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1 The exploratory analysis of autocorrelation in animal
2 movement studies

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14

15 **Abstract:**

16 Studies of animal movements has been popularized for many large and shy
17 species by the increasing use of radio telemetry methods (VHF and GPS tech-
18 nologies). Data are collected with high sampling frequency, and consist of
19 successive observations of the position of an individual animal. The statistical
20 analysis of such data poses several problems due to the lack of independence
21 of successive observations. However, the statistical description of the tempo-
22 ral autocorrelation between successive steps is rarely performed by ecologists
23 studying the patterns of animals movements. The aim of this paper is to warn
24 ecologists against the consequences of failing to consider this aspect. We discuss
25 the various issues related to analysing autocorrelated data, and show how the
26 exploratory analysis of autocorrelation can both reveal important biological in-
27 sights, and help to improve the accuracy of movement models. We suggest some
28 tools that can be used to measure, test and adjust for temporal autocorrelation.
29 A short ecological illustration is presented.

30 *Keywords: autocorrelation function; GPS; independence test; radio telemetry;*
31 *permutation test*

32 1 Introduction

33 Radio telemetry *has become increasingly popular as a convenient means of studying move-*
34 *ments of wildlife* (Dunn and Gipson 1977) and it can be used to collect data that consist of
35 successive observations of the locations of an individual animal. The recent development
36 of GPS technology makes it possible to collect relocation data automatically, at short,
37 regular intervals. However, as the time interval decreases, the dependence between succes-
38 sive observations usually increases so that the problem of autocorrelation must be taken
39 into considered in the analysis. Autocorrelation can be defined as a property of random
40 variables, which means that values from samples taken near to each other tend to be ei-
41 ther more similar (positive autocorrelation) or less similar (negative autocorrelation) than
42 would be expected from a random arrangement. This nearness can be defined in space
43 (spatial autocorrelation), or in time (temporal autocorrelation). The main difference is
44 that an observation is only influenced by past values in temporal autocorrelation whereas
45 spatial dependence extends in all directions. Autocorrelation is often seen as an obsta-
46 cle, as it interferes with standard statistical hypothesis testing (Legendre 1993), and many
47 approaches have been developed to eliminate it by restricting data prior to analysis. How-
48 ever, autocorrelation is often an intrinsic property of biological data, so that eliminating
49 it could reduce the relevance of ecological studies. In the context of animal movement,
50 which is by definition a non-independent phenomenon, De Solla et al. (1999) summarized
51 the situation clearly: *Animals typically move in a non-random fashion, and thus ecolo-*
52 *gists are frequently faced with strongly autocorrelated data sets, particularly when frequent*
53 *observations are collected using radiotelemetry.*

54 Solow (1990) distinguished two approaches in the literature on animal movements: one
55 focusing on relocations, and the other on the movements between relocations. The question
56 of autocorrelation must be (and indeed has been) considered in different ways in these two
57 approaches. Any temporal autocorrelation between the coordinates of successive reloca-
58 tions must be taken into account when the analysis is based on relocations. For instance,
59 in the context of home range estimation, this problem has been discussed in a number of

60 papers (e.g., Dunn and Gipson 1977, Swihart and Slade 1985a;b, De Solla et al. 1999), and
61 so we will not consider it any further here. On the other hand, the analysis of movements
62 between relocations raises the question of the temporal autocorrelation between succes-
63 sive steps (i.e. the displacement between two successive relocations). The development of
64 models of realistic animal movement is a very active field of research at present (Patterson
65 et al. 2008, Schick et al. 2008). The aim of these studies is to understand why, how and
66 where animals move, and to see how this could affect the spatial dynamics at higher levels
67 of organization (population, community, etc). Recent methodological developments have
68 improved the ability of models to handle the biological complexity of animal movements
69 (Nathan et al. 2008), and to account for multiple behavior modes (e.g. searching, resting,
70 etc), characteristics of landscape (e.g. patchiness) or environmental variations (e.g. spatial
71 distribution of resources). The various internal (e.g. behavioral) or external (e.g. environ-
72 mental) factors influencing organisms could induce temporal autocorrelation in movement
73 data. For instance, autocorrelation in steps could be due to the animal's switching between
74 different movement strategies. Hence, autocorrelation is usually considered as an emergent
75 property in a modelling framework and its exploratory analysis is rarely performed by
76 authors.

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

89 2 Description of movement paths

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

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

104 The parameters d_n and ρ_n have been widely used since the early work of Siniff and Jessen
105 (1969), while R_n^2 has been popularized by Kareiva and Shigesada (1983). GPS collars are
106 often programmed to collect regular data, so that we assume from here on that the time
107 lag between two relocations is constant. Despite improvements in this technology, GPS
108 telemetry can still result in missing data in the form of failed location attempts. If this
109 happens, data are still considered to be regular, as the steps connecting a relocation to a
110 missing value are missing, but still characterized by the same time interval as the observed
111 steps (see Calenge et al. 2009). The presence of missing data can be due for example to
112 the behaviour of the animal or to the habitat structure (e.g., Frair et al. 2004, Graves and
113 Waller 2006, Bourgoin et al. 2009). It is then important to deal with missing observations

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

120 *Illustration* — Fig. 2a shows an example of a movement path. The data set contains
121 the 336 relocations (extending over one week, with a recording interval of 30 minutes) of a
122 female brown bear monitored using a GPS collar in July 2004 in Sweden.

123 **3 Autocorrelation and the analysis of movement paths**

124 3.1 Definition of theoretical models

125 Understanding how animals move is often based on a confrontation of the observed data
126 with theoretical models. The observed distribution of some of the parameters defined
127 above may be compared to the distribution expected under the assumption of the theoret-
128 ical model. These comparisons could be performed using graphical tools (e.g., Kareiva and
129 Shigesada 1983) or traditional testing procedures. The random walk (RW) and the corre-
130 lated random walk (CRW) are the models most often used (e.g., Marsh and Jones 1988).
131 RW corresponds to a succession of random steps, whereas the CRW model assumes that
132 the movement of animals exhibits directional persistence (“correlated”). In a mathematical
133 context, the CRW model differs from the RW model, because it assumes a unimodal and
134 symmetric distribution (about zero) of the turning angles whereas the RW model assumes
135 a uniform distribution. Both models also require the independence of successive turning
136 angles and step lengths. Turchin (1998, p. 135) stated that *CRW formulation assumes that*
137 *the move durations, speeds, and turning angles are not serially correlated, an assumption*
138 *that should be tested statistically.* This advice has sometimes been followed in the liter-
139 ature (e.g., Bergman et al. 2000, Nolet and Mooij 2002, Revilla et al. 2004, Bailey and
140 Thompson 2006, Dumont et al. 2007). For instance, Root and Kareiva (1984) tested the

141 autocorrelation for distances and turning angles using Pearson's correlation coefficients. If
142 no tests of independence are performed, the probability that a model (e.g. RW, CRW)
143 will be rejected when it is false (i.e. statistical power) is lower than expected, because it is
144 assumed *a priori* that independence assumptions are met.

145 3.2 Computation of mean squared net displacement and related tools

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

160 3.3 Standard hypothesis tests on movement descriptors

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

168 hypothesis tests on movement descriptors.

169 In his note on the analysis of angular data, Cain (1989, p. 1542) stated that *statistical*
170 *tests [...] are based on the assumption that observed angles are independent, a condition*
171 *that may not be satisfied when multiple angles are recorded from a single individual.* He
172 conducted a survey of the literature and showed that independence tests are rarely per-
173 formed before hypothesis tests on angular data, and concluded that *a lack of independence*
174 *among successive angles not only violated hypothesis test assumptions, it also has important*
175 *movement consequences: organisms that alternate right and left turns, for example, will*
176 *displace farther than those whose turning angles are independent.* A short review of the
177 recent literature demonstrated that some authors did test independence (e.g., Fortin et al.
178 2005, Bailey and Thompson 2006), but many others did not check the independence as-
179 sumptions before carrying out standard hypothesis tests (e.g., Bowne et al. 1999, Cardona
180 et al. 2005, Lorch et al. 2005, Parks et al. 2006). More surprisingly, several authors (e.g.,
181 Bergman et al. 2000, Austin et al. 2004, Lancaster et al. 2006) performed independence
182 tests (usually to check CRW assumptions), rejected the hypothesis of independence and
183 then used wrongly standard tests on autocorrelated data.

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

187 **4 Independence testing procedures**

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

191 4.1 The autocorrelation function

192 In the literature, some authors (Bergman et al. 2000, Austin et al. 2004, Bailey and Thomp-
193 son 2006), following the recommendations of Turchin (1998), used autocorrelation functions
194 (ACF, Diggle 1990), a standard tool for the analysis of time series which consists of plot-

195 ting the values of autocorrelation measured for different time lags against the corresponding
 196 lags. For a real-valued random variable X taking values x_1, \dots, x_N , the sample autocorre-
 197 lation function for a given time lag h is:

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

198 For a significance level α , we conclude that data are not independent if $\sqrt{n}|\hat{\rho}(h)|$ exceeds
 199 the standard gaussian $(1 - \frac{\alpha}{2})$ -quantile. Note that the autocorrelation function for lag 1
 200 (i.e. $\hat{\rho}(1)$) is sufficient to test for independence (Diggle 1990). For the first order lag (i.e.,
 201 $h = 1$), we have:

$$\begin{aligned} \hat{\rho}(1) &= \frac{\sum_{i=1}^{N-1} z_i \cdot z_{i+1}}{\sum_{i=1}^N z_i^2} \\ &= 1 - \frac{1}{2N\hat{\sigma}^2} \left(z_1^2 + z_N^2 + \sum_{i=1}^{N-1} (z_i - z_{i+1})^2 \right) \end{aligned}$$

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

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

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

213 missing observations for linear and angular descriptors.

214 4.2 Linear descriptors

215 Among the different linear descriptors, tests of independence are often used for the length
 216 of the step. Several authors have used the Pearson product-moment correlation coefficient
 217 and its associated t -test (Nolet and Mooij 2002, Banks and Yassenak 2003, Lancaster et al.
 218 2006) to evaluate the significance of the correlation of the variable of interest (e.g. the
 219 length) and a time-shifted version of itself. Others have preferred to use Spearman's rank
 220 correlation coefficient (Cain et al. 1991, Dumont et al. 2007) on the same data. As explained
 221 below, standard tests (including t -test) assume independence of observations, and this
 222 kind of approach violates this basic assumption. A correct way to test for independence is
 223 provided by permutation procedure. For a path with N steps, a measure of autocorrelation
 224 (von Neumann 1941, von Neumann et al. 1941) of step lengths is given by:

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

225 where $N_d = N - 1$ is equal to the number of summed squared differences. Our presen-
 226 tation focused on step lengths, but the method can also be used for other linear descriptors
 227 (e.g., δx_n , δy_n). The principles of the randomization procedure are as follows:

- 228 (i). Compute a reference value of S_L using original data.
- 229 (ii). Randomly permute the values of the step lengths, and recompute the S_L statistic.
 230 This operation is repeated a number of times (e.g., 999), to provide a set of values of
 231 the statistic under the null hypothesis of independence (H_0).
- 232 (iii). Compare the observed statistic to the distribution containing the values obtained by
 233 permutation as well as the reference value; compute the associated probability and
 234 take the appropriate statistical decision (reject or fail to reject the null hypothesis of
 235 independence).

236 Depending on the alternative hypothesis (H_1), the third step will involve different pro-
 237 cedures. If the alternative hypothesis is the presence of positive autocorrelation, using a
 238 significance level equal to α , a p-value is estimated as: (number of random values equal to
 239 or less than the observed value + 1)/(number of permutations + 1). The null hypothesis
 240 is rejected if the p-value is below the threshold of significance (α). If the alternative hy-
 241 pothesis is the presence of negative autocorrelation, a p-value is estimated as: (number of
 242 random values equal to or greater than the observed value + 1)/(number of permutations
 243 + 1). Again, the null hypothesis is rejected if the p-value is below the threshold of signifi-
 244 cance (α). Lastly, if the alternative hypothesis is the presence of autocorrelation (positive
 245 or negative), a two-sided test can be used. The estimation of the p-value is equivalent to
 246 the second procedure described above, except that random and observed values are first
 247 centered (using the average of random values), and then transformed into their absolute
 248 values.

249 In the case of missing data, the computation of S_L is restricted to the N_d pairs of
 250 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
 251 computed) and only observed data are permuted (i.e. the structure of the missing data is
 252 kept constant under permutation).

253 Our procedure can also be used to construct a correlogram by plotting the statistic
 254 $S_L(h) = \frac{1}{N_{d(h)}} \sum_{n=1}^{N-h} (d_{n+h} - d_n)^2$ against the time lag h . The significance of $S_L(h)$ is
 255 assessed using the permutation procedure, as described above. Since tests are performed
 256 for various time lags, results could be corrected using a multiple adjustment method such
 257 as Bonferroni or Holm's sequential procedure (Legendre and Legendre 1998).

258 *Illustration* — A correlogram (Fig. 2b) computed on the bear step length data indicated
 259 a significant positive autocorrelation for the three first lags, and also for several lags between
 260 14 and 27 (7-13h30) and lag 43 (21h30). This seems to reflect a recurrent periodic structure
 261 related to diel movement patterns.

262 4.3 Angular descriptors

263 In the literature, angular autocorrelation has been analyzed using both qualitative and
264 quantitative measurements (Turchin 1998). There have been a few attempts to use quan-
265 titative measures: Lancaster et al. (2006) used the circular coefficient of correlation of
266 Jammalamadaka and Sengupta (2001) while Nolet and Mooij (2002) used the coefficient of
267 Jupp and Mardia (1980). Tests based on qualitative measurements involve transforming
268 angles as right (R) or left (L) deviations from the previous direction for turning angles,
269 or from the X axis for absolute angles (Cain 1989). Then one can use a runs test on
270 the sequence of R and L (e.g., Bailey and Thompson 2006). An alternative approach is
271 to construct the contingency table with the four possible values of successive steps (LL,
272 RR, LR, RL) as entries. Independence is then tested using a χ^2 test with one degree of
273 freedom (e.g., Cain et al. 1991, Banks and Yassenak 2003). Schaeffer and Messier (1997)
274 transformed left and right deviations into 0 and 1, and then computed an ACF on this
275 binary variable (see also Bergman et al. 2000). Transforming angular data into qualitative
276 information undoubtedly leads to a loss of information. Moreover, we do not think that the
277 R-L transformation, which considers only two directions, is really suitable for the analysis
278 of movement data. Indeed, if an animal moves in a given direction with slight deviations to
279 the left and then to the right, this would lead to a negative association (LR) but we would
280 assume a positive autocorrelation as the movement is always in the same main direction.

281 On the other hand, if an animal moves in given direction and then in the opposite with
282 slight deviations to the left for both steps, this would lead to a positive association (LL) but
283 we would assume a negative autocorrelation as the main direction has completely changed.

284 If we consider the turning angles, it seems natural to assume that positive autocorrela-
285 tion means that the direction taken for the n -th step is similar to the previous one, while
286 negative autocorrelation means that the direction of the n -th step is opposite to that of
287 the previous step. Hence, it would be preferable to use a qualitative measurement that
288 considers the four possible directions corresponding to different values of turning angles
289 (Fig. 3): turn right (R, $-\pi/2$), turn left (L, $\pi/2$), go forwards (F, 0) or go backwards (B, π)

290 or $-\pi$). It makes sense to consider the sequences LL, RR, FF or BB as positive associations,
 291 and LR, RL, FB or BF as negative associations.

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

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

297 Like the linear descriptors, the angular autocorrelation can be tested using the permu-
 298 tation procedures described above. A correlogram can also be computed.

299 *Illustration* — Correlograms of absolute and turning angles computed on the bear data
 300 did not highlight any autocorrelation structure, and are not reported here.

301 5 Understanding autocorrelation and detrending

302 Autocorrelation is a very general property of ecological variables. Unfortunately, it is also
 303 an obstacle in ecological studies as it violates the basic assumptions of standard statistical
 304 hypothesis testing. Autocorrelation is usually viewed as a form of bias, and a common
 305 procedure is to eliminate it before analysing the data by subsampling (Turchin 1998, p.
 306 130). However, we do not think that subsampling of relocations or steps should be routinely
 307 used before the analysis of movement paths. The first reason for this is that computing
 308 some descriptors requires two relocations (e.g., distance) or two steps (turning angle),
 309 and in such circumstances, subsampling will reduce the accuracy of the estimates. The
 310 second reason is that autocorrelation is often the consequence of ecological processes. This
 311 is particularly true for long-time surveys obtained with GPS monitoring, for which the
 312 animal's "switching behaviour" is often responsible of the presence of autocorrelation. In
 313 some cases, this autocorrelation can be generated by a process unrelated to the focus issue
 314 (e.g., the mechanistic aspects of the locomotion process), which would justify eliminating it

315 prior to the analysis. However, we stress that the preliminary analysis of the autocorrelation
316 and identifying its causes are essential if we are to gain a better understanding of the
317 patterns of animal movements.

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

339 *Illustration* — The daily pattern of step lengths is represented in Fig. 2c, and is
340 characterized by two peaks of activity corresponding to long step lengths. This circadian
341 pattern with two peaks is common, and has been demonstrated for several species (Aschoff
342 1966). Hence, this circadian pattern must be taken into account before attempting any
343 other analysis of step lengths.

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

353 6 Concluding remarks

354 In these days of state-space and hierarchical Bayesian modelling (Patterson et al. 2008,
355 Schick et al. 2008), our approach may look rather old-fashioned. What is the point of data
356 exploration when models of realistic movements are available? Answers to this question
357 can be found in the old debate initiated by Tukey (1977; 1980) about exploratory and
358 confirmatory analyses. Data exploration allows one to extract what the data says, without
359 any *a priori* hypothesis. It can be useful for generating new questions/ideas, improving
360 the sampling design or guiding the choice of subsequent analyses. In the field of animal
361 movement, autocorrelation is an important property of the data that could reveal infor-
362 mation about how animals move. Patterns revealed by its exploratory analysis help to
363 generate new hypotheses about the behavioral processes related to animal mobility. These
364 hypotheses can then be tested by introducing new parameters into animal movement mod-
365 els. For instance, our example suggests that a model integrating the time of the day (e.g.
366 Preisler et al. 2004) should be used to analyse brown bear movement data. Exploratory
367 analysis and modelling of animal movements should therefore not be opposed, but rather
368 considered as two complementary approaches. The reader could consult Brillinger et al.
369 (2004) for a nice example of an exploratory analysis of animal movement data.

370 We hope that this paper will help to improve the way we tackle the question of auto-

371 correlation in animal movement analysis. An appropriate approach would consist of the
372 following steps:

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

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

- 377 • detrend the data so that autocorrelation (corresponding to processes analyzed in the
378 previous step) is eliminated;
- 379 • use detrended data in the analysis. Standard statistical tools can now be used, as
380 the observations are now independent.

381 or

- 382 • incorporate new parameters in movement models that account for the hypothesised
383 processes.

384 In order to help ecologists, functions that can be used to store and manage animal move-
385 ment paths and to measure and test autocorrelation have been included in the `adehabitat`
386 package (Calenge 2006) for the R software. The reader could consult Calenge et al. (2009)
387 for more details about these functions. Appendix 1 provides a complete example corre-
388 sponding to the brown bear illustration used in this paper.

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517 **7 Figure legend**

518 FIG. 1: Parameters used to describe steps. The n -th step is associated to its length (d_n),
 519 the increments in the X and Y directions (δx_n and δy_n), the absolute angle (α_n), the
 520 turning angle (ρ_n) and the squared net displacement (R_n^2).

521 FIG. 2: Analysis of brown bear data. (a) representation of the movement path. (b)
 522 correlogram of step lengths ($S_L(h)$). The gray area corresponds to a 95% confidence
 523 interval obtained by permutation procedure (999 permutations). The gray dotted line
 524 depicts the median of the values of the statistic computed on permuted data. Empty
 525 circles represent non-significant autocorrelation, while black squares correspond to
 526 significant values. (c) Boxplots of the daily pattern of step lengths. The line with white
 527 circles corresponds to average values. Correlogram for the detrended step lengths (d) and
 528 the trend (e). The trend corresponds to the predictions of the linear model with step
 529 length as response variable and 9 Moran's eigenvectors maps as explanatory variables;
 530 detrended data correspond to the residuals of this model.

531 FIG. 3: Using the chord distance to measure the autocorrelation for the turning angles.
 532 (a) A path of 4 steps encompasses 3 successive turning angles ρ_1 , ρ_2 and ρ_3 . (b) Small
 533 chord length corresponds to positive association between successive angles ρ_1 and ρ_2 and
 534 large chord length corresponds to "negative association" between successive angles ρ_2 and
 535 ρ_3 .

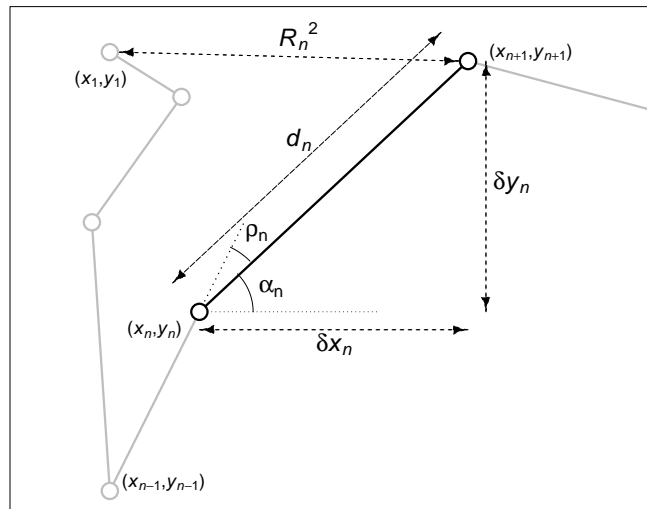


Fig. 1

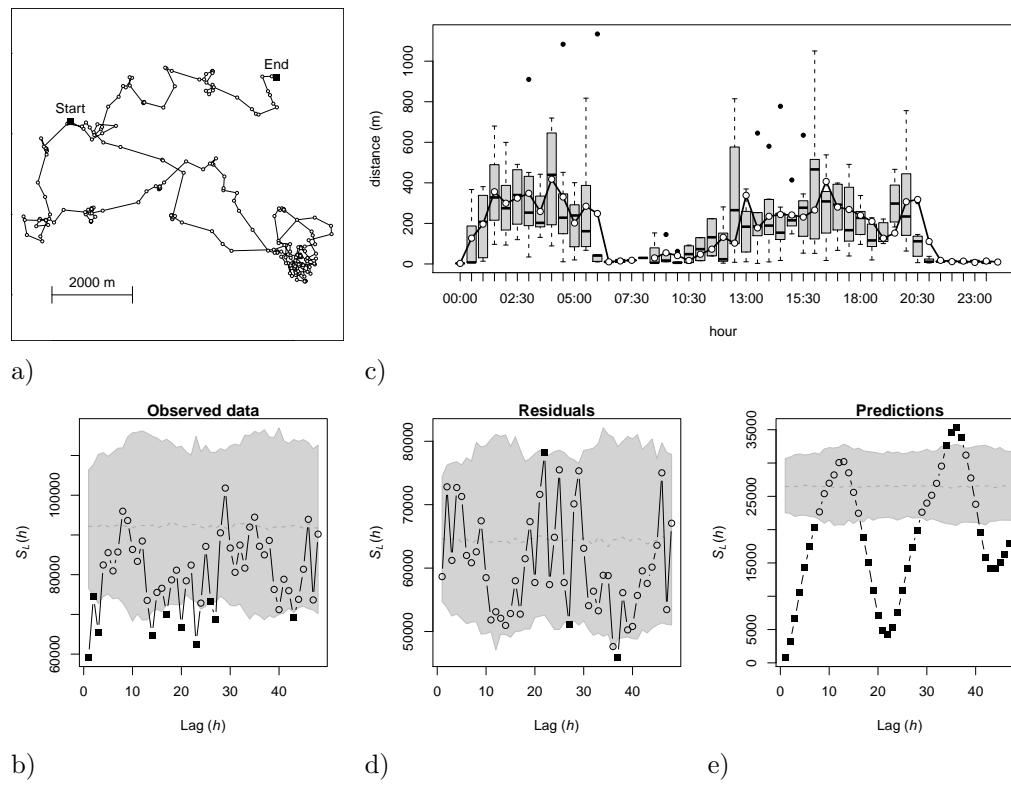
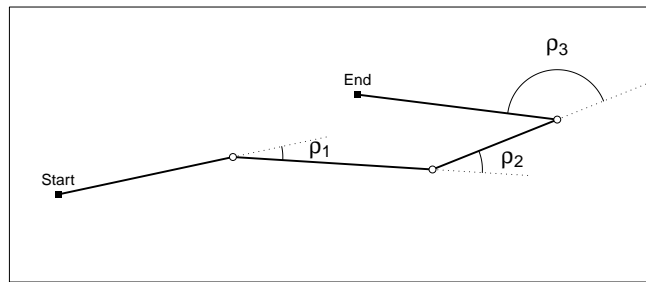
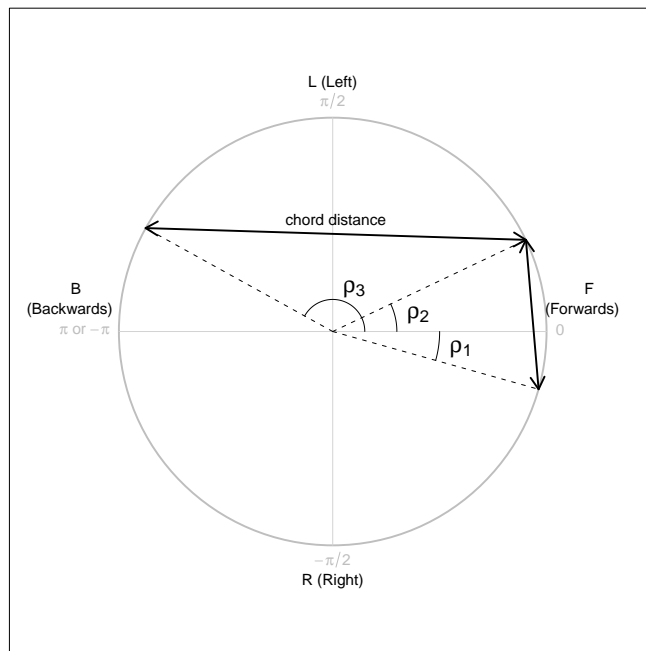


Fig. 2



a)



b)

Fig. 3