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► **To cite this version:**

Clément Calenge, S. Dray, Manuela Royer-Carenzi. The concept of animals trajectories from a data analysis perspective. *Ecological Informatics*, 2009, 4 (1), pp.34-41. 10.1016/j.ecoinf.2008.10.002 . hal-00428328

HAL Id: hal-00428328

<https://hal.science/hal-00428328>

Submitted on 18 Feb 2022

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The concept of animals trajectories from a data analysis perspective

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Abstract

The Global positioning system (GPS) has been increasingly used during the past decade to monitor the movements of free-ranging animals. This technology allows to automatically relocate fitted animals, which often results into a high-frequency sampling of their trajectory during the study period. However, depending on the objective of trajectory analysis, this study may quickly become difficult, due to the lack of well designed computer programs. For example, the trajectory may be built by several “parts” corresponding to different behaviours of the animal, and the aim of the analysis could be to identify the different parts, and thereby the different activities, based on the properties of the trajectory. This complex task needs to be performed into a flexible computing environment, to facilitate exploratory analysis of its properties. In this paper, we present a new class of object of the R software, the class “ltraj” included in the package *adehabitat*, allowing the analysis of animals’ trajectories. We developed this class of data after an extensive review of the

literature on the analysis of animal movements. This class of data facilitates the computation of descriptive parameters of the trajectory (such as the relative angles between successive moves, distance between successive relocations, etc.), graphical exploration of these parameters, as well a numerous tests and analyses developed in the literature (first passage time, trajectory partitioning, etc.). Finally, this package also contains numerous examples of animal trajectories, and a working example illustrating the use of the package.

Key words: adehabitat, Global Positioning System, animal movements, R software, trajectory analysis.

1 Introduction

Ecological data analysis finds its place at the intersection of three scientific fields (Chessel, 1992). On one hand, the Biology provides the data, the biological concepts underlying the study, and the questions asked for in a given analysis. On the other hand, the Mathematical theory provides general models permitting the development of statistical methods. Finally, Computer Science is at the junction of Biology and Mathematics: object classes are defined from the data provided by the biologists, and computational tools are designed from mathematical theory to manage and analyze these classes. Research in data analysis should develop new statistical methods, and organise them into a consistent approach of data analysis, to help biologists, to answer their questions. This statistical approach of data analysis should be developed into a flexible computing environment, to take into account the wide diversity of both

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14 questions and data collected by the biologists, and to allow an easy implemen-
15 tation.

16 Animal movements provide a good example of the complexity of ecological
17 data and of the wide variety of questions related to their analysis. There has
18 been several studies carried out to understand how the animals' space use is
19 related to both their internal constraints (e.g., biological rhythms) and their en-
20 vironment (e.g., habitat, competitors, predators). Thus, this kind of study has
21 been carried out at the individual scale to identify the external factors affect-
22 ing these movements, such as the effect of landscape heterogeneity (Johnson
23 et al., 1992; Morales and Ellner, 2002) and of patch boundaries (Schtickzelle
24 and Baguette, 2003), the seasonality of these movements (Bergman et al.,
25 2000), or the orientation mechanisms of the animals (Séguinot et al., 1998).
26 At a larger scale, several authors have used individual movements to model
27 the spatial distribution of populations (Turchin, 1996, 1998) and the whole
28 dynamics of a group of animal (Couzin et al., 2005).

29 Because of the numerous aims and data types involved in the analysis of
30 animals trajectories, a wide variety of mathematical tools have been developed.
31 Several models, such as the correlated random walk (Kareiva and Shigesada,
32 1983) or the stochastic differential equations (Brillinger et al., 2002) have been
33 developed to describe these movements. As well, several statistical methods
34 relying on these models have been proposed to reach one or the other aim of
35 trajectory analysis (e.g., Fauchald and Tveraa, 2003).

36 However, to our knowledge, no computing environment exists presently for
37 the implementation of these analyses, as animals' trajectories are complex ob-
38 jects requiring to define new data class. Indeed, common statistical softwares

39 generally provide only the most common data structures (e.g., data tables)
40 and standard statistical approaches. These softwares have generally been de-
41 veloped for commercial use, and are poorly designed for research (Tufto and
42 Cavallini, 2005; Calenge, 2006). Consequently, it is often difficult to manage
43 complex ecological objects, such as animal trajectories, in these “canned” pro-
44 grams, which hampers the research for new statistical methods.

45 In this context, open source softwares offer an alternative to standard commer-
46 cial softwares. In particular, the R software is especially suitable for ecological
47 data analysis (Tufto and Cavallini, 2005; Calenge, 2006). This software, ini-
48 tially developed by Ross Ihaka and Robert Gentleman to provide a statistical
49 environment to their laboratory in 1992, has been released as an open-source
50 software in 1995. It is now increasingly used in the scientific community, and
51 especially among ecologists. This free software relies on the programming lan-
52 guage S, a language designed to “turn ideas into softwares” (Chambers, 1998).
53 Because the number of users of the R software increases regularly, and because
54 the authors of the language S have designed it to encourage the users “to slide
55 into programming without noticing” (Chambers, 1998), more and more sta-
56 tistical methods are becoming available in the R environment. In addition,
57 the R software provides simple means to define object classes, which gives it
58 a desirable flexibility for ecological data analysis.

59 In this paper, we focus on the computational aspects of trajectories analysis.
60 We present a new object class, the class “ltraj”, developed for the R software,
61 which we designed to make it closely fit to the requirements of the biologists.
62 We first describe an overview of the existing points of view on this analysis in
63 the ecological literature. We discuss about the biological aims, the data types,
64 the parameters used to describe the trajectories, and the mathematical models

65 used in trajectory analysis. We also describe how the class “ltraj” closely fits
66 with the existing points of view in the literature. This class is available in the
67 package adehabitat (Calenge, 2006) for the free R software (R Development
68 Core Team, 2006).

69 **2 A classification of trajectories**

70 *2.1 What about the time?*

71 Basically, the trajectory is the curve described by the animal when it moves.
72 Because this movement is continuous, the sampling of the trajectory implies a
73 step of discretization, i.e., the division of this continuous curve into a number
74 of discrete “steps” connecting successive relocations of the animal (Turchin,
75 1998). Depending on the sampling protocol, two main classes of trajectories
76 can be distinguished: the trajectories of type I for which the time is not pre-
77 cisely known or not taken into account for the relocations of the trajectory,
78 and the trajectories of type II for which the time is known for each relocation.

79 On one hand, the trajectories of type I are made of a collection of relocations
80 characterised by their coordinates X and Y, as well as by an ordered factor G
81 giving the order of the relocations in the trajectory. These trajectories can be
82 obtained by sampling the tracks of the animals in the snow (Nams and Bour-
83 geois, 2004) or in the sand (Ward and Saltz, 1994). Some more specialised
84 techniques have also been used, such as thread trailing to monitor turtles
85 (Claussen et al., 1997; Iglay et al., 2006), or a fluorescent powder to monitor
86 the American Woodcock broods (Steketee and Robinson, 1995). In most cases,
87 these trajectories are characterised by equal step lengths (Turchin, 1998). The

88 pure geometrical analysis of such trajectories allow to derive interesting bio-
89 logical conclusions concerning the behaviour of an animal. For example, the
90 tortuosity of the trajectory may bring information on the foraging strategies
91 of an animal (Benhamou, 2004).

92 On the other hand, for trajectories of type II, the factor G is replaced by the
93 time T at which relocations were collected. These trajectories are generally
94 sampled using telemetry techniques (Johnson et al., 2002a,b; Franke et al.,
95 2004; Frair et al., 2005) or direct observation (Root and Kareiva, 1984; Morales
96 and Ellner, 2002). These modes of data collections often result in trajectories
97 characterised by constant time lag, which we call “regular trajectories” in the
98 rest of this paper.

99 2.2 The class “ltraj”

100 We designed the class “ltraj” in the package adehabitat (Calenge, 2006) to
101 manage and analyze animals’ trajectories in the R software. An object “ltraj”
102 may contain data collected on several animals, with several trajectories per
103 animal. Basically, an object of class “ltraj” is a list of tables (named “data
104 frames” in R), each table containing: (i) the coordinates of the relocations
105 in the trajectory (a “burst” of relocations), (ii) either their timing (type II)
106 or a numeric variable indicating their order (type I) in the trajectory, and
107 (iii) several descriptive parameters of the steps (see below). Each trajectory is
108 characterised by an attribute “ID” defining the ID of the monitored animal,
109 and an attribute “burst” giving a unique ID for each trajectory in the object.
110 The package adehabitat provides functions allowing to manage the content of
111 such objects. It is easy to subset the data, keeping only given animals or given

112 trajectories, or parts of the trajectories corresponding to specified criteria (e.g.,
113 given time limits).

114 When trajectories of type II are under study, the class “ltraj” is mainly de-
115 signed to store regular trajectories (constant time lag between relocations).
116 Indeed, recent advances in the technics for monitoring of animal movements
117 facilitate such designs, and it is generally more convenient for the biologist
118 to define a constant time lag before data collection. In addition, most models
119 used to describe animal movements (e.g., the correlated random walk, Kareiva
120 and Shigesada, 1983) and most statistical approaches (e.g., time series anal-
121 ysis, Diggle, 1990) suppose this regularity. Moreover, some of the descriptive
122 parameters of the trajectory generally used in the analysis (see below) do
123 not have any biological meaning when the time lag varies. For example, the
124 distribution of relative angles (angles between successive steps) depends on a
125 given time scale; the angle between two 10-min steps of a migrating whitestork
126 does not have the same biological meaning as the angle between two 1-day
127 steps. If the time lag varies, the underlying process varies too. For this reason,
128 most functions of `adehabitat` have been developed for “regular” trajectories.
129 Furthermore, several functions are intended to help the user to transform an
130 object of class “ltraj” into a regular object. Nevertheless, the class “ltraj” can
131 be used to store irregular trajectories, which often occurs with some modes of
132 data collection (e.g., with Argos collars).

133 The class “ltraj” deals with missing relocations in the trajectories. Missing
134 values are frequent in the trajectories of animals collected using telemetry: for
135 example, GPS collar may not receive the signal of the satellite at the time of
136 relocation, due for example to the habitat structure obscuring the signal (Frair
137 et al., 2004), or to the behaviour of the animal (e.g., a sleeping animal affects

138 the position of the collar relative to the sky, D'Eon and Delparte, 2005; Graves
139 and Waller, 2006). Because the frequency of missing values in a trajectory
140 may sometimes be high (reaching more than 20-30% on some study areas,
141 e.g. on the ibex in mountainous area, see the dataset `ibex` in the `adehabitat`
142 package), and because they may be related to biologically important variables,
143 the analysis of the patterns of missing values should be part of trajectory
144 analysis (Graves and Waller, 2006). This preliminary analysis is allowed with
145 the class “`ltraj`”. For example, runs tests can be used to test whether the
146 missing values are randomly distributed over time (function `runsNALtraj`).

147 **3 Description of trajectories**

148 *3.1 Common Descriptive parameters of the trajectories*

149 A set of parameters is needed to characterise the different aspects of the animal
150 movement (Fig. 1). Actually, the descriptive parameters used in studies of
151 animals trajectories can be categorised according to the scale at which they
152 describe the trajectory.

153 First, some parameters describe the basic unit of the trajectory - the step.
154 These measures are calculated from the coordinates of the two relocations
155 defining the step, to describe its length and orientation in space. These pa-
156 rameters include the distance between these relocations (Jones, 1977; Root
157 and Kareiva, 1984; Marsh and Jones, 1988; Morales and Ellner, 2002; Ramos-
158 Fernandez et al., 2004; Franke et al., 2004), the time lag (Siniff and Jessen,
159 1969), the speed (Siniff and Jessen, 1969; Johnson et al., 2002a; Brillinger
160 et al., 2004), the increment in the X (East-West) and Y (North-South) direc-

161 tions (Brillinger et al., 2004; Wiktorsson et al., 2004), or the “absolute” angles
162 between the step and the X direction (Marsh and Jones, 1988).

163 Moreover, some parameters describe the position of a given step relative to
164 the other steps of the trajectory. These measures include the mean squared
165 distance between the first relocation of the trajectory and the last relocation
166 of the current step (Kareiva and Shigesada, 1983; Root and Kareiva, 1984;
167 Marsh and Jones, 1988; Bovet and Benhamou, 1988; Johnson et al., 1992;
168 Ward and Saltz, 1994; Morales and Ellner, 2002; Ramos-Fernandez et al.,
169 2004; Wiktorsson et al., 2004), or the “relative” angle between the current
170 step defined by the relocations $[i, (i+1)]$ and the next one (sometimes called
171 “turning angles”, Siniff and Jessen, 1969; Jones, 1977; Root and Kareiva, 1984;
172 Marsh and Jones, 1988; Bovet and Benhamou, 1988; Zollner and Lima, 1999;
173 Morales and Ellner, 2002; Ramos-Fernandez et al., 2004; Franke et al., 2004).

174 Finally, the above statistics are often used to derive other statistics measuring
175 some particular features characterizing the whole trajectory. In this case, it
176 is supposed that the trajectory is statistically stationnary, i.e., that the sta-
177 tistical distribution of these parameters are the same all along the trajectory.
178 Thus, the tortuosity of the trajectory is an aspect reflecting the intensity of
179 the search for food by animals, and is for this reason one of the most studied
180 properties. It has been estimated by the fractal dimension of the trajectory
181 (Claussen et al., 1997; Laidre et al., 2004; Nams and Bourgeois, 2004), its
182 spectral dimension (Johnson et al., 1992), and various coefficients of tortu-
183 osity related to the variance of the the circular distribution of the relative
184 angles (Bovet and Benhamou, 1988; Benhamou, 2004; Claussen et al., 1997).
185 For very long trajectories, home range estimators of sedentary animals can be
186 understood as indices reflecting both the length and the tortuosity of this tra-

187 jectory (Benhamou, 1998). For a given trajectory, the above statistics assume
188 that the trajectory is stationary. When it is not, it has been advised to use
189 them for subparts of the trajectories, e.g., using sliding windows (Benhamou,
190 2004).

191 Note that the computation of a given parameter depends on the type of avail-
192 able data. Thus, it does not make sense to work on the time lag between
193 successive relocations for regular trajectories of type II. On the other hand,
194 as noted above the computation of relative angles is not suitable for irregular
195 trajectories of type II.

196 *3.2 Descriptive parameters in the objects of class "ltraj"*

197 Owing to Marsh and Jones (1988), a good description of the trajectory is
198 achieved when the following criteria are fulfilled: (i) the description is achieved
199 using a limited set of relatively easily measured parameters; (ii) the rela-
200 tionships between these parameters are precisely defined (with the help of
201 a model), and (iii) the parameters and the relationships between them are
202 sufficient to reconstruct characteristic tracks without losing any of their sig-
203 nificant properties. Thus, for each relocation of an object of class "ltraj", a
204 minimum set of descriptive parameters of the steps is automatically computed
205 and included in the table describing each burst (Fig. 1). For a given relocation
206 i , the increment of the step in the X and Y directions (i.e., $\delta X_i = X_i - X_{i-1}$
207 and $\delta Y_i = Y_i - Y_{i-1}$), as well as the time lag ($\delta t = t_i - t_{i-1}$) are computed.
208 These three parameters are sufficient to reconstruct the trajectory, and are
209 used by several mathematical models to describe the trajectories (stochastic
210 differential equations, Brillinger et al., 2002).

211 Another family of models (see below) characterise the step defined by the
212 relocations $[(i - 1), i]$ by its length and either the “absolute” angle between
213 this step and the X direction (e.g., biased random walk, Marsh and Jones,
214 1988), or the “relative” angle between this step and the previous step defined
215 by the relocations $[i, (i + 1)]$ (e.g., correlated random walk). The increment in
216 X and Y can be used to derive the length of the step, and both the relative and
217 absolute angles are automatically computed when an object of class “ltraj” is
218 created.

219 Finally, for each relocation, the squared net displacement between the cur-
220 rent relocation and the first relocation of the trajectory is also automatically
221 computed, as a large amount of research has been performed on this measure
222 during the last decades and theoretical values are available for several models,
223 for example for the correlated random walk (Kareiva and Shigesada, 1983;
224 Bovet and Benhamou, 1988), or the brownian motion (Jammalamadaka and
225 SenGupta, 2001).

226 4 Statistical analyses

227 4.1 Models describing animals trajectories

228 Most often the analysis implies the use of models to identify the patterns in
229 the trajectories, or to summarise the trajectory with a small set of parameters.

230 Two broad classes of trajectory models have been used by ecologists until now.

231 The first class includes models developed by physicians to describe the move-
232 ment of particles. They generate theoretical trajectories sequentially, using the

233 last step of the trajectory as a reference to build an additional step. These
234 models generally describe a step of the trajectory by the relative angle between
235 the step and the preceding step (randomly drawn from a circular distribution),
236 and by the length of this step. Note that trajectories of type II are supposed
237 to be regular (as the relative angle only has a sense at a given time scale).
238 Several models developed in physics are used for a long time in ecology, such
239 as the correlated random walk (Kareiva and Shigesada, 1983), or the biased
240 random walk (Marsh and Jones, 1988). The main quality of these models
241 is their simplicity, which explains their success (Ward and Saltz, 1994). Note
242 that other models used in physical science have been introduced more recently
243 in ecology, such as the Lévy flight (Viswanathan et al., 1996, 1999; Ramos-
244 Fernandez et al., 2004). Actually, several authors have noted that advances in
245 physics can be of use for ecologists (e.g., Johnson et al., 1992).

246 The second class of models has been developed in probability, and especially
247 in the field of random processes analysis. Such models have been widely used
248 in financial sciences to model economic processes (e.g., Osborne, 1972). In
249 ecology, they are intended to model trajectories of type II (time known), and
250 do not make any assumption on the regularity of the trajectories (continuous
251 time). The position of the relocation at time t is generally determined by
252 adding to the relocation collected at time $t - 1$ a bivariate vector describing
253 the increment in X and Y of the trajectory. The Ornstein-Uhlenbeck process is
254 probably the first model belonging to this class that has been used in ecology to
255 describe animals movements (Dunn and Gipson, 1977; Blackwell, 1997). Other
256 models, such as state-space models (Bayesian approach of trajectory analysis,
257 Jonsen et al., 2003) or stochastic differential equations (Brillinger et al., 2002,
258 2004; Preisler et al., 2004) have also been proposed. Their complexity make

259 them more difficult to use, but they are generally highly parametrizable,
260 allowing to take into account a wide variety of patterns.

261 No model will ever allow to take into account the whole complexity of the
262 animal behavior. However, all the above models can be used as reference to
263 which the observed trajectories are compared (i.e., null models). For exam-
264 ple do the studied trajectory exhibit smaller relative angles than theoretical
265 trajectories generated by this model (indicating some autocorrelation in the
266 direction chosen by the animal from one step to the next)? Are the relative an-
267 gles autocorrelated in the trajectory, indicating possible changes in behaviour?

268 *4.2 Analysis of trajectories in adehabitat*

269 Many approaches have been used in the literature to analyze animals trajec-
270 tories. However, as noted above the questions of the biologists are various and
271 the types of data are even more diverse. Consequently, each study is particular,
272 and no universal recipe to analyze animals trajectories can be given. However,
273 a set of tools is provided by the package adehabitat to help the biologist to
274 build an analytic approach, given the data at hand (Fig. 2).

275 First, the package adehabitat contains functions allowing a dynamical explo-
276 ration of the trajectory (function `trajdyn`). The graphical exploration of the
277 statistical distribution of the descriptive parameters is also facilitated by func-
278 tions of the powerful R environment (histograms, quantile plots, etc., Cleve-
279 land, 1993).

280 An important aspect of trajectory analysis is the question of the indepen-
281 dence of the descriptive parameters within the trajectory (Root and Kareiva,

282 1984). For example, under the hypothesis that the trajectory has been gener-
283 ated by a correlated random walk, the relative angles associated to the steps
284 should be independently distributed within the trajectory. If there is a pos-
285 itive autocorrelation of the relative angles (i.e., a small angle is followed by
286 a small angle), this indicates that some parts of the trajectories are charac-
287 terised by linear movements (between-patch movements) and others by more
288 sinuous movements (e.g., foraging movements inside a patch of resource): the
289 trajectory is not stationnary. Dray et al. (in prep.) provided criteria to test
290 the independence of each one of the parameters (function `testang.ltraj` for
291 the absolute and relative angles, `indmove` for a simultaenous test of the inde-
292 pendence of increment in the X and Y direction, `testdist.ltraj` for the step
293 length, and `wawotest` for separate tests in the X and Y directions). Based on
294 these criteria, they also developed methods allowing to identify the degree of
295 the autocorrelation of these parameters, i.e. whether a given step i is depen-
296 dent only on the step $i - 1$, or also of the step $i - 2$, $i - 3$, etc. (functions
297 `acfdist.ltraj` and `acfang.ltraj`). Note that, under certain models, some
298 parameters are expected to be independent, whereas they are expected to be
299 autocorrelated under other models. For example, the increments in the X di-
300 rection are expected to be independent under the Brownian process, whereas
301 they are expected to to be autocorrelated with the Ornstein-Uhlenbeck process
302 (Royer-Carenzi et al. in prep.).

303 The issue of the non-stationnarity of the trajectories raises the question of the
304 identification of these behavioural bouts based on the shape of the trajectory
305 (Fauchald and Tveraa, 2003; Schwager et al., 2007), and of their organisation
306 according to the environment and the internal constraints (seasonnal or circa-
307 dian rythms) of the animal (Johnson et al., 2002a; Morales and Ellner, 2002;

308 Franke et al., 2004). As noted by Morales and Ellner (2002), “the main chal-
309 lenge for scaling up movement patterns resides in the complexities of individual
310 behavior rather than in the spatial structure of the landscape”. The package
311 `adehabitat` provides functions allowing to investigate the non-stationnarity of
312 the descriptive parameters of the trajectories: functions allow to draw time
313 plots (function `plotltr`), to apply a smoothing function to the parameters
314 describing the trajectory in a sliding window (function `sliwinltr`). Further
315 studies may imply the partition of a trajectory into segments corresponding to
316 a stationnary behaviour of the animal, e.g., using the K-means algorithm (as
317 recommended by Schwager et al., 2007, function `kmeans`). The study of the
318 non-stationnarity can also be done using time series analysis (Diggle, 1990),
319 easily implemented in the R environment (e.g., functions `spectrum` for the
320 periodogram, `acf` for the autocorrelation function, etc.).

321 Note that it can be useful to compare the distribution of descriptive param-
322 eters computed for one trajectory with the distribution expected with theo-
323 retical models for the trajectory, using simulations. Therefore, we also imple-
324 mented several models of animal trajectories in `adehabitat`. Thus, the function
325 `simm.brown` simulates a Brownian motion. The function `simm.mba` simulates
326 the arithmetic Brownian process (takes into account a potential drift in the
327 move, and/or a correlation structure between the increments in the X and
328 Y direction, Royer-Carenzi et al. in prep.). The function `simm.mou` simulates
329 a bivariate Ornstein-Uhlenbeck process (Blackwell, 1997; Dunn and Gipson,
330 1977). These three functions simulate special cases of process belonging to
331 the family of the stochastic differential equation (Brillinger et al., 2002, 2004;
332 Preisler et al., 2004). We also included a function named `simm.crw` to simulate
333 the correlated random walk (takes into account a unimodal distribution of the

334 relative angles between successive steps). Finally, the function `simm.levy` im-
335 plements an algorithm to simulate the Levy walk (Viswanathan et al., 1999;
336 Bartumeus et al., 2005) a family of models taking into account an exponential
337 distribution of the steps length).

338 In case of stationnarity, if an acceptable model has been chosen for the trajec-
339 tory, then the whole trajectory can be summarised by the parameters of the
340 model, and a study at a larger scale can be carried out to compare the value
341 of these parameters with those of trajectories sampled in different conditions
342 (different animals, different time period, etc.). The R environment contains
343 numerous functions facilitating this study. For example, the R package `Circ-`
344 `Stats` contains several functions implementing tests for circular data, so that it
345 is straightforward to compare the concentration parameters of the distribution
346 of relative angles between two or more trajectories.

347 More complex cases can however arise, for example when several trajectories
348 of an animal show a significant autocorrelation of a given parameter, whereas
349 other do not. It might be, for example, because the biological constraints dif-
350 fer between the two trajectories (some trajectories might have been collected
351 during the rutting period and the other during rearing-young period). It is
352 difficult to give here any universal recipe to deal with such cases: The decision
353 should be taken case-by-case according to the data and the biological aims.

354 Note that several functions have been implemented in `adehabitat` to facilitate
355 the study of the effect of the time or spatial scale of the study on the descriptive
356 parameters of the trajectories. Thus, the function `subsample` allows to change
357 the time lag between successive relocation for regular trajectories of type II
358 (e.g., to compute a trajectory sampled every 20 minutes instead of 10 min-

359 utes). When trajectories of type I are under study, the function `redisltraj`
360 can be used to discretize the trajectory into steps of specified length, as
361 recommended by several authors (Bovet and Benhamou, 1988; Turchin, 1998;
362 Benhamou, 2004). The function `fpt` (for regular trajectories of type II) can
363 be used to identify the scale at which animals concentrate their search when
364 they forage (Fauchald and Tveraa, 2003).

365 Finally, other functions of `adehabitat` may be used to manage vector or raster
366 maps of environmental variables (Calenge, 2006). Several basic operations can
367 be performed with this package: a buffer can be computed around the tra-
368 jectories (i.e., identify the area comprised within a specified distance of the
369 trajectory), an operation sometimes needed to compute some descriptive pa-
370 rameters of the trajectories not automatically computed in the object of class
371 “`ltraj`” (Doerr and Doerr, 2005). The value of mapped environmental variables
372 can be determined for each relocation, allowing analyses of habitat selection.

373 **5 Discussion**

374 For a long time, animals trajectories have been mainly studied on insects,
375 which are easy to monitor visually (Jones, 1977; Root and Kareiva, 1984;
376 Johnson et al., 1992; Schultz, 1998). However, for large and “shy” species such
377 as ungulates, direct observation of the animals was not possible, and the study
378 of movements often relied on radio-tracking (e.g., Maillard, 1996). However,
379 the collection of relocations at short time lags on several animals requires
380 an important staff and a heavy protocol, so that these studies were rather
381 scarce in the ecological literature. The recent development of GPS (Global
382 Positioning System) has facilitated this type of study. Indeed, GPS collars

383 allow the automatic collection of animals' relocations, so that the movements
384 are often sampled at regular and short time lag. The increasing use of GPS
385 collars now renders possible the study of movement on species for which this
386 kind of study was difficult before (Johnson et al., 2002a,b; Franke et al., 2004;
387 Frair et al., 2005).

388 In this paper, we presented a new class of data, the class "ltraj", intended to
389 manage and analyze animals trajectories in the R software. Designing a class
390 of object for R is interesting from a methodologist perspective: the structure
391 of the class reflects a point of view of the programmer on the biological object
392 and on its analysis. Thus, we had to identify the different types of trajectories
393 that can be encountered (time recorded or not, regular or not, etc.); numerous
394 decisions had to be made concerning the class itself - for example, we did
395 not allow additional variables (e.g., environmental variables, or measures of
396 precision of the relocations) to be included in the object "ltraj" with other
397 descriptive parameters of the steps, as this class is intended to store only
398 purely geometrical properties of the trajectory.

399 This point of view was developed after an extensive review of the ecologi-
400 cal literature on trajectory analysis, which we summarized in this paper. We
401 also based our reflexion on a large amount of trajectories collected on a large
402 diversity of species (bears, wild boars, albatross, hooded seals, porpoise, roe
403 deer, moufflons, ibex, etc.), monitored mainly using telemetry modes of data
404 collection (GPS, Argos, radio-tracking). For this reason, the package adehabi-
405 tat contains a large number of example trajectories, which shows the large
406 diversity of data that can be encountered in biological studies. All the func-
407 tions are documented in help files, which present examples of their use in the
408 context they are to be used. Note also that typing `demo(managltraj)` in the

409 R console performs a sample session giving examples of use of the package
410 for management of trajectories, and typing `demo(analysisltraj)` provides a
411 working example of trajectory analysis.

412 This class was developed within a group of researchers composed of numerous
413 biologists, methodologists and mathematicians. The discussions between spe-
414 cialists of these three fields allowed to develop this class, which in turn was
415 discussed to develop an approach of statistical analysis of animal trajectories
416 (Dray et al. in prep.; Royer-Carenzi et al. in prep). We hope that the present
417 approach will serve as a basis for future methodological developments.

418 **Acknowledgements**

We are grateful to the Agence nationale pour la recherche (project “mobilité”
number ANR-05-BDIV-008) and to the Office national de la chasse et de la
faune sauvage for their financial support. We warmly thank the members of the
GRHA (groupe de recherche sur l’habitat) for the fruitful discussions about
trajectory analysis.

419 **References**

- 420 Bartumeus, F., da Luz, M., Viswanathan, G., Catalan, J., 2005. Animal search
421 strategies: a quantitative random-walk analysis. *Ecology* 86, 3078–3087.
- 422 Benhamou, S., 1998. Le domaine vital des mammifères terrestres. *Rev. Ecol.*
423 - *Terre Vie* 53, 309–334.
- 424 Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal’s

425 path: straightness, sinuosity, or fractal dimension? *J. Theor. Biol.* 229, 209–
426 220.

427 Bergman, C., Schaefer, J., Luttich, S., 2000. Caribou movement as a correlated
428 random walk. *Oecologia* 123 (364-374).

429 Blackwell, P., 1997. Random diffusion models for animal movement. *Ecol.*
430 *Model.* 100, 87–102.

431 Bovet, P., Benhamou, S., 1988. Spatial analysis of animal’s movements using
432 a correlated random walk model. *J. Theor. Biol.* 131, 419–433.

433 Brillinger, D., Preisler, H., Ager, A., Kie, J., 2004. An exploratory data anal-
434 ysis (EDA) of the paths of moving animals. *J. Stat. Plan. Infer.* 122, 43–63.

435 Brillinger, D., Preisler, H., Ager, A., Kie, J., Stewart, B., 2002. Employing
436 stochastic differential equations to model wildlife motion. *Bulletin of the*
437 *Brazilian Mathematical Society* 33, 385–408.

438 Calenge, C., 2006. The package adehabitat for the r software: a tool for the
439 analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519.

440 Chambers, J., 1998. *Programming with data*. Springer, New York.

441 Chessel, D., 1992. *Echanges interdisciplinaires en analyse de données*
442 *écologiques*. Mémoire d’habilitation, Université Claude Bernard Lyon 1,
443 Lyon.

444 Claussen, D., Finkler, M., Smith, M., 1997. Thread trailing of turtles: methods
445 for evaluating spatial movements and pathway structure. *Can. J. Zool.* 75,
446 2120–2128.

447 Cleveland, W., 1993. *Visualizing data*. AT&T Bell Laboratories/Hobart Press,
448 Murray Hill.

449 Couzin, I., Krause, J., Franks, N., Levin, S., 2005. Effective leadership and
450 decision making on the move. *Nature* 433, 513–516.

451 D’Eon, R., Delparte, D., 2005. Effects of radio-collar position and orientation

452 on GPS radio-collar performance, and the implication of DPDOP in data
453 screening. *J. Appl. Ecol.* 42, 383–388.

454 Diggle, P., 1990. *Time Series. A biostatistical introduction.* Clarendon press,
455 Oxford.

456 Doerr, E., Doerr, V., 2005. Dispersal range analysis: quantifying individual
457 variation in dispersal behaviour. *Oecologia* 142, 1–10.

458 Dunn, J., Gipson, P., 1977. Analysis of radio telemetry data in studies of home
459 range. *Biometrics* 33, 85–101.

460 Fauchald, P., Tveraa, T., 2003. Using first passage time in the analysis of area
461 restricted search and habitat selection. *Ecology* 84, 282–288.

462 Frair, J., Merrill, E., Visscher, D., Fortin, D., Beyer, H., Morales, J., 2005.
463 Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in
464 forage resources and predation risk. *Landscape Ecol.* 20, 273–287.

465 Frair, J., Nielsen, S., Merrill, E., Lele, S., Boyce, M., Munro, R., Stenhouse,
466 G., Beyer, H., 2004. Removing GPS collar bias in habitat selection studies.
467 *J. Appl. Ecol.* 41, 201–212.

468 Franke, A., Caelli, T., Hudson, R., 2004. Analysis of movements and behaviour
469 of caribou (*Rangifer tarandus*) using hidden markov models. *Ecol. Model.*
470 173, 259–270.

471 Graves, T., Waller, J., 2006. Understanding the causes of missed global posi-
472 tioning system telemetry fixes. *J. Wildlife Manage.* 70, 844–851.

473 Iglay, R., Bowman, J., Nazdrowicz, N., 2006. A comparison of two methods
474 for studying box turtle movements. *Wildlife Soc. B.* 31, 208–209.

475 Jammalamadaka, S., SenGupta, A., 2001. *Topics in circular statistics. Vol. 5*
476 *of Series on Multivariate analysis.* World scientific, London.

477 Johnson, A., Wiens, J., Milne, B., Crist, T., 1992. Animal movements and
478 population dynamics in heterogeneous landscapes. *Landscape Ecol.* 7, 63–

479 75.

480 Johnson, C., Parker, K., Heard, D., Gillingham, M., 2002a. Movement param-
481 eters of ungulates and scale-specific responses to the environment. *J. Anim.*
482 *Ecol.* 71, 225–235.

483 Johnson, C., Parker, K., Heard, D., Gillingham, M., 2002b. A multiscale be-
484 havioral approach to understanding the movements of woodland caribou.
485 *Ecol. Appl.* 12, 1840–1860.

486 Jones, R., 1977. Movement patterns and egg distribution in cabbage butter-
487 flies. *J. Anim. Ecol.* 46, 195–212.

488 Jonsen, I., Myers, R., Flemming, J., 2003. Meta-analysis of animal movement
489 using state-space models. *Ecology* 84, 3055–3063.

490 Kareiva, P., Shigesada, N., 1983. Analysing insect movement as a correlated
491 random walk. *Oecologia* 56, 234–238.

492 Laidre, K., Heide-Jorgensen, M., Logsdon, M., Hobbs, R., Dietz, R., VanBlari-
493 com, G., 2004. Fractal analysis of narwal space use patterns. *Zoology* 107,
494 3–11.

495 Maillard, D., 1996. Occupation et utilisation de la garrigue et du vignoble
496 méditerranéens par le sanglier (*sus scrofa l.*). Ph.D. thesis, Université de
497 droit, d'économie et des sciences d'Aix-Marseille III.

498 Marsh, L., Jones, R., 1988. The form and consequences of random walk move-
499 ment models. *J. Theor. Biol.* 133, 113–131.

500 Morales, J., Ellner, S., 2002. Scaling up animal movements in heterogeneous
501 landscapes: the importance of behavior. *Ecology* 83, 2240–2247.

502 Nams, V., Bourgeois, M., 2004. Fractal analysis measures habitat use at dif-
503 ferent spatial scales: an example with American marten. *Can. J. Zool.* 82,
504 1738–1747.

505 Osborne, M., 1972. Random nature of stock market prices. *Journal of Eco-*

506 nomics and Business 6, 220–233.

507 Preisler, H., Ager, A., Johnson, B., Kie, J., 2004. Modeling animal movements
508 using stochastic differential equations. *Environmetrics* 15, 643–657.

509 R Development Core Team, 2006. R: A Language and Environment for Statis-
510 tical Computing. R Foundation for Statistical Computing, Vienna, Austria.
511 URL <http://www.R-project.org>

512 Ramos-Fernandez, G., Mateos, J., Miramontes, O., Cocho, G., 2004. Levy walk
513 patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*).
514 *Behav. Ecol. Sociobiol.* 55, 223–230.

515 Root, R., Kareiva, P., 1984. The search for resources by cabbage butterflies
516 (*Pieris Rapae*): Ecological consequences and adaptive significance of Marko-
517 vian movements in a patchy environment. *Ecology* 65, 147–165.

518 Schtickzelle, N., Baguette, M., 2003. Behavioural responses to habitat patch
519 boundaries restrict dispersal and generate emigration-patch area relation-
520 ships in fragmented landscapes. *J. Anim. Ecol.* 72, 533–545.

521 Schultz, C., 1998. Dispersal behavior and its implications for reserve design in
522 a rare Oregon butterfly. *Conserv. Biol.* 12, 284–292.

523 Schwager, M., Anderson, D., Butler, Z., Rus, D., 2007. Robust classification
524 of animal tracking data. *Computer and Electronic in Agriculture* in press.

525 Séguinot, V., Cattet, J., Benhamou, S., 1998. Path integration in dogs. *Anim.*
526 *Behav.* 55, 787–797.

527 Siniff, D., Jessen, C., 1969. A simulation model of animal movement patterns.
528 *Adv. Ecol. Res.* 6, 185–219.

529 Steketee, A., Robinson, W., 1995. Use of fluorescent powder for tracking Amer-
530 ican woodcock broods. *Auk* 112, 1043–1045.

531 Tufto, J., Cavallini, P., 2005. Should wildlife biologists use free software?

532 Wildlife Biol. 11, 67–76.

533 Turchin, P., 1996. Fractal analyses of animal movement: a critique. Ecology
534 77, 2086–2090.

535 Turchin, P., 1998. Quantitative analysis of movement. Sinauer Associates, Sun-
536 derland, MA.

537 Viswanathan, G., Afanasyev, V., Buldyrev, S., Murphy, E., Prince, P., Stanley,
538 E., 1996. Lévy flight search patterns of wandering albatrosses. Nature 381,
539 413–415.

540 Viswanathan, G., Buldyrev, S., Havlin, S., da Luz, M., Raposo, E., Stanley,
541 E., 1999. Optimizing the success of random searches. Nature 401, 911–914.

542 Ward, D., Saltz, D., 1994. Foraging at different spatial scales: dorcas gazelles
543 foraging for lilies in the negev desert. Ecology 75, 48–58.

544 Wiktorsson, M., Ryden, T., Nilsson, E., Bengtsson, G., 2004. Modelling the
545 movement of a soil insect. J. Theor. Biol. 231, 497–513.

546 Zollner, P., Lima, S., 1999. Search strategies for landscape-level interpatch
547 movements. Ecology 80 (3), 1019–1030.

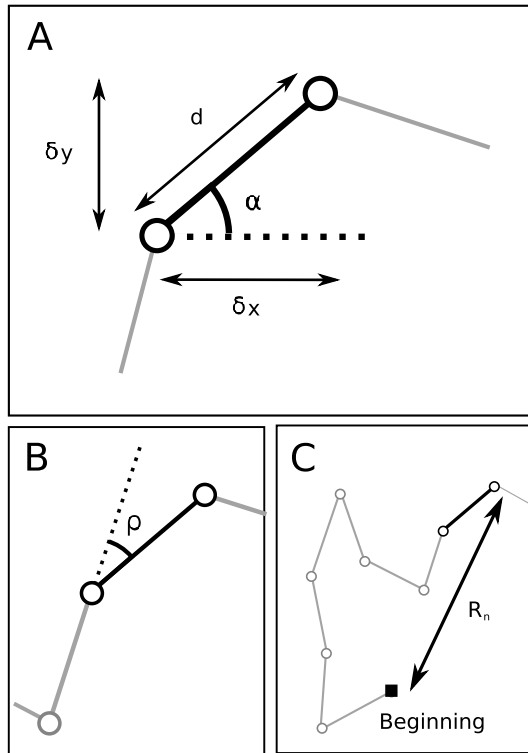


Figure 1. Descriptive parameters of a trajectory automatically computed by ade-habitat in an object of class “ltraj”: (A) parameters describing the basic unit of the trajectory – the step: increments in the X and Y direction, respectively δx and δy , the step length d and the absolute angle between the step and the X direction α ; (B) the relative angle ρ measures the angle between the current step and the direction of the previous step; (C) the mean squared displacement R_n^2 is the square of the distance between the first relocation and the current relocation of the animal.

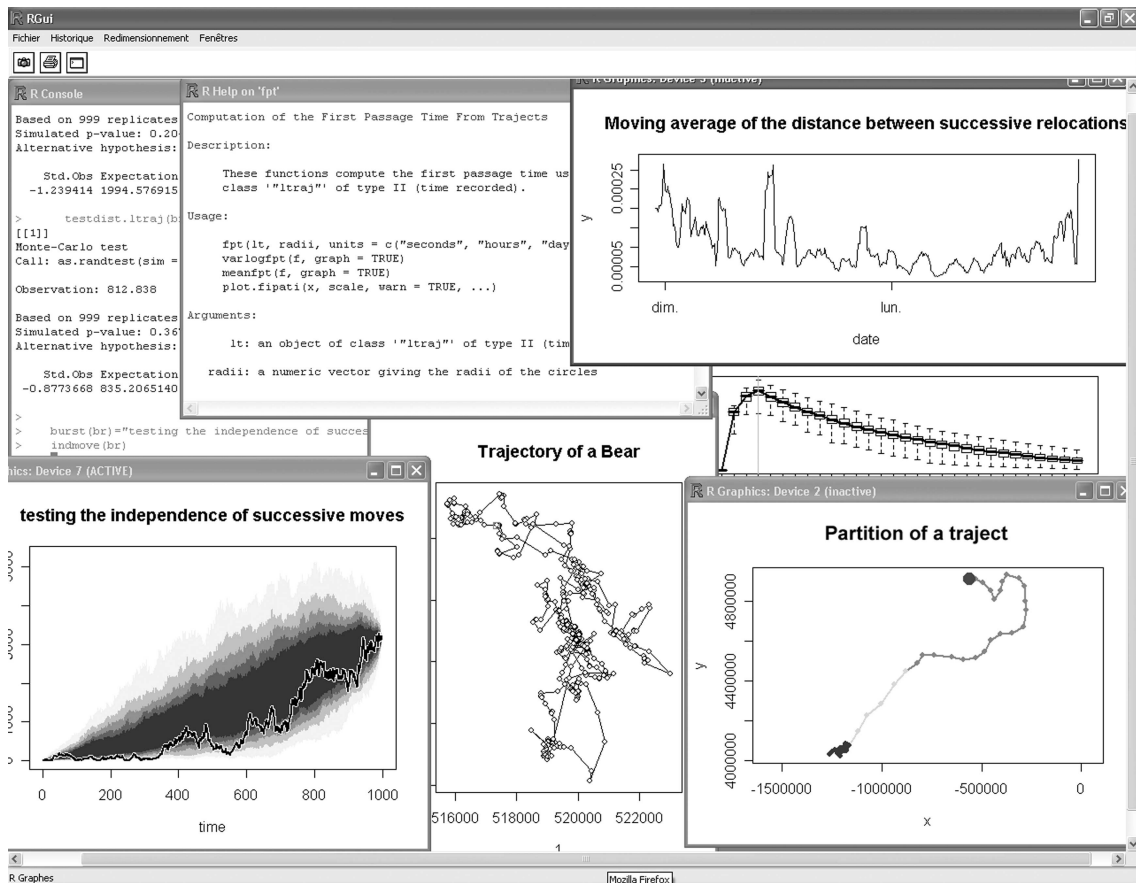


Figure 2. Capture screen of one R session with adehabitat, showing a small portion of the analysis possibilities with the class “ltraj”.