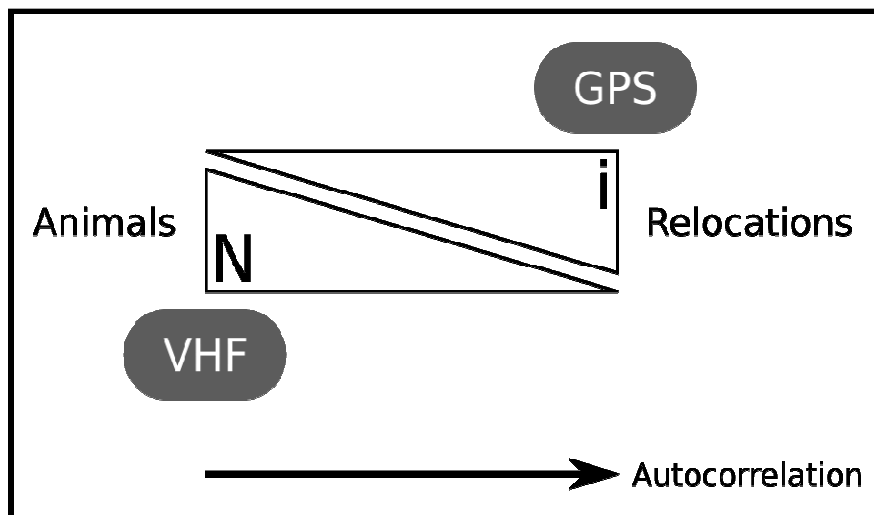


Figure 5. The sampling strategy, at a fixed cost, is the result of a trade-off between the number of individuals marked (N) and the number of relocations per individual (i). Typically, VHF monitoring allows a large number of individuals with fewer relocations per individual (thus no autocorrelation), whereas GPS monitoring allows fewer individuals with more relocations (thus autocorrelation).

CONCLUSION

Despite some budget limitations, GPS technology offers interesting avenues for our understanding of the habitat selection process. The shorter time intervals between relocations allow for the study of more rapidly changing decisions of habitat selection at small spatio-temporal scales. The increased temporal autocorrelation also allows the detailed investigation of different behavioral states with different movement characteristics. Whereas *static* approaches of habitat selection often rely on the assumption of statistical independence of

relocations, the development of newer methods, driven by the collection of relocations with a shorter time lag, now allow the use of autocorrelation for more *dynamic* approaches. We expect such dynamic habitat selection studies to become even more common in the near future, as ecologists become more familiar with the use of methods from time-series analysis like state-space models (Patterson et al. 2008). Coupling habitat selection and movement analyses should provide new perspective to understand how individuals react to environmental heterogeneity during their lifetime.

The use of GPS technology in wildlife management or conservation issues, however, often is motivated by technological advantage rather than biological questions. The appealing nature of GPS data (through higher precision and frequency, as well as automation of the data collection) often results in sampling strategies targeting large amounts of data. This often leads afterwards to data-dredging that can cause mismatches between the scale of the monitoring and the scale of the biological processes of interest. We warn every user of GPS devices about the statistical and conceptual changes induced by this technology used for studying habitat selection (Figure 5). In answer to the potential increase in autocorrelation due to higher fix frequency following technological developments in telemetry, we call for a paradigmatic shift in the study of animal habitat selection from static patterns towards dynamic processes. Especially with critical management or conservation issues, we stress that every ecologist should take care to start from the biological question at hand in making his choice of the most appropriate monitoring technology.

ACKNOWLEDGEMENTS

Financial support has been provided by the ANR (project “Mobilité” ANR-05-BDIV-008). We thank Jean-Michel Gaillard (Laboratoire de Biométrie et Biologie Evolutive; Université Lyon1, France) and our referee Eloy Revilla (Estación Biológica de Doñana, Sevilla, Spain) for their useful comments on the manuscript. We also are grateful to the working group “Trajectory” (Laboratoire de Biométrie et Biologie Evolutive; Université Lyon1, France) for earlier discussions on the topic.

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