Applying Step Selection Functions to Data with Data Gaps: Simulation and Case Study on African wild dogs

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July 11, 2022

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Running Title: None

Keywords: step selection functions, gps data, animal movement, Lycaon pictus, irregular data

Abstract

Animal movement data collected in the field is often noisy and incomplete, thus confronting movement ecologists with temporal irregularities in their data. Step selection functions have become a popular tool to analyse movement data and to infer a species movement or preferences, yet they are based on the assumption of equal temporal gaps between consecutive datapoints. To adhere to this requirement, researchers typically only consider bursts of consecutive relocations with equal step-durations, thus discarding large portions of their data. Here, we use simulated data to question this practice and we examine whether including temporally irregular can improve estimates from step-selection models. In addition, we explore the usefulness of multiple methods to account for temporal irregularity in movement data. Our results show that including irregular data improves model estimates substantially. By applying methods that account for the irregularity in the data, the precision of model estimates can further be improved, albeit only marginally.

Contents

1 Introduction

GPS data is usually collected on fixed temporal intervals (could do a quick and dirty analysis on MoveBank) ranging from a few minutes, to multiple hours or even days between subsequent reolocations. Nevertheless, GPS devices regularly fail to adhere to the anticipated fixrate schedule due to cloud cover or other unfavorable conditions, thus resulting in irregular data. In other cases, the GPS schedule is not strictly fixed but may be subject to change. For example, **?** increased the fixrate of their GPS collars once per week from 4 to 8 fixes per day, aiming to collect more fine scaled data for a limited time. We chose to coin this type of data *irregular*, because it is not collected on the anticipated fixrate schedule and therefore not directly comparable to the vast majority of the collected data.

Step selection analysis is a powerful framework that enables researchers to study habitat and movement preferences of their focal species. The method works by comparing spatial covariates at locations where the studied animal has been observed, to a set of locations where the animal was presumably absent. For this, the collected GPS data is converted into steps, where a step represents the straight line movement between two consecutive GPS fixes. One can then compare covariates experienced along observed steps to covariates along potential alternative steps and thus infer preferred or avoided features. By restricting the availability domain to a set of steps, SSA is specifically intended to account for spatio-temporal autocorrelation inherent to data collected using GPS collars and is therefore one of the preferred methods for analysing such data. However, it is considered good practice to only consider steps with similar step durations in step-selection models. Depending on the amount of available data and depending on the number of missing GPS fixes, this practice might entail little sacrifice. In some situations, however, removing irregular data implies a substantial loss of information. Additionally, recent developments in the SSA realm have brought forward several improvements to SSA that might allow to relax the assumption of regular step-durations. This includes the *integrated* SSA approach presented by (**?**), in which inference on habitat *and* movement preferences are possible thanks to the inclusion of movement descriptors in the respective model. More recently, the method has been further refined by (**?**), who coined the term *time-varying integrated* SSA. This method was developed for high frequency data which has been rarified using a change-point detection algorithm, thus also resulting in irregular step-durations. In case of missing steps, in contrast, steps durations are not entirely random but usually clustered.

Here, we questioned the practice of removing any irregular data in SSA and investigated whether such data could be used to inform step selection models. For this, we conducted a

simulation study where we simulated movement trajectories with known preferences across a virtual landscape. We then artifically rarified the "observed" data by removing GPS fixes and we analysed this data using SSA. This allowed us to investigate if and how the inclusion of irregular data affected model estimates. We also varied the degree of irregularity in the data and we tested for the effects of adjusting the parametric step-length and turning distributions to different step-durations. Besides the simulation study, we also analysed a dataset collected on dispersing African wild dogs and examined the implications considering or discarding irregular data.

We hypothesized that the precision of model estimates would decrease as we increased the missingness in the data. We also expected that the inclusion of irregular data would not improve the precision of estimates and rather lead to biased values. However, we anticipated that such biases, at least in estimated movement kernel parameters, could be reduced by appropriately adjusting the availability domain.

2 Methods

2.1 Simulation Study

2.1.1 Spatial Covariates

We simulated a virtual landscape comprising three spatial covariate layers, each with a resolution of 300 x 300 pixels (Figure 2) spanning across x- and y-coordinates from 0 to 300. The first layer (water) represented water-bodies and was simulated using a random cluster nearest-neighbour neutral landscape model (?), with the cluster-proportion set to 0.5 and the patch occupancy of water fixed to 20%. The second layer (elev) resembled an elevation layer and was simulated using a Gaussian random fields neutral landscape model (?), with an autocorrelation range of 10, magnitude of variation of the landscape of 1, and a magnitude of variation in scale of 0. We simulated both of these layers using the r-package NLMR (?). The third layer (dist) simply indicated the distance (in pixels) to the center of the virtual landscape ($x = 150, y = 150$), and can be understood as the distance to the center of an animal's home-range. We computed spatial distances using the r-package raster (?). We normalized the values from all layers to a range between zero and one.

2.1.2 Movement Simulation

To simulate movement across the above generated virtual lanscape, we employed an "inverted" step-selection function, which proceeded as follows. First, we generated a random

starting location. To prevent starting points in the vicinity of map borders, we restricted sampled locations to x- and y-coordinates between 50 and 250 (white dotted rectangle in Figure 2). Second, we generated a set of 10 random steps originating from the sampled starting point. We then generated random steps by sampling turning angles from a von Mises distribution with concentration parameter $\kappa = 0.5$ and location parameter $\mu = 0$, and step lengths from a gamma distribution with shape parameter $k = 3$ and scale parameter $\theta = 1$. Third, we extracted covariate values along each random step from the underlying covariate layers and computed the average of each covariate along every step. Fourth, we predicted for each step the probability of being chosen by applying **??**. The vector of relative habitat preferences used to make predictions was set to $\beta_{water} = -1$, $\beta_{elev} = 0.5$, and $\beta_{dist} = -15$. Fifth, we sampled one of the random steps based on predicted probabilities and computed the new position of the simulated individual. We the repeated these steps until a total of 100 steps were realized and we replicated the simulation 100 times, thus resulting in 100 independent movement trajectories (Figure 3). Note that by excluding interactions among habitat covariates and step metrics we implicitly assume independent habitat and movement kernels (**?**). Although measurement error would have been straight forward to implement, this was not the main focus of our analysis and so we assumed GPS locations to be 100 percent accurate.

2.1.3 Step Selection Analysis

To assess the consequences of missing GPS data in when employing step-selection functions, we analysed the simulated GPS data under different conditions **??**. Specifically, we varied the degree of data-missingness (0% to 80%), the forgiveness when analysing the data (1 to 5 fixes), and the parametric distributions from which random steps were generated (static vs. dynamic distributions). We replicated each combination of conditions 100 times and computed averages and standard deviations from the resulting model estimates.

In this context, missingness and forgiveness are complementary terms. While missingness describes the fraction of data that has not been collected, we use the term forgiveness to describe how much missingness a modeler is willing to accept. A modeler with forgiveness of one, for instance, only considers steps with a step-duration of one (i.e. fixes that are regularly spaced). In contrast, a modeler with forgiveness of two would also accept steps with a step-duration of two, thus pardoning a single missing fix.

The idea of the multiple imputation approach is as follows...

Data Rarefication   We rarefied the simulated GPS data by randomly removing a fixed fraction of GPS fixes. To assess the impact of different degrees of "missingness", we incrementally increased the fraction of missing fixes from 0.0 (complete dataset) to 0.8 (80% missing) with 10% increments. The removal of GPS fixes introduced irregular temporal intervals between remaining fixes; we will refer to these intervals as "step-times", where the "step" refers to the straight line movement between two consecutive GPS fixes (**?**). In the complete dataset, a step-time of one was assumed, whereas the step-time increased by one for every fix that was missing between subsequent fixes. For instance, a single missing fix between two other fixes directly increased the step time from one to two.

Identifying Bursts and Computing Step Metrics   We used the generated data to compute movement bursts. A movement burst consisted of a sequence consecutive GPS fixes with step-times that did not exceed the accepted forgiveness. For instance, if the forgiveness was one, already a single missing GPS fix introduced a new burst. In contrast, if the forgiveness was set to two, step-times of two units were allowed, without introducing a new step.

We will use the term "forgiveness" to indicate how many missing fixes were accepted before a new burst was enforced. For instance, a forgiveness of one implied that a single missing fix did not result in a new burst. We then converted the GPS fixes belonging to the same burst into steps, where each step resembled the straight line movement between two GPS fixes (**?**). For each step we computed a set of step metrics. This includd the step length, its logarithm, the turning angle and its cosine.

Step Selection Function   To conduct step selection analysis, we paired each observed step with 10 random steps. We generated random steps by sampling turning angles from a von Mises distribution and step lengths from a gamma distribution. Depending on the study design, we either sampled turning angles and step lengths from fixed or fixed or dynamic distributions (cfr. Section ...). Along observed and random steps, we extracted underlying covariates and computed their averages along steps.

Step Length and Turning Angle Distributions   To generate random steps, we employed three competing approaches, coined *uncorrected*, *naïve*, and *dynamic* approach, respectively. In the uncorrected approach, we sampled step-lengths and turning-angles from parametric gamma and von Mises distributions that were fitted to observed steps with step-duration of one. In the *naïve* approach, we sampled step lengths and turning angles from the

same distributions, yet we linearly scaled sampled step lengths to the actual step-duration. For instance, for any step with a step-duration of two, we doubled the sampled step length. This approach is representative of the time-varying SSF approach proposed by **?**. Finally, in the *dynamic* approach, we sampled step lengths and turning angles from distributions that were fit to different step-durations. That is, we fitted separate step length and turning angles distributions to every possible step duration. To achieve this, we subsampled the observed data to 50% of the fixes, which resulted in varying step-durations. We then and fitted step length and turning angle distributions to the steps from different step-durations. We repeated this procedure 1000 times and averaged the parameter estimates across replicates.

Regression Model We estimated ... using conditional logistic regression, implemented using the r-package survival (**?**). We followed **?** and **?** and employed *integrated* SSA. That is, aside from the habitat covariates (water, elev, dist), we also included descriptors of the step length and turning angle (sl, log(sl), cos(ta)) in our regression model. The model call was as follows:

$$case_- \sim water + elev + dist + sl + log(sl) + cos(ta)$$

2.2 Case Study

because wild dogs move comparably little in the hours between xx and xx, we made the simplyfing assumption that the 8-hour period from xx to xx is comparable to a 4-hour period.

3 Results

4 Discussion

Results from our simulation study demonstrate that the inclusion of GPS fixes can be used to gain information on relative habitat preferences of the focal species. While the inclusion of steps from irregular sampling schemes resulted in substantial biases for estimates related to step metrics, we showed that these biases can effectively be mitigated by generating step lengths and turning angles from distributions that are separately fit to steps from different step durations. Regardless of biases in beta coefficients for step metrics, we found that habitat selection estimates were unbiased, even when including irregular steps. Even more,

the inclusion of irregular steps drastically reduced model uncertainty, thus suggesting that such data can be used to gain information that would otherwise be lost.

5 Authors' Contributions

D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B., G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O. assisted with modeling; D.D.H., D.M.B., and G.C. wrote the first draft of the manuscript and all authors contributed to the drafts at several stages and gave final approval for publication.

6 Data Availability

GPS movement data of dispersing wild dogs is available on dryad (**?**). Access to R-scripts that exemplify the application of the proposed approach using simulated data are provided through Github (`https://github.com/DavidDHofmann/DispersalSimulation`). In addition, all codes required to reproduce the African wild dog case study will be made available through an online repository at the time of publication.
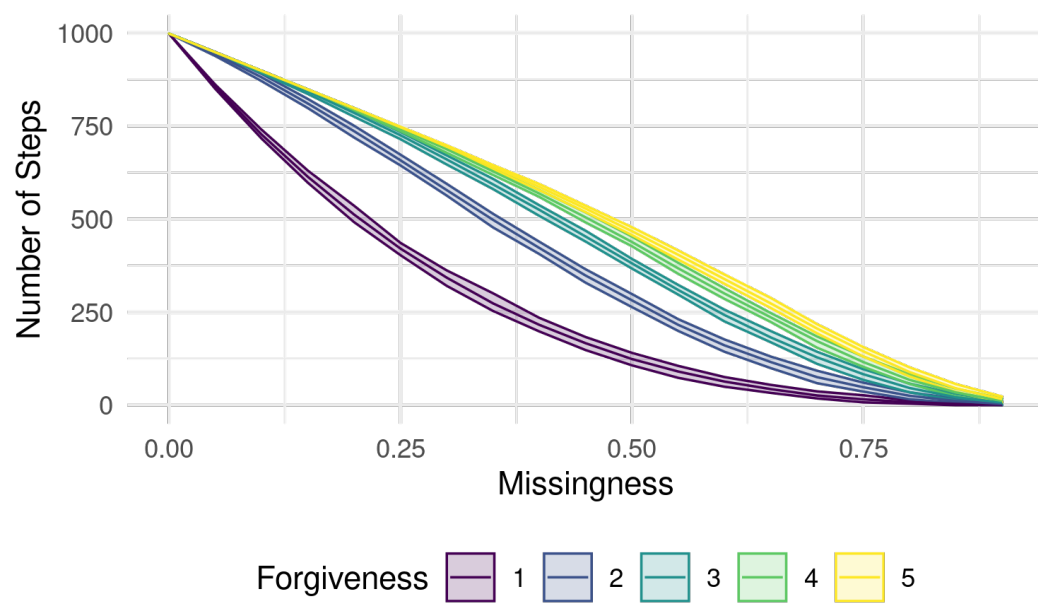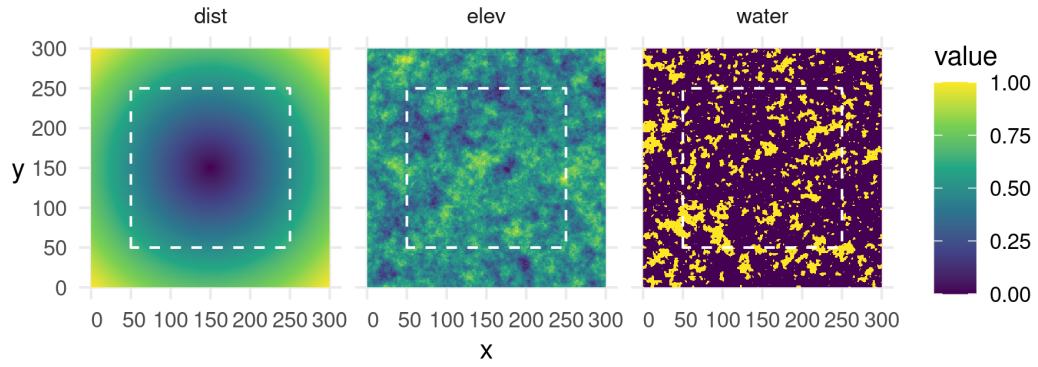
7 Acknowledgements

Figure 1

Figure 2: Virtual landscape across which we simulated movement trajectories. All layers have a resolution of 300 x 300 pixels and were generated randomly. Simulated individuals were initiated within the white dashed rectangle, which ensured that they would not be released directly at a map border.
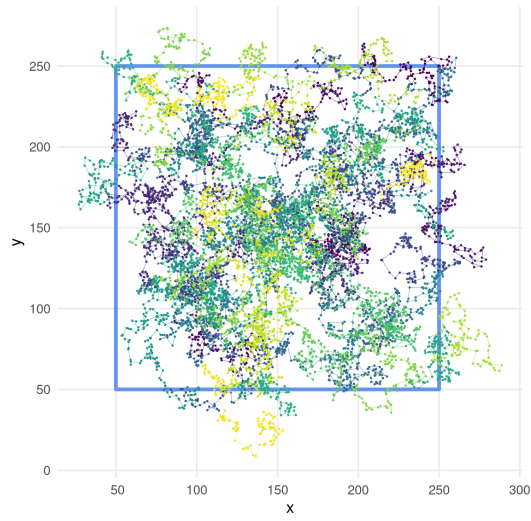
Figure 3: 100 Simulated movement trajectories, each comprising of 100 steps. Simulated individuals were initiated within the blue rectangle to mitigate edge effects.