



**HAL**  
open science

## Statistics of animal movement

Geoffroy C.B. Berthelot, Vincent Bansaye, C. Calenge

► **To cite this version:**

Geoffroy C.B. Berthelot, Vincent Bansaye, C. Calenge. Statistics of animal movement. [Technical Report] Centre de Mathématiques Appliquées, École Polytechnique, France. 2013. hal-01792314

**HAL Id: hal-01792314**

**<https://insep.hal.science/hal-01792314v1>**

Submitted on 15 May 2018

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Statistics of animal movement

G. Berthelot, V. Bansaye, C. Calenge

Tuesday 13<sup>th</sup> August, 2013

## 1 Introduction

The tracking of animals using the modern global positioning system telemetry (GPS) allowed for the collection of important datasets on animal locations. They are often used for the analysis of the home range behavior and, more generally, to better understand the spatial and temporal behavior of animals [1]. Classical and modern approaches for the modeling of animal movements include a wide range of methodologies, partly borrowed from the field of statistical physics: biased and correlated random walks (BCR) [2, 3, 4, 5], Lévy Flight [6, 7], Stochastic Differential Equation (SDE) [8, 9, 10, 11], etc. Lévy Flight have convenient patterns but ecological motivations on the behavior are scarce. BCR and its derivatives are well fitted for the interpretation in discrete time, which is adapted to GPS data [12] and it is what was considered as a model in the current case. SDE being the continuous analog or Brownian bridge and Movement Model [13] may be used to interpolate the trajectory between two points. These approaches include a drift (directional) and one or several random diffusion processes [12, 11]. This study aims at modeling animal motion on sufficiently large scales, short periods without reproduction and no cohort or group effects.

We focus on BCR models in order to make the ecological interpretation fit with the data and let the model be mathematically tractable. The parameters of a BCR can be directly interpreted in terms of the behavior of the animal and correspond in particular to the attraction of some points, the inertia and memory feature of its movement, time dependence of its behavior, local interactions with other individuals, etc. Moreover, the discrete time is well adapted to regular GPS data. We here want to identify the significant ecological parameters of such a model and put in light ‘simple models’, which could be investigated mathematically and sophisticated later on. In this paper, the BCR model is tested on both the way it gives a good description of the animal behavior and the fact that it yields a good model to investigate censusing issues. More precisely, we compare several BCR models with real data by considering several statistics linked to these questions, as detailed below.

When investigating the whole trajectory of an animal, different behaviors are observable and we take into account the random aspects, advection component and aim to later include the effect of the landscape or time inhomogeneity and interactions.

- *Diffusion* term: it corresponds to a random movement, where the individuals have the same probability to go in each direction. In the discrete model we consider even weights in each of the eight closest neighbors of  $\mathbb{Z}^2$ . In the continuous space analogue, we are considering a random angle with uniform distribution, whereas the continuous time analogue yields the brownian component  $\sigma$  of the SDE.
- *Home attraction*: the motion of the animal is not isotropic (Fig. 8) and is confined in an area or domain, according to Burt [14] and recent studies [15]. A natural way to include these features is to increase the probability to go to a fixed attractive point named *deme*. The attraction may depend on the distance from the deme [16]. This yields a drift or advection term in the direction of the home, introduced as an additional weight  $p_F$  in the transition matrix in the direction of the estimated home location.
- *Inertia and Behavior*: The motion of the animal is also shaped by searching(exploration)/foraging tasks where the animal alternates exploration periods with straightforward movements [17]. It is

taken into account by adding an additional term *inertia* to follow the previous directions of the movement and is implemented as a weight  $p_I$ . We referred to [18] for discussions about the memory of the animal and the influence on its motion.

- *Immobility*: When plotting the distribution of the covered Euclidean distances between two successive observations, some cases are observed where the animals did not covered a significant distance (ie.  $< 10\text{m.}$ , Fig. 7). This can be accredited to technological limitations with the satellite telemetry due to a weak GPS signal strength (ie. due to natural elements: when the animal was standing underneath a rock or due to dense clouds, dust particles, mountains, flying objects, such as airplanes). However, this can also be part of the behavior of the animals, in specific occasions: sleep cycle for instance. We include a specific term of spatial immobility  $p_s$ , and use a truncated law to draw the distance covered between two successive steps of the simulation.
- *Time inhomogeneity*: When investigating the whole trajectory of an animal, different behaviors were observed, depending on the time: according to Morales et al. the animal sometimes move less with a mainly diffusive movement [17]. In the initial approach, the behavior just depends on the time of the day and we do not yet consider a hidden Markov chain yielding the behavior of the animal. This is supported by Morales et al, as they suggest that having two possible behaviors is important, more than the way they occur [19]. Time inhomogeneity may affects many parameters, including inertia and distance covered.

As a first approach, we here consider one individual of a given specie with no interaction and simulate its motion in 2 dimensions. Both issues are mathematically difficult to implement and this work was intended as a first step before including more complicated environmental aspects of individual motion.

The random motion of the animal is modeled by a chain  $X_n$  characterized by a transition matrix. We use a data-set to calibrate and validate our model. The data consists in 13 animals from 3 different species: 5 deers, 3 mouflons and 5 bears. The GPS observations are used to estimate the different parameters of the model, compare the animals and species and test the different assumptions of the model: memory, inertia, ... Accordingly the model is tuned and simulated a number of times to test the different hypotheses. Each simulation is evaluated against the real data through 4 simple statistics that provide the features of an individual's motion. Statistics are designed to test the model on (i) angular distribution of two successive steps, (ii) home-range of the individual and (iii) censusing issues. We use an estimate of the living area using the approach of [20] and by dilatation of the trajectory. Censusing statistics are performed on counting an animals positions from a fixed or moving localization. We compute statistics for both the simulated and real trajectories and compare the results. In the first part, we describe the method and vocabulary. In the second part, we make the estimations of the parameters, test the assumptions and compare/comment. In the final part, we consider the statistics of interest of this paper regarding the motivations questions.

The following issues arise from the observed trajectories: memory feature of animal motion (do we get some Markov property ?), cycles (ie. periodicity of the motion) and U-turns (backward-like motion). Those features are mathematically tricky and we use a reduced number of simple parameters as a first approximation of animal motion.

## 2 Materials and methods

### 2.1 Data

We gather the GPS observations of 13 animals (5 deers, 3 mouflons and 5 bears, table ??). The standard deviation (s.d.) and missing data on the time between two observations in both the mouflons and bears are significant. In order to avoid irregular observation frequencies, we focus on the deers.

Animal	$n$	period of collection	average time between 2 observations (min.) $\pm$ s.d.	TOTAL distance (km.)	time (days)	average speed ( $10^{-2}$ m.s $^{-1}$ )
Deer 1	29520	09/01/2010 00:00:00 - 11/08/2010 23:50:00	$10.49 \pm 3.18$	945.67	214.99	5.09
Deer 2	27324	10/12/2009 00:00:00 - 24/06/2010 23:50:00	$10.38 \pm 3.69$	1030.97	196.99	6.06
Deer 3	23301	16/03/2010 00:00:00 - 07/09/2010 23:41:00	$10.88 \pm 8.67$	876.33	175.99	5.76
Deer 4	24735	22/01/2010 00:00:00 - 21/07/2010 23:51:00	$10.54 \pm 5.16$	898.38	180.99	5.74
Deer 5	21451	16/01/2010 00:01:00 - 24/06/2010 07:31:00	$10.69 \pm 10.11$	785.93	159.31	5.71
Mouflon 1	4957	18/06/2006 03:00:00 - 09/09/2007 23:00:00	$130.39 \pm 1560.06$	401.78	448.83	1.04
Mouflon 2	5913	15/07/2007 03:03:13 - 13/10/2008 20:21:05	$111.23 \pm 1344.36$	357.12	456.72	0.90
Mouflon 3	5028	12/08/2007 03:01:17 - 19/10/2008 18:20:32	$124.48 \pm 1419.33$	396.12	434.63	1.05
Bear 1	766	15/07/2006 00:02:39 - 16/06/2007 00:02:22	$631.64 \pm 7401.31$	292.36	335.99	1.01
Bear 2	735	15/05/2006 05:21:12 - 16/04/2007 00:00:34	$657.85 \pm 6463.03$	128.27	335.78	0.44
Bear 3	837	15/06/2006 00:22:18 - 16/06/2007 00:00:23	$629.65 \pm 8408.82$	93.21	365.98	0.29
Bear 4	273	15/05/2006 17:10:12 - 16/08/2006 00:02:10	$486.78 \pm 4470.25$	78.64	92.29	0.98
Bear 5	605	14/11/2006 18:01:46 - 02/12/2007 00:01:15	$909.82 \pm 8121.37$	196.72	382.25	0.60

Table 1: **Data summary.** For each animal, the total number of observations  $n$  is given along with the period of collection (date and time), the average time between 2 observations (in min.), corresponding standard deviation, total distance is given (in kilometers), total recording time (in days) and average speed.

## 2.2 The model

Five animals  $I_{s1}, \dots, I_{s5}$  are simulated in discrete time and continuous space with discrete spatial motion. A reduced number of parameters are used in order to be mathematically tractable. Each simulation is performed over  $j = 1, 2, \dots, n$  steps and at each time step, the simulated individual may move in one direction. We use the log-normal law to draw the distance covered by the animal between each time step (see sec. 6). The distances traveled during the simulation are gathered and the simulation ends when the sum of the distances covered is greater or equal to the total distance covered by the real animal.

The movement of the individual is a BCR driven by 3 weights: inertia  $p_I$ , immobility  $p_i$  and attraction of the deme  $p_F$ . If  $p_I = p_i = p_F = 0$  the movement of a simulated individual resumes to a two-dimensional random walk with a log-normal step size distribution. At each time step  $j$ , we use the transition matrix:

$$\begin{bmatrix} 1 & 1 + p_I & 1 \\ 1 & p_s & 1 \\ 1 + p_F & 1 & 1 \end{bmatrix} \quad (1)$$

where the weight  $p_I, p_F$  are placed in the matrix according to the last position of the animal, and the estimated deme. In the presented case in eq. 1 the last motion of the animal is considered as coming from the down part of the matrix (ie. vertical trajectory) and the deme is supposed to lie somewhere in the bottom left part of the actual position of the individual. We take into account the distance of the deme, such as each weight can be write as  $p_I(C_k), p_i(C_k)$  and  $p_F(C_k)$ .

## 2.3 Estimates of parameters

As a first step, features of the five individuals trajectories  $I_1, \dots, I_5$  are used to estimate the parameters of the model for each simulated individual  $I_{s1}, \dots, I_{s5}$ . In a second step, we test the model by setting different parameters values. The distance covered by a simulated individual at each time step is drawn for a log-normal distribution. Parameters  $\ln \mathcal{N}(\mu, \sigma)$  of the distribution are estimated over the observations of the individual (see sec. 6). We note  $X_i = [X_i^1, X_i^2]$  the successive locations of the individual  $I_1, \dots, I_5$ , with  $i = 1, 2, \dots, n$ . The estimated deme of one individual is the average position:

$$X_F = \bar{X} = \left[ \overline{X^1}, \overline{X^2} \right] = \frac{1}{n} \sum_{i=1}^n X_i \quad (2)$$

### 2.3.1 Classes of distances

The Euclidean distance between two observations  $X_1, X_2$  is  $d(X_1, X_2)$ . For each individual, we define  $K$  classes of distances  $C_k$   $k = 1, \dots, K$  from  $X_F$ , that forms a partition of the observations, such as all

the  $X_i$  are distributed in the classes (see Fig. 8):

$$n = \sum_{k=1}^K \text{card}(C_k) \quad (3)$$

### 2.3.2 State

Let a state be the 2-tuple containing the actual  $X_i$  and previous observation  $X_{i-1}$ . We define the set of conflicting state where a conflict occurs between attraction ( $F$ ) and inertia ( $I$ ) as:

$$\mathcal{H}_{IF} := \{i : \widehat{X_{i-1}X_iX_F} \leq \pi/8\} \quad (4)$$

It corresponds to a state where the individual is heading towards the deme. Identically, for idle state ( $s$ ):

$$\mathcal{H}_s := \{i : d(X_{i-1}, X_i) \leq 10\} \quad (5)$$

such that the next step of the individual is eventually small, leading to an almost fixed position. We define the non-conflicting states as

$$\mathcal{H} := \{1, \dots, n\} - \mathcal{H}_{IF} - \mathcal{H}_s \quad (6)$$

### 2.3.3 Motion

Let a motion be the 3-tuple containing the immediate contiguous observations of  $X_i$ :  $X_{i-1}$  and  $X_{i+1}$ . We take into account three features of animal motion: Inertia  $E_I$ , immobilism  $E_s$  and attraction  $E_F$ :

$$E_I := \{i : -\pi + \pi/8 < \widehat{X_{i-1}X_iX_{i+1}} \leq \pi + \pi/8\} \quad (7)$$

$$E_s := \{i : d(X_i, X_{i+1}) \leq 10\} \quad (8)$$

$$E_F := \{i : |\widehat{X_{i-1}X_iX_{i+1}} - \widehat{X_{i-1}X_iX_F}| \leq \pi + \pi/8\} \quad (9)$$

all other motions are purely diffusive.

### 2.3.4 Estimates of $p_I$ , $p_s$ , $p_F$

Estimates of the 3 weights are performed on  $I_1, \dots, I_5$  provided the animal is in one and only one particular state (eq. 6, 4 or 5). We define  $x_1$ ,  $x_2$  and  $x_3$  as:

$$\begin{cases} \hat{x}_1 = \frac{\#E_I \cap \mathcal{H}}{\#\mathcal{H}}; & x_1 := \frac{1 + p_I}{\chi} \\ \hat{x}_2 = \frac{\#E_s \cap \mathcal{H}}{\#\mathcal{H}}; & x_2 := \frac{1 + p_s}{\chi} \\ \hat{x}_3 = \frac{\#E_F \cap \mathcal{H}}{\#\mathcal{H}}; & x_3 := \frac{1 + p_F}{\chi} \end{cases} \quad (10)$$

Assuming  $\chi$  was the sum of matrix 1 for a given class of distance:

$$\chi = 8 + p_I + p_s + p_F \quad (11)$$

The values of  $x_1$ ,  $x_2$  and  $x_3$  were computed for each subset  $A_{0,1,2}$  for each  $C_k$  and for each animal's motion. Solving eq. 10 for  $\chi$  yields:

$$\chi = \frac{5}{1 - (x_1 + x_2 + x_3)} \quad (12)$$

Replacing in eq. 10:

$$\begin{cases} p_I = x_1\chi - 1 \\ p_s = x_2\chi - 1 \\ p_F = x_3\chi - 1 \end{cases} \quad (13)$$

We tested the independence hypothesis in all the first-order conflicting cases  $A_{1,2}$ .

## 2.4 Time inhomogeneity

Periodicity in animal motion is studied with a periodogram [21] and we find peaks at the 24h frequency. When analyzing the distances covered at each time in a 24h-cycle and taking into account the monthly variation, we find a strong activity peaks at around 6pm and 6am. Both peaks are correlated in time with daylight duration: activity peaks are earlier in summer and later in winter.

When investigating the angular distribution between two movements in a 24h time-frame and taking into account the monthly variation, we find that the motion has a stronger linear trend during activity peak than during the rest of the day (Fig. 1).

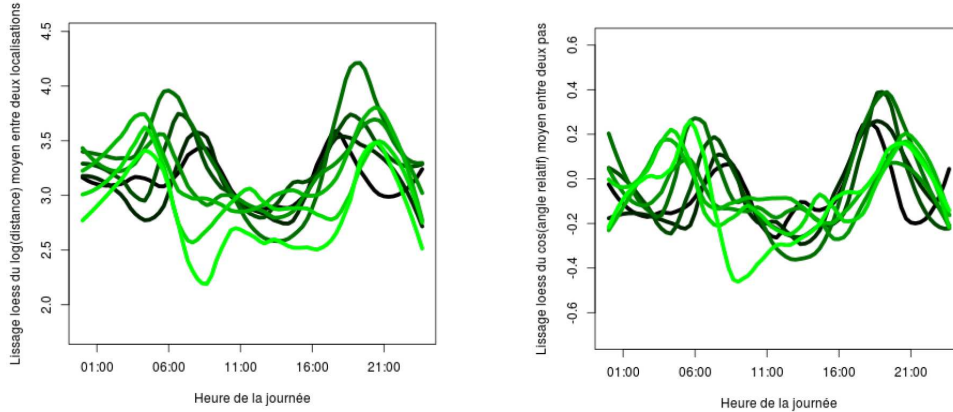


Figure 1: Relation between time of the day / distance covered between two observations (left panel) and time of the day / angular value between observations (right panel). Variations are smoothed and lighter green curves correspond to the summer months and darker green curves correspond to winter period.

## 2.5 Evaluation of memory feature

In order to test the memory feature of animal motion, we computed:

$$S_{nX_i} = \left[ \left\{ \overrightarrow{X_{i-1}, X_i} + \overrightarrow{X_{i-2}, X_i} + \dots + \overrightarrow{X_{i-n}, X_i} \right\}, X_i \right] \quad (14)$$

where  $n$  was the range of the memory.

## 3 Statistics for describing animal motion

Descriptive statistics of animal motion are provided in Supplementary Information (see section 6). Four statistics were evaluated over each trajectory to describe animal motion. Each of the 4 statistics are compared on both the real and simulated trajectories in order to evaluate the performance of our model. We focus on 2 statistics describing *i*) the features of animal movement (home range, turning angles) *ii*) counting issues based on observations made by idle and mobile observers (or agents). We evaluate the 4 statistics on the model set up using the parameters estimated from the data  $I_1, \dots, I_5$  and on the model set up with different parameters values.

### 3.1 Distribution of turning angles

For each  $I_{s1, \dots, s5}$  The distribution of turning angles ( $\widehat{X_{i-1} X_i X_{i+1}}$ ) is gathered and compared to the distribution of real individuals  $I_{1, \dots, 5}$ .

### 3.2 Home range (kernel)

We use a kernel method as a typical estimator of the animal home range. The approach of Z.I. Botev provide an estimate of observations density [20] using a bivariate kernel with diagonal bandwidth matrix. The kernel is assumed to be Gaussian. We compute the estimated area for various values of the estimated density (ie. 100, 99, 95, 90, 80, ..., 20, 10% of the density).

### 3.3 Idle observers

We consider  $j = 1, 2, \dots, n_{io}$  idle observers that count each time they see the animal in their line of sight (see sec. 6) and gather the total number of observations  $S$  realized by each of them:

$$S = \sum_o c_o \quad (15)$$

for each area of observation  $c_o$  of each observer  $o$ . Results are gathered for a fixed value of  $c_o = 200\text{m}$  (ie. a fixed line of sight, see sec. 6).

### 3.4 Mobile observers

We define  $l = 1, 2, \dots, n_{mo}$  mobile observers as observers that follow a defined trajectory at a given speed as time increase. Two types of movements are defined: linear and clockwise rotation. Linear observers move in a straightforward linear trajectory while rotating observers perform circles from a fixed center. Mobile observers  $o$  have a radius of observation  $r$  and count each time the animal  $a$  enters  $r$ , ie when:

$$(X_{a,t}^1 - X_{o,t}^1) + (X_{a,t}^2 - X_{o,t}^2) < r^2$$

where  $X_{a,t}^1$  is the position of the animal,  $X_{o,t}^2$  the position of the observer at a given time  $t$ . When simulating mobile observers, both the animal and mobile observers start to move at the same time. The initial position of the animal is  $X_1$  and the initial position of the observers is  $X_1$  or  $X_F$  (sec. 6). The total count of animal is gathered as in eq. 15.

## 4 Results

We run 50 simulations for each model and compare the following models:

1. initial model (labeled as ‘Model 1’:  $p_I(C_k)$ ,  $p_i(C_k)$ ,  $p_F(C_k)$ , presented in green color)
2. diffusion model (two-dimensional random walk with a log-normal step size distribution, presented in pink color)
3. initial model including time inhomogeneity (labeled as ‘Model 3’:  $p_I(C_k)$ ,  $p_i(C_k)$ ,  $p_F(C_k)$  are estimated for two periods of time (active / non active), according to fig. 1 and presented in cyan color)

#### 4.0.1 distribution of angles

Distribution of the angular values are presented in the following figure:

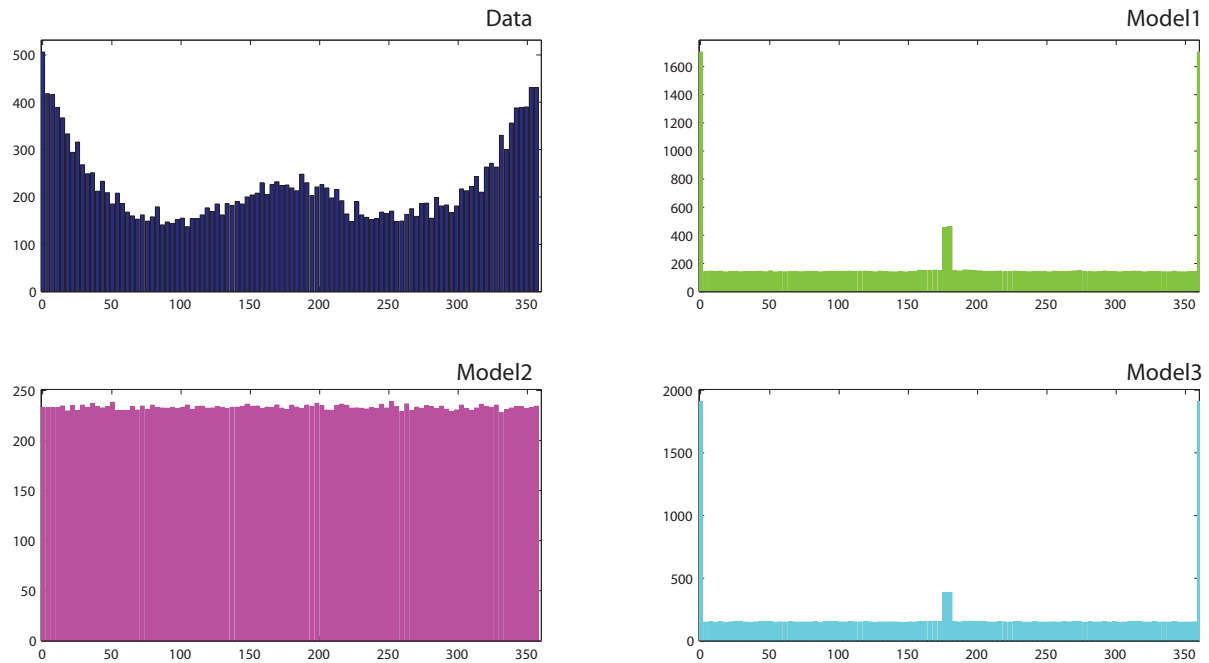


Figure 2: Distribution of averaged angular values for the 3 models (50 simulations for each model) and the data (upper left panel) for the deer 1.

#### 4.0.2 Home range estimation (kernel)

The simulated animals seem to cover a wider area than real animals (Fig. 3). This may be due to the fact that real animals may re-use customary paths while we do not include this feature in the model. When comparing the two models, it appears that the initial model (model 1 & 3) performs better than the diffusive model (model 2). It seems, after 50 simulations of the model 3, that the inter-variability of area covered between each simulation for this model is smaller compared to model 1, leading to a lesser overall dispersion when repeating the model.

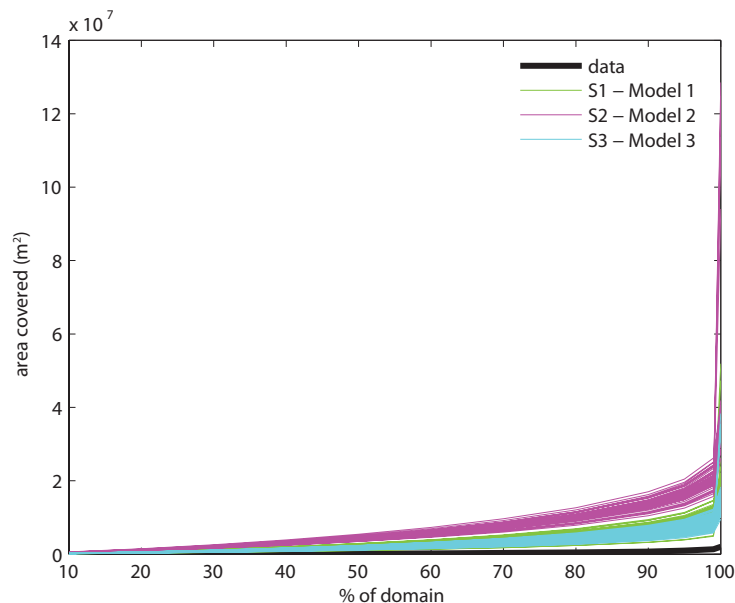


Figure 3: Estimated area covered by  $x\%$  of the estimated domain for the deer 1 (black line) and 50 simulations of model 1 (green lines), model 2 (pink lines) and 3 (cyan lines). As  $x$  increases, the area covered increases.



### 4.0.3 Fixed observers

When comparing the two models, the model 1 performs better than the model 2 and 3. On the opposite of domain estimates, the dispersion of the simulations of model 3 is greater than model 1 and 2.

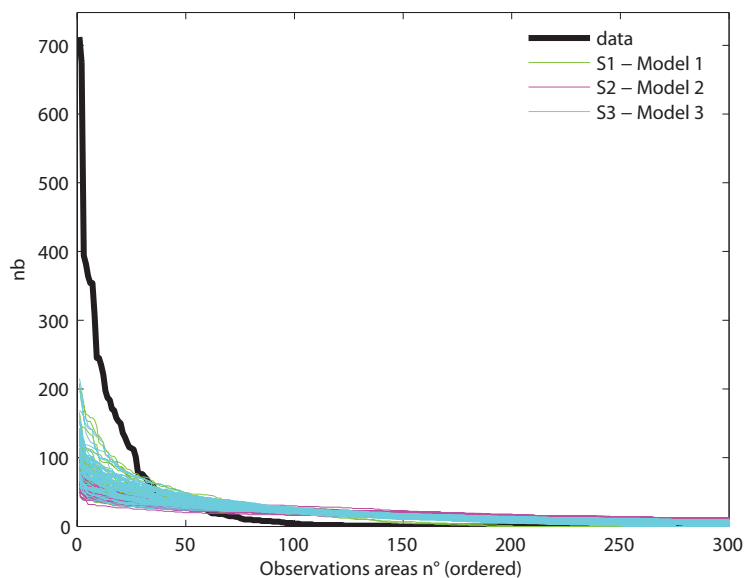


Figure 4: Total count of fixed observers for the deer 1 (black line) and 50 simulations of model 1 (green lines), model 2 (pink lines) and model 3 (cyan lines). Observation areas are sorted in decreasing order.

### 4.0.4 Mobile observers

Concerning the mobile observers, the difference between the two models is difficult to measure, and the results are not clear between models 1 and 3. More simulations are needed in order to increase the statistical power when comparing multiple observers with various size of observations and various speeds. Concerning the rotating observers, it appears that the model 2 is less efficient than model 1 and 3 (Fig. 6).

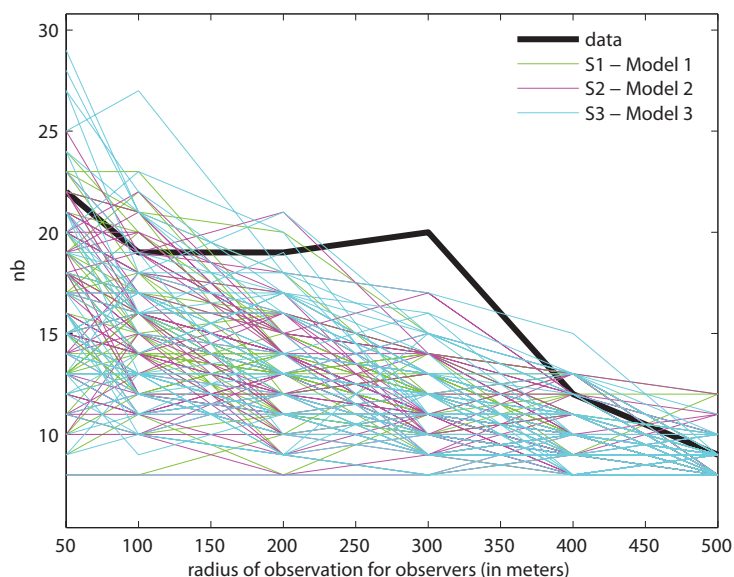


Figure 5: Total count of (linear) mobile observers for various radius of observation for the deer 1 (black line) and 50 simulations of model 1 (green lines), model 2 (pink lines) and model 3 (cyan lines).

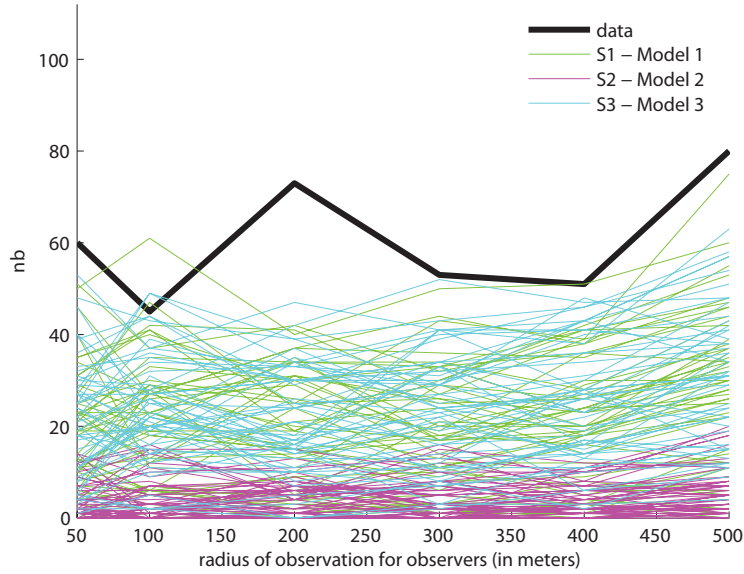


Figure 6: Total count of (rotating) mobile observers for various radius of observation for the deer 1 (black line) and 50 simulations of model 1 (green lines), model 2 (pink lines) and model 3 (cyan lines).

## 5 Discussion

**Perspectives.** We do not consider landscape/habitat effect nor interactions with other animals, and whereas both may influence individual motion. Some areas are attractive, while other are repulsive. The data-set clearly showed that the animals tend to follow levels sets (same altitude), reusing customary paths and reinforcing their trajectory and affecting Inertia and distance covered. We assume that dynamic or static interactions are important in the movement (ie. attractions or repulsions). In the static cases, the past trajectory of an animal acts upon the motion of other animals by attracting or repulsing them via the marks it laid. Both interactions and topological issues will be included in a future work in order to assess their impact other the simulated trajectories. Another point of interest is the development of the continuous space model.

## 6 Supplementary Information

Here are provided supplementary methodology and figures.

### 6.1 Distances covered

The distribution of distances between two successive observations of each animal are gathered and three distributions are tested for each animal  $I_1, \dots, I_5$ : log-normal, Weibull and gamma. The log-normal distribution appears to fit the data accordingly (Fig. 7).

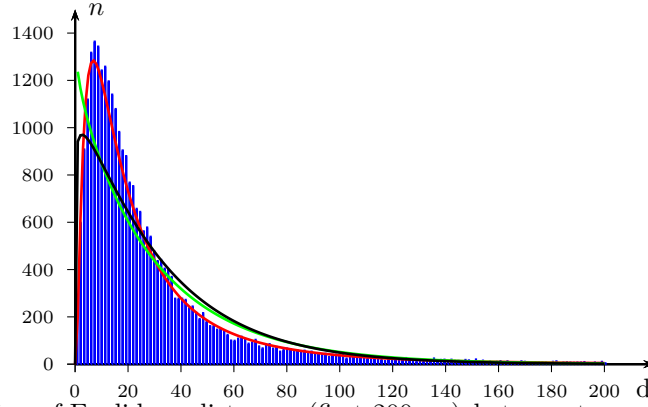


Figure 7: Distribution of Euclidean distances (first 200 m.) between two successive observations for  $I_1$  (blue bars). Three distributions are adjusted to the data: the log-normal (red line, parameters:  $\mu = 2.94$ ,  $\sigma = 1.01$ ), the Weibull (green line,  $\lambda = 31.43$ ,  $k = 0.97$ ) and the gamma (black line,  $k = 1.08$ ,  $\theta = 29.42$ ).

### 6.2 Distributing $M_i$ in distance classes

Let  $D_m$  be the highest distance from the deme:

$$D_m = \max(d(X_F, X_i)) \quad (16)$$

The radius  $R_{C_k}$  of a given class  $k$  is:

$$R_{C_k} = s_1\left(\frac{k}{K}D_m\right) \quad (17)$$

where  $s_1(x)$  is the ceil function that rounds  $x$  to the nearest integer greater than or equal to  $x$ . All the movements are distributed in the classes according to:

$$M_i \in C_k \text{ if } d(X_F, X_i) > R_{C_{k-1}} \text{ and } d(X_F, X_i) < R_{C_{k+1}} \quad (18)$$

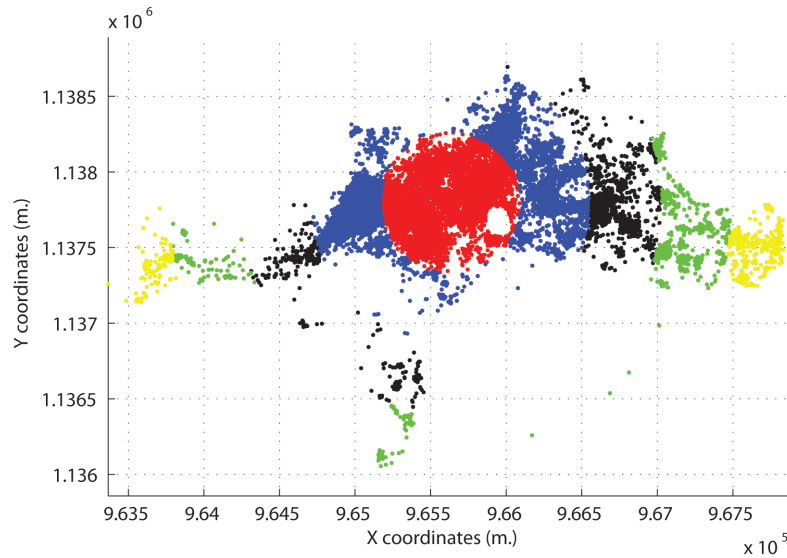


Figure 8: . GPS observations for  $I_1$  (deer) are clustered in distances classes with  $K = 5$  classes.

### 6.3 Descriptive statistics

As a first approach, we investigated the distributions of angular values of animal motion in each trajectory, by gathering the values of  $\widehat{E}_X$ .

### 6.4 Observers

We investigate different values of fixed observers  $n_{io}$  and set  $n_{mo} = 16$  with linear trajectory,  $n_{mo} = 2$  with rotating trajectory. Linear mobile observers start at two fixed initial positions: half of mobile observers start at  $X_{o,t_0} = X_1$  and the other half at  $X_{o,t_0} = X_F$ . Each of the two rotating observers has a distinct center of rotation:  $c = X_1$  for the first observer and  $c = X_F$  for the second observer.

#### 6.4.1 Idle observers

A mesh  $m$  is defined with  $r$  nodes that encapsulate all the observations of the animal (Fig. 9):

$$\begin{aligned} x_0 &= \min(X_i^1) \\ y_0 &= \min(X_i^2) \\ x_M &= \max(X_i^1) \\ y_M &= \max(X_i^2) \end{aligned} \tag{19}$$

$[x_0, y_0]$  and  $[x_M, y_M]$  being the boundaries of  $m$  with a constant spacing value  $a$  between each node. Observer counts are then gathered and ordered in increasing order. We previously compared several

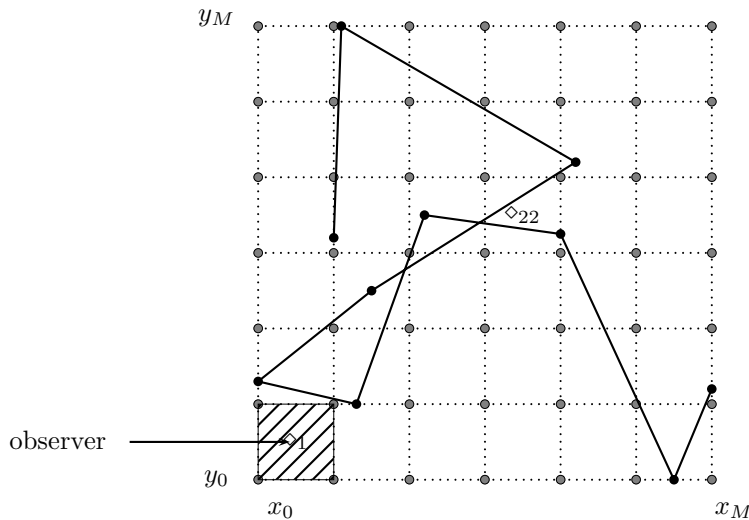


Figure 9: A mesh of  $n_{ibos} = 36$  idle observers and  $r = 49$  nodes. Each cell of the mesh corresponds to an observation area of one idle observer. The shaded area of the lower left cell corresponds to the area of vision of the observer  $\diamond_1$ . Observers are ordered in a column zig-zag way. The trajectory (black line and dots) is counted in each cell, such that the value of  $\diamond_1$  is 0 and  $\diamond_{22} = 2$ .

meshes with different resolutions (ie. different values of  $a, r$ ) and it only impacted the results by a scale factor.

#### 6.4.2 Mobile observers

The issue is to find the location of both the animal and the mobiles observers at each time step.

#### Location of the animal

The trajectory of the animal is interpolated from the discrete observations  $X_i$ . One can see the trajectory of the animal as a piecewise linear function of the observations:

$$X_i^2 = \begin{cases} \alpha_1 \cdot X_1^1 + \beta_1 & \text{if } t \leq t_{X_2} \\ \alpha_2 \cdot X_2^1 + \beta_2 & \text{if } t_{X_1} < t \leq t_{X_3} \\ \dots & \\ \alpha_n \cdot X_n^1 + \beta_n & \text{if } t_{X_{n-1}} < t \leq t_{X_n} \end{cases} \quad (20)$$

such that, for any time  $t$  we can find the corresponding observation  $X_i$  and define the segment  $[X_i, X_{i+1}]$  where the animal is located (Fig. 10). Thus the corresponding location of the animal is:

$$X_t = \lambda X_{i+1} + (1 - \lambda) X_i \quad (21)$$

with:

$$\lambda = \frac{t - t_{X_i}}{t_{X_{i+1}} - t_{X_i}} \quad (22)$$

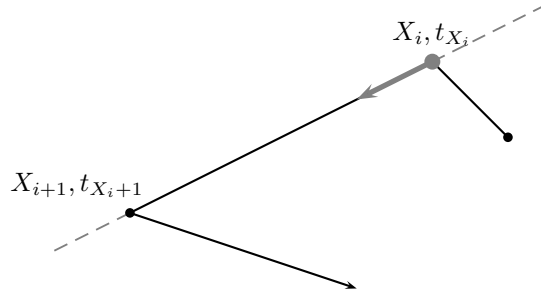


Figure 10: The trajectory of an animal considered as a piecewise linear movement.

### Location of the mobile linear observer

Let  $s$  be the speed of observers and  $\delta$  the time step. The trajectory of a linear observer with time is:

$$X_{t+\delta} = \begin{cases} X_{t+\delta}^1 = X_t^1 \pm q \cdot s \cdot \delta \\ X_{t+\delta}^2 = X_t^2 \pm q \cdot s \cdot \delta \end{cases} \quad (23)$$

where  $q = \{0, 1\}$  depending on vertical or horizontal trajectories.

### Location of the rotating observer

The trajectory of a clockwise rotating observer with time is defined by:

$$X_{t+\delta} = \begin{cases} X_{t+\delta}^1 = -r \cos\left(\alpha_t + \frac{s \cdot \delta}{r}\right) + c \\ X_{t+\delta}^2 = -r \sin\left(\alpha_t + \frac{s \cdot \delta}{r}\right) + c \end{cases} \quad (24)$$

with radius  $r$ , center  $c$  and  $\left(\alpha_t + \frac{s \cdot \delta}{r}\right) = 0$  at  $t_0$ .

## References

- [1] M. Hebblewhite and D.T. Haydon. Distinguishing technology from biology: a critical review of the use of gps telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550):2303–2312, 2010.
- [2] S. Benhamou. Spatial memory and searching efficiency. *Animal Behaviour*, 47:1423–1433, 1994.

- [3] S. Benhamou. Detecting an orientation component in animal paths when the preferred direction is individual-dependent. *Ecology*, 87:518–528, 2006.
- [4] E.A. Codling, M.J. Plank, and S. Benhamou. Random walk models in biology. *Journal of the Royal Society Interface*, 5:813–834, 2008.
- [5] O. Ovaskainen. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. *Ecology*, 85:242–257, 2004.
- [6] G.M. Viswanathan, S.V. Buldyrev, S. Havlin, M.G.E. da Luzk, E.P. Raposok, and H.E. Stanley. Optimizing the success of random searches. *Nature*, 401:911–914, 1999.
- [7] S. Benhamou. How many animals rally do the lévy walk? *Ecology*, 88:1962–1969, 2007.
- [8] D.R. Brillinger, K.P. Haiganoush, A.A. Ager, J.G. Kie, and B.S. Stewart. Employing stochastic differential equations to model wildlife motion. *Bull Braz Math Soc*, 33:385–408, 2002.
- [9] D.R. Brillinger. Simulating constrained animal motion using stochastic differential equations. *Lecture Notes-Monograph Series*, 41:pp. 35–48, 2003.
- [10] H.K. Preisler, A.A. Ager, B.K. Johnson, and J.G. Kie. Modeling animal movements using stochastic differential equations. *Environmetrics*, 15:643–657, 2004.
- [11] P.E. Smouse, S. Focardi, P.R. Moorcroft, J.G. Kie, J.D. Forester, and J.M. Morales. Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550):2201–2211, 2010.
- [12] S. Benhamou. Dynamic approach to space and habitat use based on biased random bridges. *PLoS ONE*, 6:e14592, 2011.
- [13] J.S. Horne, E.O. Garton, S.M. Krone, and J.S. Lewis. Analyzing animal movements using brownian bridges. *Ecology*, 88:2354–2363, 2007.
- [14] W.H. Burt. Territoriality and home range concepts as applied to mammals. *J. Mammal.*, 24:346–352, 1943.
- [15] L. Börger, B.D. Dalziel, and J.M. Fryxell. Are there general mechanisms of animal home range behaviour? a review and prospects for future research. *Ecology Letters*, 11(6):637–650, 2008.
- [16] Paul R. Moorcroft and Maura A. Lewis. *Mechanistic Home Range Analysis*. Princeton University Press, 2006.
- [17] J. M. Morales and S. Ellner. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *the Ecological Society of America*, 83:2240–2247, 2002.
- [18] Arild O. Gautestad, Leif E. Loe, and Atle Mysterud. Inferring spatial memory and spatiotemporal scaling from gps data: comparing red deer cervus elaphus movements with simulation models. *Journal of animal Ecology*, 2013.
- [19] J. M. Morales, D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, 85:2436–2445, 2004.
- [20] Z.I. Botev, J.F. Grotowski, and D.P. Kroese. Kernel density estimation via diffusion. *Annals of Statistics*, 38:2916–2957, 2010.
- [21] P. Diggle. *Time series. A biostatistical introduction*. Oxford University Press, Oxford, 1990.