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Temporal variation and scale in movement-based resource selection functions

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ABSTRACT

A common population characteristic of interest in animal ecology studies pertains to the selection of resources. That is, given the resources available to animals, what do they ultimately choose to use? A variety of statistical approaches have been employed to examine this question and each has advantages and disadvantages with respect to the form of available data and the properties of estimators given model assumptions. A wealth of high resolution telemetry data are now being collected to study animal population movement and space use and these data present both challenges and opportunities for statistical inference. We summarize traditional methods for resource selection and then describe several extensions to deal with measurement uncertainty and an explicit movement process that exists in studies involving high-resolution telemetry data. Our approach uses a correlated random walk movement model to obtain temporally varying use and availability distributions that are employed in a weighted distribution context to estimate selection coefficients. The temporally varying coefficients are then weighted by their contribution to selection and combined to provide inference at the population level. The result is an intuitive and accessible statistical procedure that uses readily available software and is computationally feasible for large datasets. These methods are

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demonstrated using data collected as part of a large-scale mountain lion monitoring study in Colorado, USA.

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1. Introduction

An explosion of recent papers on the statistical analysis of animal movement indicates rapid growth in this emerging area of animal ecology. The formal mathematical description of animal movement is quite old, dating back hundreds of years, and even though the seminal text on the topic written by Turchin [47] is quite relevant, it is currently out of print and lacks a contemporary statistical perspective. Despite the existence of highly technical literature describing ways to model animal movement (e.g., [7,15]), most applied studies that have actual management or conservation objectives have sought to focus more on what is termed “space use”, in which they seek to characterize the geographical and/or environmental space used by either individual animals or populations or both.

Types of space use analyses vary widely and include: (1) describing an individual’s home range or core area (e.g., [52]) (2) describing the spatial distribution (probability density function or “utilization distribution”, e.g. [34]) from which individual’s locations (\mathbf{s}_t , for time $t \in \mathcal{T}$) might arise and (3) the estimation of resource selection functions (or RSFs, e.g., [32]). In the latter, statistical inference is focused on identifying the probability of resource use *given* resource availability (i.e., selection).

1.1. Traditional resource selection

The basic statistical approach put forth by Manly et al. [32], and since extended in several different directions (e.g., [23,30,24,29]), specifies that the distribution of use $[\mathbf{x}]_u$ is equal to a weighted distribution of availability $[\mathbf{x}]_a$:

$$\begin{aligned} [\mathbf{x}]_u &= \frac{g(\mathbf{x}, \boldsymbol{\beta})[\mathbf{x}]_a}{\int g(\mathbf{v}, \boldsymbol{\beta})[\mathbf{v}]_a d\mathbf{v}}, \\ &= c g(\mathbf{x}, \boldsymbol{\beta}) [\mathbf{x}]_a, \\ &= [\mathbf{x}|\boldsymbol{\beta}]_u, \end{aligned} \tag{1}$$

where, the square bracket notation ‘[...]’ denotes a probability density function, \mathbf{x} corresponds to a vector of resource covariates, $\boldsymbol{\beta}$ is a set of selection parameters (often regression coefficients), c is a normalizing constant, and $g(\mathbf{x}, \boldsymbol{\beta})$ is the resource selection function (often the inverse logit or exponential function, depending on the desired inference). The last line in (1) is not commonly used elsewhere, but is a notation that we will make use of in what follows.

Importantly, as others point out (e.g., [40,30,49,12]), the equation in (1) is referred to as a “weighted distribution” and can be arrived at by an application of Bayes rule. Making a slight modification to the typical weighted distribution specification, we index the resource observations by the location \mathbf{s}_t at which they were observed at time t . Thus, without loss of generality we may write:

$$\begin{aligned} [\mathbf{x}(\mathbf{s}_t)]_u &= \frac{g(\mathbf{x}(\mathbf{s}_t), \boldsymbol{\beta})[\mathbf{x}(\mathbf{s}_t)]_a}{\int g(\mathbf{x}(\mathbf{s}), \boldsymbol{\beta})[\mathbf{x}(\mathbf{s})]_a d\mathbf{s}}, \\ &= [\mathbf{x}(\mathbf{s}_t)|\boldsymbol{\beta}]_u. \end{aligned} \tag{2}$$

Now, assuming independent observations $\mathbf{x}(\mathbf{s}_t)$ for $t = 1, \dots, T$ and a known availability distribution $[\mathbf{x}(\mathbf{s}_t)]_a$, the likelihood can be written as the product of the right-hand-side of (2):

$$\prod_{t=1}^T [\mathbf{x}(\mathbf{s}_t)|\boldsymbol{\beta}]_u, \tag{3}$$

and can be maximized with respect to the selection coefficients $\boldsymbol{\beta}$, given the data, as long as the integral in the denominator of (2) can be computed. Conveniently, it has been shown that the likelihood in

(3) can be maximized, under certain conditions, using logistic regression and a “case-control” design (e.g., [23,49]). Thus, computational methods for fitting resource selection models to telemetry data are accessible to animal ecologists. All that is needed is a binary regression data set consisting of ones and zeros, where ones correspond to the observed telemetry locations (and associated covariates $\mathbf{x}(\mathbf{s})$) and the zeros correspond to a background sample that is typically drawn from a uniform spatial distribution over the study area or home-range of an individual animal. Then this most commonly employed method for estimating resource selection proceeds by fitting a logistic regression model to the augmented binary data set and associated set of covariates while omitting the intercept term (β_0) in the model. It has been shown that the intercept is not identifiable as a model parameter; this arises because of the standardization of $g(\mathbf{x}, \boldsymbol{\beta})$ in the likelihood.

These ideas are certainly not new in the statistical literature, but their application to animal space use studies has only relatively recently become common [32]. Further, it should be noted that this basic approach to estimating resource selection is actually equivalent to many of the approaches proposed for species distribution modeling (e.g., [50,12]) where so-called presence-only data are collected and a background sample is taken to numerically compute the necessary integral in the denominator of (2). In fact, [50] show that the integral in the denominator of (2) can be more efficiently computed using numerical quadrature rather than Monte Carlo integration as is implicit in the random background data sampling used in the logistic regression method.

1.2. Emerging issues with contemporary telemetry data

Animals move in a non-independent fashion with respect to resources and our monitoring techniques are becoming so sophisticated that the temporal resolution of fixes (i.e., location observations in time, \mathbf{s}_t) is quite fine; hours or minutes typically, using global positioning system (GPS) telemetry devices. Thus, wildlife biologists have a movement process evident in most of their recent telemetry data and conventional methods for estimating resource selection are not equipped to explicitly address this. Furthermore, in programming telemetry devices (which is the only control over the design once the animal is tagged) most studies opt for regular fix rates, though not all fixes may be successful given terrain, atmospheric conditions, or other landscape features [35]. Therefore, irregularly spaced temporal data at a very fine resolution are common and result in hundreds or thousands of observations depending on the extent of the study. Fig. 1 shows a subset of telemetry locations from two of the animals used in our study. Notice how, even with a fine temporal fix rate (3 h between locations) there exists much uncertainty pertaining to the use of the resource shaded in gray (let alone selection).

The well-cited work of Swihart and Slade [45,46] provides a means to assess autocorrelation under certain types of monitoring designs (e.g., known home range). However, if these methods are employed at all, they are often only used to “thin” data sets prior to further modeling. The downside to thinning is that the full potential of the monitoring technology cannot be utilized. Also, the selection of resources can depend on the behavioral state of the animal and other exogenous factors that are dynamic in time. Examples of these could include diurnal activity patterns, satiation, and weather events. Although becoming less of an issue as the monitoring technology improves, another problem common with satellite telemetry observations (e.g., Argos and to a lesser extent GPS) is the potential presence of measurement error or location uncertainty.

To some extent, many (but not all) of these problems have been addressed in animal movement models that explicitly consider a movement process with built-in environmental effects on movement as a form of selection function (e.g., [42,19,17,33]). This is a rapidly growing area of statistical modeling research, but so far these methods have not been widely adopted by the wildlife biologists who need them most. This lack of adoption may be due to the sophistication and specialization of the models for certain species and the lack of available software. Thus, most applied ecological studies of animal space use still rely on logistic regression routines to estimate resource selection functions [27].

Johnson et al. [24] and Forester et al. [14] describe methods for estimating resource selection while considering the autocorrelation due to movement, and while others (e.g., [38,13]) have argued that

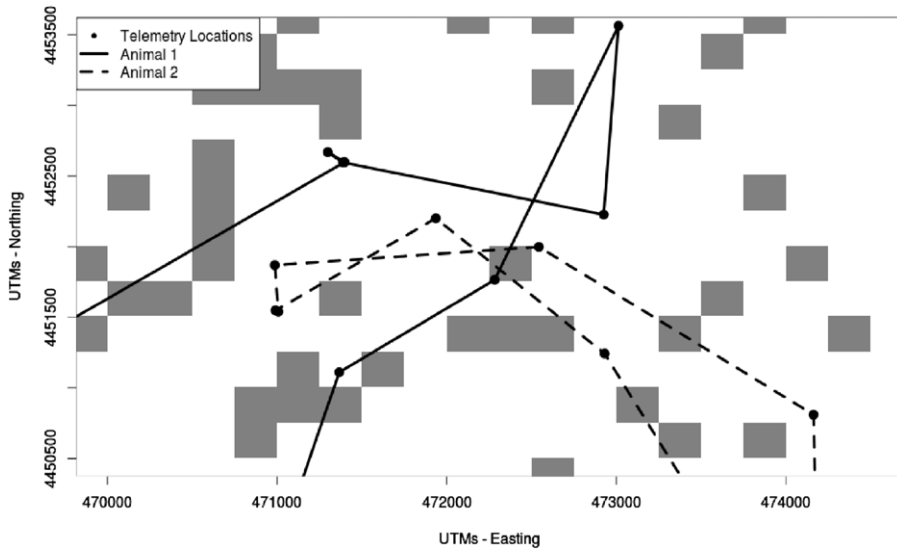


Fig. 1. A portion of the path and telemetry data for two different mountain lions. The gray shaded cells in the background represent one landtype (specifically, shrub type) used as a covariate in the analyses. Lines between telemetry locations are only shown to indicate the individual and sequence of fixes.

population level studies need not be concerned with such forms of autocorrelation, conventional weighted distribution approaches are simply not appropriate for use with modern forms of telemetry data.

1.3. Roadmap

In what follows, we describe an approach that: (1) allows for resource selection inference while utilizing all of the available data, (2) explicitly accommodates location uncertainty, (3) allows for the scale of selection to be user defined before and after the data are collected, and (4) provides a very flexible framework for incorporating more sophisticated modeling if desired. The methodology that we present relies on a constraint (i.e., model for movement) that is placed on the movement process which allows for both interpolation and prediction of locations at a regular set of time intervals (the scale of which is a user decision). Specifically, movement-related use and availability distributions are estimated from telemetry data and then put in a time-specific weighted distribution context to obtain selection coefficients β_t . These β_t coefficients represent time-varying effects of the resource covariates on selection over the period of $(t - \Delta t, t]$ for all t of interest. The simplest form of desired inference often pertains to the mean and variance of β_t , but much more complicated models on β_t may allow for inference on population-level selection, changes in individual and population behavior over time, intra- and interspecific interaction, and synchrony of selection with other time-varying environmental variables. These methods are intuitive and relatively simple to implement using readily available software, falling somewhere between the over-simplified logistic regression approaches to estimating resource selection and the more sophisticated and specialized animal movement models that have appeared in the recent literature.

Beginning in the *Methods* section, we describe how to frame the selection problem in a movement context directly, how to estimate time-varying selection, and how to summarize selection over the temporal extent of interest. In the *Application* section, we demonstrate the utility of this new approach using telemetry data from a population of mountain lions (*Puma concolor*) in Colorado, USA. Finally, in the *Conclusion* section, we summarize our approach and provide several promising novel methodological directions as well as potential future applications.

2. Methods

2.1. Modeling movement

One of the simplest models for animal movement is based on a random walk. Typically this takes the form of a state-space model where the random walk is correlated and framed in either discrete time (e.g., [25]) or in continuous time (e.g., [22]). In principle, either approach could be employed here, however our focus is on determining the two critical distributions for estimating resource selection: use and availability. As we show next, both distributions arise naturally in a local time setting as a byproduct of the movement model.

Consider the continuous-time correlated random walk (CTCRW) model of Johnson et al. [22] where the true underlying continuous movement of an individual is assumed to be dynamic according to an Ornstein–Uhlenbeck process (i.e., stochastic differential equation involving Brownian motion). When the dynamical system is discretized to accommodate a finite set of data as well as to facilitate computation, the geographical location process (μ_t) is not Markovian over the interval $(t - \Delta t, t]$. However, a combined dynamic process containing the locations and velocities can be constructed such that it is Markov. That is, a Brownian motion process can be specified in terms of a set of coupled velocity (\mathbf{v}_t) and location (μ_t) equations (using a parenthetical indexing notation to handle non-regular time intervals and ignoring the multivariate notation for simplicity):

$$v(t) = \theta_1 + \frac{\theta_2 e^{-\theta_3 t}}{\sqrt{2\theta_3}} \omega(e^{2\theta_3 t}),$$

$$\mu(t) = \mu(0) + \int_0^t v(u) du, \quad (4)$$

where the θ parameters control the motion and $\omega(t)$ is a standard Brownian motion process with $E(\omega(t)) = 0$, $\text{Var}(\omega(t)) = t$, and $\text{Corr}(\omega(t), \omega(\tau)) = \frac{\min(t, \tau)}{\max(t, \tau)}$ (e.g., [22]). When discretized, this serves as a model for the true underlying movement process where, for $\mathbf{z}_t = (\mu_t, \mathbf{v}_t)'$ we have:

$$\mathbf{z}_t = \mathbf{M}_t \mathbf{z}_{t-\Delta t} + \eta_t, \quad (5)$$

such that $\eta_t \sim N(\mathbf{0}, \Sigma_z)$ and \mathbf{M}_t is a propagator matrix consisting of elements that perform the necessary combination of previous $\mathbf{z}_{t-\Delta t}$ using nonlinear functions of θ and Δt as weights in the sums resulting from the matrix multiply: $\mathbf{M}_t \mathbf{z}_{t-\Delta t}$.

To construct a statistical model, we describe a likelihood that gives rise to the data. In this case, we assume the observed telemetry locations \mathbf{s}_t depend stochastically on the true locations μ_t and some measurement error (e.g., perhaps due to inaccuracy of the sensor and/or weather and terrain conditions). Thus, Johnson et al. [22] show that the data model can be written:

$$\mathbf{s}_t = \mathbf{H}_t \mathbf{z}_t + \epsilon_t, \quad (6)$$

where, $\epsilon_t \sim N(\mathbf{0}, \Sigma_s)$ and the transformation matrix \mathbf{H}_t simply maps the state-space to the data-space. In the 2-D movement situation, each \mathbf{H}_t will be a 2×4 matrix with rows $(1, 0, 0, 0)$ and $(0, 1, 0, 0)$, respectively. Note that (5) and (6) combine to form a state-space model that fits within the general spatio-temporal modeling framework proposed by Wikle and Hooten [51].

2.2. Use and availability distributions

Given its convenient state-space form, the hierarchical movement model in (5) and (6) can be implemented using likelihood and Kalman methods for state estimation [22]. Using either Kalman methods or finding the associated full-conditional distributions for \mathbf{z}_t given different portions of the entire latent state process, we can arrive at the filter, smoother, and predictor distributions for \mathbf{z}_t . These terms are commonly used in the time series literature (e.g., [43]) and specifically, the smoother distribution corresponds to our best understanding of \mathbf{z}_t given all of the data, while the predictor distribution describes the uncertainty concerning \mathbf{z}_t given only the preceding data. Though the filter

distribution has great utility in time series modeling, we are only concerned with the smoother and predictor distributions herein.

In translating the smoother and predictor concepts to the animal movement setting, the smoother distribution pertaining to the marginal location process μ_t can be thought of as our understanding of an animal’s true location at time t given all of the data, and the predictor distribution of μ_t represents a prediction of where the animal might be at time t given the best knowledge of its location at times $t - \Delta t$ and earlier. To be consistent with the animal space-use literature, we refer to these two distributions, smoother and predictor, as the use, $[\mu_t]_u$, and availability, $[\mu_t]_a$, distributions, respectively. Using the Kalman filter-smoother algorithm one can obtain the parameters $\phi_t = E[\mu_t|\{s_t, \forall t\}]$ and $\Omega_t = \text{Var}[\mu_t|\{s_t, \forall t\}]$ for, $[\mu_t]_u = N(\phi_t, \Omega_t)$ (details presented in [22]). Thus from (5), we have $[\mu_t]_a = N(\tilde{M}_t \phi_{t-\Delta t}, \tilde{M}_t \Omega_{t-\Delta t} \tilde{M}_t + \tilde{\Sigma}_z)$, where \tilde{M}_t and $\tilde{\Sigma}_z$ are the upper 2×2 submatrices of M_t and Σ_z , respectively.

Note that these two distributions give rise to a geographical vector rather than a resource vector as in (2). Fig. 2 illustrates the use and availability distributions for a single individual at a given time t . Due to the differences between the Kalman smoother and predictor, both the mode and diffuseness of the distributions can vary, though more temporal information is used by the smoother and this induces a more precise use distribution than availability distribution.

As a point of clarification, we note that the term “smoother” is somewhat misleading in this context because in fact, the use distribution (i.e., smoother distribution) will be less diffuse than the availability distribution (i.e., predictor distribution). The term “smoother” arises in the time series literature to denote that the process is being updated from both sides (from behind as well as ahead in time), thus it should be less diffuse in the space of the latent state than the predictor distribution, which is based on forecasting only (hence inducing extra variation in the distribution). In our case, the latent state of interest is the animal’s true location, thus the smoother provides the most precise information we have about the use of space by the animal, while the predictor indicates where the animal is forecast to be at some time in the future. This forecast identifies the likely spatial locations that are available to the animal at a future time step.

2.3. Estimating the selection coefficients

Employing the use and availability (i.e., smoother and predictor) distributions with respect to location, we can rewrite the weighted distribution from (2) as:

$$\begin{aligned}
 [\mu_t]_u &\approx \frac{g(\mathbf{x}(\mu_t), \beta_t)[\mu_t]_a}{\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t}, \\
 &\approx [\mu_t|\beta_t]_u.
 \end{aligned}
 \tag{7}$$

Aside from the use and availability distributions depending on covariates rather than locations (e.g., [1]), note that the other inherent difference between (7) and (2), is the time-specific nature of selection as denoted by the time index on β_t . Thus, the left hand side of (7) should be approximated with the right hand side depending on the selection coefficients β_t . In conventional resource selection approaches, the product over the weighted distribution equations (similar to the right hand side of (7)) results in a likelihood that can be maximized with respect to β because the left hand side of (7) is not known. Here, we actually know (or can estimate) both $[\mu_t]_u$ and $[\mu_t]_a$ based on the available data and assumed movement model in (5) and (6). Thus, we need only find the time-specific selection coefficients β_t that minimize the discrepancy between $[\mu_t]_u$ and $[\mu_t|\beta_t]_u$ from (7). In what follows, we approach the necessary optimization problem from an information theoretic perspective.

The Kullback–Leibler divergence from $[\mu_t|\beta_t]_u$ to $[\mu_t]_u$ can be written as:

$$\begin{aligned}
 D_{KL}(\beta_t) &= \int \log \left(\frac{[\mu_t]_u}{[\mu_t|\beta_t]_u} \right) [\mu_t]_u d\mu_t, \\
 &= E_u \left(\log \left(\frac{[\mu_t]_u}{[\mu_t|\beta_t]_u} \right) \right), \\
 &= E_u(\log[\mu_t]_u) - E_u(\log[\mu_t|\beta_t]_u),
 \end{aligned}
 \tag{8}$$

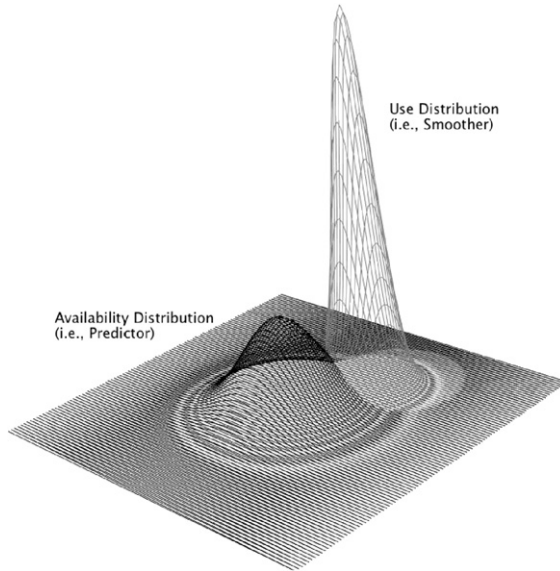


Fig. 2. An example of the use (smoother) and availability (predictor) distributions for temporal prediction grain of 1 h for a single individual. The more diffuse surface (dark gray) represents the availability distribution while the less diffuse surface (light gray) represents the use distribution for one time point.

and, since the Kullback–Leibler divergence is non-negative by Gibbs’ inequality [31] and finite since μ_t is Gaussian in our case, a numerical algorithm can be constructed to obtain an estimator of β_t based on Kullback–Leibler loss:

$$\hat{\beta}_t = \operatorname{argmin}_{\beta_t} \{D_{\text{KL}}(\beta_t)\}, \tag{9}$$

such that $[\mu_t | \hat{\beta}_t]_u$ is as close as possible to $[\mu_t]_u$ as desired in (7). In fact, since $E_u(\log[\mu_t]_u)$ does not contain β_t , to minimize $D_{\text{KL}}(\beta_t)$, we only need to maximize $E_u(\log[\mu_t | \beta_t]_u)$. That is, we maximize the criterion:

$$q(\beta_t) = \int \log[\mu_t | \beta_t]_u [\mu_t]_u d\mu_t, \tag{10}$$

with respect to β_t .

The implications of this movement-constrained weighted distribution approach are that we can characterize time-specific selection coefficients β_t using the inherent relationship between the use and availability distributions at each time of interest. Further, since we can find the use and availability distributions at any time throughout the extent of the study, we can obtain $\hat{\beta}_t$ over a quasi-continuous set of times controlled computationally by Δt .

2.4. Infinite point process equivalence

As noted by Warton and Shepherd [50] and Aarts et al. [1], many of the species distribution models and resource selection approaches can be equivalently thought of in a spatial point process framework. As we show below, the same result arises here, though because of the animal movement constraint, we have continuous knowledge of the use distribution $[\mu_t]_u$ in space. This continuity implies that, at each time t , instead of a finite point process of animal locations in space, we “observe” an entire spatial distribution due to the uncertainty associated with the true individual location μ_t . One way to illustrate the equivalence is to show that maximizing the optimization criterion $q(\beta_t)$ in (10) is

equivalent to maximizing the likelihood from an infinite inhomogeneous point process. Recall, to minimize the Kullback–Leibler divergence $D_{KL}(\beta_t)$, and thus maximize the efficiency of representing $[\mu_t]_u$ with $[\mu_t|\beta_t]_u$, we can maximize the criterion $q(\beta_t)$ with respect to β_t . Expanding $q(\beta_t)$, we have,

$$\begin{aligned} q(\beta_t) &= \int \log[\mu_t|\beta_t]_u [\mu_t]_u d\mu_t, \\ &= \int \log\left(\frac{g(\mathbf{x}(\mu_t), \beta_t)[\mu_t]_a}{\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t}\right) [\mu_t]_u d\mu_t, \\ &= \int \log(g(\mathbf{x}(\mu_t), \beta_t)[\mu_t]_a) [\mu_t]_u d\mu_t - \int \log\left(\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t\right) [\mu_t]_u d\mu_t, \\ &= q_1(\beta_t) - q_2(\beta_t). \end{aligned} \tag{11}$$

We note that $q_2(\beta_t)$ can be written as

$$\log\left(\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t\right) \int [\mu_t]_u d\mu_t,$$

which is the same as $\log(\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t)$ only, since $\int [\mu_t]_u d\mu_t = 1$. Thus, rather than maximize $q(\beta_t)$ directly with respect to β_t , it is equivalent to maximize

$$E_u(\log(g(\mathbf{x}(\mu_t), \beta_t))) - \log E_a(g(\mathbf{x}(\mu_t), \beta_t)), \tag{12}$$

which has a similar form as the point process likelihood described by Cressie [10, p. 651] and referred to as the “conditional inhomogeneous Poisson point process” (CIPP) by Aarts et al. [1]. In fact, since Warton and Shepherd [50] show that maximizing the likelihood of the Poisson generalized linear model results in the same inference as the logistic regression approaches that approximate a weighted distribution likelihood, and, Aarts et al. [1] show that inference under the CIPP model is equivalent, then we only have to show that the fit using the weighted distribution likelihood yields the same objective function as (12).

To show this, consider a likelihood based on (7), where we are interested in obtaining inference for β_t :

$$\begin{aligned} L(\beta_t) &= \prod_{i=1}^M [\mu_{i,t}|\beta]_u, \\ &= \prod_{i=1}^M \frac{g(\mathbf{x}(\mu_{i,t}), \beta_t)[\mu_{i,t}]_a}{\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t}, \end{aligned}$$

where the corresponding log likelihood is

$$\begin{aligned} l(\beta_t) &= \sum_{i=1}^M \log[\mu_{i,t}|\beta]_u, \\ &\propto \sum_{i=1}^M \log(g(\mathbf{x}(\mu_{i,t}), \beta_t)) - \sum_{i=1}^M \log\left(\int g(\mathbf{x}(v_t), \beta_t)[v_t]_a dv_t\right). \end{aligned}$$

Since we know the use distribution $[\mu_t]_u$ in this context, we can sample a large point process from it such that $\mu_{i,t} \sim [\mu_t]_u$ for $i = 1, \dots, M$. Now, if $M \rightarrow \infty$, then the sums in the log likelihood approximate the required integrals in (12) and the log likelihood is linearly related to (12) and will maximize at the same value of β_t .

The utility of this equivalence between our Kullback–Leibler minimization and the infinite point process is that we can use the approaches of Warton and Shepherd [50] to find $\hat{\beta}_t$. That is, using a Poisson generalized linear model approach on a fine grid with a very large set of grid cell counts, we obtain the same values for $\hat{\beta}_t$ as if we numerically performed the integration in (8).

2.5. Selection inference

The selection of resources by animals varies with temporal scale in both grain and extent [21,6]. From the grain perspective, when Δt is small and an animal moves from location $\mu_{t-\Delta t}$ to μ_t it has less opportunity to actually select resources because of the inherently correlated nature and physics of movement. However, as Δt increases, the animal has more of an opportunity to make decisions based on environmental cues. Thus, temporal selection grain is an important, but relatively unaddressed aspect in most space-use studies. Therefore, we have the opportunity to study resource selection across different temporal scales by varying Δt in our model. Further, the inferential scale often pertains to the extent of the study. For example, it is common to want inference about selection summarized over the temporal extent of the study. That is, if an animal is tracked during a breeding season, say for a set of time \mathcal{T} , and breeding season level inference is desired, then we may be interested in $E(\hat{\beta}_t)$ for all $t \in \mathcal{T}$.

As an animal moves through its environment, it will perform varying amounts of resource selection based on its momentum (or memory) and available resources. The extent to which the animal is influenced by our chosen environmental covariates at any given time is expressed in our estimate for selection $\hat{\beta}_t$ and the contribution of those coefficients in transforming the availability distribution into the use distribution. After reconciling use and availability by optimizing β_t , we are left with the minimized Kullback–Leibler divergence ($D_{\min}^{(t)}$) such that $0 \leq D_{\min}^{(t)} \leq D_{au}^{(t)}$, where $D_{au}^{(t)}$ represents the Kullback–Leibler divergence from $[\mu_t]_a$ to $[\mu_t]_u$. Note that when $D_{au}^{(t)}$ is small (i.e., close to zero) the use and availability distributions are very similar, implying that the movement model is able to reconcile selection without any influence from covariates. Therefore, we are only able to learn about selection due to our chosen covariates when there is a large difference between $D_{au}^{(t)}$ and $D_{\min}^{(t)}$. Thus consider the quantity $\Delta^{(t)} = D_{au}^{(t)} - D_{\min}^{(t)}$; this $\Delta^{(t)}$ provides us with a measure of the potential amount of selection due to our chosen covariates after accounting for the environmentally homogeneous physics of movement. For example, when $\Delta^{(t)}$ is large, it implies that the covariates were able to help reconcile use and availability, but when $\Delta^{(t)}$ is close to zero, it implies that either the movement model was able to predict selection by itself, or that our covariates were not very helpful in reconciling the use and availability distributions.

In this case, we would want an estimator for $E(\hat{\beta}_t)$ to be more heavily influenced by $\hat{\beta}_t$ when $\Delta^{(t)}$ is large. Thus, consider the weighted estimator $\bar{\beta}$:

$$\bar{\beta} = \sum_{t \in \mathcal{T}} w_t \hat{\beta}_t, \tag{13}$$

where, w_t are weights indicating which $\hat{\beta}_t$ coefficients contribute the most to our knowledge of selection during period \mathcal{T} . To construct the weights themselves, consider the quantity $e^{-\Delta^{(t)}}$; after some trivial algebra, this yields the quantity $e^{-D_{au}^{(t)}}/e^{-D_{\min}^{(t)}}$ which can be recognized as the “ratio of evidence” discussed by Burnham and Anderson [9, p. 78]. Note that this quantity can also approximately be considered a (1) likelihood ratio [2,8] where the Kullback–Leibler divergences are approximated using an information criterion multiplied by 1/2 and (2) a Bayes factor [26,18] where the prior model weights are equal. In this case, since $D_{au}^{(t)} \geq D_{\min}^{(t)}$, the ratio will be positive and bounded above by 1. Furthermore, it pertains to the ratio of evidence in favor of the homogeneous CTCRW model over the resource selection model. Thus, when $e^{-\Delta^{(t)}} = 1$ we have no evidence of selection. This implies that the quantity $1 - e^{-\Delta^{(t)}}$ provides a Kullback–Leibler measure of the evidence for selection at time point t and can be normalized over all times $t \in \mathcal{T}$ to create weights for temporal averaging:

$$w_t = \frac{1 - e^{-\Delta^{(t)}}}{\sum_{\tau \in \mathcal{T}} 1 - e^{-\Delta^{(\tau)}}}. \tag{14}$$

We note that our approach directly relates to information theory and maximum entropy concepts. When we minimize the Kullback–Leibler divergence from the availability distribution to the use

distribution, we are, in effect, obtaining a model that loses a minimum amount of information in the data as compared to the null model of environmentally homogeneous movement. Further, given the well-known negative relationship between Kullback–Leibler divergence and entropy, we are also implicitly maximizing the mean entropy, or maximizing the “noise” associated with movement, leaving only the information about selection [20,3]. The Kullback–Leibler differences $\Delta^{(t)}$ measure the amount of information we gain about movement when covariates are used in a resource selection framework.

Returning now to the estimator of mean selection (13), it is easily shown that $\bar{\beta}$ yields an unbiased estimator of $E(\hat{\beta}_t)$ under certain conditions (e.g., $\sum_t w_t = 1$ for $w_t \geq 0$). Similarly, the unbiased weighted covariance estimator of $\hat{\Sigma}_{\beta} \equiv \text{var}(\hat{\beta}_t)$ is

$$\hat{\Sigma}_{\beta} = \frac{\sum_{t \in \mathcal{T}} w_t (\hat{\beta}_t - \bar{\beta})(\hat{\beta}_t - \bar{\beta})'}{1 - \sum_{t \in \mathcal{T}} w_t^2}, \tag{15}$$

where the covariance matrix of the weighted mean, $\bar{\beta}$, can then be estimated with

$$\hat{\Sigma}_{\bar{\beta}} = \sum_{t \in \mathcal{T}} w_t^2 \hat{\Sigma}_{\hat{\beta}_t}. \tag{16}$$

For population-level inference, each selection estimator $\hat{\beta}_j$ will be indexed by individual j for $j = 1, \dots, J$ (and hence $\hat{\Sigma}_{\hat{\beta}_j}$ will also be indexed by j). Conventional frequentist inference can be obtained for the population by computing summary statistics using the $\hat{\beta}_j$ over all individuals. That is, for population-level inference we desire the estimates $\bar{\beta}_{\text{pop}}$ and $\widehat{\text{var}}(\bar{\beta}_{\text{pop}})$ given the individual-level information $\hat{\beta}_j$ and $\hat{\Sigma}_{\hat{\beta}_j}$ for $j = 1, \dots, J$. This is essentially a meta-analysis problem and there are numerous approaches for combining the information across individuals, many of which are analytical approximations or require further model-based estimation methods (e.g., [16]). For the analysis that follows, we obtain $\bar{\beta}_{\text{pop}}$ and $\widehat{\text{var}}(\bar{\beta}_{\text{pop}})$ using a parametric bootstrap procedure (Appendix) primarily for its relative simplicity as compared with other methods.

Many further extensions can be made to compare subpopulation selection (e.g., differences among varying demographics) as well as temporal subsets such as varying day periods or biologically relevant cycles (e.g., breeding vs. non-breeding season). Further, given the propensity for some species to exhibit periodic behavior, functional data analysis methods can be applied within this same framework.

3. Application: mountain lion resource selection

3.1. Background

The mountain lion (*Puma concolor*) is a carnivore native to North America whose range has diminished substantially since European settlement. Despite the dramatic reduction in the spatial extent of mountain lions during the past two centuries, thriving populations currently exist in various portions of the country. There are numerous mountain lion studies across the Western United States, however our understanding of mountain lion ecology is nascent in this area largely due to the difficulty and expense of studying such an elusive, wide-ranging, and solitary species [39]. Technological advances, such as GPS telemetry, have increased the ability of researchers to gather valuable information on mountain lions, but such research has just begun, such as the Uncompahgre Plateau research project. Even less information is known about mountain lion spatial ecology within urban and exurban environments.

Other studies have documented the impacts of urban environments on mountain lion temporal and spatial use patterns. Ordenana et al. [36] documented an overall decrease in mountain lion occurrence associated with proximity and density of urban landscapes. Other studies have shown that dense

housing developments can act as movement barriers to mountain lions [37] or that mountain lions will become more nocturnal in urban areas [28]. Similarly, studies have shown selection of home ranges, use within home ranges, general movements, and dispersal can be affected by roads, road densities and/or traffic volumes [48,5,4,44,11,37]. Preliminary investigations suggest that mountain lions in the front-range of Colorado are similarly affected by urbanization as nocturnal behaviors and changes in use relative to human density have been observed with GPS collared mountain lions during the study.

3.2. Telemetry and covariate data

As part of a larger study on Colorado Front-Range mountain lions, GPS telemetry data have been obtained for 66 individuals at a fairly regular fix interval of approximately 3 h in an ongoing Colorado Parks and Wildlife (CPW) monitoring effort. The observation windows for these 66 mountain lions vary; some individuals have location histories for the past 5 years, while others have only recently been captured and fitted with a telemetry device. We focused on the month of June, 2011 for our analysis of population-level resource selection and examined telemetry data collected from 25 mountain lions in the Colorado Front-Range study during this month.

One of the main objectives of the Colorado Front-Range mountain lion study is to examine how the population of mountain lions are selecting resources in a mosaic of urban and exurban environments. The availability of fine scale, highly accurate, GPS data provides the potential to look at selection patterns in great detail. For spatial covariates, we used a set of land cover types (i.e., classified as urban, agricultural, shrub, and bare ground) as well as continuous elevation to assess resource selection (Fig. 3); note that a sixth covariate (i.e., forest land cover type) is implicitly considered in the analysis as a baseline category. For each individual, the telemetry devices were programmed to provide approximately 7 fixes per day for the month of June, 2011. In our analysis, we desired inference on a relatively small temporal scale, and thus chose a one hour temporal grain for selection. This implies that we seek to learn about how mountain lions select resources during a one hour time period.

3.3. Data analysis

The full estimation procedure for mountain lion selection involves a sequence of steps that are easily summarized. First, we fit the continuous-time correlated random walk movement model described in (5) and (6) using the telemetry data from June, 2011 (\mathcal{T}) for each of the 25 individuals in our study. Second, in fitting the movement model, we obtain the use and availability distributions for all $t \in \mathcal{T}$ and individuals; these arise naturally as the Kalman smoother and predictor distributions pertaining to the fitted movement path. This can all be accomplished using the ‘crawl’ package [22] in the R Statistical Computing Environment [41].

Next, we reconcile the use and availability distributions by minimizing the Kullback–Leibler divergence (8) between them. Fortunately, this step can be accomplished using a standard generalized linear model fitting algorithm [50]. Specifically, we sample a large spatial point process from each of the use and availability distributions then sum the points over a fine grid and fit a Poisson regression model with the use counts (u) as the response variable and the availability counts (a) as an offset in the model (i.e., $u \sim \text{Pois}(a\lambda)$ where $\log(\lambda) = \beta_0 + \mathbf{x}\beta$) for each animal at $t \in \mathcal{T}$. The result is a set of selection coefficients $\hat{\beta}_{j,t}$ for each individual j at every time t . The resource selection for each individual was then estimated with $\bar{\beta}_j$ (13) and combined for population-level inference using the bootstrapping approach described in the previous section.

In Fig. 4 we provide the estimated selection coefficient $\hat{\beta}_t$ for the urban land type covariate and the weight w_t over the complete set of hourly selection periods in June, 2011 for a single individual (i.e., mountain lion # 2, an adult female). These results indicate that an individual’s resource selection likely varies over time (as we expected) as does the amount of selection (as evidenced by w_t). The “spikes” in these time series of $\hat{\beta}_t$ and w_t coincide with times where telemetry location data exist. This behavior can be explained by the fact that the use and availability distributions are quite similar at points distant in time from telemetry data (at least in this example) and the Kullback–Leibler minimization cannot

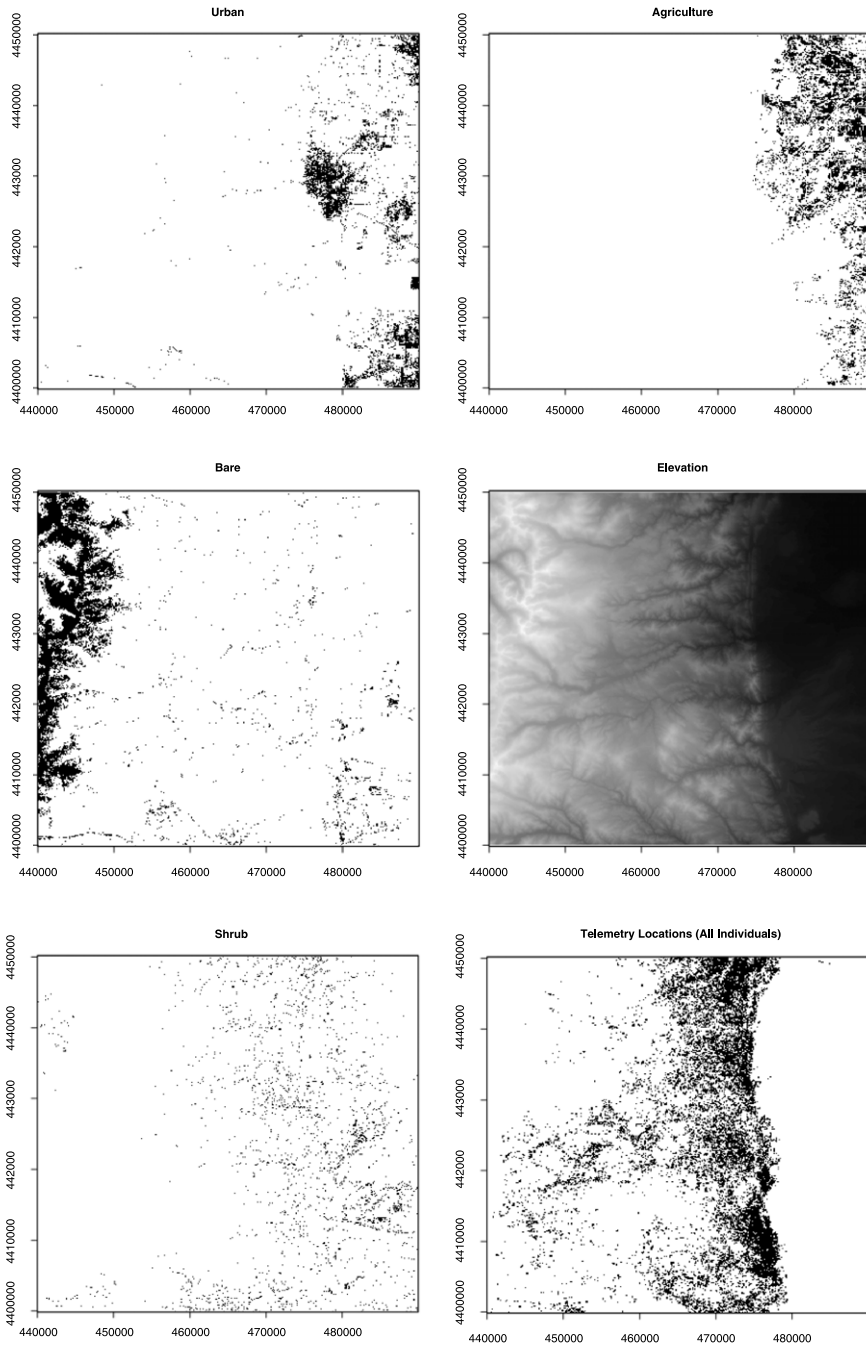


Fig. 3. Maps showing the spatial covariates used in the mountain lion analysis as well as the full set of telemetry locations for all individuals in the study.

make use of the covariate information, hence estimating the coefficients to be near zero. At points near the telemetry data, the opposite occurs: at these times, we have a large discrepancy between use

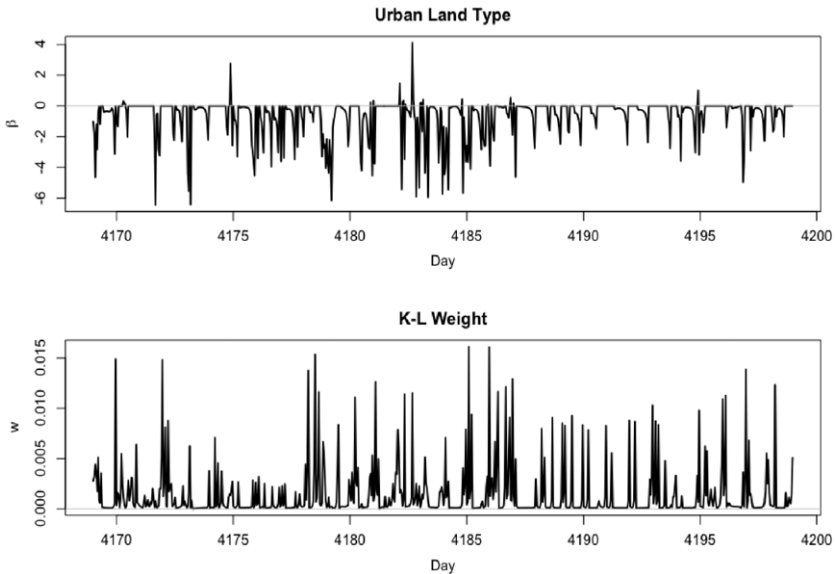


Fig. 4. Time series plot showing the estimated $\hat{\beta}_t$ for mountain lion # 2 (adult female) and the associated weight. Large values for w_t indicate important times for inferring selection based on our chosen covariates.

and availability distributions and the RSF model has a chance to learn about the selection parameters. An advantage of the weighted estimator (13) is that the coefficients at times when little information is available about selection will be down-weighted appropriately. We note that as the number of observed telemetry locations in the original dataset increases, we will see a corresponding increase in the w_t spikes and this will, in turn, provide more precise estimates of $\hat{\beta}_j$ with lower variance due to the increased effective sample size.

In our analysis, the results for each individual showed similar variation in selection and divergence, although each displayed somewhat different patterns. In this study, our analysis was focused on the estimation of resource selection at the population-level, but it is important to point out that various data mining methods could be employed to better illuminate patterns of resource selection resulting from output similar to that shown in Fig. 4.

Table 1 summarizes the estimates for population-level resource selection based on all 25 individuals in our study. Note that the estimates for all land types (i.e., urban, agricultural, shrub, and bare ground), as well as the elevation coefficient, are significantly negative. The negative population-level coefficients for land types imply that this population of mountain lions select most strongly for the forest land type (not shown because it is implicit in the baseline category). In fact, in order of selection for the categorical covariates (i.e., selection for that resource), Table 1 indicates that forest is first, with agricultural land next, then urban land, then bare ground, with shrub last. These results suggest that, during June, 2011, the selection for urban land type by this mountain lion population is significantly less than the selection for forest. Similar implications hold for the other land types and elevation as well.

4. Conclusion

We have proposed a statistical method for estimating resource selection using high-resolution animal telemetry data. Though alternative methods for assessing movement-based RSFs exist (e.g., [24,22,14]), our approach differs in several critical features. First and foremost, by conditioning on movement, we obtain naturally arising use and availability distributions that allow us to estimate individual-based selection at each time of interest for a pre-specified selection period. Further, our estimation of individual-based selection using Kullback–Leibler minimization provides insight into

Table 1

Population-level inference for selection coefficients based on monthly analysis and a 1 h temporal selection grain.

Parameter	Est.	Std. error	95% CI
β_1 (urban)	−1.19	0.042	(−1.28, −1.01)
β_2 (agricultural)	−0.22	0.021	(−0.26, −0.17)
β_3 (shrub)	−1.95	0.059	(−2.07, −1.83)
β_4 (bare)	−1.76	0.057	(−1.87, −1.64)
β_5 (elevation)	−0.002	0.0004	(−0.003, −0.001)

when a given animal appears to be selecting resources (based on our chosen covariates) and can be used to weight the selection coefficients based on how much information each is contributing to our understanding of global selection. To our knowledge, this is the first resource selection approach that allows the researcher to investigate the degree of selection learning possible throughout an individual's path.

Finally, the methods we present are intuitive, easy to implement, and highly generalizable. Many recent models for animal movement (e.g., [19,17,33]) are perhaps useful, but, due to their complexity, may be inaccessible to wildlife biologists and managers who need the inference for scientific inquiry and for wildlife and resource management. Our method couples well-understood animal movement models [22] with commonly used RSF approaches to provide inference about resource selection at fine temporal scales using high-resolution telemetry data. Despite the complex optimization procedure that is required (10), we show that readily available and familiar statistical software can be used to perform the estimation.

In terms of computational efficiency, the bulk of required calculations are “embarrassingly parallel” in that the individual animals can be processed separately to find the sequences of use and availability distributions. The Kullback–Leibler optimization can also be parallelized and performed using sparse matrix calculations reducing computing burden even further by distributing the load among several processors. Still, in our case, without parallelizing the code, computing for each animal occurred on the order of a few minutes. Given the massive size of the covariate grids (approximately 1.5 million pixels), the compute times we experienced indicate that this methodology can be applied to real datasets spanning large spatial landscapes.

It is important to point out that this method is heavily based on an underlying mechanistic movement model. In fact, these methods are similar in spirit to a meta-analysis and exploit the fact that the current (i.e., use) and future (i.e., availability) location distributions of the animals under study can be estimated using the available telemetry data. If the observed telemetry locations are too temporally distant, then a fine scale movement model like the continuous-time correlated random walk model used herein may not provide the information needed to identify time-varying use and availability distributions. As a general rule of thumb we would not advise using any time-varying resource selection method unless the data include a distinct “movement” signal. That is, if one can envision a realistic animal path connecting the telemetry location data, then typically these sorts of models work well. In terms of guidance on scales for inference, if the temporal change Δ_t is too small then there will be very little difference between use and availability distributions and thus only minimal information will be available about selection. Finally, if seasonal (i.e., periodic) animal behavior is expected, it should be accounted for so that one does not obtain misleading inference. For example, animals may exhibit varying amounts and types of resource selection during different photoperiods (e.g., day or night). A simple way to deal with this might be to summarize results from night and day periods separately. Finally, like with all statistical models, if the telemetry fix rate (i.e., sampling) is itself correlated with environmental variables then there is a potential to obtain biased inference for resource selection. A potential area of future research with this type of analysis would be to simultaneously model fix rate and resource selection.

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Appendix. Implementation

The approach to fitting resource selection models for animal movement data described in the METHODS section requires a sequence of steps that are outlined below. Due to the complexities of specific datasets, we provide a mixture of software syntax in the R Statistical Computing Environment [41] and pseudo-code that demonstrate how one would actually implement the fitting procedure on their own dataset. First we assume that the user has already obtained telemetry data (containing a “movement signal” as discussed in CONCLUSION) for J individuals, gridded covariate data over the spatial domain of interest, and has a temporal scale for selection in mind (Δ_t). Then, the following steps can be used to implement the described inference procedure:

1. Fit the CTCRW model (i.e., ‘crawl’ R package; [22]) to each set of telemetry observations from each individual using the ‘crwMLE’ R function. Then use the ‘crwPredict’ R function to obtain the posterior predictive distribution for the complete path of each individual at selection scale of interest. By setting the ‘getUseAvail=TRUE’ flag in the ‘crwPredict’ function one can output the use and availability (i.e., smoother and predictor, respectively) distributions at each time point t in terms of the first two moments of the distributions (since they are both Gaussian). See the help documentation for the ‘crawl’ R package for further details on syntax. Once these use and availability moments (mean vector and covariance matrix) have been stored the remainder of output can be discarded. Furthermore, it is important to point out that each animal is processed individually, thus this step can be parallelized.
2. Once the use and availability distributions have been obtained using ‘crawl,’ the Kullback–Leibler divergence ($D_{au}^{(t)}$) between the use and availability distributions can be approximated for each time point t by approximating the necessary integrals (i.e., $\int \log([\mu_t]_u) [\mu_t]_u d\mu$ and $\int \log([\mu_t]_a) [\mu_t]_a d\mu_t$) using either numerical quadrature or Monte Carlo integration. The Monte Carlo integration approach would proceed by sampling several location realizations μ_t from the use distribution, computing the quantities $\log([\mu_t]_u)$ and $\log([\mu_t]_a)$, arithmetically average each of these, and then subtract them.
3. Minimize the Kullback–Leibler divergence using the Poisson point process model described in Section 2.4. One method for implementation is, for each time t , sample two very large spatial point processes (on the order of thousands of samples from each to approximate the distribution); one from the use distribution and the other from the availability distribution. Compute the cell frequencies for each point process over a very fine grid spanning the convex hull of all points. Let the ‘use’ cell frequencies be the response variable in a Poisson regression (e.g., using the ‘glm’ R function) where the ‘availability’ cell frequencies serve as the offset and the covariates are associated with each grid cell. The estimates $\hat{\beta}_t$ resulting from this fit serve as our temporally indexed selection coefficients.
4. Given the coefficients $\hat{\beta}_t$, the minimized Kullback–Leibler divergence $D_{\min}^{(t)}$ can be approximated numerically as described in step 2 above.
5. Obtain the individual-level averaged selection coefficients by first subtracting the Kullback–Leibler divergences to get $\Delta^{(t)} = D_{au}^{(t)} - D_{\min}^{(t)}$, computing the weights (14), then using the estimators (13), (15) and (16) to get $\bar{\beta}_j$ and $\hat{\Sigma}_{\bar{\beta}_j}$ for all individuals $j = 1, \dots, J$.
6. Finally, population-level inference can be obtained via a meta-analysis of the individual-level estimates. One approach for estimating the population-level mean and standard error is a parametric bootstrap. It is trivial to implement such a bootstrap and should not be too computationally intensive if the number of individuals is relatively small. Within a bootstrap loop with K iterations, the first step is to sample a realization from each individual-level multivariate Gaussian distribution with mean $\bar{\beta}_j$ and covariance $\hat{\Sigma}_{\bar{\beta}_j}$ such that we have J temporary samples in each iteration of the bootstrap loop. We then simply compute the sample mean and covariance of these samples and save for each of the K bootstrap iterations. This approach uses a Gaussian assumption for the β_j , but given that these coefficient vectors are means, Gaussianity is reasonable.

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