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Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data

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Abstract. An animal's trajectory is a fundamental object of interest in movement ecology, as it directly informs a range of topics from resource selection to energy expenditure and behavioral states. Optimally inferring the mostly unobserved movement path and its dynamics from a limited sample of telemetry observations is a key unsolved problem, however. The field of geostatistics has focused significant attention on a mathematically analogous problem that has a statistically optimal solution coined after its inventor, *Krige*. Kriging revolutionized geostatistics and is now the gold standard for interpolating between a limited number of autocorrelated spatial point observations. Here we translate Kriging for use with animal movement data. Our Kriging formalism encompasses previous methods to estimate animal's trajectories—the Brownian bridge and continuous-time correlated random walk library—as special cases, informs users as to when these previous methods are appropriate, and provides a more general method when they are not. We demonstrate the capabilities of Kriging on a case study with Mongolian gazelles where, compared to the Brownian bridge, Kriging with a more optimal model was 10% more precise in interpolating locations and 500% more precise in estimating occurrence areas.

Key words: autocorrelation; Brownian bridge; CRAWL; Krige; Mongolian gazelle; Procapra gutturosa; *telemetry error; tracking data; tracking data gaps; utilization distribution.*

Introduction

Understanding the drivers and mechanisms of animal movement informs our understanding of many ecological processes, from the individual to the population level. When considering an animal's activities and behaviors, many quantities of interest must be conditioned upon that individual's movement trajectory. These quantities include, but are not limited to, distance traveled, speed, regions occupied, environmental covariates utilized, behavioral states, and energy expended. Many of these quantities would be straightforward to calculate if we knew the animal's trajectory—i.e., the coordinates $\mathbf{r}(t) = (x(t), y(t))$ at all times t. For example, an animal's velocity is given by

differentiation, $\mathbf{v}(t) = \dot{\mathbf{r}}(t)$, its speed by the absolute value of velocity, $v(t) = |\mathbf{v}(t)|$, and distance traveled by integrating speed, $d(t_1, t_2) = \int_{t_1}^{t_2} v(t)\mathrm{d}t$. However, we never know an animal's trajectory exactly as we only sample it a limited number of times, often with substantial telemetry error.

The existing probabilistic approaches to trajectory estimation are the Brownian bridge (BB) (Horne et al. 2007, Benhamou 2011, Kranstauber et al. 2012, 2014, Pozdnyakov et al. 2014) and the continuous-time correlated random walk library (CRAWL) (Johnson et al. 2008). Discrete-time approaches that assume subsequent observations are connected by straight lines, such as the correlated random walk (Kareiva and Shigesada 1983), provide no way to reliably estimate most of the quantities we consider. Though the BB and CRAWL are typically used for different purposes—estimating occurrence distributions with the BB vs. smoothing and simulating data with CRAWL—as we will show, they both happen to be examples of Kriging with a predetermined movement model. The Kriging approach

we introduce here allows users to select between these special case models, or other candidate models, and identify the most appropriate model for their data.

It is important to note that for any given dataset the generalized distribution we introduce here estimates occurrences rather than range (Fleming et al. 2015a). The occurrence distribution specifies the probability that the animal occurred within an area at a randomly chosen time within the observation period. In general terms, estimating "range" involves extrapolating where an animal will travel over a long span of time if similar movement behaviors persist, while estimating "occurrence" involves interpolating where an animal traveled during the observation period. Notably, "range" considers all realizations of the movement process that could occur, while "occurrence" pinpoints the one realization of the movement process that did occur. The true range distribution is sampling independent, with a home-range area that reflects the animal's needs, while the occurrence distribution is sampling dependent, with a coverage area that reflects our uncertainty in the underlying movement path—we refer to this area as an "occurrence area". And while the occurrence distribution does converge to the range distribution in the limit of data with infinite duration and fixed sampling rate, occurrence estimators are relatively biased and inefficient estimators of range because they make no attempt at extrapolating this future space use. On the other hand, proper range estimators (By a "proper" range estimator, we mean to imply one that has its assumptions met by the data, rather than assuming, for example, that strongly autocorrelated data are independently sampled. As can be seen from the results in Fleming et al. (2015a), ignoring autocorrelation causes a downward bias in the range estimator that muddles this distinction) are relatively biased and inefficient estimators of occurrence because they do extrapolate space use. In addition to this conceptual clarification, Fleming et al. (2015a) derived an autocorrelated kernel density estimator to rigorously estimate the range distribution from autocorrelated tracking data. Here we turn our attention in the other direction and show how to estimate an animal's occurrence distribution, and many other trajectory-related quantities, in a statistically rigorous way via probabilistic path reconstruction.

KRIGING

A general and statistically rigorous solution to the problem of how to extract and leverage the most information from tracking data is to solve for the distribution of all possible trajectories conditioned upon the data. Mathematically, this problem has been addressed in geostatistics, engineering, and computer science, where its solution is referred to as Kriging, filtering and smoothing, and stochastic process regression respectively (Cressie 1993, Durbin and Koopman 2001, Rasmussen and Williams 2006). While the Krige is a familiar tool in spatial and statistical ecology (Legendre and Fortin

1989), its full statistical framework has never before been translated to animal-tracking time series. The Krige estimates missing or erroneous locations in a manner consistent with trends in the data and correlations to other data points. For the type of problem we consider, the Krige has been rigorously proven to be statistically optimal under readily satisfied assumptions (Stein 1988, Cressie 1993).

Kriging is a two-step process. The first step is to select a movement model, such as Brownian motion, that best describes the data (Fleming et al. 2014a,b). At minimum, a movement model provides a mean function $\mu(t)$, that reflects deterministic trends such as migration, and an autocorrelation function $\sigma(t,t')$ (Appendix S1), that reflects stochastic movements such as diffusion. The most appropriate movement model for an animal tracking dataset is determined not only by the animal's true movement behaviors, but also by how well those behaviors are resolved by the data. Once the best model for the data has been selected, the parameterized mean and autocorrelation functions for that model can be fed into the Krige. The second step is then to solve for the probability of the animal's location $\mathbf{r}(t)$, conditioned upon both the observed data and a selected movement model (Appendix S1).

An important advantage of the Kriging framework is that it has well understood and rigorously proven statistical properties (Stein 1988, Cressie 1993). If an animal's locations $\mathbf{r}(t)$ are realizations of a Gaussian stochastic process then Kriging with the true autocorrelation model provides the minimum variance unbiased (MVU) estimate, while for other distributions Kriging with the true autocorrelation model still provides the best linear unbiased estimate (BLUE) (Cressie 1993). Unbiased estimators yield the true value on average, MVU estimators then minimize the squared error on average, and BLUEs minimize this variance specifically among estimators that are linear functions of the data (Lehmann and Casella 1998). The true model is never known, so it is important to understand how the Krige performs with a misspecified model. On this point, Stein (1988) proved that the Krige will still be asymptotically efficient as long as the misspecified model process has the same number of continuous derivatives as the true process. An asymptotically efficient estimator is one that becomes as good as MVU for large amounts of data (Lehmann and Casella 1998).

On the other hand, Newtonian mechanics places strict constraints on what models can be appropriate. Realistic animal movement processes must have continuous positions, velocities, and accelerations, but a finite sampling rate may not reveal all of the process' continuity (Fleming et al. 2015b, and Appendix S2). Therefore, to achieve asymptotic efficiency, Stein's proof necessitates modeling every degree of continuity supported by the data. For example, in many ungulates continuous-position models are necessary even when sampling intervals range from weeks to months, as this is the scale at which the ungulates' sequential locations appear related (McNay et al. 1994, Rooney et al. 1998, Boyce et al. 2010, Fleming et al.

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2014*a,b*). In contrast, continuous-velocity models may not become necessary for ungulates unless one is working with sampling intervals comparable to an hour, as this is the scale at which directional persistence is perceptible (Fleming et al. 2014*a,b*). Further continuity beyond what is apparent in the data is not required because the differences in predictions between the "true" model and an effective model—one negligibly different at the resolved timescales—will also be negligible.

The Krige and its Products

The Krige yields a distribution of trajectories $\mathbf{r}(t)$ conditioned upon the data $\mathbf{R}$, which is Gaussian with mean and autocorrelation functions defined

$$
\begin{aligned}
\boldsymbol{\mu}_K(t) &\equiv \langle \mathbf{r}(t) | \mathbf{R} \rangle, \\
\boldsymbol{\sigma}_K(t,t') &\equiv \langle [\mathbf{r}(t) - \boldsymbol{\mu}_K(t)] \left[\mathbf{r}(t') - \boldsymbol{\mu}_K(t') \right]^T | \mathbf{R} \rangle,
\end{aligned}
\tag{1}
$$

which are derived in Appendix S1 and given by Eqs (S1:6) and (S1:9), where $\langle \mathbf{A} | \mathbf{B} \rangle$ denotes the expectation value of $\mathbf{A}$ conditioned upon $\mathbf{B}$. The distribution of a single, unknown location is therefore normally distributed with mean $\boldsymbol{\mu}_K(t)$ and covariance $\boldsymbol{\sigma}_K(t,t)$ or

$$
p(\mathbf{r}(t) | \mathbf{R}) = \mathcal{N}(\boldsymbol{\mu}_K(t), \boldsymbol{\sigma}_K(t,t)).
\tag{2}
$$

In the absence of location error, the Krige interpolates observed locations. Otherwise, it yields predictions of true locations for sampled times that depend on the movement model, data, and observation error. In either case, the location of the animal at times not sampled can be estimated. We note that the conditional probability distribution here in Eq. (2) is equivalent to that of the BB and CRAWL. Specifically, Kriging based on a Brownian motion model is equivalent to the BB, while Kriging based on an integrated Ornstein–Uhlenbeck model (IOU, Appendix S3) is equivalent to the CRAWL.

The occurrence distribution is obtained by averaging (2) over a set window of time

$$
p(\mathbf{r}(t_A < t < t_B) | \mathbf{R}) = \frac{1}{t_B - t_A} \int_{t_A}^{t_B} dt \, \mathcal{N}(\boldsymbol{\mu}_K(t), \boldsymbol{\sigma}_K(t,t)),
\tag{3}
$$

which results in the probability distribution of the locations of the tracked animal during intermediate times. Occurrence distribution (3) generalizes the Brownian bridge and CRAWL derived utilization distributions (UDs) (Horne et al. 2007, Johnson et al. 2011), in that selecting Brownian motion yields the BB UD, while selecting IOU motion yields the CRAWL UD, and we may equivalently refer to both as the BM Krige and IOU Krige, respectively. A key advantage of the Kriging framework is that the most appropriate movement model for the data, whether BM, IOU, or otherwise, can be used to derive the occurrence distribution. Occurrence distributions leverage autocorrelation to filter and interpolate where the animal was located, though they do not typically reflect an animal's home range in any given

dataset. However, if we want to know what environmental covariates the animal experienced in its travel, then the occurrence distribution is the appropriate quantity for this task.

In addition to resource utilization, many other quantities can be obtained from the distribution of trajectories. As a particularly salient example, the Krige can estimate how far an animal travels, say, on a daily or yearly basis. How to rigorously estimate kinematic quantities such as distance traveled from movement data has been an open question in movement ecology (Rowcliffe et al. 2012). Like the home-range area, these should be sampling independent quantities that can be meaningfully compared across species and sampling schedules, yet estimators that ignore autocorrelation render such comparisons uninformative. The distance/time estimator, in particular, will underestimate speed in coarse data because it assumes minimal-distance straight-line motion between sampled times (Rowcliffe et al. 2012), while overestimating speed in fine data because it confounds error with movement (Ranacher et al. 2016). Kriging based on a model of Brownian motion is also not helpful for this task because BM predicts an infinite, fractal distance traveled between any two times. In contrast, Kriging based on a continuous-velocity model (e.g., IOU) can be used to estimate kinematic quantities in a rigorous way. Speeds are particularly convenient to estimate in CRAWL's hidden-Markov IOU model; however, as we derive in Appendix S1: Eq. 1, kinematic quantities like velocity can be estimated from the Krige even if they are not hidden-state variables, provided that the data and selected model support these features.

Movement Model Selection

Selecting an appropriate model for the data is a key step in Kriging that strongly affects the quality of trajectory and occurrence distribution estimates. The full specification of a "model" requires both a movement process model and an error process model. As a demonstration of model selection within the Kriging framework, we consider the five basic continuous-time movement models that have been applied to animal-tracking data: bivariate normal (Winkle 1975), Brownian motion (BM, Horne et al. 2007, Pozdnyakov et al. 2014), Ornstein–Uhlenbeck motion (OU, Uhlenbeck and Ornstein 1930, Dunn and Gipson 1977), integrated OU motion (IOU, Johnson et al. 2008, Gurarie and Ovaskainen 2011), and a hybrid IOU-OU model coined OUF after the ballistic foraging behavior observed in grazing ungulates (Fleming et al. 2014*a*). These models—summarized in Table 1 and described in Appendix S3—specify the autocorrelation function of the movement process, while deterministic trends such as migration events are straightforward to implement in the mean function.

GPS telemetry data now come standard with "dilution of precision" (DOP) estimates, which ameliorate much of the need to model telemetry error as an unknown process. When telemetry errors cannot be estimated or

Table 1. Comparison of movement models: Bivariate normal (BN), Brownian motion (BM), Ornstein–Uhlenbeck motion (OU), integrated Ornstein–Uhlenbeck (IOU), and Ornstein–Uhlenbeck–F motion (OUF)

Model	Range	Position	Velocity
BN	Finite	Discontinuous	Discontinuous
BM	Infinite	Continuous	Discontinuous
OU	Finite	Continuous	Discontinuous
IOU	Infinite	Continuous	Continuous
OUF	Finite	Continuous	Continuous

calibrated independently, an error model can be fit to the data simultaneously with the movement model (e.g., Johnson et al. 2008). However, this should be done sparingly and cautiously, and we only consider this possibility as an exercise. If not carefully constrained, sporadic movements that occur over durations shorter than the sampling interval can easily be "explained" by an error model when in fact there is far less error to explain.

To make optimal predictions, we base model selection on AIC rather than BIC (Yang 2005). The selected model should also be compared to the *x*-*y* scatter plot and empirical variogram (Fleming et al. 2014*a*) to ensure that it explains the most significant features of the data. In short, substantial telemetry error would correspond to an initial discontinuity in the variogram, continuous velocities correspond to the positive curvature at short time lags, Brownian motion corresponds to linearity in the variogram, and range residence corresponds to an asymptote in the variogram (qualitatively similar to Appendix S3: Fig. 1). Variogram, model selection, and basic Kriging functionality is provided in the ctmm R package (v 0.3.0, Fleming and Calabrese 2015), which we demonstrate in the supplement.

As we will demonstrate, Kriging based on the selected model has a strong tendency to make better predictions than Kriging based on higher-AIC models. Especially given the proof of Stein (1988), under-performance is often a forseeable consequence of Kriging based on a model that does not adequately account for the key features in the data. First, the BM and OU movement models exhibit infinite, discontinuous velocities (Appendix S1: Fig. 1) and therefore they will not be asymptotically efficient for data that are sampled finely enough to reveal finite, continuous velocities. In this case, diffusion is overestimated at scales shorter than the sampling interval, which comprise the bulk of occurrence estimation, and the general effect is to overestimate the occurrence area (Appendix S3: Fig. 1). Second, the BM and IOU models exhibit endless diffusion and will therefore overestimate diffusion in large gaps, which makes their occurrence distributions more sensitive to gapping in the data (Appendix S4: Fig. 2). As a specific example, if a maned wolf patrols its territory daily and there is a month-long gap in the data, then a BM or IOU Krige will project an occurrence area during that month extending far beyond the wolf's territory. In contrast,

Kriging based upon a model featuring restricted space use (e.g., OU & OUF) would predict an occurrence area bound by the territory size.

EMPIRICAL EXAMPLE

To compare the capabilities of Kriging based on a selected movement model relative to the special cases of the BM and IOU models on a real tracking data set, where the true model is not known, we used GPS tracking data from 36 Mongolian gazelles (*Procapra gutturosa*) collected over a span of 5 yr, with individual time series up to 2.5 yr in length, and individual sampling intervals ranging from 1 to 25 h (Fleming et al. 2013). In Appendix S4, we performed the same comparative analysis on a longer and more regularly sampled fisher (*Martes pennanti*) dataset (LaPoint, et al. 2013*a*, *b*), where the performance differences were comparable to the gazelles.

Our model selection was performed on an individual basis. All of the individuals we considered were range resident (not migratory) and so we only fit stationary mean functions. Both circular and elliptical covariances were included in the model selection. An OUF process was selected for 33 gazelles, while an OU process was selected for the remaining three gazelles. The continuous-velocity OUF model was supported for all individuals with hourly data, but not for all individuals with more coarsely sampled data. 23 of the selected covariances were elliptical, while 13 were circular.

The gazelles' GPS fixes were not annotated with "dilution of precision" (DOP) estimates, but blanketly assigned a 5-m spatial resolution. The mean distance between sequential observations was ~ 6 km across all 36 animals. Relative to these observed displacements, spatial error on the observations (~ 5 m) was small enough to be neglected, though we still included it to demonstrate the methodology. We selected among three error models: one with no telemetry error, one with a fixed 5-m error, and one with an unknown error variance for each individual gazelle that is on the order of 5 m. The default 5-m error model was selected for all 36 gazelles, though the AICc only improved on-average by 0.02 over the zero-error model. For the individually-tailored error model, the errors' standard deviations were generally estimated to be close to 5 m, but ranged up to 15 m and degraded the AICc in all cases, even if only compared to the zero-error model. Concordant with these estimates, we previously analyzed the locations of dead gazelles and found the collars typically consistent to within 1–3 m, but occasionally up to 20–30 m (Fleming et al. 2014*a*). On the other hand, the fisher example in Appendix S4 had DOP estimates provided that were found to be significant (ΔAICc >20), as the fisher moved shorter distances between observations relative to his telemetry errors.

We next compared Kriging with a selected best model to Kriging based on an a priori assumption of BM or IOU motion via leave-one-out cross validation, all with the fixed 5-m telemetry error. In each case we estimated the
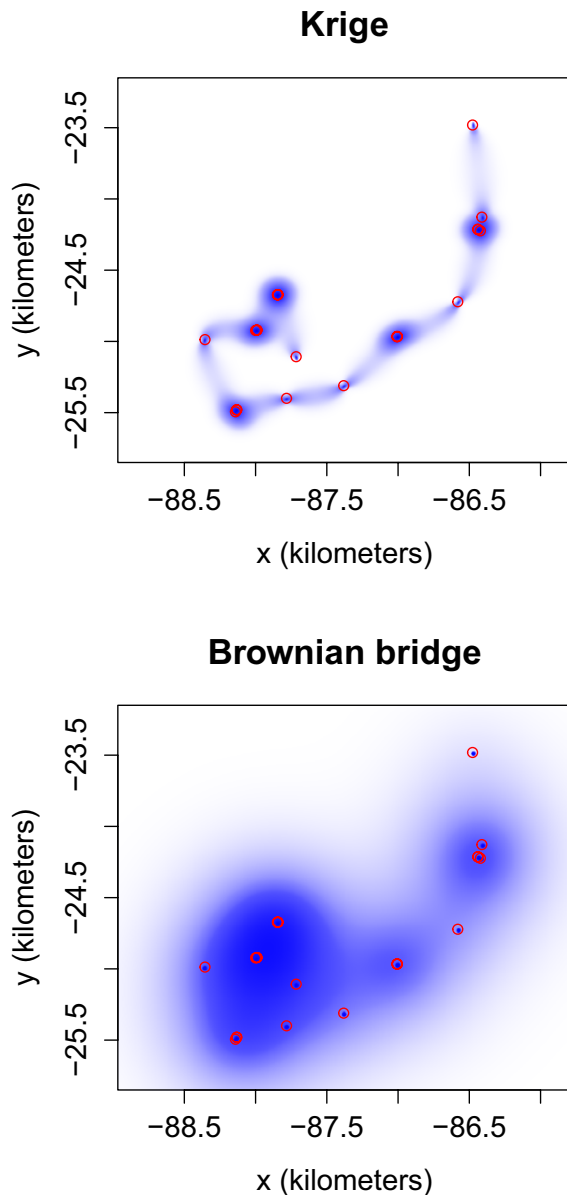
FIG. 1. Two occurrence distribution estimates (blue) for the same hourly sampled segment of gazelle timeseries (red). On the top is the Kriged distribution using the selected OUF movement model, while on the bottom lies the Brownian bridge. For this high-resolution data, the Brownian bridge is inappropriately large, as can be confirmed by cross validation. Persistence of motion is highly visible in these data, which also suggests that a continuous-velocity movement model is appropriate.

model parameters using the full time series of the focal gazelle, and then for each time t_i we removed the ith point from the data set and predicted the known location $\mathbf{r}(t_i)$. More accurately, the ith point should also be left out of the autocorrelation estimation step, but with long time series, the computational cost of this differentiation is prohibitive and the parameter estimates will be negligibly different.

To assess the relative accuracy of the point estimates, we fit a normal distribution to the residuals—e.g., $\mathbf{d}(t_i) = \boldsymbol{\mu}_K(t_i) - \mathbf{r}(t_i)$. Zero fell well within the 95% CI on the mean residual for all methods, indicating a general lack of bias in the point estimates. However, on average, Kriging with the selected model produced a point estimate that was 0.9–1.3 km (95% CI) closer to the true value than the BM Krige in terms of the square root of the difference in the variances, which corresponds to a 10% increase in precision. In contrast, the average model-selected Krige estimate was an insignificant 0.0–0.9 km closer to the true value than the IOU Krige, reflecting the fact that the IOU and OUF models are both likely to be asymptotically efficient at the short timescales being probed. The IOU and OUF models differ only at longer timescales, where the OUF model exhibits range-resident behavior while the IOU model diffuses endlessly. Unfortunately the timeseries did not have large enough gaps, relative to the gazelles' ranging timescales, to highlight where these models differ with the gazelle data. However, with the longer fisher dataset we were able to demonstrate the robustness against gapping that can be obtained with a range-resident model in Appendix S4: Fig. 2.

To compare the reliability of the confidence regions, we fit a normal distribution to the standardized residuals, which amounts to $\mathbf{z}(t_i) = \boldsymbol{\sigma}_K(t_i,t_i)^{-1/2} \left[\boldsymbol{\mu}_K(t_i) - \mathbf{r}(t_i) \right]$. As expected, the BM Krige generally overestimated occurrence area, as shown in Fig. 1, and the predicted occurrence area was 56–63% larger than the cross-validated occurrence area on average. As a result, occurrence distributions estimated by the BM Krige on this dataset are wider than they should be, such as in Fig. 1 where there is ~5 km2 excess predicted area (a 600% over-prediction). For the model-selected and IOU Krige, the standardized residuals were much closer to falling from a standard normal distribution, in that on average the cross-validated occurrence area was only larger than the predicted occurrence area by 4–9%—a 500% increase in precision over the BB.

The fact that both the selected OUF and related IOU models perform comparatively well relative to the higher-AIC BM and OU models (results not shown) strongly suggests that the efficiency difference here is due to the ability to model continuous velocity, as this is the sole difference between the BM and IOU movement models. The resolution of continuous velocities was a visually apparent feature of this dataset's population variogram (Fleming et al. 2014a) and manifests in the curves and fine detail of the occurrence distribution (Fig. 1). On the other hand, Appendix S4: Fig. 2 demonstrates that the range resident OU and OUF models are less sensitive to large gaps in the data.

DISCUSSION

We have introduced time-series Kriging as a general and statistically optimal method for estimating trajectory information from animal-tracking data. Trajectory estimation is a fundamental problem in movement ecology because it
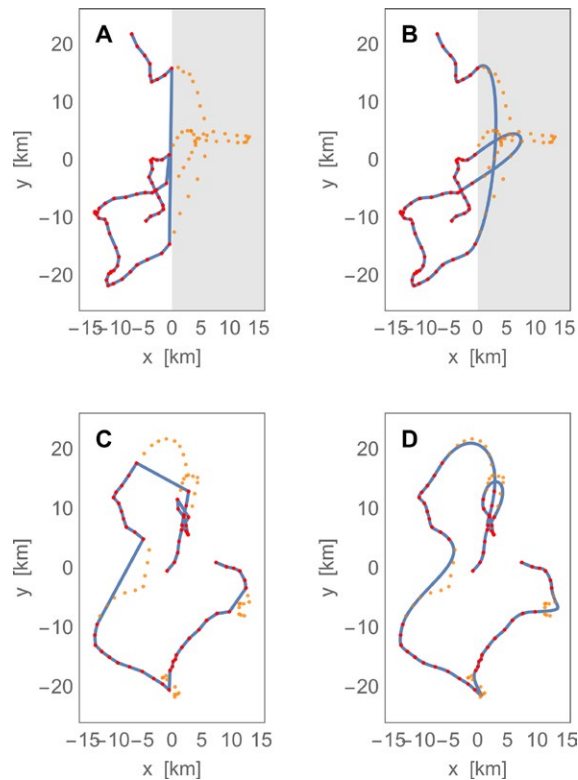
FIG. 2. Simulation and interpolation of the best-fit gazelle model. In panels A–B, the right half of the spatial plane is missing (gray), for example because of canopy cover that blocks out location fixes (orange). In A, which uses Brownian Bridge interpolation, the occurrence area is biased along the boundary. In B, which uses the Krige estimate, continuity in the observed data is leveraged to more accurately predict the region where missing observations occur. In this example, the Krige point estimate lacks details in the unobserved region because the gap is large compared to the velocity timescales, though the corresponding confidence regions sufficiently cover these details. Panels C–D present high resolution data (red) with a periodic loss of signal (orange). In C, distance traveled is significantly underestimated in the BB, whereas in D, the Kriged estimate leverages continuity and autocorrelation structure present in the observed data to more accurately predict the missing locations.

provides the statistical backbone for making inferences about a wide variety of animal behaviors, from energy expenditure to resource utilization. Our framework includes within it the Brownian bridge (BB Krige) and CRAWL (IOU Krige), and allows users to select among a set of candidate models to let the data decide which is most appropriate. As we have demonstrated with real data, the selected model can significantly outperform higher-AIC models in a predictable manner. The improvements in occurrence-area estimation are of practical importance because they translate into improved resolution of passageways and better sampling of the environmental covariates that animals encounter as they move. As ongoing technological advances facilitate increasingly finely sampled datasets, the usefulness of these techniques will improve commensurately.

Persistence of motion has long been viewed as critically absent from the BB and several attempts have been made

to address this issue from within the Brownian-motion paradigm. Benhamou (2011) extended the Brownian motion model by including a linear drift term. However, as pointed out by Kranstauber et al. (2014) and as we derive in Appendix S3: Eq. 1.1, this modification to the movement model only changes the Brownian bridge's diffusion rate. Kranstauber et al. (2014) then proposed a model of anisotropic Brownian motion, wherein the diffusion rate is allowed to take one value in the direction of motion and another value in the perpendicular direction. As we discuss in Appendix S3: Eq. 1.2, there are some issues with this model due to the fact that a Brownian particle has no well-defined heading. The approach we advocate here—Kriging the data based on a selected movement model—naturally incorporates persistence of motion when and how it is revealed in the data. Essentially, a solution for this particular problem already existed in CRAWL (Johnson et al. 2008), which predates both Benhamou (2011) and Kranstauber et al. (2014), yet these connections were not noticed. A similar story played out with the incorporation of telemetry errors, which were not correctly implemented in the BB until Pozdnyakov et al. (2014). Telemetry errors had already been correctly implemented in CRAWL by Johnson et al. (2008) in a manner that is more computationally efficient than the method of Pozdnyakov et al. (2014). A key contribution of our work, therefore, is to place these related approaches under a generalized framework for probabilistic path reconstruction and occurrence estimation.

We have presented the general Kriging relations for any movement model, with which trajectories and occurrence distributions can be estimated from sparse and noisy tracking data in a statistically efficient way. We note the critical need for more general software packages, that allow for any of the mentioned models to be selected and any of the mentioned outputs to be calculated, including occurrence distributions, location estimates, and trajectory simulations (Fig. 2). In this way the movement model can be decoupled from the biological question of interest, so that model selection can facilitate statistically-optimal solutions. Second, Kalman filtering techniques, such as those introduced by Johnson et al. (2008), are absolutely necessary for large tracking datasets because of their vastly superior computational efficiency. Future development of Kalman-filter implementations for a diverse array of continuous-time movement models would allow the Kriging techniques introduced here to be efficiently applied to the ever-larger tracking datasets that are becoming the norm in movement ecology. Many of these features are presently included in the ctmm R package (v 0.3.0, Fleming and Calabrese 2015, and R supplement). Finally, we note that many unsolved ecological questions are straightforward to address within the Kriging framework. Co-Kriging (Cressie 1993, Diggle and Ribeiro 2007), in particular, allows for multiple, related data sources to be simultaneously Kriged with a model that accounts for the correlation between them. For instance, improved trajectory estimates could be obtained by co-Kriging GPS-derived estimates of both location and velocity data, based on a

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movement model that accounts for position autocorrelation, velocity autocorrelation, and their cross-correlation. Three-dimensional accelerometry data combined with elevation, altitude, and depth information would allow for an even more detailed co-Kriged estimation, though continuous-acceleration models, such as those introduced by Fleming et al. (2015b), would be necessary.

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