ORIGINAL ARTICLE

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The exploratory analysis of autocorrelation in animal-movement studies

Abstract Studies of animal movements have been pop-ularized for many large and shy species by the increasing use of radio telemetry methods (VHF and GPS tech-nologies). Data are collected with high sampling fre-quency, and consist of successive observations of the position of an individual animal. The statistical analysis of such data poses several problems due to the lack of independence of successive observations. However, the statistical description of the temporal autocorrelation between successive steps is rarely performed by ecolo-gists studying the patterns of animals movements. The aim of this paper is to warn ecologists against the con-sequences of failing to consider this aspect. We discuss the various issues related to analyzing autocorrelated data, and show how the exploratory analysis of auto-correlation can both reveal important biological insights and help to improve the accuracy of movement models. We suggest some tools that can be used to measure, test, and adjust for temporal autocorrelation. A short eco-logical illustration is presented.

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Introduction

Radio telemetry "has become increasingly popular as a convenient means of studying movements of wildlife" (Dunn and Gipson 1977) and it can be used to collect data that consist of successive observations of the locations of an individual animal. The recent develop-ment of GPS technology makes it possible to collect relocation data automatically, at short, regular inter-vals. However, as the time interval decreases, the dependence between successive observations usually increases, so that the problem of autocorrelation must be taken into considered in the analysis. Autocorrela-tion can be defined as a property of random variables, which means that values from samples taken near to each other tend to be either more similar (positive autocorrelation) or less similar (negative autocorrela-tion) than would be expected from a random arrange-ment. This nearness can be defined in space (spatial autocorrelation), or in time (temporal autocorrelation). The main difference is that an observation is only influenced by past values in temporal autocorrelation whereas spatial dependence extends in all directions. Autocorrelation is often seen as an obstacle, since it interferes with standard statistical hypothesis testing (Legendre 1993), and many approaches have been developed to eliminate it by restricting data prior to analysis. However, autocorrelation is often an intrinsic property of biological data, so that eliminating it could reduce the relevance of ecological studies. In the context of animal movement, which is by definition a non-independent phenomenon, De Solla et al. (1999) sum-marized the situation clearly: "Animals typically move in a non-random fashion, and thus ecologists are fre-quently faced with strongly autocorrelated data sets, particularly when frequent observations are collected using radiotelemetry".

Solow ([1990](#)) distinguished two approaches in the literature on animal movements: one focusing on relocations, and the other on the movements between relocations. The question of autocorrelation must be (and indeed has been) considered in different ways in these two approaches. Any temporal autocorrelation between the coordinates of successive relocations must be taken into account when the analysis is based on relocations. For instance, in the context of home range estimation, this problem has been discussed in a number of papers (e.g., Dunn and Gipson [1977](#); Swihart and Slade [1985a](#), [b](#); De Solla et al. [1999](#)), and so we will not consider it any further here. On the other hand, the analysis of movements between relocations raises the question of the temporal autocorrelation between successive steps (i.e., the displacement between two successive relocations). The development of models of realistic animal movement is a very active field of research at present (Patterson et al. [2008](#); Schick et al. [2008](#)). The aim of these studies is to understand why, how, and where animals move, and to see how this could affect the spatial dynamics at higher levels of organization (population, community, etc). Recent methodological developments have improved the ability of models to handle the biological complexity of animal movements (Nathan et al. [2008](#)), and to account for multiple behavior modes (e.g., searching, resting, etc), characteristics of landscape (e.g., patchiness), or environmental variations (e.g., spatial distribution of resources). The various internal (e.g., behavioral) or external (e.g., environmental) factors influencing organisms could induce temporal autocorrelation in movement data. For instance, autocorrelation in steps could be due to the animal's switching between different movement strategies. Hence, autocorrelation is usually considered as an emergent property in a modeling framework and its exploratory analysis is rarely performed by authors.

The interest of the empirical study of autocorrelation has been affirmed in the recent special issue of PNAS on movement ecology by Wittemyer et al. ([2008](#)). They stated that "the role of autocorrelation, at different temporal scales, in the movement pathways of animals is an important understudied phenomenon that is critical for predictive modeling of population spatial properties". Following this idea, the aim of this paper is to demonstrate that movement ecology could benefit from a deeper exploratory analysis of the empirical data, with a special emphasis on temporal autocorrelation. We present the various problems linked to the analysis of autocorrelated data, and show how the study of autocorrelation can reveal important biological insights, help to develop new biological hypotheses, and thus make it possible to improve the accuracy of movement models. We suggest some tools that can be used to measure, test, and adjust for temporal autocorrelation. An ecological illustration is presented.

Description of movement paths

The analysis of movements involves recording the path of an individual through space and time. Animal movement is a continuous process, but its observation using radio telemetry technologies leads to a discrete representation. The data gathered consist of a sequence of successive relocations (x_i, y_i) of an individual collected at time i. Steps are defined as the displacement between two successive relocations. As this displacement is usually represented as a straight-line, a path is represented as a series of straight-lines. Following Marsh and Jones ([1988](#)), several descriptors (Calenge et al. [2009](#)) can be associated with each step to quantify animal movements (see Fig. [1](#)). For example, the nth step can be characterized by:

- its length (d_n)
- the increment in the X and Y directions (δx_n and δy_n)
- the absolute angle between the step and the X direction (α_n)
- the relative (or turning) angle between the nth step and the previous one (ρ_n)
- the squared net displacement after n consecutive steps (R_n^2)

The parameters d_n and ρ_n have been widely used since the early work of Siniff and Jessen ([1969](#)), while R_n^2 has been popularized by Kareiva and Shigesada ([1983](#)). GPS collars are often programmed to collect regular data, so that we assume from here on that the time lag between two relocations is constant. Despite improvements in this technology, GPS telemetry can still result in missing data in the form of failed location attempts. If this happens, data are still considered to be regular, as the steps connecting a relocation to a missing value are missing, but still characterized by the same time interval as the observed steps (see Calenge et al. [2009](#)). The presence of missing data can be due for example to the behavior of the animal or to the habitat structure (e.g., Frair et al. [2004](#); Graves and Waller [2006](#); Bourgoin et al. [2009](#)). It is then important to deal with missing observations when
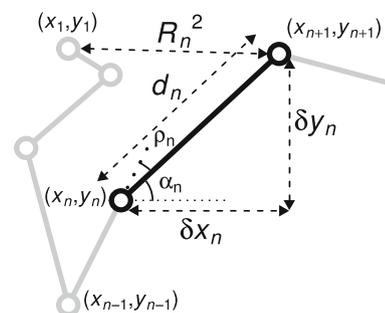
Fig. 1 Parameters used to describe steps. The nth step is associated with its length (d_n), the increments in the X and Y directions (δx_n and δy_n), the absolute angle (α_n), the turning angle (ρ_n) and the squared net displacement (R_n^2)
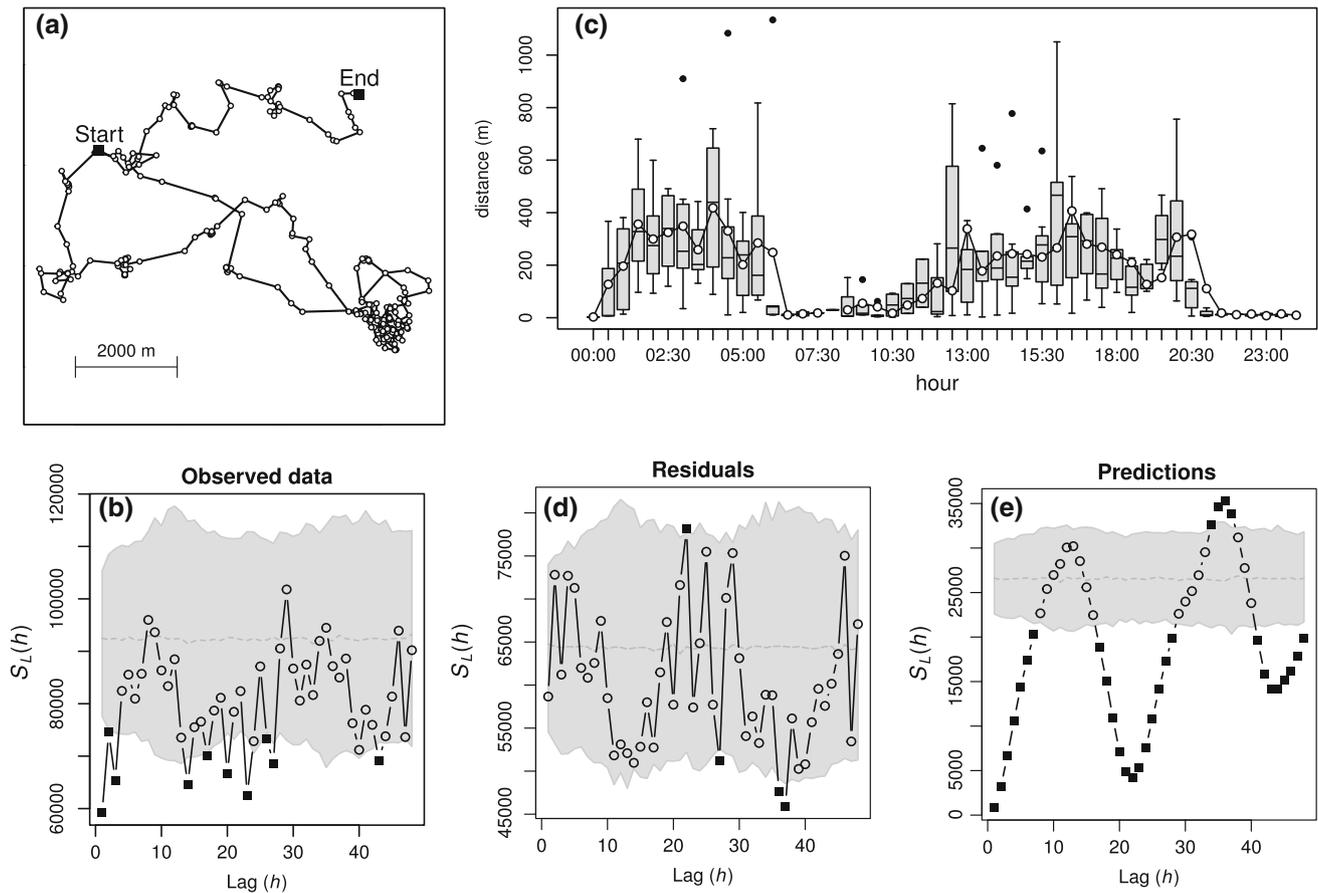
Fig. 2 Analysis of brown-bear data. **a** Representation of the movement path. **b** Correlogram of step lengths [$S_L(h)$]. The *gray area* corresponds to a 95% CI obtained by permutation procedure (999 permutations). The *gray dotted line* depicts the median of the values of the statistic computed on permuted data. The *empty circles* represent non-significant autocorrelation, while the *black squares* correspond to significant values. **c** *Boxplots* of the daily pattern of step lengths. The *line with white circles* corresponds to average values. Correlogram for the detrended step lengths (**d**) and the trend (**e**). The trend corresponds to the predictions of the linear model with step length as response variable and nine Moran's eigenvectors maps as explanatory variables; detrended data correspond to the residuals of this model

analyzing movement data because their structure could be related to important biological variables and thus gives some information about movement characteristics. In this context, Calenge et al. (2009) suggests that "the analysis of the patterns of missing values should be a part of trajectory analysis" (p. 36). As missing data are a key component of GPS data, we propose several procedures that have the ability to deal with them when analyzing autocorrelation structures.

Illustration: Fig. 2a shows an example of a movement path. The data set contains the 336 relocations (extending over 1 week, with a recording interval of 30 min) of a female brown bear monitored using a GPS collar in July 2004 in Sweden.

Autocorrelation and the analysis of movement paths

Definition of theoretical models

Understanding how animals move is often based on a confrontation of the observed data with theoretical models. The observed distribution of some of the parameters defined above may be compared to the distribution expected under the assumption of the theoretical model. These comparisons could be performed using graphical tools (e.g., Kareiva and Shigesada 1983) or traditional testing procedures. The random walk (RW) and the correlated random walk (CRW) are the models most often used (e.g., Marsh and Jones 1988). RW corresponds to a succession of random steps, whereas the CRW model assumes that the movement of animals exhibits directional persistence ("correlated"). In a mathematical context, the CRW model differs from the RW model because it assumes a unimodal and symmetric distribution (about zero) of the turning angles whereas the RW model assumes a uniform distribution. Both models also require the independence of successive turning angles and step lengths. Turchin (1998, p. 135) stated that "CRW formulation assumes that the move durations, speeds, and turning angles are not serially correlated, an assumption that should be tested statistically". This advice has sometimes been followed in the literature (e.g., Bergman et al. 2000; Nolet and Mooij

2002; Revilla et al. 2004; Bailey and Thompson 2006; Dumont et al. 2007). For instance, Root and Kareiva (1984) tested the autocorrelation for distances and turning angles using Pearson's correlation coefficients. If no tests of independence are performed, the probability that a model (e.g., RW, CRW) will be rejected when it is false (i.e., statistical power) is lower than expected, because it is assumed a priori that independence assumptions are met.

Computation of mean squared net displacement and related tools

Kareiva and Shigesada (1983) proposed an explicit formula of the expected mean squared net displacement $E(R_n^2)$ for (C)RW models. They insisted on the notion of independence of parameters (e.g., p. 235, the word "independent" is italicized) to obtain a correct derivation of $E(R_n^2)$. The algorithm proposed by McCulloch and Cain (1989) to compute the variance in squared displacement $V(R_n^2)$ for a CRW, and the expected value of the Δ statistic presented by Marsh and Jones (1988) to distinguish between the CRW and the biased random walk (BRW) models are also based on the assumption of independence of some parameters. Marsh and Jones (1988, p. 129) stated that the information given in their paper can be used "to construct a simple test to distinguish between the two models" but pointed out that "we must, of course, have other reasons for restricting consideration to just these two types of model". One of these reasons is that the underlying assumptions of independence have been confirmed. In this context, using these tools without checking the independence of parameters (see e.g., Odendaal et al. 1989; Firle et al. 1998; Morales and Ellner 2002) makes no sense.

Standard hypothesis tests on movement descriptors

The various descriptors (see the previous section) are routinely used in standard statistical procedures (e.g., ANOVA, t-test for linear descriptors; Rayleigh test of uniformity for angular descriptors) to test hypotheses concerning animal movements. Usually, these procedures require the independence of observations. If data are positively autocorrelated, classical tests are biased because "computed statistics are too often declared significant under the null hypothesis" (Legendre 1993, p. 1660). Hence, the hypothesis of independence (i.e., absence of autocorrelation) should be tested and not rejected before using standard hypothesis tests on movement descriptors.

In his note on the analysis of angular data, Cain (1989, p. 1542) stated that "statistical tests [...] are based on the assumption that observed angles are independent, a condition that may not be satisfied when multiple angles are recorded from a single individual". He conducted a survey of the literature and showed that independence tests are rarely performed before hypothesis tests on angular data, and concluded that "a lack of independence among successive angles not only violated hypothesis test assumptions, it also has important movement consequences: organisms that alternate right and left turns, for example, will displace farther than those whose turning angles are independent". A short review of the recent literature demonstrated that some authors did test independence (e.g., Fortin et al. 2005; Bailey and Thompson 2006), but many others did not check the independence assumptions before carrying out standard hypothesis tests (e.g., Bowne et al. 1999; Cardona et al. 2005; Lorch et al. 2005; Parks et al. 2006). More surprisingly, several authors (e.g., Bergman et al. 2000; Austin et al. 2004; Lancaster et al. 2006) performed independence tests (usually to check CRW assumptions), rejected the hypothesis of independence and then used wrongly standard tests on autocorrelated data.

Testing for the independence of path descriptors is essential, and is probably the first step that should be carried out when analyzing movement data. This can be done by means of several procedures.

Independence testing procedures

Several approaches have been used in the literature to test the independence of descriptors. Among the different descriptors, angular data require a particular attention due to their nature and must be analyzed using appropriate circular statistics (Cain 1989).

The autocorrelation function

In the literature, some authors (Bergman et al. 2000; Austin et al. 2004; Bailey and Thompson 2006), following the recommendations of Turchin (1998), used autocorrelation functions (ACF, Diggle 1990), a standard tool for the analysis of time series which consists of plotting the values of autocorrelation measured for different time lags against the corresponding lags. For a real-valued random variable X taking values $x_1,...,x_N$, the sample autocorrelation function for a given time lag h is:

$$\widehat{\rho}(h) = \frac{\sum_{i=1}^{N-h} z_i \cdot z_{i+h}}{\sum_{i=1}^{N} z_i^2} \quad \text{where } z_i = x_i - \frac{1}{N}\sum_{i=1}^{N} x_i.$$

For a significance level α, we conclude that data are not independent if $\sqrt{n}|\widehat{\rho}(h)|$ exceeds the standard Gaussian $(1 - \frac{\alpha}{2})$-quantile. Note that the autocorrelation function for lag 1 (i.e., $\widehat{\rho}(1)$) is sufficient to test for independence (Diggle 1990). For the first-order lag (i.e., $h = 1$), we have:

$$\widehat{\rho}(1) = \frac{\sum_{i=1}^{N-1} z_i \cdot z_{i+1}}{\sum_{i=1}^{N} z_i^2}$$

$$= 1 - \frac{1}{2N\widehat{\sigma}^2}\left(z_1^2 + z_N^2 + \sum_{i=1}^{N-1}(z_i - z_{i+1})^2\right)$$

where $\widehat{\sigma}^2 = \frac{1}{N}\sum_{i=1}^{N} z_i^2$.

The foregoing equations allow us to link the ACF to the two methods generally used to measure the autocorrelation. The first method considers the products $z_i \cdot z_{i+1}$ (Wald and Wolfowitz 1943), while the second considers the local differences $(z_{i+1} - z_i)^2$ (von Neumann et al. 1941, von Neumann 1941). In this paper, we will focus on the second approach, which has been implemented in the *adehabitat* package (Calenge 2006) for the R software.

ACF is not designed to handle missing data. Consequently, the previous testing procedure cannot be used for data sets with missing observations. Fortunately, similar tools have been developed in the context of spatial analysis, particularly the correlogram (Legendre and Legendre 1998, p. 714), which can easily be modified to accept missing values. In the following sections, we propose statistics and procedures adapted to movement data with missing observations for linear and angular descriptors.

Linear descriptors

Among the different linear descriptors, tests of independence are often used for the length of the step. Several authors have used the Pearson product-moment correlation coefficient and its associated *t*-test (Nolet and Mooij 2002; Banks and Yasenak 2003; Lancaster et al. 2006) to evaluate the significance of the correlation of the variable of interest (e.g., the length) and a time-shifted version of itself. Others have preferred to use Spearman's rank correlation coefficient (Cain et al. 1991; Dumont et al. 2007) on the same data. As explained below, standard tests (including *t*-test) assume independence of observations, and this kind of approach violates this basic assumption. The correct way to test for independence is provided by permutation procedure. For a path with N steps, a measure of autocorrelation (von Neumann 1941, von Neumann et al. 1941) of step lengths is given by:

$$S_L = \frac{1}{N_d}\sum_{n=1}^{N-1}(d_{n+1} - d_n)^2$$

where $N_d = N - 1$ is equal to the number of summed squared differences. Our presentation focused on step lengths, but the method can also be used for other linear descriptors (e.g., $\delta x_n, \delta y_n$). The principles of the randomization procedure are as follows:

(1) Compute a reference value of S_L using original data.
(2) Randomly permute the values of the step lengths, and recompute the S_L statistic. This operation is repeated a number of times (e.g., 999), to provide a set of values of the statistic under the null hypothesis of independence (H_0).
(3) Compare the observed statistic to the distribution containing the values obtained by permutation as well as the reference value; compute the associated probability and take the appropriate statistical decision (reject or fail to reject the null hypothesis of independence).

Depending on the alternative hypothesis (H_1), the third step will involve different procedures. If the alternative hypothesis is the presence of positive autocorrelation, using a significance level equal to α, a *p*-value is estimated as: (number of random values equal to or less than the observed value + 1)/(number of permutations + 1). The null hypothesis is rejected if the *p*-value is below the threshold of significance (α). If the alternative hypothesis is the presence of negative autocorrelation, a *p*-value is estimated as: (number of random values equal to or greater than the observed value + 1)/(number of permutations + 1). Again, the null hypothesis is rejected if the *p*-value is below the threshold of significance (α). Lastly, if the alternative hypothesis is the presence of autocorrelation (positive or negative), a two-sided test can be used. The estimation of the *p*-value is equivalent to the second procedure described above, except that random and observed values are first centered (using the average of random values), and then transformed into their absolute values.

In the case of missing data, the computation of S_L is restricted to the N_d pairs of successive observed data (i.e., if d_n is missing, $(d_n - d_{n-1})^2$ and $(d_{n+1} - d_n)^2$ are not computed) and only observed data are permuted (i.e., the structure of the missing data is kept constant under permutation).

Our procedure can also be used to construct a correlogram by plotting the statistic $S_L(h) = \frac{1}{N_{d(h)}}\sum_{n=1}^{N-h}(d_{n+h} - d_n)^2$ against the time lag h. The significance of $S_L(h)$ is assessed using the permutation procedure, as described above. Since tests are performed for various time lags, results could be corrected using a multiple adjustment method such as Bonferroni or Holm's sequential procedure (Legendre and Legendre 1998).

Illustration: a correlogram (Fig. 2b) computed on the bear step length data indicated a significant positive autocorrelation for the three first lags, and also for several lags between 14 and 27 (7–13h30) and lag 43 (21h30). This seems to reflect a recurrent periodic structure related to diel movement patterns.

Angular descriptors

In the literature, angular autocorrelation has been analyzed using both qualitative and quantitative measurements (Turchin 1998). There have been a few attempts to

use quantitative measures: Lancaster et al. ([2006]) used the circular coefficient of correlation of Jammalamadaka and Sengupta ([2001]) while Nolet and Mooij ([2002]) used the coefficient of Jupp and Mardia ([1980]). Tests based on qualitative measurements involve transforming angles as right (R) or left (L) deviations from the previous direction for turning angles, or from the X axis for absolute angles (Cain [1989]). Then one can use a runs test on the sequence of R and L (e.g., Bailey and Thompson [2006]). An alternative approach is to construct the contingency table with the four possible values of successive steps (LL, RR, LR, RL) as entries. Independence is then tested using an χ^2 test with one degree of freedom (e.g., Cain et al. [1991]; Banks and Yasenak [2003]). Schaeffer and Messier ([1997]) transformed left and right deviations into 0 and 1, and then computed an ACF on this binary variable (see also Bergman et al. [2000]). Transforming angular data into qualitative information undoubtedly leads to a loss of information. Moreover, we do not think that the R-L transformation, which considers only two directions, is really suitable for the analysis of movement data. Indeed, if an animal moves in a given direction with slight deviations to the left and then to the right, this would lead to a negative association (LR) but we would assume a positive autocorrelation as the movement is always in the same main direction. On the other hand, if an animal moves in a given direction and then in the opposite with slight deviations to the left for both steps, this would lead to a positive association (LL) but we would assume a negative autocorrelation as the main direction has completely changed.

If we consider the turning angles, it seems natural to assume that positive autocorrelation means that the direction taken for the nth step is similar to the previous one, while negative autocorrelation means that the direction of the nth step is opposite to that of the previous step. Hence, it would be preferable to use a qualitative measurement that considers the four possible directions corresponding to different values of turning angles (Fig. 3): turn right (R, $-\pi/2$), turn left (L, $\pi/2$), go forwards (F, 0), or go backwards (B, π or $-\pi$). It makes sense to consider the sequences LL, RR, FF, or BB as positive associations, and LR, RL, FB, or BF as negative associations.

As an alternative, we propose to use a quantitative coefficient (the chord distance) to measure angular autocorrelation (Fig. 3b). Chord distance is low when two successive angles are similar. In the case of sequences LR, RL, FB, or BF, the distance reaches its maximum, and is equal to 2. For a sequence of N turning angles, we propose measuring the autocorrelation as the sum of the squared chord distances:

$$S_A = \frac{1}{N_d} \sum_{n=1}^{N-1} \left[(\cos \rho_{n+1} - \cos \rho_n)^2 + (\sin \rho_{n+1} - \sin \rho_n)^2 \right]$$

$$= \frac{2}{N_d} \sum_{n=1}^{N-1} 1 - \cos(\rho_{n+1} - \rho_n)$$
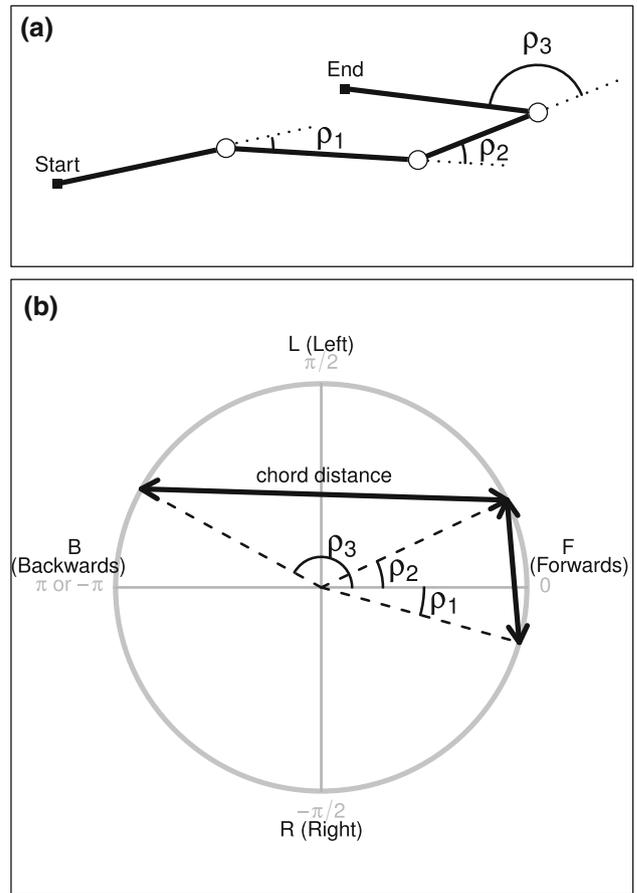
Fig. 3 Using the chord distance to measure the autocorrelation for the turning angles. **a** A path of four steps encompasses three successive turning angles ρ_1, ρ_2, and ρ_3. **b** Small chord length corresponds to positive association between successive angles ρ_1 and ρ_2 and large chord length corresponds to "negative association" between successive angles ρ_2 and ρ_3

Like the linear descriptors, the angular autocorrelation can be tested using the permutation procedures described above. A correlogram can also be computed.

Illustration: correlograms of absolute and turning angles computed on the bear data did not highlight any autocorrelation structure, and are not reported here.

Understanding autocorrelation and detrending

Autocorrelation is a very general property of ecological variables. Unfortunately, it is also an obstacle in ecological studies as it violates the basic assumptions of standard statistical hypothesis testing. Autocorrelation is usually viewed as a form of bias, and a common procedure is to eliminate it before analyzing the data by subsampling (Turchin [1998], p. 130). However, we do not think that subsampling of relocations or steps should be routinely used before the analysis of movement paths. The first reason for this is that computing some descriptors requires two relocations (e.g., distance) or two steps (turning angle), and in such circumstances,

subsampling will reduce the accuracy of the estimates. The second reason is that autocorrelation is often the consequence of ecological processes. This is particularly true for long-time surveys obtained with GPS monitoring, for which the animal's "switching behavior" is often responsible for the presence of autocorrelation. In some cases, this autocorrelation can be generated by a process unrelated to the focus issue (e.g., the mechanistic aspects of the locomotion process), which would justify eliminating it prior to the analysis. However, we stress that the preliminary analysis of the autocorrelation and identifying its causes are essential if we are to gain a better understanding of the patterns of animal movements.

Legendre (1993) stated that spatial structures observed in ecological communities can arise from two independent processes. Environmental factors that influence species distributions are spatially structured and, as a result of an indirect process, communities of species are also spatially structured (induced spatial dependence). Spatial autocorrelation can also be created directly at the community level as a result of contagious biotic processes. By analogy, two processes can be considered to be a potential cause of temporal autocorrelation of successive steps (Martin et al. 2008). If movement parameters are dependent on local environmental conditions, then environmental variability can induce temporal autocorrelation of movement descriptors (Turchin 1998, p. 135). Here, "environment" is used in a very broad sense, and includes both abiotic (e.g., altitude) and biotic factors (e.g., distribution of preys and predators). Temporal autocorrelation can also be the consequence of internal (individual) processes (e.g., circadian activity). When the origins of autocorrelation have been identified, it can then be eliminated before carrying out the other analyses. This requires tools to describe temporal patterns explicitly in order to detrend the data, and perform subsequent analyses on the residual (or detrended) data. Several methods exist for detrending time series including the variate difference method, Fourier series (Wittemyer et al. 2008), or harmonic regression (see for instance Legendre and Legendre 1998, Ch. 12 for details). Tools developed for the analysis of spatial autocorrelation (e.g., Dray et al. 2006) can also be useful. The reader could consult Frair et al. (2005) for an example of the detrending of animal-movement data. Detrending of angular data is more complicated, and involves the use of circular regression methods (Fisher 1996, Ch. 6).

Illustration: the daily pattern of step lengths is represented in Fig. 2c, and is characterized by two peaks of activity corresponding to long step lengths. This circadian pattern with two peaks is common, and has been demonstrated for several species (Aschoff 1966). Hence, this circadian pattern must be taken into account before attempting any other analysis of step lengths.

We modeled the temporal constraint as a linear graph with 336 nodes, and computed Moran's eigenvector maps (Dray et al. 2006) for the associated weighting matrix. This approach can be used to construct a set of predictors in order to model an autocorrelated signal in ecological data (Peres-Neto 2006). Detrending was performed using the procedure proposed in Griffith and Peres-Neto (2006) with a significance level equal to 0.05. The correlogram computed on detrended data (Fig. 2d) demonstrated that the autocorrelation structure corresponding to the circadian rhythm has been removed. The correlogram for the trend (Fig. 2e) corresponds to a periodic pattern (the period is around 10–14 h). The detrended data can then be used for subsequent analysis.

Concluding remarks

In these days of state-space and hierarchical Bayesian modeling (Patterson et al. 2008; Schick et al. 2008), our approach may look rather old-fashioned. What is the point of data exploration when models of realistic movements are available? Answers to this question can be found in the old debate initiated by Tukey (1977, 1980) about exploratory and confirmatory analyses. Data exploration allows one to extract what the data says, without any a priori hypothesis. It can be useful for generating new questions/ideas, improving the sampling design, or guiding the choice of subsequent analyses. In the field of animal movement, autocorrelation is an important property of the data that could reveal information about how animals move. Patterns revealed by its exploratory analysis help to generate new hypotheses about the behavioral processes related to animal mobility. These hypotheses can then be tested by introducing new parameters into animal-movement models. For instance, our example suggests that a model integrating the time of the day (e.g., Preisler et al. 2004) should be used to analyze brown bear movement data. Exploratory analysis and modeling of animal movements should therefore not be opposed, but rather considered as two complementary approaches. The reader could consult Brillinger et al. (2004) for a nice example of an exploratory analysis of animal-movement data.

We hope that this paper will help to improve the way we tackle the question of autocorrelation in animal-movement analysis. An appropriate approach would consist of the following steps:

- measure and test autocorrelation using appropriate procedures;
- if autocorrelation is detected, its structure must be studied as it can reflect ecological processes of interest.

Then, depending on the type of subsequent analysis, one can:

- detrend the data so that autocorrelation (corresponding to processes analyzed in the previous step) is eliminated;

- use detrended data in the analysis. Standard statistical tools can now be used, as the observations are now independent.

or

- incorporate new parameters in movement models that account for the hypothesized processes.

In order to help ecologists, functions that can be used to store and manage animal-movement paths and to measure and test autocorrelation have been included in the *adehabitat* package (Calenge 2006) for the R software. The reader could consult Calenge et al. (2009) for more details about these functions. Appendix 1 in Electronic supplementary material provides a complete example corresponding to the brown bear illustration used in this paper.

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