

A Notions of space use and their estimators

Here we describe how the two most common notions of space use answer different biological questions and have different appropriate estimators, even though they have been often conflated in the literature. On the one hand there is Burt’s notion of the “home range” (Burt, 1943):

that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.

This concept is, in spirit, estimated by kernel-density estimation (KDE), minimum convex polygon (MCP), and mechanistic home-range analysis (MHRA) when the data are independently sampled, and by autocorrelated Gaussian density estimation (AGDE) when the process is Gaussian. The estimation target of all of these techniques is the range distribution, which addresses the long-term area requirements of an animal, assuming its movement behaviors do not significantly change, and the estimated quantity is independent of the sampling schedule, allowing it to be meaningfully compared across individuals.

On the other hand, the question of where the animal was located during the observation period is addressed by the occurrence distribution. The occurrence distribution is estimated by the Brownian bridge density estimator (BBDE) when the animal movement is Brownian, as we will discuss. This latter distribution is explicitly sampling dependent, cannot be compared across individuals, and is not generally related to Burt’s home range. Instead, the occurrence distribution is more appropriate than the range distribution when the goal is to correlate space use with environmental covariates, such as for analyses like Marzluff et al. (2004) and Millsaugh et al. (2006). In other words, these two distributions and their respective estimators, though often conflated in the literature, answer different biological questions. The criticism leveled by Kie et al. (2010)—are traditional estimators relevant given high quality data?—only pertains to estimating occurrence. We therefore strongly recommend that ecologists carefully determine what biological questions they wish to answer, what properties their data exhibit (e.g., with variogram analysis Fleming et al., 2014a), and what estimator is appropriate. An overview of each space-use estimator’s applicability is given in table A.1.

A.1 Kernel-density estimation

As we prove in App. B.4, the conventional kernel-density estimate collapses to the movement path in the limit of continuously sampled data even though it estimates the home range in the limit of uncorrelated data. From this fact, one might be inclined to conclude that the conventional KDE estimates both home range and occurrence, even though this is not logically possible. However, in contrast with BBDE, conventional KDE does not estimate occurrence correctly for any finite amount of data. The way that the occurrence estimator fills in the gaps should depend on the movement process, because the movement process imparts a distribution of interpolated locations. KDE is generally incorrect for this purpose because it can only take this limit in one way, regardless of the animal’s movement, while BBDE fills gaps between the sampled locations differently for different diffusion coefficients.

Estimator	Target	Assumptions
KDE	range [†]	IID
MCP	range	IID
MHRA	range	IID/Markovian [‡]
AGDE	range	normal
AKDE	range	none
BBDE	occurrence	Brownian

Table A.1: An overview of the data requirements and applicability of different space-use estimators. Both KDE and MCP assume IID data and will return underestimated home-range areas with short samples of location data. BBDE assumes Brownian motion, which requires the data to be sampled coarsely enough that velocities appear uncorrelated. †: While KDE does collapse to the movement path for continuously sampled data, it does not correctly estimate occurrence for finite amounts of data (App. A.1). ‡: MHRA can be fit under the assumption of a Markov process, similar to BBDE, but many applications of this approach assume IID data (App. A.2).

A.2 Mechanistic home-range analysis

Mechanistic models of home-range formation provide parametric estimators with both mechanistic insight as to why animals move and increased statistical efficiency over non-parametric estimators such as KDE and MCP. Mechanistic analysis was first popularized by the population-level advection-diffusion equation approach of Moorcroft *et al.* (1999, 2006) and Moorcroft and Lewis (2006), but now encompasses a broader range of approaches including individual-based models (Potts *et al.*, 2013) and step-selection functions (Moorcroft and Barnett, 2008; Potts *et al.*, 2014; Potts and Lewis, 2014). As we discuss below, the traditional—and still used (Potts *et al.*, 2013; Bateman *et al.*, 2014)—statistical estimation methods assume independently sampled data because they employ marginal likelihoods, while the step-selection function approach can account for Markov-process autocorrelations in the data. However, no mechanistic approach can currently account for non-Markovian-process autocorrelations in the data, though we describe how this could be accomplished in future efforts. Accounting for the appropriate degree (or lack) of autocorrelation—*independent, Markovian, or non-Markovian*—is an important determination to make for a dataset. Animal movement data are often highly autocorrelated, and these autocorrelations can persist over very long periods of time (McNay *et al.*, 1994; Rooney *et al.*, 1998; Boyce *et al.*, 2010; Polansky *et al.*, 2010; Fleming *et al.*, 2014a), ranging up to months and years. Therefore, it can require a considerable degree of coarsening to make the data (approximately) independently sampled. In somewhat less coarsely sampled datasets (e.g., 1-2 day resolution in many ungulates), Markovian process and estimation techniques are appropriate, as they can account for autocorrelation between subsequent locations. However, moving animals must feature correlated velocities on short time scales (Johnson *et al.*, 2008; Fleming *et al.*, 2014a) both because the degree to which animals can change their velocity in small increments of time is physically limited (i.e., animals are not capable of infinite acceleration), and because animals frequently tend to maintain similar velocities when displaying certain behaviors (e.g., commuting between foraging sites). When data are sampled finely enough to reveal velocity autocorrelation

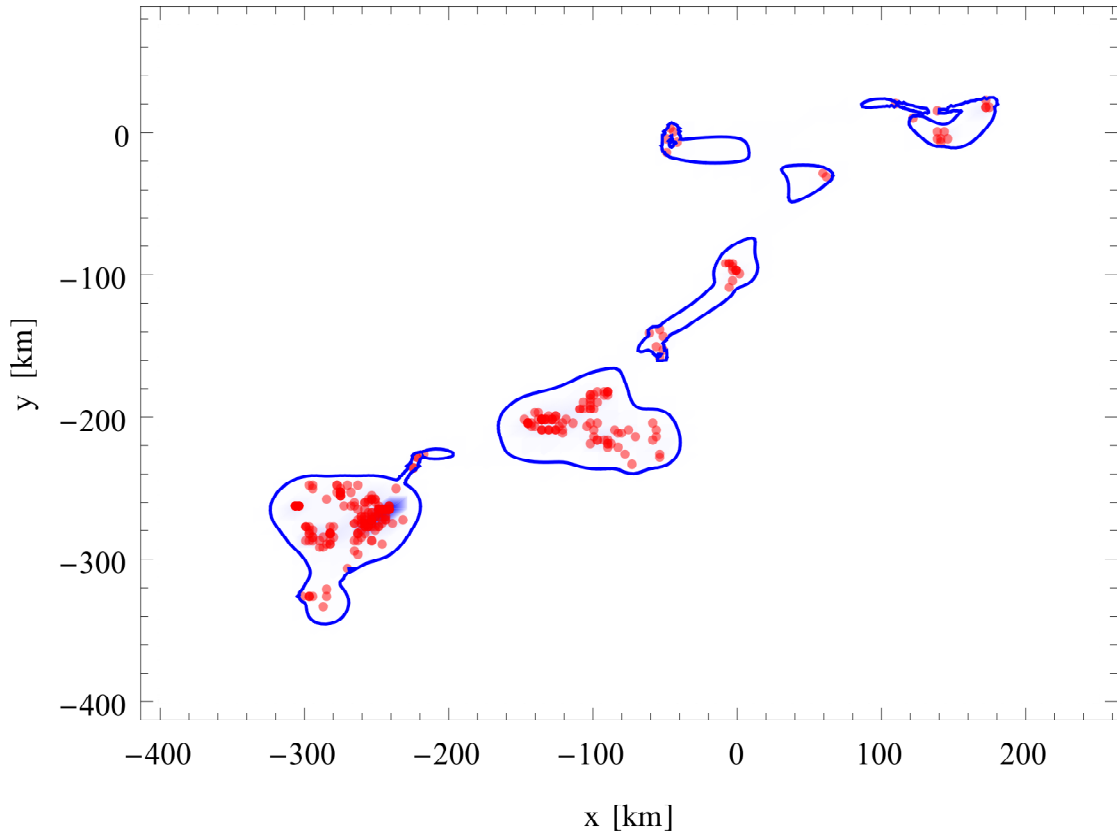


Figure A.1: Brownian-bridge home-range estimate for 2.5 years of Mongolian gazelle relocations (red dots ●) with 95% occurrence area (blue contours –). In this case the telemetry errors were measured to be within 10-20 meters, whereas gazelles travel hundreds of kilometers. Aside from the large gaps throughout the data, the gazelle’s location is fairly well known and so the Brownian-bridge space-use estimate is even more spatially constrained and fragmented than the conventional KDE.

(e.g., < 1 day resolution for many ungulates), as is increasingly the case with modern GPS datasets (Johnson et al., 2008; Kuhn et al., 2009; Gurarie and Ovaskainen, 2011; Hanks et al., 2011; Fleming et al., 2014a), Markovian analyses are biased (Fleming et al., 2014b) and inefficient (Stein, 1988). Instead, non-Markovian methods (Johnson et al., 2008; Fleming et al., 2014b) must be employed to properly account for velocity autocorrelation and to yield accurate estimates.

By construction, individual-based correlated random-walk models (Potts et al., 2013), step-selection functions (Fortin et al., 2005; Forester et al., 2009; Potts et al., 2014; Potts and Lewis, 2014) and redistribution kernels (Moorcroft and Barnett, 2008), can only be fit to short-ranged Markovian autocorrelations in the data, as only for a Markov process can the joint likelihood function of the time-series record be decomposed into a product of transitional probabilities, which these methods rely upon for their model fitting. Less clear, however, is that this is also the case when working with partial differential (Fokker–Planck) equations for the population densities rather than stochastic differential (Langevin) equations for the trajectories. To avoid any possible confusion stemming from the non-

Markovian density-density interactions in MHRA, let us simply consider the dynamics of one individual, whereupon the MHRA advection-diffusion equations do not depend on past values of the individual’s density function. The question of interest is how to construct a joint (multi-time) likelihood function appropriate for autocorrelated location data. With Langevin equations this is straightforward, as the Langevin equations themselves provide a method to simulate processes that fall from the joint probability distribution. However, as discussed in [Calzetta et al. \(2003\)](#), Fokker–Planck equations do not provide a framework to calculate multi-time correlations or multi-time probabilities unless the dynamics are Markovian.

Though MHRA has greatly evolved since its inception ([Moorcroft, 2012](#); [Potts and Lewis, 2014](#)), the statistical methods behind the traditional MHRA remain in use as recently as [Bateman et al. \(2014\)](#). The traditional MHRA fitting method proceeds by numerically solving for steady states $p_{ss}(\mathbf{r}|\boldsymbol{\theta})$ as a function of the animal location \mathbf{r} and model parameters $\boldsymbol{\theta}$, and then maximizing the likelihood function

$$L(\boldsymbol{\theta}|\mathbf{r}(t_1), \dots, \mathbf{r}(t_n)) = \prod_{i=1}^n p_{ss}(\mathbf{r}(t_i)|\boldsymbol{\theta}). \quad (\text{A.1})$$

However, note that this explicitly assumes that the data are independently sampled because for autocorrelated data the joint (multi-time) probability distribution is not given by the product of its marginal distributions.

$$p(\mathbf{r}(t_1), \dots, \mathbf{r}(t_n)|\boldsymbol{\theta}) \neq \prod_{i=1}^n p(\mathbf{r}(t_i)|\boldsymbol{\theta}). \quad (\text{A.2})$$

This assumption of independent data is still made in the recent non-stationary analyses of [Potts et al. \(2013\)](#) and [Bateman et al. \(2014\)](#), and so this remains a relevant issue even though these papers excel at capturing the transient dynamics of multi-individual home-range formation. The only exception to this standard, marginal likelihood approach of which we are aware is the redistribution-kernel method of [Moorcroft and Barnett \(2008\)](#) and its related step-selection function method ([Potts et al., 2014](#); [Potts and Lewis, 2014](#)), which are fit to data with the transition probabilities from one time to the next. In this way, the autocorrelation of first-order Markov processes can correctly be taken into account.

All of the above issues could potentially be resolved to produce mechanistic analyses suitable for data featuring multi-scale, non-Markovian-process autocorrelations, which would provide parametric home-range estimators capable of outperforming AKDE. First, for reasons discussed, modeling efforts need to be based upon mathematical formalisms, such as Langevin equations, that are capable of generating and describing strong multi-scale and multi-time autocorrelation among observations, such as in [Johnson et al. \(2008\)](#) and [Fleming et al. \(2014a\)](#). Second, the full joint likelihood function ([Johnson et al., 2008](#); [Fleming et al., 2014b](#)) of the time series must be employed rather than fitting with products of marginal distributions or transition probabilities. For this task, fitting methods such as those employed by [Blackwell \(2003\)](#) could be used.

A.3 Brownian-bridge density estimation

In [Fig. A.1](#), we plot the Brownian-bridge estimate ([Horne et al., 2007](#)) of a long Mongolian gazelle track. As previously noted, the BBDE does not estimate the range distribution and

thus is not a home-range estimator. In the case of home-range estimates obtained through KDE, AGDE, and MHRA approaches, the home-range area corresponds to a confidence region of the location variable's probability distribution for all realizations of the movement process (i.e., the range distribution). In contrast, the BBDE estimates the occurrence distribution, which corresponds to the location variable's probability distribution during the observed timespan, conditioned upon the data. In other words, the occurrence distribution estimated by BBDE only addresses the question of where the specific animal was located during the observation period. Other plausible realizations of the underlying movement process are excluded. The area estimated by the BBDE is not an estimate of the animal's home range, but instead a reflection of our ignorance as to where the animal was located. If the telemetry errors are small and the sampling interval is short, then the animal's location is well known for the observed timespan. As a result, the BBDE becomes singularly defined upon the observed movement path, estimating a vanishing area for any confidence region, as is particularly apparent in Fig. A.1.

References

- Bateman, A. W., M. A. Lewis, G. Gall, M. B. Manser, and T. H. Clutton-Brock. 2014. Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: a mechanistic modelling approach. *Journal of Animal Ecology* 84:260–271.
- Blackwell, P. G. 2003. Bayesian inference for Markov processes with diffusion and discrete components. *Biometrika* 90:613–627.
- Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2213–2219.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:436–352.
- Calzetta, E., A. Roura, and E. Verdaguer. 2003. Stochastic description for open quantum systems. *Physica A* 319:188–212.
- Fleming, C. H., J. M. Calabrese, T. Mueller, K. A. Olson, P. Leimgruber, and W. F. Fagan. 2014a. From fine-scale foraging to home ranges: A semi-variance approach to identifying movement modes across spatiotemporal scales. *The American Naturalist* 183:E154–E167.
- . 2014b. Non-Markovian maximum likelihood estimation of autocorrelated movement processes. *Methods in Ecology and Evolution* 5:462–472.
- Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology* 90:3554–3565.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone national park. *Ecology* 86:1320–1330.

- Gurarie, E., and O. Ovaskainen. 2011. Characteristic spatial and temporal scales unify models of animal movement. *The American Naturalist* 178:113–123.
- Hanks, E. M., M. B. Hooten, D. S. Johnson, and J. T. Sterling. 2011. Velocity-based movement modeling for individual and population level inference. *PLoS ONE* 6:e22795.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–63.
- Johnson, D. S., J. M. London, M.-A. Lea, and J. W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–1215.
- Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B* 365:2221–2231.
- Kuhn, C. E., D. S. Johnson, R. R. Ream, and T. S. Gelatt. 2009. Advances in the tracking of marine species: using GPS locations to evaluate satellite track data and a continuous-time movement model. *Marine Ecology Progress Series* 393:97–109.
- Marzluff, J. M., J. J. Millsbaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller’s jays. *Ecology* 85:1411–1427.
- McNay, R. S., J. A. Morgan, and F. L. Bunnell. 1994. Characterizing independence of observations in movements of Columbian black-tailed deer. *The Journal of Wildlife Management* 58:422–429.
- Millsbaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.
- Moorcroft, P. R. 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy* 93:903–916.
- Moorcroft, P. R., and A. Barnett. 2008. Mechanistic home range models and resource selection analysis: A reconciliation and unification. *Ecology* 89:1112–1119.
- Moorcroft, P. R., and M. A. Lewis. 2006. *Mechanistic Home Range Analysis*. Princeton University Press.
- Moorcroft, P. R., M. A. Lewis, and R. L. Crabtree. 1999. Home range analysis using a mechanistic home range model. *Ecology* 80:1656–1665.
- . 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* 273:1651–1659.

- Polansky, L., G. Wittemyer, P. C. Cross, C. J. Tambling, and W. M. Getz. 2010. From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. *Ecology* 91:1506–1518.
- Potts, J. R., S. Harris, and L. Giuggioli. 2013. Quantifying behavioral changes in territorial animals caused by sudden population declines. *The American Naturalist* 182:E73–E82.
- Potts, J. R., and M. A. Lewis. 2014. How do animal territories form and change? lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society of London B: Biological Sciences* 281.
- Potts, J. R., K. Mokross, and M. A. Lewis. 2014. A unifying framework for quantifying the nature of animal interactions. *Journal of The Royal Society Interface* 11.
- Rooney, S. M., A. Wolfe, and T. J. Hayden. 1998. Autocorrelated data in telemetry studies: Time to independence and the problem of behavioural effects. *Mammal Review* 28:89–98.
- Stein, M. L. 1988. Asymptotically efficient prediction of a random field with a misspecified covariance function. *Ann. Stat.* 16:55–63.