Computational Statistics and Data Analysis 105 (2017) 76–95

Contents lists available at ScienceDirect

Computational Statistics and Data Analysis

journal homepage: www.elsevier.com/locate/csda

A general hidden state random walk model for animal movement☆

Aurélien Nicosia[a,*], Thierry Duchesne[a], Louis-Paul Rivest[a], Daniel Fortin[b]

[a] Département de mathématiques et de statistique, Université Laval, pavillon Alexandre-Vachon, 1045, av. de la Médecine, bureau 1056, Québec (Qc), G1V 0A6, Canada

[b] Département de biologie, Université Laval, pavillon Alexandre-Vachon, 1045, av. de la Médecine, bureau 3058, Québec (Qc), G1V 0A6, Canada

ARTICLE INFO

Article history:
Received 2 December 2015
Received in revised form 11 July 2016
Accepted 13 July 2016
Available online 25 July 2016

Keywords:
Angular regression
Biased correlated random walk
Circular–linear process
Directional persistence
Directional statistical model
Filtering–smoothing algorithm
Markov model
Multi-state model
von Mises distribution

ABSTRACT

A general hidden state random walk model is proposed to describe the movement of an animal that takes into account movement taxis with respect to features of the environment. A circular–linear process models the direction and distance between two consecutive localizations of the animal. A hidden process structure accounts for the animal's change in movement behavior. The originality of the proposed approach is that several environmental targets can be included in the directional model. An EM algorithm that enables prediction of the hidden states of the process is devised to fit this model. An application to the analysis of the movement of caribou in Canada's boreal forest is presented.

1. Introduction

In animal ecology, being able to understand and model the movement of animals is fundamental (Nathan et al., 2008). For example, animal behaviorists want to see to what extent animals have preferred movement directions or are attracted towards several environmental targets, such as food-rich patches and previously visited locations (spatial memory effect) (Latombe et al., 2014). The development of Global Positioning System (GPS) technology permits the collection of a large amount of data on animal movement. This can be combined to data available from geographic information systems (GIS) to investigate how the environment influences animal displacement. To achieve this goal, robust statistical techniques and flexible animal movement models are required.

Discrete time models for animal movement are actively being developed and investigated (Holyoak et al., 2008). Because displacement in discrete time can be characterized by the distance and the direction between two consecutive localizations, circular–linear processes can be used to model movement in 2D. A basic model is the biased correlated random walk (BCRW) of Turchin (1998); it predicts the next motion angle as a compromise between the current one (often called directional persistence) and the direction towards a specific target (also called directional bias). Several authors have built models to

☆ A real dataset and R functions with documentation are available as annexes in the electronic version of the manuscript.

* Corresponding author.
E-mail address: aurelien.nicosia.1@ulaval.ca (A. Nicosia).

http://dx.doi.org/10.1016/j.csda.2016.07.009

List of symbols

Data

T	Number of observed animal's locations.
y_t	Direction between the animal's locations at time steps t and $t+1$
$y_{0:T}$	Set of all observed directions $y_0, \ldots, y_T$
d_t	Distance between the animal's locations at time steps t and $t+1$
$d_{0:T}$	Set of all observed directions $d_0, \ldots, d_T$
x_{it}	Value of ith explanatory angle variable
z_{it}	Value of ith explanatory real variable
$\mathcal{F}_t^o$	Observed information: directions, distances and explanatory variables gathered from time 0 up to time t

Hidden process

S_t	State (behavior) in which the animal is at time step t
S_{kt}	Indicator function equal to 1 if $S_t = k$ and 0 otherwise
$S_{0:T}$	Set of all states $S_0, \ldots, S_T$
$\mathcal{F}_t^c$	Complete information: information in $\mathcal{F}_t^o$ and the hidden states $S_0, \ldots, S_t$
$p(S_t \mid \mathcal{F}_{t-1}^c)$	Conditional probability mass of the hidden state S_t
π_{hk}	State transition probability $\mathbb{P}(S_t = k \mid S_{t-1} = h)$

Observed trajectory

$h(y_t, d_t \mid S_t, \mathcal{F}_{t-1}^c)$	Conditional joint density of the observed data (y_t, d_t)
$f(y_t \mid S_t, \mathcal{F}_{t-1}^c)$	Conditional density of the direction y_t
f_k	Density of the direction y_t given that the hidden state is k at time t
$\kappa^{(k)}$	Vector of parameters of f_k
$\mu_t^{(k)}$	Mean direction of the von Mises density f_k
$\ell_t^{(k)}$	Concentration parameters of the von Mises density f_k
$g(d_t \mid S_t, \mathcal{F}_{t-1}^c)$	Conditional density of the distance d_t
g_k	Density of the distance d_t given that the hidden state is k at time t
$\lambda_1^{(k)}, \lambda_2^{(k)}$	Shape and scale parameters of g_k

adapt or generalize the BCRW so that it can be applied in different contexts. Jonsen et al. (2005) directly model the (x, y)-coordinates at a given time-step as a function of coordinates at the previous time-step with bivariate normal distributions to deal with data acquired at irregular time intervals. An alternative formulation of this model is proposed by Shimatani et al. (2012), but this formulation of the BCRW does not allow to include multiple directional biases. Despite the rapid increase in the development of movement analysis, most quantitative techniques still consider only two directional targets when estimating the mean direction of BCRWs. However, habitat selection studies demonstrate that animal movement can be influenced simultaneously by more than one or two environmental features (Moreau et al., 2012). Our first generalization of the BCRW is therefore to make the mean direction of the process depend upon several directional targets. To do so, we embed the directional model recently proposed by Rivest et al. (2016) within the BCRW and show how it is easily interpretable. We also show that its estimation is numerically more stable than other BCRW models.

Often, the movement trajectory of animals involves multiple movement states or behaviors (Fryxell et al., 2008). For instance, in their analysis of bison movement, Langrock et al. (2012) identified two states, "exploratory" and "encamped". The former has long traveled distances and turning angles between two consecutive locations that tend to be concentrated around zero, while the latter is characterized by short distances and almost uniformly distributed turning angles. Multiple movement behaviors can be accounted for by introducing hidden states in the models. Leonard and Baum (1966) give a general presentation of these models and Morales et al. (2004), Jonsen et al. (2005), Holzmann et al. (2006) and Langrock et al. (2012) are examples of the use of hidden state models to analyze angular-distance data in ecological applications. The second main contribution of our work is to introduce more flexible hidden state models that can accommodate directional persistence as well as the simultaneous influence of several environmental targets that can vary from state to state. Further, by using the EM algorithm to fit the model, we are able to compute the posterior probabilities of the hidden state for each step of the animal's trajectory. Because these probabilities take into account the targets that are important in each hidden state, they can be used to understand the relative roles of these individual targets on the overall movement and space-use patterns of individuals. They can also serve as input values in movement simulations, such as individual-based movement models (e.g., Latombe et al., 2014). Finally, these probabilities can highlight some regions in the landscape to be identified as patches of interest.