

Estimating utilization distributions from fitted step-selection functions

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Abstract. Habitat-selection analyses are often used to link environmental covariates, measured within some spatial domain of assumed availability, to animal location data that are assumed to be independent. Step-selection functions (SSFs) relax this independence assumption, by using a conditional model that explicitly acknowledges the spatiotemporal dynamics of the availability domain and hence the temporal dependence among successive locations. However, it is not clear how to produce an SSF-based map of the expected utilization distribution. Here, we used SSFs to analyze virtual animal movement data generated at a fine spatiotemporal scale and then rarefied to emulate realistic telemetry data. We then compared two different approaches for generating maps from the estimated regression coefficients. First, we considered a naïve approach that used the coefficients as if they were obtained by fitting an unconditional model. Second, we explored a simulation-based approach, where maps were generated using stochastic simulations of the parameterized step-selection process. We found that the simulation-based approach always outperformed the naïve mapping approach and that the latter overestimated home-range size and underestimated local space-use variability. Differences between the approaches were greatest for complex landscapes and high sampling rates, suggesting that the simulation-based approach, despite its added complexity, is likely to offer significant advantages when applying SSFs to real data.

Key words: habitat selection; home range; integrated step-selection analysis; integrated step-selection function; mechanistic home range; movement ecology; resource-selection function; step-selection analysis; step-selection function; utilization distribution.

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INTRODUCTION

Understanding how environmental drivers shape space-use patterns of animals is of great interest to both theoretical and applied ecologists. Historically, the importance of environmental covariates was inferred by comparing sites that animals were known to use with sites that were deemed available to the animal. Such use-availability designs for resource-selection analysis (Boyce and McDonald 1999, Manly et al. 2007) required independent observations and an

adequately defined spatial domain representing the extent of available habitat. Treating observations as independent was frequently justified under the assumption that observations were spaced far enough apart in time to allow an individual to travel to any location within the availability domain (McNay et al. 1994). Under this assumption, habitat availability may be quantified by randomly sampling locations within the assumed geographical availability domain (e.g., the animal's home range; Johnson 1980, Beyer et al. 2010). A major drawback of this approach

is that the resulting inference is sensitive to the somewhat subjective definition of the availability domain (Beyer et al. 2010, Prokopenko et al. 2016).

Technological advances in animal tracking over the last two decades have led to an increase in animal position data by several orders of magnitude (Tomkiewicz et al. 2010, Kays et al. 2015). These new data sets allow researchers to address new research questions regarding how animals interact with their environment. Data collected at fine temporal resolution, however, tend to be autocorrelated in position and velocity, violating the independence assumption of traditional resource-selection analysis (Fieberg et al. 2010). Ignoring the temporal sequence of location data can also lead to a loss of information about factors influencing animal movement (Horne et al. 2007, Fleming et al. 2016).

Step-selection functions (SSFs) were developed to address concerns related to positional autocorrelation (Fortin et al. 2005, Thurfjell et al. 2014). Step-selection functions define availability conditional on the previous location, the time between successive locations, and movement characteristics of the study animal, and are appealing because they relax the assumption of independence (from full independence among all locations to independent transitions between successive locations). Models can be fit using conditional logistic regression with strata formed by pairing each observed location (at time t) with a set of control locations determined by generating random movement steps (straight lines connecting two observed locations) from the previous observed location (at time $t - 1$). After its initial introduction to study the movement behavior of elk in the presence of wolves (Fortin et al. 2005), subsequent studies adapted and modified SSFs to include movement-related covariates to make inference to both the selection and movement processes, or to control one process while investigating the other (Forester et al. 2009, Dancose et al. 2011, Latombe et al. 2014a, Avgar et al. 2015).

Many management and conservation applications require maps depicting habitat importance or habitat use or derived quantities such as animal home ranges, yet it is not always clear how to generate such maps based on a fitted model. Under certain formulations, fitting an SSF results in a parametrized mechanistic movement model (also termed an integrated SSF; Avgar et al. 2016), a

model for the pattern-generating process of the observed relocation data. Thus, SSFs provide a relatively simple analytical framework for fitting mechanistic home ranges (Moorcroft and Barnett 2008), which can be used to project expected space use under current and future conditions. This contrasts with most traditional home-range estimators, such as kernel density estimators (Worton 1989), which only provide summaries of the observed data, a single realization of the underlying stochastic process. The synoptic home-range model of Horne et al. (2008) offers an alternative to SSF-based estimation, but with the disadvantage of assuming full independence among animal locations.

Simulation offers an intuitive approach for estimating space use from fitted SSFs, yet it is also common to produce SSF-based maps, by multiplying resources by their corresponding selection coefficients (hereafter referred to as the naïve approach; Squires et al. 2013, McLean et al. 2016), an approach that originates from traditional resource-selection analysis. Alternatively, Zeller et al. (2016), in an attempt to account for the conditional formulation of step-selection models, choose to produce maps by averaging movement kernels across a larger availability domain. This approach assumes individuals are equally likely to be found at any location within this domain, which is inconsistent with the underlying logic of the analysis. In their discussion, Zeller et al. (2016) suggested individual-based simulations might be needed to more properly weight these movement kernels. Others have used individual-based models (Latombe et al. 2014b) to derive home-range sizes from fitted SSF, or stochastic simulations (Avgar et al. 2016) to estimate the utilization distribution (UD), the two-dimensional relative frequency distribution of space use of an animal (Van Winkle 1975), from fitted SSFs.

Our objective here is to compare performance of the naïve approach and the more computationally demanding simulation-based approach when estimating the true UD, with the expectation that the latter should lead to more accurate estimates. This expectation follows from the work of Barnett and Moorcroft (2008), who developed an analytical framework for exploring links between fine-scale space-use behavior and the resulting steady-state UD (SSUD). They showed that if the animal is free to access any part of the availability domain at any time, a 1:1 relationship exists

between the SSUD and the habitat-selection function embedded in a dispersal kernel. However, as movement or cognitive limitations become more restrictive, the SSUD will begin to deviate from the underlying habitat-selection function. In the diffusive (Fokker-Planck) limit, the SSUD should equal the habitat-selection function raised to the power of two (Barnett and Moorcroft 2008). Hence, the more limited the redistribution capacity of the animal is relative to spatial environmental variability, the less accurate the naïve approach should be in estimating the UD.

Here, we compare the naïve and simulation-based estimators of the UD using simulated data where the animal's movement capacity is fixed, but we vary landscape complexity, strength of selection for local habitat features, and the rate at which positions are sampled. Based on the findings of Barnett and Moorcroft (2008), we predicted that (1) the naïve and simulation-based approaches would yield similar results for relatively simple landscapes, (2) the naïve approach would oversmooth the UD compared to the simulation-based approach in more complex landscapes, (3) differences between the naïve and simulation-based approach would become larger as animals select more strongly for local habitat features, thereby shrinking their effective redistribution kernel, and (4) differences between the naïve and simulation-based approaches would become larger as sampling rates are increased (again, due to a shrinking redistribution kernel).

METHODS

Movement data generation

We generated animal movements in discrete space and time using a stepping-stone process similar to Avgar et al. (2016). We created a simulation domain representing an area of 2.5×10^7 m², comprised of 10^6 quadratic cells (25 m² each). At each time step t , we denote the position of the animal as vector $\mathbf{x}_t = (x_t, y_t)$ containing the x - and

y -coordinates of the animal's position at time t . All else being equal, the animal could either move to one of its four nearest neighboring cells, with probability p_m , or stay at its current position (with probability $1 - p_m$). In the simplest case, the position of the animal at time step $t + \tau$ (where τ is duration of a single simulation step = 15 s) only depended on the basal movement probability and the squared distance to the home-range center. The dispersal kernel in this case is given by Eq. 1.

Here, $d(\cdot)$ is the squared distance between the cell occupied at time $t + \tau$ and the home-range center, α is the basal movement cost given by $\log(-4(p_m - 1)/p_m)$, and ω_1 controls the strength of attraction toward the home-range center. We used the squared distance to the home-range center ($d(\cdot)$), because this model converges at steady state to a bivariate-normal distribution peaking at the home-range center, with a scaling parameter σ given by $(4\omega_1)^{-0.5}$ (Moorcroft and Barnett 2008). This model can also be seen as a discrete approximation of the well-studied bivariate Ornstein-Uhlenbeck process (Dunn and Gipson 1977, Blackwell 1997, Fieberg 2007).

More generally, Eq. 1 can be extended to include k covariates reflecting resources, risks, or environmental conditions (Avgar et al. 2016), by Eq. 2, where $\mathbb{1}(\cdot)$ is an indicator function valued 1 if the expression is valid and 0 otherwise, $\|\cdot\|$ stands for the euclidean norm, ω_j is the selection coefficient for resource z_j , and n is the number of cells in the domain. We will consider two covariates: z_1 , the squared distance to the home-range center, and z_2 , an indicator for favorable ($z_2 = 1$) and unfavorable ($z_2 = 0$) habitat patches.

We ran the movement generation process for 1 yr, after a burn-in phase of 3.5 d (2×10^4 time steps). Animals were initially placed at a random location within the landscape. The home-range center was at $x = 500$ and $y = 500$, that is, the center of the landscape. We then rarefied the track to simulate a typical sampling design, where a GPS collar is programmed to record the

$$p(\mathbf{x}_{t+\tau}) \propto \begin{cases} \exp(-\omega_1 d(\mathbf{x}_{t+\tau})) & \text{stay in the current cell,} \\ \exp(-\alpha - \omega_1 d(\mathbf{x}_{t+\tau})) & \text{move to a neighbor,} \\ 0 & \text{otherwise.} \end{cases} \quad (1)$$

$$p(\mathbf{x}_{t+\tau}) = \frac{\mathbb{1}(\|\mathbf{x}_t - \mathbf{x}_{t+\tau}\| \leq 1) \exp(-\alpha \|\mathbf{x}_t - \mathbf{x}_{t+\tau}\| + \sum_{j=1}^k \omega_j z_j)}{\sum_{i=1}^n \mathbb{1}(\|\mathbf{x}_t - \mathbf{x}_{i,t+\tau}\| \leq 1) \exp(-\alpha \|\mathbf{x}_t - \mathbf{x}_{i,t+\tau}\| + \sum_{j=1}^k \omega_j z_j)} \quad (2)$$

position of the animal every 0.5, 1, 3, 6, and 12 h. Since we included attraction to the home-range center, animals never encountered the border of the simulation domain.

We assumed animals moved (all else being equal) with a probability of 0.3 (from Eq. 2). We explored a range of values for $\omega = (\omega_1, \omega_2)$. We began by considering a scenario where movement depended on only the squared distance to the home-range center ($\omega = (-0.05, 0)$; Fig. 1A). We then considered a scenario in which animals also selected locations depending on local environmental features at the end of each step (with varying selection strength). In particular, we considered a binary covariate indicating whether or not the habitat was favorable, with the strength of selection given by $\omega = (-0.05, 2)$; Fig. 1B). Further, we explored a range of scenarios where we kept $\omega_1 = -0.05$ and varied $\omega_2 = (0, 1, 2, 3)$ for the 6-h sampling rate only. The spatial distribution of the habitat covariate was created using a modified version of the random cluster algorithm (Saura and Martinez-Millan 2000) as implemented in Efford (2016). The random cluster algorithm generates landscapes based on spatial autocorrelation of habitat patches controlled through a fragmentation parameter p and the expected amount of favorable habitat A (we kept both constant at 0.5). For an example of such a simulated landscape, see Appendix S1: Fig. S1.

Step-selection analysis

For each trajectory, we estimated space-use drivers at the scale of the observed (rarefied) locations using a SSF with movement-related covariates. For each observed step, we generated 10 control steps. Lengths of control steps were drawn from a gamma distribution with parameters estimated using maximum likelihood (package `fitdistrplus::fitdist` in R; Delignette-Muller and Dutang 2014) applied to the observed step-length distribution associated with each generated trajectory individually. Turning angles were distributed uniformly between $-\pi$ and π . We then extracted the value of the covariates of interest (squared distance to home-range center and habitat) at the end of each observed and control step. We modeled usage as a function of the squared distance to the home-range center and a indicator variable if a step landed in suitable habitat or not (results shown in Appendix S3), and extended

this model by additionally including the step length and the natural logarithm of step length (as modifiers of the original step-length distribution; Avgar et al. 2016). By including these additional terms, the SSF estimates parameters of the movement and resource-selection process simultaneously. We used `survival::clogit` in R to fit the models (Therneau and Grambsch 2000, R Development Core Team 2007).

Estimating utilization distributions

We were interested in two types of UD. The SSUD is the long-term (asymptotically infinite) expectation of the space-use distribution across the landscape. The transient UD (TUD) is the expected space-use distribution over a short time period and is thus sensitive to the initial conditions (e.g., the starting point; for further details, see discussion and appendix S1 in Avgar et al. 2016). Here, we focus on predicting the TUD for 5 d into the future. We used numerical methods to estimate the *true* SSUD and TUD, running the data-generating process for $n = 2.0736 \times 10^8$ time steps (SSUD), or running 500 replicates of $n = 2.888 \times 10^4$ (=5 d at 15 s) time steps and then averaging the results (TUD). For the *true* SSUD, we began the simulation at the first tracking position (after the burn-in), whereas for simulations of the *true* TUD we started at the last tracking position. Although there is a single true SSUD associated with any set of parameters, ω , each simulated data set will have associated with it a unique *true* TUD due to its dependence on the starting point (see also Appendix S1: Fig. S2 for a schematic outline of the whole simulation and estimation procedure).

For each simulated trajectory, we also estimated the SSUD and TUD with the naïve and the simulation-based approaches. For the naïve approach, we multiplied selection coefficients obtained from our fitted SSF with the resources, summed and exponentiated the resulting values pixel-wise and divided by the sum across the domain to ensure the estimated UD summed to 1 (for both SSUD and TUD; Fig. 1C, D). For the simulation-based approach, we simulated animal movement by drawing turning angles distributed uniformly between $-\pi$ and π , and step lengths from a gamma distribution (we adjusted the scale and shape parameter of the gamma distribution by correcting these with the coefficients of the of step length and log of step length from the conditional

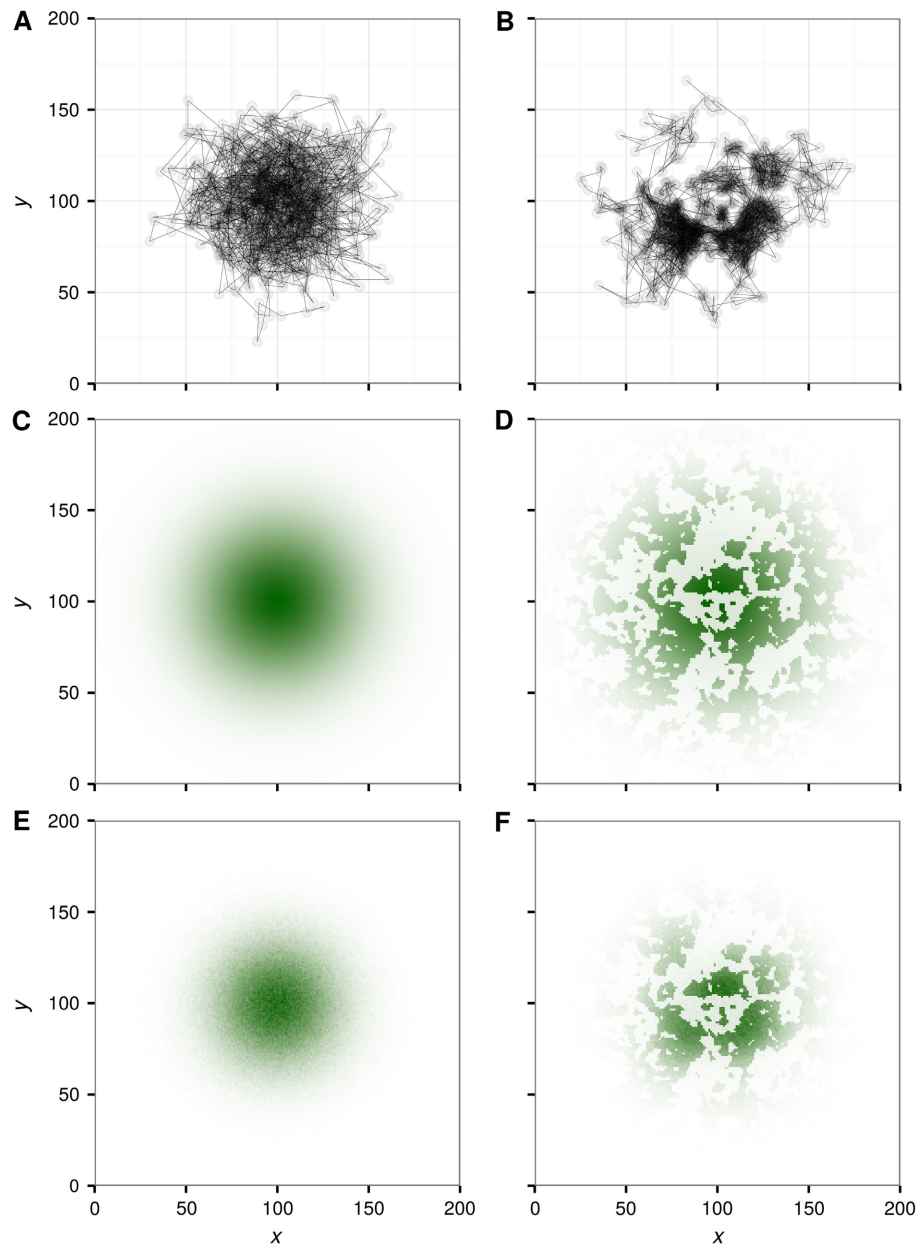


Fig. 1. Simulated movement data and corresponding estimated utilization distributions (UDs). Animals selected either for the squared distance to the home-range center (panel A; $\omega_1 = -0.05$) or for the squared distance to the home-range center and habitat (panel B; $\omega_1 = -0.05$ and $\omega_2 = 2$). Next, we estimated steady-state UD from a fitted step-selection function using the naïve (panels C and D) and the simulation-based approach (panels E and F).

logistic regression as described in appendix S2 of Avgar et al. (2016)). To estimate SSUDs, we simulated a single trajectory for 10^6 time steps starting at the first observed relocation. To estimate TUDs, we simulated steps for 5 d at the sampling rate, starting from the last observed

relocation; we repeated this process 10^4 times and then averaged results across these simulations. The accuracy of SSUD and TUD estimates will be influenced by Monte Carlo error (the length of the simulation for the SSUD and the number of simulations for TUD). In practice, one should run

simulations until estimates converge. In our example, SSUDs and TUDs converged after 10^5 steps and 5000 to 10^4 replicates, respectively (Appendix S1: Figs. S3, S4). A detailed step-by-step description of how we estimated the UD can be found in Appendix S3.

Performance of UD estimation

We compared the estimated SSUD/TUD to the *true* SSUD/TUD using Bhattacharyya's affinity (BA; Bhattacharyya 1943, Fieberg and Kochanny 2005). Bhattacharyya's affinity provides a measure of agreement between two distributions and ranges from 0 (no overlap) to 1 (identical in distribution). To quantify differences between estimation approaches in ecological terms, we compared estimates of home-range size of the UDs using the two methods of estimation (naïve, simulation-based) for 6-h sampling rate only. We used the 95% isopleth to determine home-range size for both the *true* UD and the estimated UDs.

We replicated the whole process (data generation, fitting SSFs, and UD estimation) 1000 times for two representative scenarios ($\omega = (-0.05, 0)$ and $\omega = (-0.05, 2)$). For the second scenario

($\omega = (-0.05, 2)$), we created 10 landscape realizations (using the random habitat algorithm as described above) and used one landscape per 100 replicates. In further scenarios, we kept $\omega_1 = -0.05$ and explored a range of values for $\omega_2 = (0, 1, 2, 3)$. For each of these scenarios, we used the same landscape and replicated the simulation and estimation process 100 times.

RESULTS

The relative performance of the naïve and simulation-based estimators depended on the estimation target (SSUD or TUD), simulation scenario, and sampling rates. We present results for 6-h sampling rates here. Overall, the naïve approach always oversmoothed the UD, resulting in biased estimates and poor performance compared to the simulation-based approach (e.g., Fig. 1, lower four panels). The simulation-based estimator always outperformed the naïve estimator regardless of landscape complexity or estimation target (BA statistics were closer to 1 and exhibited less variability across simulated data sets; Figs. 2, 3). As selection strength for

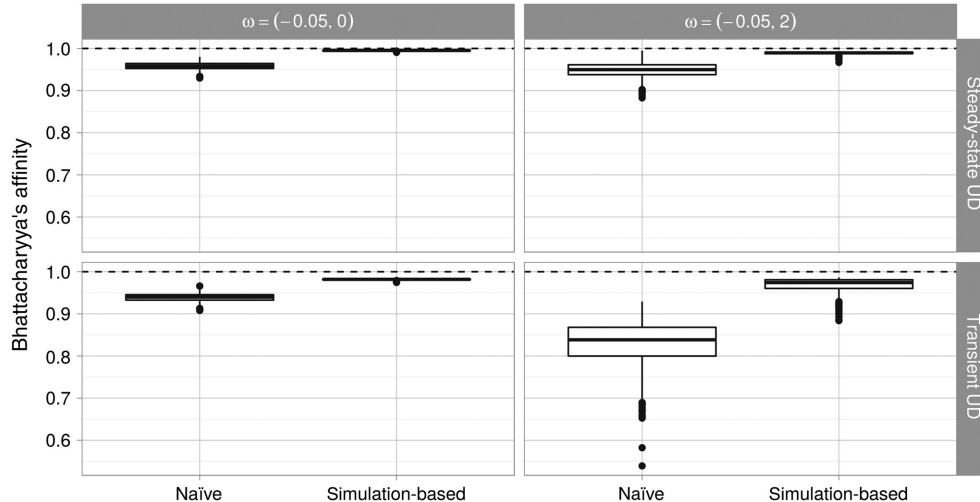


Fig. 2. Agreement between the *true* underlying utilization distribution (UD) and the estimated UD by multiplying estimated selection coefficients with resources (naïve) and simulating space use from the fitted step-selection model (simulation-based) for two simulation scenarios (columns). Bhattacharyya's affinity provides a measure of agreement between two distributions and ranges from 0 (no overlap) to 1 (identical in distribution). We simulated tracking data mimicking a collar with a 6-h sampling rate. Results are shown for the steady-state UD (top row) and for the transient UD (bottom row) predicting space use for 5 d. We show results for two representative scenarios where the animal selects for either the home-range center (left column) or the home-range center and habitat (right column). Box plots show the distribution of 1000 replicates.

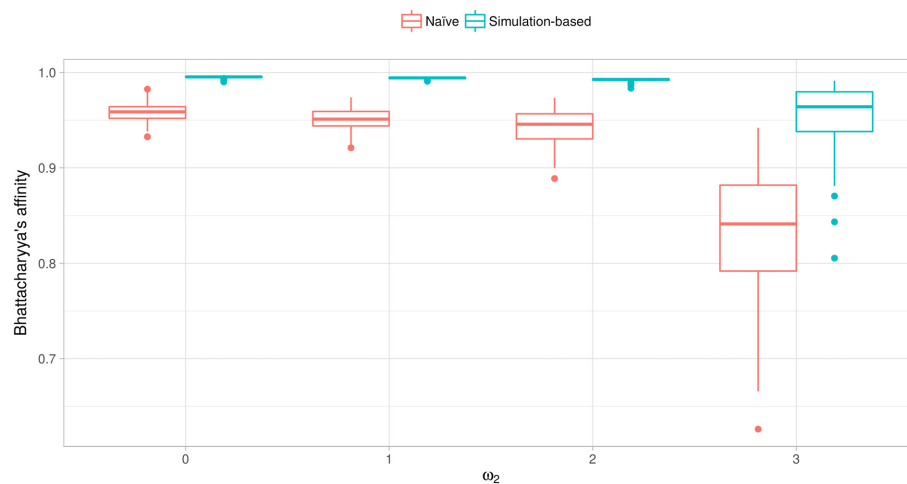


Fig. 3. Agreement between the *true* underlying utilization distribution (UD) and steady-state UD estimates using the naïve and simulation-based approaches for a range of values representing the strength of habitat selection (ω_2). We show results for a 6-h sampling rate. Bhattacharyya's affinity provides a measure of agreement between two distributions and ranges from 0 (no overlap) to 1 (identical in distribution). Box plots show the distribution of 100 replicates.

habitat (ω_2) increased, estimated and *true* UD began to diverge, particularly for the naïve approach (Fig. 3).

The simulation-based estimator of home-range size was nearly unbiased, whereas the naïve estimator was biased high in all scenarios we considered (Fig. 4). The simulation-based estimators of the UD and of the size of the home range also exhibited less variability than the corresponding naïve estimators across all scenarios (Figs. 2–4).

Differences between estimators were similar for different sampling rates, but were more pronounced at higher sampling rates (Appendix S1: Figs. S7, S9). Lastly, in contrast to the often large differences in performance between estimation approaches (naïve and simulation-based), there were minimal differences between the SSF with and without using movement parameters as covariates (see Appendix S2 for the same results using a SSF without movement-related covariates).

DISCUSSION

Results of the simulation study agreed with the predictions we outlined in the *Introduction*. Differences between the naïve and simulation-based estimators were small in relatively simple

landscapes (prediction 1), but became larger as we increased the selection strength for more complex habitat structure (prediction 3; Fig. 3). Confirming prediction (2), we found that the naïve approach oversmoothed the UD to a much greater extent for the two representative scenarios ($\omega = (-0.05, 0)$ and $\omega = (-0.05, 2)$), leading to discrepancies between the estimated and *true* UD (Fig. 2) and substantially greater bias in derived quantities such as the size of the animal's home range (Fig. 4).

In line with our prediction (4), we found differences between the two estimators were visible for 6-h sampling rates, but were even stronger for finer sampling rates (e.g., 30 min) and weaker for higher sampling rates (e.g., 12 h; see also Appendix S1: Figs. S7, S9). These observations provide further support for the hypothesis that the naïve approach might be sufficient for low sampling rates where the animal may be able to reach any point within its home range from its current position, but for tracking data with high temporal resolution (where the step lengths for the animal are small compared to the habitat features), a simulation-based approach is necessary for estimating long-term space-use patterns. These findings are in line with the theoretical predictions of Barnett and Moorcroft (2008) that

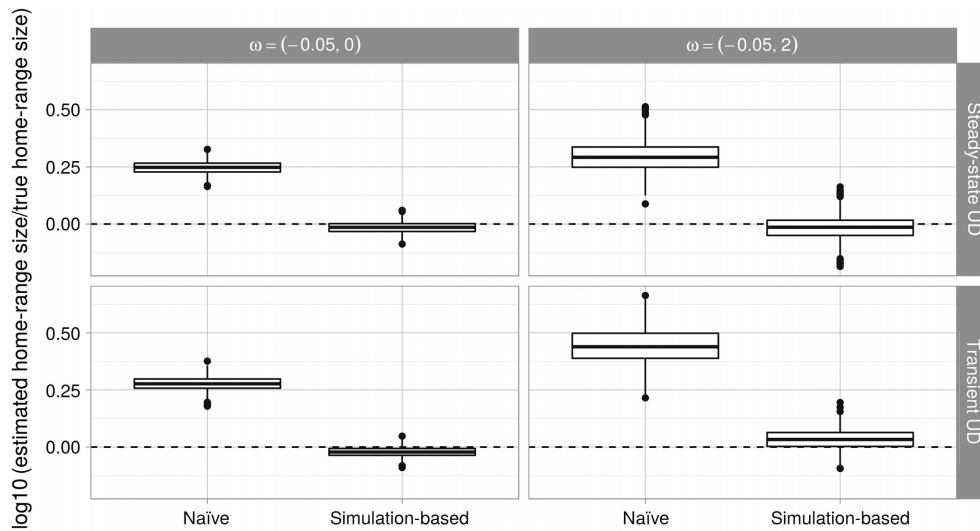


Fig. 4. Bias of home-range size estimates derived from utilization distributions (UD) that were obtained by the naïve and simulation-based approaches, for steady-state UD (top row) and transient UD (bottom row) predicting space use for 5 d. We used the 95% isopleth of the UD and compared the size of the estimated home range to the size of the *true* home range (obtained from the *true* UD). We show results for two representative scenarios where the animal selects for either the home-range center (left column) or the home-range center and habitat (right column). Box plots show the distribution of 1000 replicates, and horizontal dashed lines indicate equivalence between estimated and true home-range size.

if step lengths of an animal become shorter relative to environmental features (or equivalently, the spatial autocorrelation in the landscapes increases), the relationship between the habitat-selection function (our naïve estimation approach) and the UD changes from linear to quadratic. It should be noted that at low sampling rate, the use of a conditional analysis (SSF) may be considered unnecessary to begin with.

Our focus here was on approximating both the transient and SSUD. It is worth noting how these concepts relate to similar terms used in the literature. The SSUD has also been referred to as the “equilibrium distribution” (Dunn and Gipson 1977), and, more recently, as the “range distribution” (Fleming et al. 2015, 2016, Calabrese et al. 2016). As its name suggests, it is the distribution of animal density (or the probability density of animal occurrence) across space after a very long time (or many iterations of the same stochastic process). It is thus independent of the animal’s starting position and of time itself. The TUD is the expected distribution of animal occurrence conditional on its starting position and is thus dependent on both the starting position and time. It is however

different from the concept of the “occurrence distribution” (Fleming et al. 2015, 2016, Calabrese et al. 2016), which estimates the path taken during a particular tracking interval. A TUD, as it was defined and used here, is the expectation of space-use distribution averaged over many realizations of the movement process. As we have demonstrated, SSF-based simulations are particularly useful in approximating such TUDs, as unconditional formulations (such as traditional resource-selection analysis or the naïve approach described here) are not equipped to accommodate temporal and positional dependencies.

Besides the traditional use of SSFs to study resource selection and derived quantities (i.e., mechanistic home ranges as described in the *Introduction*), we see a second application of the simulation-based estimator for the estimation of resistances surfaces to quantify an animal’s movement capacity in the landscape. Recently, step- and path-selection functions were suggested as a means to derive movement resistance surfaces (Benz et al. 2016, Zeller et al. 2016) from telemetry data, rather than deriving such resistance surfaces from expert opinions or resource-selection

functions as is commonly done (Zeller et al. 2012). By simulating movement from source populations to other areas in the landscape, SSFs could be used to identify likely movement corridors between populations (e.g., using least cost path [Adriaensen et al. 2003] or circuit theory [McRae et al. 2008]), or to derive effective costs separating populations that can be contrasted with genetic differentiation in landscape genetic studies (Balkenhol et al. 2015).

A shortcoming and unresolved problem of SSFs in general, and hence also of our study, is the issue of scale-dependent inference. The temporal resolution of the SSF is typically determined by practical limitations, such as GPS battery life, rather than by the true scale at which the animal makes space-use decisions. Similarly, the spatial grain of the analysis is typically determined by the resolution of remote-sensed environmental data (e.g., land-cover) rather than by the spatial scale at which the animal responds to the landscape. In fact, there is no reason to believe such true scales exist as animals tend to interact with their surrounding across a multitude of scales. This does not mean the resulting inference is wrong. Rather, it is best to think of the fitted SSF as providing the best approximation at the scale of the observation. Hence, SSF-based maps should share the same spatial grain as the one used to fit the SSF, and movement simulations must be conducted at the same spatiotemporal resolution as that of the observed data.

In summary, SSFs provide users with a relatively accessible modeling framework for investigating animal space-use patterns while appropriately addressing age-old issues related to defining availability and properly accounting for positional autocorrelation. An integrated SSF can be used to further account for velocity autocorrelations (Duchesne et al. 2015, Avgar et al. 2016), which are characteristic of high-frequency GPS data. These advantages come with difficulties in interpreting and communicating the resulting inference. As we have demonstrated here, in many cases the naïve approach may be an insufficient work-around for these difficulties and stochastic simulations of the step-selection process must be employed. For applied science, the simulation-based approach provides a conceptually easy (albeit computationally more demanding) tool to translate parameter estimates

into maps that managers and applied researchers can understand and use.

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