# A comprehensive analysis of autocorrelation and bias in home range estimation

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*Abstract.*　Home range estimation is routine practice in ecological research. While advances in animal tracking technology have increased our capacity to collect data to support home range analysis, these same advances have also resulted in increasingly autocorrelated data. Consequently, the question of which home range estimator to use on modern, highly autocorrelated tracking data remains open. This question is particularly relevant given that most estimators assume independently sampled data. Here, we provide a comprehensive evaluation of the effects of autocorrelation on home range estimation. We base our study on an extensive data set of GPS locations from 369 individuals representing 27 species distributed across five continents. We first assemble a broad array of home range estimators, including Kernel Density Estimation (KDE) with four bandwidth optimizers (Gaussian reference function, autocorrelated-Gaussian reference function [AKDE], Silverman's rule of thumb, and least squares cross-validation), Minimum Convex Polygon, and Local Convex Hull methods. Notably, all of these estimators except AKDE assume independent and identically distributed (IID) data. We then employ half-sample cross-validation to objectively quantify estimator performance, and the recently introduced effective sample size for home range area estimation ($\hat{N}_{area}$) to quantify the information content of each data set. We found that AKDE 95% area estimates were larger than conventional IID-based estimates by a mean factor of 2. The median number of cross-validated locations included in the hold-out sets by AKDE 95% (or 50%) estimates was 95.3% (or 50.1%), confirming the larger AKDE ranges were appropriately selective at the specified quantile. Conversely, conventional estimates exhibited negative bias that increased with decreasing $\hat{N}_{area}$. To contextualize our empirical results, we performed a detailed simulation study to tease apart how sampling frequency, sampling duration, and the focal animal's movement conspire to affect range estimates. Paralleling our empirical results, the simulation study demonstrated that AKDE was generally more accurate than conventional methods, particularly for small $\hat{N}_{area}$. While 72% of the 369 empirical data sets had >1,000 total observations, only 4% had an $\hat{N}_{area}$ >1,000, where 30% had an $\hat{N}_{area}$ <30. In this frequently encountered scenario of small $\hat{N}_{area}$, AKDE was the only estimator capable of producing an accurate home range estimate on autocorrelated data.

　　*Key words:　animal movement; kernel density estimation; local convex hull; minimum convex polygon; range distribution; space use; telemetry; tracking data.*

## INTRODUCTION

　　Studying how animals use their habitat is fundamental for understanding their behavior and ecology (Mueller and Fagan 2008, Nathan et al. 2008, Schick et al. 2008), and critical for developing effective conservation strategies (Law and Dickman 1998, Macdonald 2016). A crucial component of space use is the notion of an individual's home range (Powell 2000), where Burt's (1943) early conceptual definition "…the 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…" is still the most widely referenced. While advances in animal tracking technology, and its increasing use, have dramatically increased our capacity to collect data to support home range analysis (Tomkiewicz et al. 2010, Kays et al. 2015), translating Burt's

conceptual definition into a rigorous statistical method that can be applied to these data has remained challenging (Powell 2000, Hemson et al. 2005, Kie et al. 2010, Walter et al. 2015). A primary reason for this difficulty is that tracking data are often strongly autocorrelated, while most home range estimators assume statistically independent data.

　　With tracking data, temporal autocorrelation occurs when the values of a target quantity that are close together in time are more similar to each other than values that are farther apart temporally, on average. Autocorrelation can occur among positions and velocities, and data from a single individual may simultaneously feature autocorrelation in both of these (Swihart and Slade 1985, Blundell et al. 2001, Cushman et al. 2005, Fleming et al. 2014c, Morato et al. 2016). All else being equal, the shorter the time interval between samples, the more the autocorrelation structure of a particular movement path

will be revealed, and the characteristic time scales over which autocorrelations decay can vary by target quantity, species, and individual (Fleming et al. 2014c, Gurarie and Ovaskainen 2015). Notably, autocorrelation in position tends to decay more slowly than autocorrelation in velocity. For example, for many range-resident ungulate species, the characteristic time scales for position and velocity autocorrelation are on the order of days and hours, respectively (Fleming et al. 2014c, Calabrese et al. 2016). Because of the longer persistence, the time scale over which autocorrelation in position decays, $\tau_p$, is a key parameter for home range estimation (Fleming and Calabrese 2017): data sets featuring a sampling interval $\gg \tau_p$ will have locations that are effectively independent, whereas those with a sampling interval $< \tau_p$ will have autocorrelated positions. For this reason, the time scale over which autocorrelation in position decays beyond significance has historically been referred to as the time to independence (Swihart and Slade 1985, Worton 1989, De Solla et al. 1999).

Autocorrelation is a critical issue when operationalizing Burt's home range definition for tracking data, because all home range estimators currently in widespread use are based on an assumption of statistical independence among location observations. In particular, conventional Kernel Density Estimation (KDE; Worton 1989) explicitly assumes that location data are independent and identically distributed (IID). Kernel methods benefit from being the most statistically efficient nonparametric density estimators—nonparametric, meaning that KDE does not make assumptions about the form of the underlying distribution of the data beyond the IID assumption (Silverman 1986, Izenman 1991, Turlach 1993, Millspaugh and Marzluff 2001). However, when the IID assumption is violated, recent studies have demonstrated that KDEs underestimate home range areas (Fleming et al. 2015a, Fleming and Calabrese 2017, see also Swihart and Slade 1985). Geometric methods such as the Minimum Convex Polygon (MCP; Mohr 1947) and Local Convex Hull (LoCoH; Getz and Wilmers 2004) are also routinely used for estimating home ranges (Laver and Kelly 2008), and are popular because they are straightforward to understand, and easy to implement. Though often not explicitly stated, geometric methods also make the IID assumption. To see this, consider that these estimators are invariant under permutations of the time ordering of the data, which only makes sense for IID data. Similar to the case with KDE, recent work has suggested that geometric methods also tend to underestimate home range areas on autocorrelated data (Burgman and Fox 2003, Börger et al. 2006, Walter et al. 2015).

Here, we aim to provide a comprehensive evaluation of the effects of autocorrelation on home range estimation. The idea that autocorrelation may affect home range estimates is certainly not new, and many studies have explored this topic (e.g., Swihart and Slade 1985, Rooney et al. 1998, De Solla et al. 1999, Blundell et al.

2001, Hemson et al. 2005, Börger et al. 2006, Kie et al. 2010, Walter et al. 2015). However, we argue that the role that autocorrelation plays in home range estimation has yet to be fully resolved for three key reasons.

First, modern data sets generally feature far stronger autocorrelation than that considered by past assessments of autocorrelation on home range estimation. For example, of three very influential earlier studies that all concluded that autocorrelation was not an issue for home range estimation (De Solla et al. 1999, Blundell et al. 2001, Fieberg 2007), none considered autocorrelation as strong as that routinely observed in modern tracking data (Fig. 1). More strongly autocorrelated data sets are a direct result of the higher frequencies with which current tracking devices can record location observations, and this trend will continue as technological advances facilitate ever-finer sampling of movement paths (Kays et al. 2015). Conclusions based on the examination of older, coarsely sampled tracking data sets (e.g., intervals of $\geq 1$ d) may therefore no longer hold on modern data with much shorter sampling intervals (Fig. 1). Despite this mismatch, the classical studies of De Solla et al. (1999), Blundell et al. (2001), and Fieberg (2007) continue to be widely cited as justification for ignoring autocorrelation in modern tracking data sets.

Second, there has been a historical lack of objective metrics that quantify (1) the performance of home range estimators on empirical data, where the true home range area is not known, and (2) how the interplay between study design and movement behavior affects the information content of a tracking data set. In the absence of the former, some studies have used estimates based on the full empirical data set as the "truth" (e.g., Rooney et al. 1998, Girard et al. 2002, Börger et al. 2006, Walter et al. 2015),



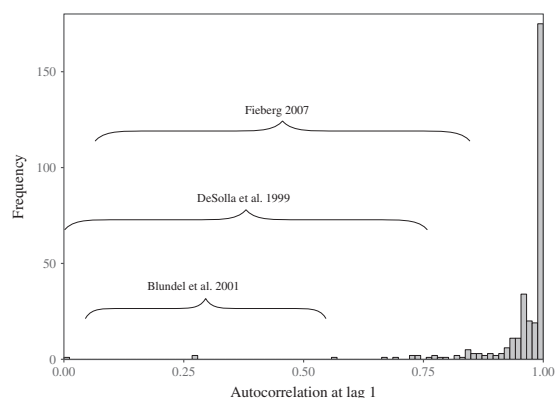FIG. 1. Histogram depicting the amount of autocorrelation at lag 1 in the empirical tracking data for each of the 369 individuals used in the present study, in comparison to the range of values addressed by previous studies. Note how previous conclusions on the influence of autocorrelation on home range estimation were based on weakly autocorrelated data that are not representative of the majority of modern GPS data.

while others have simply shown empirical results without reference to their accuracy (e.g., De Solla et al. 1999, Dougherty et al. 2017). In the absence of the latter, researchers have been encouraged to obtain a threshold number of locations (Seaman et al. 1999, Girard et al. 2002) or days (e.g., Börger et al. 2006, Signer et al. 2015), but the precise conditions under which autocorrelation and movement behavior can a priori be expected to influence these thresholds have remained obscure.

Third and finally, many existing studies predate the availability of appropriate methods for working with and modeling autocorrelated tracking data. For example, continuous-time stochastic movement models (Johnson et al. 2008, Gurarie et al. 2009, Fleming et al. 2014c, Blackwell et al. 2015, Péron et al. 2017), which can naturally model the kind of multi-dimensional, multi-scale autocorrelation apparent in modern tracking data, have only recently been embraced by the literature (but see Dunn and Gipson 1977, Blackwell 1997, Brillinger et al. 2002). Related statistical tools for quantifying and visualizing complex autocorrelation structures (Fleming et al. 2014b, Péron et al. 2016), and for simulating realistically autocorrelated data (Johnson et al. 2008, Fleming et al. 2017) are also recent advances. In particular, the ability to simulate data where the strength of autocorrelation can be systematically manipulated, and where the true home range is exactly known has been a key missing ingredient. Such simulations could help tease apart the influences of different, potentially interacting, sources of bias, and would help to put empirical results in their proper context.

As a solution to these issues, we base our analysis on an extensive empirical data set, comprising GPS locations from 369 individuals across 22 mammalian, four avian, and one reptilian species from study sites on five continents. All individual data sets were collected between 2005 and 2017, ensuring that our database is representative of modern trends in tracking data. We then assemble a broad array of home range estimators, including KDE with four bandwidth optimization methods (the Gaussian reference function, Silverman's rule of thumb, least squares cross-validation, and the autocorrelated-Gaussian reference function), MCP, and $k$-LoCoH. Collectively, this set covers all of the most commonly used home range estimators in the ecological literature (Laver and Kelly 2008, Kie et al. 2010, Signer and Balkenhol 2015). To evaluate estimator performance on these empirical data, we employ half-sample cross-validation, which provides an objective measure of how well a given estimator satisfies Burt's time-honored definition of the home range. Importantly, this approach does not assume any particular home range estimator, and thus should be impartial with respect to the estimators used. We also demonstrate how the recently introduced effective sample size for home range estimation, $\hat{N}_{area}$ (Calabrese et al. 2016, Fleming and Calabrese 2017), provides a more generally reliable estimate of the information content of a data set than the sampling

duration, or number of locations. Consequently, $\hat{N}_{area}$ can be used to pinpoint the conditions under which estimators assuming IID data can be expected to produce biased estimates, and suggest the qualitative magnitude of that bias. To contextualize our empirical results, we perform a detailed simulation study. Specifically, we use continuous-time movement models (Johnson et al. 2008, Gurarie et al. 2009, Fleming et al. 2014c, Blackwell et al. 2015, Péron et al. 2017) to precisely manipulate the degree of autocorrelation in the simulated data, which allows us to tease apart how sampling frequency, sampling duration, and the focal animal's movement behavior conspire to affect range estimates.

## METHODS

### Home range estimation

*Estimator selection criteria.*—For our comparison, we selected home range estimators based on the target probability distribution being estimated. Fleming et al. (2015a, 2016) recently distinguished between *range* estimators, such as MCP, KDE, and AKDE, and *occurrence* estimators such as the Brownian bridge (Horne et al. 2007), the continuous-time correlated random walk library (Johnson et al. 2008), time-dependent LoCoH (T-LoCoH; Lyons et al. 2013), and time-series Kriging (Fleming et al. 2016). Home range estimators correspond to Burt's traditional notion of the home range and estimate space use assuming the focal movement process continues into the future. Occurrence estimators, in contrast, quantify our ignorance about where the focal individual was located *during the sampling period*, even at times not sampled (Fleming et al. 2016). In other words, range estimators *extrapolate* space use into the future (i.e., answering the question "How much space does an animal need?"), while occurrence estimators *interpolate* within the sampling period (i.e., answering the question "Where did the animal go during the study period?"). Fully exploring the range/occurrence distinction requires detailed mathematical arguments and additional analyses that are beyond the scope of this paper and will be fully explored in a subsequent publication, but we note briefly that, under broad conditions, occurrence estimators perform poorly at estimating home range areas. Based on these considerations, we therefore selected MCP, $k$-LoCoH, and KDE with four bandwidth optimization methods (the Gaussian reference function, Silverman's rule of thumb, Least squares cross-validation, and the autocorrelated-Gaussian reference function) for our comparison, which covers all of the most commonly used home ranged estimators (Laver and Kelly 2008, Kie et al. 2010, Signer and Balkenhol 2015).

*Minimum convex polygon (MCP).*—The MCP approach (Mohr 1947) is the most widely used home range estimator in ecological research (Laver and Kelly

2008). MCP defines an animal's home range as the smallest convex polygon that contains $X\%$ of locations from the original data set. Home range areas were estimated using the MCP method implemented in the R package adehabitatHR (Calenge 2006).

k-*Local convex hull (*k-*LoCoH)*.—To construct a home range estimate, the $k$-LoCoH method begins by locating the $k - 1$ nearest neighbors for each location in the data set, constructs a convex hull for each of these unique sets of nearest neighbors, merges the hulls together from smallest to largest, and then divides the merged hulls at the designated isopleth (e.g., 95%, or 50%; Getz and Wilmers 2004). Here, we applied $k$-LoCoH estimation as implemented in the R package rhr (Signer and Balkenhol 2015), with the value of the tuning parameter $k$ defined as the square root of all locations (i.e., $k = \sqrt{n}$; see Getz et al. 2007). We note that in the limit where $k = n$, $k$-LoCoH and MCP will result in identical area estimates, and so area estimates using the LoCoH family can only ever be less than or equal in size to MCP estimates.

*Kernel-based home range estimation*.—To obtain a home range estimate, kernel methods construct a density function by placing small kernels of bandwidth $\boldsymbol{\sigma}_B$ at each sampled location. The mean of these kernels provides an estimate of the underlying probability density function (Silverman 1986, Worton 1989). The value of $\boldsymbol{\sigma}_B$ is crucial, and is selected to minimize the mean integrated squared error (MISE) between the true distribution and its estimate (Silverman 1986, Izenman 1991, Turlach 1993). Home range size can then be quantified as the area contained within a desired quantile of the density estimate (usually 95% or 50%; Worton 1989). A range of methods are routinely employed to determine the optimal value of $\boldsymbol{\sigma}_B$. We therefore applied KDE using four bandwidth optimization methods: the Gaussian reference function, Silverman's rule of thumb, Least squares cross-validation, and the autocorrelated-Gaussian reference function (AKDE).

*Gaussian reference function KDE*.—For Gaussian reference function KDE (henceforth simply KDE), we estimated 95% areas using the asymptotically optimal Gaussian reference function bandwidth relation (Silverman 1986), which approximates the MISE in two dimensions as

$$\text{MISE} = \frac{1}{2\pi} \left( \frac{\frac{1}{n}}{\sqrt{\det(2\boldsymbol{\sigma}_B)}} + \frac{\frac{n-1}{n}}{\sqrt{\det(2\boldsymbol{\sigma}_0 + 2\boldsymbol{\sigma}_B)}} - \frac{2}{\sqrt{\det(2\boldsymbol{\sigma}_0 + \boldsymbol{\sigma}_B)}} + \frac{1}{\sqrt{\det(2\boldsymbol{\sigma}_0)}} \right) \quad (1)$$

where $n$ is the sample size, $\boldsymbol{\sigma}_B$ is the bandwidth matrix, and $\boldsymbol{\sigma}_0$ is the covariance of the sampled locations

(Fleming et al. 2015a). The optimal bandwidth is then computed using standard numerical optimization techniques. For KDE, we also applied the small sample size bias reduction introduced in Fleming and Calabrese (2017; henceforth KDEc), and uniform weights, which are the optimal weighting relations for IID data (Fleming et al. 2018).

*Silverman's rule of thumb (Srt) KDE*.—Silverman's rule of thumb starts with the Gaussian reference function relation (Eq. 1), which approximates the probability density as being Gaussian when optimizing the bandwidth. The optimal bandwidth is then expanded asymptotically in powers of $1/n$, and to lowest order in $1/n$ (Silverman 1986), its value in two dimension is

$$\boldsymbol{\sigma}_B = n^{-1/3} \boldsymbol{\sigma}_0. \quad (2)$$

Importantly, Silverman's rule of thumb is not exactly the same as the Gaussian reference function approximation without the additional asymptotic approximation, even though it is sometimes called as much (Worton 1989). KDE using Srt bandwidth optimization (Srt-KDE) was carried out using the R package rhr (Signer and Balkenhol 2015). We note that although the adehabitatHR and rhr packages use Silverman's rule of thumb to derive the optimal bandwidth, these are incorrectly termed Gaussian reference function optimization in both packages.

*Least squares cross-validation (lscv) KDE*.—Another commonly used bandwidth optimization method is least squares cross-validation (lscv; Silverman 1986, Worton 1989). The lscv method minimizes the MISE using an error estimate evaluated at each data point, based on one KDE conditional on all the data and another excluding said data point. This estimate of the MISE is then minimized by varying the bandwidth (Silverman 1986). KDE using least squares cross-validation bandwidth optimization (lscv-KDE) was carried out using the R package rhr (Signer and Balkenhol 2015).

*Autocorrelated-Gaussian reference function KDE (AKDE)*.—Whether explicitly stated or not, all home range estimators make an assumption about the underlying movement process. For most estimators in the literature, including all those described above, that assumption is simply that the data were sampled from an IID process. However, while all methods make an assumption about the movement process, only some methods explicitly separate the movement modeling and home range estimation steps. Autocorrelated-KDE (AKDE) is a generalization of Gaussian reference function KDE that operates under the principle that autocorrelation structure in the data can first be estimated, and then conditioned upon when optimizing the bandwidth (Fleming et al. 2015a, Calabrese et al. 2016), such that the MISE is approximated by

$$\text{MISE} = \frac{1}{2\pi}\left(\frac{1}{n^2}\sum_\tau \frac{n(\tau)}{\sqrt{\det(2\boldsymbol{\gamma}(\tau) + 2\boldsymbol{\sigma}_B)}}\right.$$
$$\left. -\frac{2}{\sqrt{\det(2\boldsymbol{\sigma}_0 + \boldsymbol{\sigma}_B)}} + \frac{1}{\sqrt{\det(2\boldsymbol{\sigma}_0)}}\right) \quad (3)$$

where the semi-variance function is given by

$$2\boldsymbol{\gamma}(\tau) = 2\boldsymbol{\sigma}_0 - \boldsymbol{\sigma}(+\tau) - \boldsymbol{\sigma}(-\tau) \quad (4)$$

where $\tau$ is the time lag between any two samples, $\boldsymbol{\sigma}(\tau)$ is the autocorrelation function, and $n(\tau)$ is the number of sample pairs with time lag $\tau$ between them.

AKDE is currently available via command line interface through the R package ctmm (Calabrese et al. 2016), or through the web based graphical user interface (Dong et al. 2017; program *available online*).[38] Following the workflow described by Calabrese et al. (2016), the autocorrelation structure in the data is estimated by fitting continuous-time movement models, and the best-fit model is selected based on the approximate small-sample-size corrected Akaike Information Criterion. The choice of models includes all continuous-time stochastic models for stationary movement processes that are in current use in the ecological literature. These are: an IID process (i.e., the model assumed by conventional KDE, MCP, and *k*-LoCoH methods), which features uncorrelated positions and velocities; the Ornstein-Uhlenbeck (OU) process, which features correlated positions but uncorrelated velocities (Uhlenbeck and Ornstein 1930); and an OU-Foraging (OUF) process, featuring both correlated positions, and velocities (Fleming et al. 2014*b,c*). Home ranges areas are then estimated conditional on the selected model for each data set, via the methods implemented in the R package ctmm, with the further bias correction introduced in area-corrected AKDE (henceforth AKDEc; Fleming and Calabrese 2017), and the optimal weighting relations established by Fleming et al. (2018). This approach has the further benefit that uncertainty in the model parameters can be propagated to the area estimates (Fleming and Calabrese 2017). Importantly, AKDE is a generalization of the conventional Gaussian reference function KDE. The two estimators produce identical results in the limit of no autocorrelation, and only differ when data are autocorrelated (Fleming et al. 2015*a*). This property allows us to isolate the effects of autocorrelation per se on home range estimation, holding all other factors constant. We also note that, all else being equal, accounting for the autocorrelation in the data when optimizing $\boldsymbol{\sigma}_B$ results in wider bandwidths as compared to KDEc, generally producing larger area estimates (see Fleming et al. 2015*a*; Appendix B2.1).

### Effective sample size ($\hat{N}_{\text{area}}$)

For home range area estimation, the information content of a tracking data set is not a function of the total

number of locations, $n$ (e.g., Seaman et al. 1999, Girard et al. 2002, Börger et al. 2006), but rather the equivalent number of statistically independent locations (i.e., the effective sample size, $\hat{N}_{\text{area}}$; Calabrese et al. 2016), governed by the duration of the observation period ($T$), and the time scale over which autocorrelation in position decays ($\tau_p$)

$$N_{\text{area}} \approx \frac{T}{\tau_p}. \quad (5)$$

We note that an estimate of $\hat{N}_{\text{area}}$ first requires an estimate of $\tau_p$. Formally, $\tau_p$ can be quantified from the data as the time scale over which an individual's positional autocorrelation decays to insignificance. Specifically, if the autocorrelation in position decays exponentially in time at rate $1/\tau_p$, then $\tau_\alpha = \tau_p \ln(1/\alpha)$ where $\alpha$ is the proportion of the original position autocorrelation remaining. Setting $\alpha = 0.05$, $\tau_\alpha \sim 3\tau_p$ is the time it takes for 95% of the autocorrelation in position to decay. This is also equivalent to the mean-reversion time scale from time-series analysis (Hamilton 1994, Fleming et al. 2015*a*, Fleming and Calabrese 2017). Because $\tau_p$ quantifies the time scale over which an animal's movement process reverts to the mean, it also has the intuitive biological interpretation as being roughly equivalent to the average time it takes an individual to cross the linear extent of its home range (Rooney et al. 1998, Calabrese et al. 2016, Fleming and Calabrese 2017). In what follows, we will therefore refer to $\tau_p$ as the home range crossing time.

Within individuals, an increase in the sampling duration, $T$, will generally result in a proportional increase in $\hat{N}_{\text{area}}$. Between individuals, however, an increase in $n$ through increased sampling frequency, or duration, does not directly translate to an increase in $\hat{N}_{\text{area}}$ as range crossing times can also vary. To see this, consider an individual with a home range crossing time of 1 d, sampled for 30 d. Whether it was sampled once per day, or once per minute, it would have crossed its range $\sim 30$ times in each scenario, and so both data sets would have an $\hat{N}_{\text{area}}$ of $\sim 30$, irrespective of the differences in $n$. In contrast, an individual with a range crossing time of 30 d, sampled again for 30 d would have an $\hat{N}_{\text{area}}$ of only $\sim 1$, and increasing the sampling frequency would not change this. As such, to permit meaningful cross-study and cross-individual comparisons, we used the $\hat{N}_{\text{area}}$ of each individual's data set as our metric of information content. Notably, fitting movement models to tracking data, which is a pre-requisite to the AKDE method, also provides an estimate of the home range crossing time (Fleming et al. 2015*a*, Calabrese et al. 2016, Fleming and Calabrese 2017). This estimate was used as the basis of our $\hat{N}_{\text{area}}$ calculations.

### Estimator evaluation

Throughout this study, we treat home range estimation as a point estimation problem (see e.g., Worton 1995, Casella and Berger 2002), and evaluate estimators by their

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[38] ctmm.shinyapps.io/ctmmweb/

capacity to use samples drawn from a target distribution to recover that distribution. By restricting our analyses to home range estimators, we have set the range distribution as the target distribution (Fleming et al. 2015a, 2016), and focus our evaluation around bias and sampling variance in the estimates. While we acknowledge that other studies have framed their evaluations of home range estimators in a hypothesis testing context and attempted to quantify the probabilities of type I vs. type II error with presence-only data (e.g., White and Garrott 1990, Getz and Wilmers 2004, Getz et al. 2007, Fieberg and Börger 2012), here we treat the problem more straightforwardly as one of point estimation, which is not suited to evaluation via error probabilities.

*Empirical data.*—To evaluate home range estimators, we first compiled a data set of GPS tracking data for 22 mammalian, four avian, and one reptilian species, comprising a total of $2.33 \times 10^6$ locations of 369 individuals (Fig. 2; Table 1). Data sets were selected based on the criterion of range resident behavior, as evidenced by variograms (i.e., plots of the semi-variance in positions as a function of the time lag separating observations) with a clear asymptote at large lags (Calabrese et al. 2016, Morato et al. 2016), while data from migratory, or non-range resident individuals were excluded. To provide an accurate depiction of how home range estimators might be expected to perform in practice, we did not use habitat features (e.g., rivers, cliffs, fences, and other landforms) that may have impacted movement as a selection criteria. As a result, many of the individuals in this data set were subject to the types of hard boundaries that challenge KDEs (Worton 1995, Getz and Wilmers 2004). Data were obtained from the online animal tracking database Movebank (Wikelski and Kays 2017), or

contributed by co-authors directly, and are openly available (see Data Availability below).

*Cross-validation.*—For these empirical data, we could not quantify the bias of home range area estimates by comparing them to a known truth. However, if an estimator truly captures an individual's home range (sensu Burt 1943), an unbiased 95% area estimate generated over some observation period $T_1$, should contain 95% of that animal's locations over a subsequent observation period $T_2$, provided the animal's movement behavior does not change significantly and autocorrelation between the two cross-validation blocks is minimal. If the point-inclusion of a 95% area estimate were to consistently come out too high (i.e., including more than 95% of the subsequent locations), then it would suggest a positively biased estimate. If the point-inclusion were to consistently come out too low, it would suggest negative bias. Similarly, a 50% home range estimate generated over $T_1$, should contain 50% of an animal's locations over $T_2$. In order to assess how, given locations over $T_1$, home range estimators compared in their ability to capture space use over $T_2$, we conducted cross-validation on these empirical data (for details see Appendix S1). Because traditional leave-one-out cross-validation makes strong assumptions of independence, we subset individual data into two halves. The first half ($T_1$) consisted of the first 50% of an individual's locations; the second half ($T_2$) consisted of the second 50%. Although locations are drawn from the same individual, $T_1$ and $T_2$, are much more independent of each other than any single time $t_i$ is to the bulk of the data, which means that the core assumption of our block cross-validation approach is much more likely to be satisfied compared to that of leave-one out cross-validation (Roberts et al. 2017).
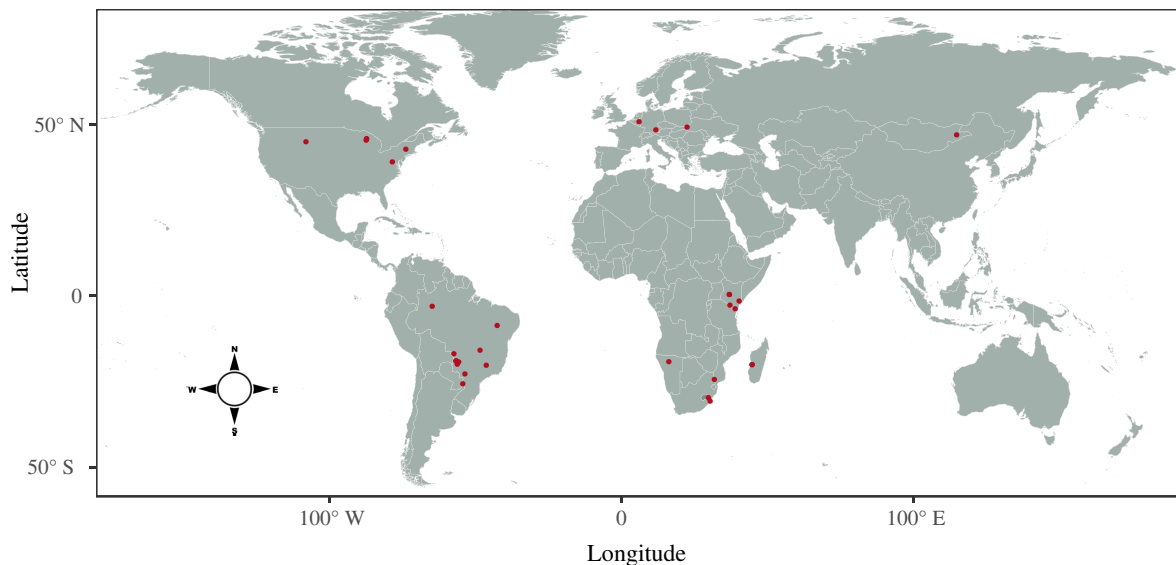


Fig. 2.    Distribution of locations from the empirical GPS tracking data set spanning 369 individuals across 22 mammalian, four avian, and one reptilian species.

TABLE 1. Summary statistics of the GPS tracking data sets.

| Binomial | Individuals | Frequency (min) | Duration (d) | Number of locations | $\hat{N}_{area}$ |
|---|---|---|---|---|---|
| *Aepyceros melampus* | 21 | 20 | 295.5 (1.5–463.4) | 19,623 (106–30,975) | 151.5 (8.2–645.3) |
| *Beatragus hunteri* | 4 | 60 | 843.7 (120.5–966.6) | 20,053 (2,839–22,568) | 93.8 (28.0–275.4) |
| *Bycanistes bucinator* | 24 | 15 | 18.2 (4.8–56.0) | 758 (165–2,303) | 35.5 (0.8–1,256.5) |
| *Canis latrans* | 20 | 15 | 210.2 (2.8–351.0) | 10,170 (10–13,935) | 164.9 (1.2–884.1) |
| *Canis lupus* | 7 | 15 | 207.0 (108.0–220.5) | 10,552 (6,876–12,576) | 47.3 (5.0–227.7) |
| *Cerdocyon thous* | 20 | 5 | 41.0 (19.7–64.2) | 8,137 (1,811–19,851) | 147.8 (8.8–260.6) |
| *Chrysocyon brachyurus* | 13 | 120 | 293.3 (58.2–996.4) | 2,565 (496–8,760) | 475.0 (52.5–2,416.0) |
| *Eulemur rufifrons* | 4 | 30 | 76.4 (26.3–122.4) | 4,019 (3,506–6,705) | 251.3 (53.6–263.1) |
| *Felis silvestris* | 5 | 120 | 82.6 (35.8–148.4) | 391 (128–2,006) | 117.3 (13.6–733.5) |
| *Glyptemys insculpta* | 12 | 300 | 76.9 (20.1–190.6) | 164 (46–453) | 47.8 (4.5–894.5) |
| *Gyps africanus* | 12 | 10 | 140.9 (12.1–536.2) | 25,231 (865–38,066) | 20.3 (4.7–480.7) |
| *Gyps coprotheres* | 5 | 5 | 483.5 (124.4–720.4) | 39,170 (3,911–46,330) | 29.1 (7.4–101.6) |
| *Lepus europaeus* | 12 | 60 | 196.3 (5.6–214.7) | 2,823 (43–4,426) | 783.2 (13.7–1,122.3) |
| *Madoqua guentheri* | 15 | 10 | 24.9 (9.0–26.1) | 2,194 (914–2,417) | 201.8 (46.0–405.8) |
| *Martes pennanti* | 14 | 10 | 20.1 (10.2–71.4) | 1,425 (446–13,925) | 30.3 (9.6–216.9) |
| *Ovis canadensis* | 6 | 420 | 1,030.3 (368.6–1,169.0) | 2,736 (1,169–3,262) | 478.8 (32.1–785.6) |
| *Panthera leo* | 3 | 420 | 627.8 (138.2–642.0) | 396 (243–1,464) | 154.1 (96.7–243.8) |
| *Panthera onca* | 33 | 90 | 193.3 (52.0–1,140.9) | 1,011 (42–7,668) | 46.1 (2.9–149.9) |
| *Papio cynocephalus* | 22 | 60 | 297.5 (87.5–299.5) | 4,097 (1,222–4,140) | 543.7 (60.3–1,455.2) |
| *Procapra gutturosa* | 23 | 1,500 | 304.2 (67.2–755.0) | 165 (28–866) | 4.5 (0.7–24.6) |
| *Propithecus verreauxi* | 28 | 15 | 100.7 (7.7–149.5) | 8,773 (687–13,258) | 332.2 (34.9–834.8) |
| *Sus scrofa* | 26 | 5 | 56.9 (25.4–213.4) | 5,676 (442–13,303) | 188.7 (28.3–680.4) |
| *Syncerus caffer* | 6 | 60 | 214.6 (106.6–471.0) | 3,986 (2,572–5,776) | 21.5 (14.1–61.4) |
| *Tapirus terrestris* | 4 | 60 | 582.3 (568.0–643.6) | 11,839 (10,842–12,203) | 2,546.5 (1,726.7–3,289.8) |
| *Torgos tracheliotus* | 3 | 10 | 379.0 (162.0–514.0) | 36,437 (26,960–37,143) | 90.7 (13.2–1,082.8) |
| *Ursus americanus* | 15 | 15 | 106.6 (29.0–718.6) | 8,608 (1,326–15,594) | 33.5 (0.9–310.8) |
| *Ursus arctos* | 12 | 60 | 193.3 (8.4–379.8) | 1,421 (62–13,423) | 17.2 (4.5–144.0) |

*Notes:* Study durations, number of locations, and $\hat{N}_{area}$ are median values with ranges in parentheses. $\hat{N}_{area}$ represents the effective sample size for home range area estimation, governed by the duration of the observation period ($T$), and the range crossing time ($\tau_p$); $\hat{N}_{area} \approx \frac{T}{\tau_p}$.

These subset halves were then used to cross-validate home range estimators via percent location inclusion. Using tracking data from $T_1$, an individual's home range was estimated using each of the home range estimators. We then calculated the percentage of locations from $T_2$ that were located within the 95% and 50% areas of each of the estimates. Because estimator performance improved with $\hat{N}_{area}$ in an asymptotic, nonlinear fashion, we fit Michaelis-Menten curves ($f(x) = Lx/(x_0 + x)$) to cross-validation results via median quantile regression to summarize trends across our datasets.

As noted above, this cross-validation technique was dependent on the assumption that an individual's movement behavior had not changed significantly between $T_1$ and $T_2$. For instance, if an individual had dispersed during the observation period (Bowler and Benton 2005), or was displaced via anthropogenic disturbance (Faille et al. 2010), cross-validation failure might not have been the result of bias in the estimate, but rather could have been due to unmodeled the change in movement behavior. To objectively confirm this assumption, we tested whether the mean and covariance of $T_1$ differed significantly from those of $T_2$. Movement models for each subset half were fit using

the methods described above, which provided estimates of the mean, $\mu$, and covariance, $\sigma$, parameters of the models' distributions. We then used the Battacharryya distance (BD; Bhattacharyya 1946, Winner et al. 2018) as a measure of dissimilarity between the normal distributions corresponding to the fitted movement models from $T_1$ and $T_2$, and asked if the CIs on this distance contained 0 (for full details see Appendix S1), where the BD can be expressed in terms of the arithmetic and geometric means of the covariance matrices (AM and GM respectively)

$$\text{AM} = \frac{\sigma_1 + \sigma_2}{2}, \qquad \text{GM} = \sqrt{\sigma_1 \sigma_2} \qquad (6)$$

and the Mahalanobis distance (MD; Mahalanobis 1936)

$$\text{MD} = \sqrt{(\mu_1 - \mu_2)^{\text{T}} \text{AM}^{-1} (\mu_1 - \mu_2)}. \qquad (7)$$

such that

$$\text{BD} = \frac{1}{8}\text{MD}^2 + \frac{1}{2}\text{tr}\log\left(\frac{\text{AM}}{\text{GM}}\right). \qquad (8)$$

Using this method, we found that 77 of 369 individuals had movement models with significantly different parameter estimates between $T_1$ and $T_2$, and so were excluded from our cross-validation test. Although an average of $\sim 90\%$ of the individuals from each study satisfied the assumption of consistent movement behavior, there was a significant relationship between those individuals that were excluded and which study the data were from ($F_{24,342} = 2.72$, $P < 0.005$).

*Empirically guided simulations.*—Simulating data from a movement model is an effective tool for evaluating estimator performance because the true distribution of a simulated process can be calculated exactly, and confounding effects can be controlled for. With simulated data, however, biases can be introduced into home range estimates in two ways: (1) the model used to simulate the data might not be providing an adequate representation of real animal movement data; and/or (2) the home range estimator may be biased even though the movement model is appropriate. To tease these apart, we used a set of empirically guided simulations to assess the correspondence between the empirical results, and simulated results that were tied to the data, but where the truth was known. Similar results in both cases would indicate that the models we simulated from were adequate representations of the real data, and that the major biases apparent in the results are occurring on the home range estimator side of the problem.

For these simulations, locations were simulated conditional on the fitted movement model for each individual using the `simulate()` function in the R package `ctmm`, with the number of locations, and sampling times corresponding to those from each individual's original data. Simulating data in this way reproduced movement with the same parameters as the fitted model. If the fitted models were not accurately describing the underlying movement, home ranges estimated from the simulated data would not be comparable to home ranges estimated from the empirical data. Conversely, comparable estimates are an indication that the simulated data appropriately reflect the empirical data, and variation between empirical area estimates was the result of biases in the estimates as opposed to model misspecification. From these simulated data, we estimated the 95% home range area using each of the estimation methods described above. This process was repeated 400 times for each of the 369 fitted models, yielding a total of 147,600 area estimates per estimator.

Our simulations revealed that bias decreased asymptotically with $\hat{N}_{area}$ in a sigmoidal fashion. To summarize this trend, we fit the median of the ratio of empirical KDEc : AKDEc 95% area estimates, vs. $\hat{N}_{area}$, to a logistic function using the R package quantreg (version 5.29; Koenker 2013). We then assessed whether the parameter estimates of the curve fit to the empirical data reflected a similar function fit to the results from the empirically guided simulations. Similar comparisons were made for the ratios between each of the estimators and AKDEc.

*Simulated data.*—After identifying a close correspondence between the empirical results and simulated results that were tied to the data, we used another series of simulations to explore how both the bias, and variance of 95% area estimates varied with sampling duration, frequency, and underlying movement processes. Data were simulated based on both an IID process, and an OUF process (Fleming et al. 2014*b,c,* for full details see Appendix S2). Simulating from an IID process generates data that satisfy the assumption of independence, whereas simulating from an OUF process generates locations that are representative of modern GPS tracking data commonly used in home range analyses (Fleming and Calabrese 2017). This was confirmed by an OUF model being selected as the best fit for 240 of the 369 individuals in our empirical GPS data set, with an IID model only being selected for one individual and an OU model for the remaining 128. We used these processes to simulate locations according to three sets of manipulations:

*1. Sampling duration.*—In our first set of simulations, we tested how 95% area estimates compared across variable sampling durations. Observations were recorded eight times per day, and we manipulated sampling duration (ranging from 1 to 4,096 d in a doubling series). For OUF simulations, the home range crossing time and the velocity autocorrelation time scale were set to one day. Notably, this parameterization was such that in these simulations the sampling duration in days exhibited a 1:1 relationship with $\hat{N}_{area}$.

*2. Sampling frequency.*—In our second set of simulations, we tested how variation in sampling frequencies influenced home range estimates. Here, the sampling duration was fixed at 30 d, and we manipulated the sampling frequency (ranging from 1 to 1,024 locations per day in a doubling series). Again, home range crossing time and the velocity autocorrelation time scale for the OUF process were set to one day. The fixed sampling duration in these simulations resulted in a constant $\hat{N}_{area}$ of 30 for the OUF process, irrespective of variation in the sampling frequency.

*3. Range crossing time.*—In our third set of simulations, we tested whether variation in the underlying movement process influenced home range estimates. We fixed the sampling duration at 365 d, with observations recorded every hour, resulting in 24 observations per day and a fixed $n$ of 8,760. The velocity autocorrelation time scale was again set to one day, but we manipulated the home range crossing time from 1 to 1,024 d in a doubling series. This resulted in $\hat{N}_{area}$ decreasing with increasing range crossing time. For an autocorrelated process like OUF this manipulation will result in data being autocorrelated for sampling intervals $< \tau_p$ (with correspondingly smaller $\hat{N}_{area}$) and the data being IID for sampling intervals $\gg \tau_p$. We therefore only performed this

manipulation for the OUF process, as this manipulation changes nothing for an IID process.

For each of these simulated data sets, we estimated the 95% home range area using each estimator (full details and visualizations of simulated movement tracks are presented in Appendix S2), and compared the bias and variance of these estimates. Results were averaged over 400 simulations per manipulation to balance the capacity to explore broad regions of parameter space against computation time. In all simulations, the true 95% area was scaled to 1 km$^2$.

We note, however, that results from simulations may reflect artifacts of the functions used to generate the simulated data, rather than provide an adequate representation of how estimators might perform on real data (Blundell et al. 2001, Hemson et al. 2005, Börger et al. 2006). We chose to simulate from Gaussian processes because the true distribution, and resulting bias, could be calculated exactly, which is not tractable for more complex distributions. Real tracking data are unlikely to be perfectly Gaussian however, as landforms such as rivers, cliffs, and fences will sometimes impact animal movement. To confirm that our rankings of estimator performance were not driven solely by the processes we used to simulated the data, in Appendix S3 we describe supplementary simulations where we simulated data with a hard boundary. In this respect, we found no difference in estimator performance between results from Gaussian and non-Gaussian simulations aside from the expected spillover by kernel methods (Worton 1995).

All analyses were performed in the R environment (version 3.4.0; R Core Team, 2016), using the home range estimation techniques implemented in the R packages ctmm (version 0.4.0; Calabrese et al. 2016, Fleming and Calabrese 2017), adehabitat (version 0.4.14; Calenge 2006), and rhr (version 1.2.909; Signer and Balkenhol 2015). The computations were conducted on the Smithsonian Institution High Performance Cluster.

## Results

### Empirical data

The median number of GPS locations in individual tracking data sets was 3,549 (range: 10–46,330), with the durations of studies ranging from 1.5 to 1,169 d (median = 121.0 d). The median effective sample size however, was only 91.4 (ranging from 0.67 to 3,289.8). Sampling intervals ranged from 2 min to 10 d but, out of 369 data sets, only one was found to be IID and free from autocorrelation: a coyote (*Canis latrans*) that was located 15 times over 28.6 d. Range crossing times also varied substantially both intra- and interspecifically, with >100-fold variation regularly observed between individuals of the same species in the same tracking study (Fig. 3).

### Cross-validation

Cross-validation of home range estimates demonstrated that when autocorrelation in animal tracking
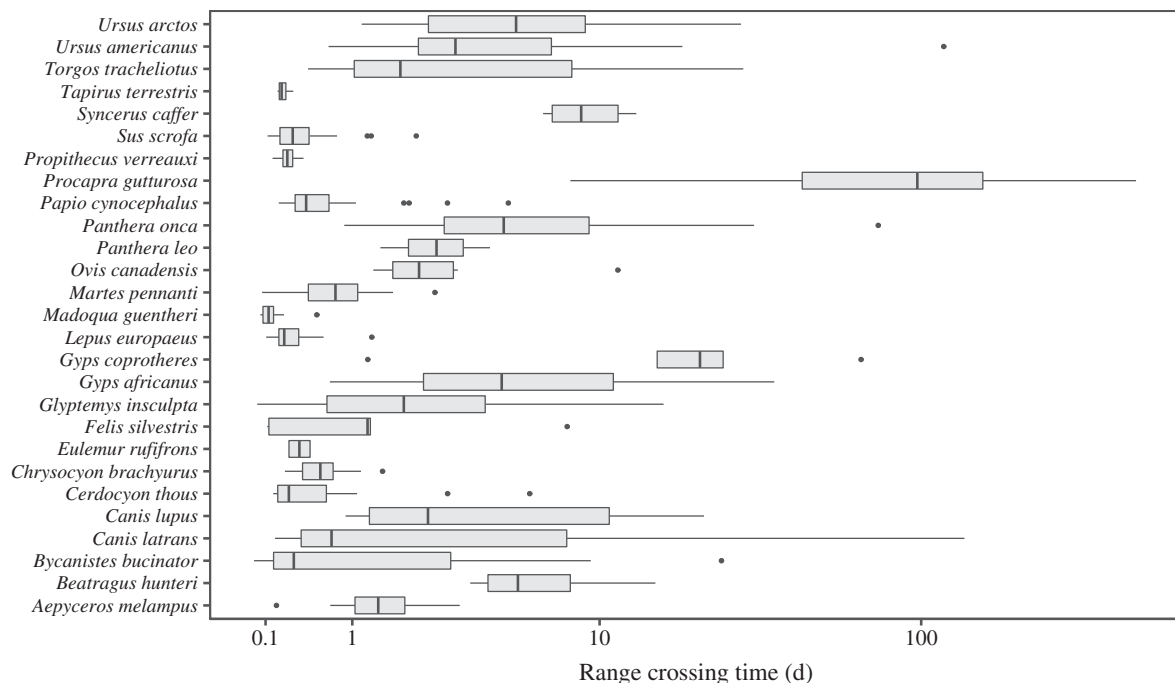


FIG. 3. Boxplots depicting the variation in range crossing times for individuals in each data set. For each boxplot, the solid vertical line depicts the median, the gray box the interquartile range (IQR; i.e., 25th and 75th quartiles), the whiskers ±1.5 × IQR, and the circles outliers. Note the log scale of the *x*-axis.

data was accounted for, estimator performance improved significantly (e.g., Fig. 4).

*95% home ranges.*—In a direct comparison between AKDEc and KDEc, we found that AKDEc 95% home ranges estimated using the first half of an individual's locations included more locations in the second half of a tracking data set for 280 individuals, vs. only 14 for KDEc, with no clustering of this effect by species ($F_{26,262} = 1.36$, $P = 0.12$). Crucially, of the expected 95%, the median number of locations included in AKDEc range estimates was 95.3% (CI: 94.3–96.4%), demonstrating that the greater number of subsequent locations included by AKDEc was not a function of estimates being overly-large, and across all data sets, AKDEc cross-validated more often at the correct rate ($F_{1,524} = 80.56$, $P < 0.001$). Similar negative biases were observed in the cross-validation rates of all other conventional home range estimators (i.e., Srt-KDE, lscv-KDE, MCP, and *k*-LoCoH).

Notably, while the percentage of locations included by conventional estimators did increase with $\hat{N}_{area}$ (Fig. 5c, e, g, i, k), the percentage of locations included by AKDEc did not vary with $\hat{N}_{area}$ ($F_{1,287} = 3.23$, $P = 0.07$; Fig. 5a), and cross-validation was consistently appropriate. As a result, the difference between AKDEc and conventional estimators was greatest at mid-low $\hat{N}_{area}$. For instance, although the number of subsequent locations included in KDEc 95% area estimates converged to 95% as $\hat{N}_{area}$ increased, at low $\hat{N}_{area}$ ($\leq 32$) AKDEc resulted in a 52.9% (CI: 19.9–85.8%) improvement over KDEc. At intermediate $\hat{N}_{area}$ ($32 < \sim\hat{N}_{area} \leq 256$) the improvement offered by AKDEc was 7.9% (CI: 3.2–12.7%), and only 1.6% (CI: 1.1–2.0%) at high $\hat{N}_{area}$ (>256).

*50% home ranges.*—The median percentage of locations included by AKDEc 50% estimates was consistently appropriate (50.1%; CI: 44.8–51.3%), and did not vary with $\hat{N}_{area}$ ($F_{1,287} = 0.02$, $P = 0.88$; Fig. 5b), whereas the
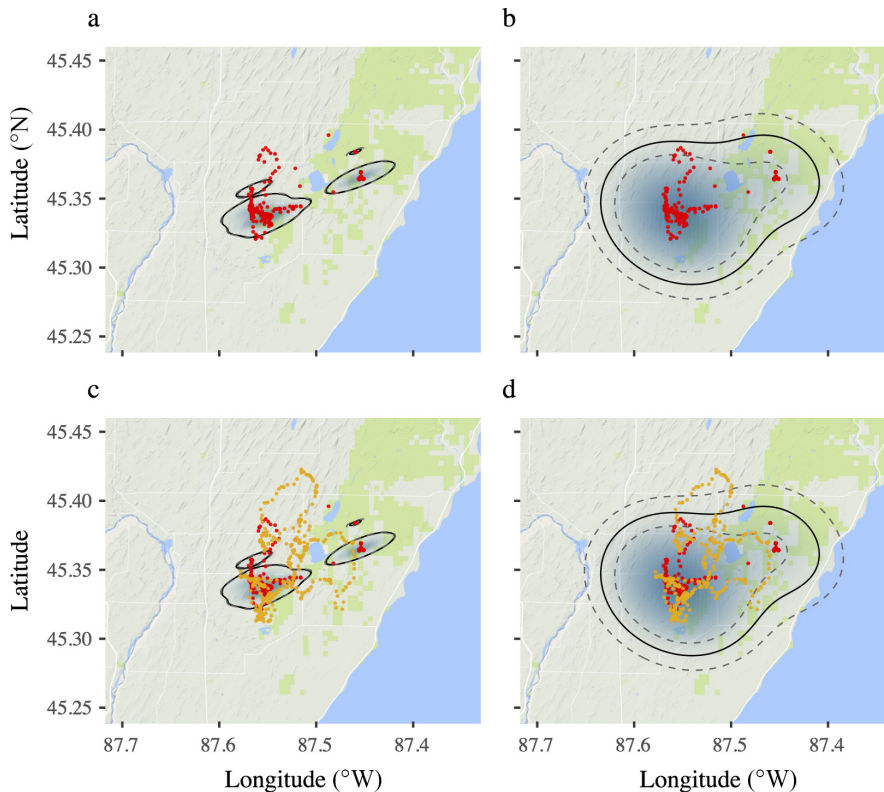


FIG. 4. Example of the location inclusion cross-validation for a black bear (*Ursus americanus*), tracked over a period of 139 d; $\hat{N}_{area} = 23$. In all panels, the range distribution estimated from the first half of locations (red dots) is shown as blue shading, a black contour line delineates the estimated 95% home range area, and two gray contour lines express the 95% confidence range. Panel a depicts the smaller range estimate and minimal estimated uncertainty produced by conventional KDEc; whereas panel b depicts AKDEc's (area-corrected autocorrelated-Gaussian reference function Kernel Density Estimation) larger range estimate, and substantial uncertainty in delineating how much area this individual would use 95% of the time. The larger range and wide confidence intervals of the AKDEc estimate are appropriate for this bear, evidenced in panel c where KDEc failed to anticipate the possibility of the long distance movements that it undertook during the second half of the monitoring period (orange dots) excluding 49.8% of its subsequent locations, whereas this possibility was accounted for by the AKDEc method in panel d, which was well informed by the autocorrelation structure present in the first half of the data and included 92.3% of this individual's subsequent locations.
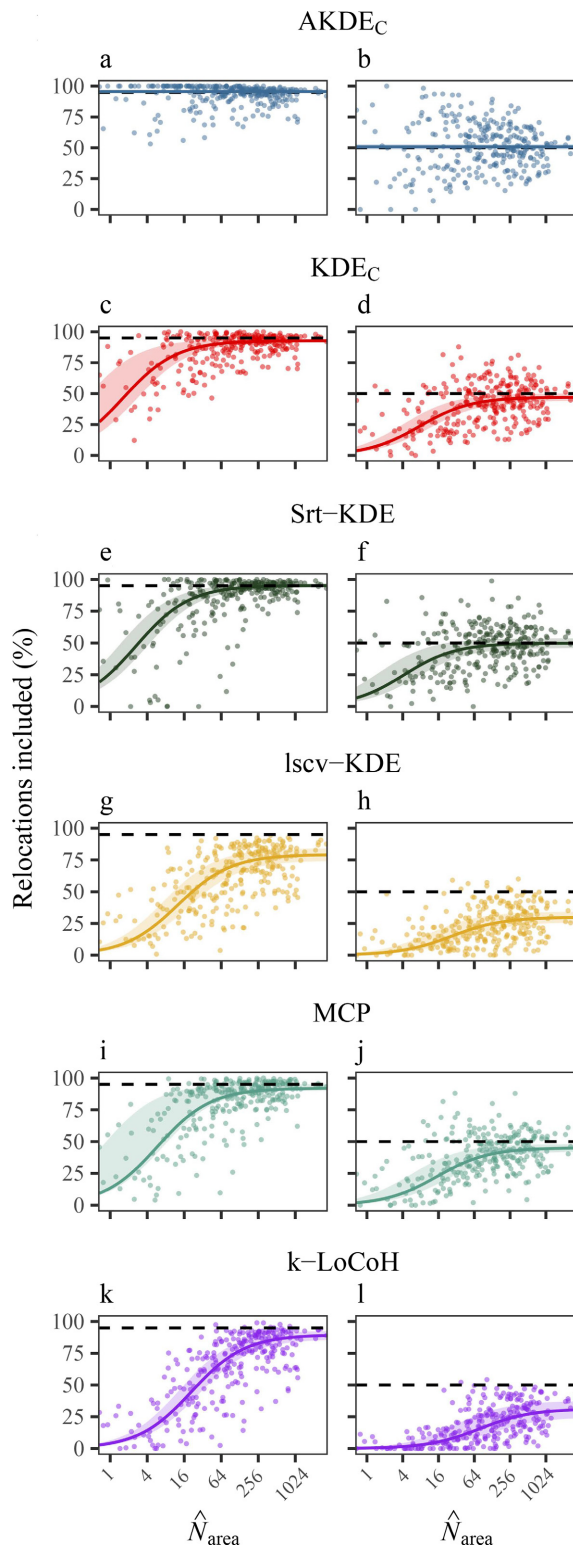
FIG. 5. Scatterplots depicting the percentage of locations from the second half of the data included in 95% and 50% home ranges estimated from the first half of the data, as a function of the effective sample size ($\hat{N}_{area}$). The solid lines represent Michaelis-Menten curves ($f(x) = Lx/(x_0 + x)$) fit to cross-validation results via median quantile regression, and the shaded regions 95% CIs of the curve fits. For AKDEc, the median number of cross-validated locations ± 95% CIs is presented (95.3%; and 50.1% respectively), as these did not vary significantly with $\hat{N}_{area}$. The dashed lines depict the values at which these estimates should cross-validate. Estimators are defined in Table 2.

TABLE 2. Mean ratio ±95% confidence intervals, between area estimates produced by AKDEc and those produced by conventional estimators, for the 369 empirical GPS data sets.

| Estimator | Mean | Lower 95% CI | Upper 95% CI | $F_{1,688}$ |
|---|---|---|---|---|
| MCP | 2.2 | 1.9 | 2.6 | 21.70 |
| $k$-LoCoH | 13.3 | 7.3 | 19.5 | 199.31 |
| KDEc | 1.9 | 1.7 | 2.1 | 22.53 |
| Srt-KDE | 2.2 | 1.6 | 2.8 | 15.74 |
| lscv-KDE | 11.0 | 7.3 | 14.6 | 352.92 |

*Notes:* All differences were significant with $P < 0.001$. AKDEc, area-corrected autocorrelated-Gaussian reference function Kernel Density Estimation; MCP, Minimum Convex Polygon; $k$-LoCoH, $k$-Local Convex Hull; KDEc, area-corrected Kernal Density Estimation; Srt-KDE, KDE using Srt bandwidth optimization; lscv-KDE, KDE using least squares cross-validation bandwidth optimization.

at small $\hat{N}_{area}$. As a result, the improvement offered by AKDEc was again greatest at low $\hat{N}_{area}$.

### Patterns in empirical area estimates

AKDEc 95% home range estimates were, on average, larger than area estimates from conventional estimators (Table 2), where there was no interaction with which study the data were from ($F_{24,688} = 0.41$, $P = 0.99$). Consistent with trends in the cross-validation study, we found that the difference between AKDEc and conventional area estimates was greatest at low $\hat{N}_{area}$, with the ratios between these and AKDEc converging to parity as $\hat{N}_{area}$ increased (Fig. 6). Crucially, the parameter estimates for these relationships did not differ significantly between logistic functions fit to the ratios of empirical area estimates and estimates of the biases observed in the empirically guided simulations, demonstrating correspondence between the simulated and empirical findings. This ratio exhibited no relationship with the number of locations ($F_{1,367} = 1.57$, $P = 0.21$; Fig. 7a), nor with the duration of the sampling period ($F_{1,367} = 1.69$, $P = 0.19$; Fig. 7b).

We also found that the width of KDEc's 95% CIs were unrelated to a data set's $\hat{N}_{area}$ (Fig. 6b); whereas the width of AKDEc 95% CIs narrowed as $\hat{N}_{area}$ increased (Fig. 6c). No other home range estimator provided CIs on area estimates, precluding additional analysis.

percentage of locations included by conventional estimators exhibited a positive relationship with the effective sample size (Fig. 5d, f, h, j, l), and were negatively biased

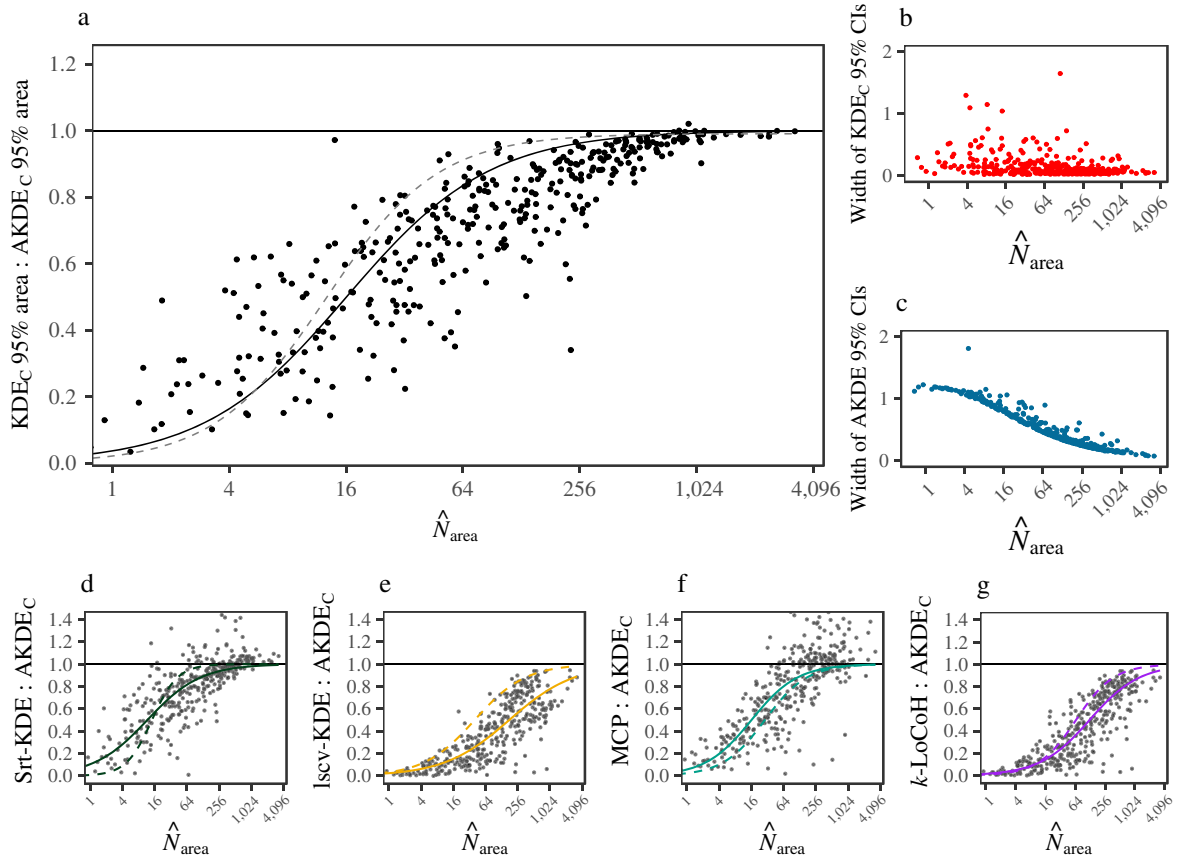FIG. 6. Summary of empirical home range analysis depicting (a) the ratio between 95% area estimates generated via KDEc and AKDEc, (b) the width of 95% CIs of KDEc estimates as a proportion of the estimated area, and (c) the width of 95% CIs of AKDEc estimates. The bottom row shows the ratio between 95% area estimates generated via (d) Srt-KDE and AKDEc, (e) lscv-KDE and AKDEc, (f) MCP and AKDEc, and (g) *k*-LoCoH and AKDEc. The horizontal lines depict parity between conventional estimators and AKDEc; the solid curves logistic functions fit to the empirical data; and the dashed curves similar function fit to data simulated from the fitted movement model for each individual. Note that for KDEc, the width of the 95% CIs was unrelated to $\hat{N}_{area}$, whereas AKDEc CIs narrowed systematically as $\hat{N}_{area}$ increased.
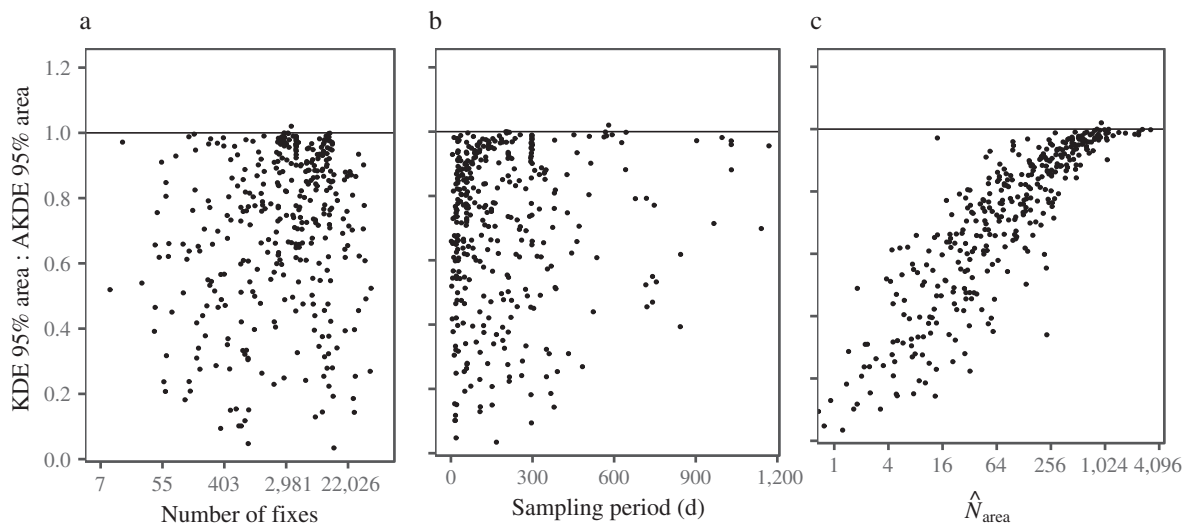


FIG. 7. Scatterplots depicting the ratio between empirical 95% area estimates generated via KDEc and AKDEc and (a) the sample size, (b) the duration of the sampling period, and (c) the effective sample size. The horizontal lines depict parity between KDEc and AKDEc.

*Simulation study*

Our simulations revealed that, when the data were IID, all estimators benefited from an increase in the total number of locations by either extending the sampling duration, or increasing the sampling frequency. When data were autocorrelated, however, AKDEc 95% area estimates were less biased than conventional estimates (i.e., MCP, $k$-LoCoH, Srt-KDE, lscv-KDE, and KDEc), and more robust to variation in sample duration, frequency, and an individual's range crossing time. Crucially, across all simulations, as the amount of information in a data set increased (i.e., larger $\hat{N}_{area}$) the sampling variance of AKDEc estimates decreased, whereas this relationship was not observed for conventional estimators.

*Sampling duration.*—For IID data, KDEc and AKDEc 95% area estimates were identical, and both estimators converged to the true 95% area as the sampling duration increased (Fig. 8a). KDE estimation using Silverman's rule of thumb and least squares cross-validation bandwidth optimization also converged to the true area, however, these methods exhibited slower convergence to the true value with increased sampling duration than KDEc and AKDEc and, at intermediate sample sizes, resulted in relatively strong positive bias. Asymptotic convergence was also observed for the MCP and $k$-LoCoH methods, but these required substantially longer sampling durations to approach the true value when compared to the kernel methods, and were the most biased across the range of sampling durations we tested. Notably, the sampling variance of all estimators also

decreased as the sample duration increased, benefiting from the greater number of locations.

For coarsely sampled, autocorrelated OUF data, all 95% area estimates eventually converged to the true 95% area as the sampling duration increased (Fig. 9a), however, convergence to the true value with increasing sample duration was considerably slower for all the conventional methods, requiring at least 128 times more data than AKDEc before achieving relatively unbiased estimates. The variance of AKDEc 95% area estimates was inversely related to the sampling duration ($F_{1,11} = 1,421$, $P < 0.001$), and was lowest when the data had the largest effective sample size. In contrast, there was no relationship between the variance of 95% area estimates from MCP, Srt-KDE, lscv-KDE, and KDEc, and the sampling duration (all $P > 0.18$), where these estimators exhibited comparable variance irrespective of the $\hat{N}_{area}$. Worryingly, the variance of the $k$-LoCoH method actually increased as $\hat{N}_{area}$ increased ($F_{1,11} = 10.66$, $P = 0.008$), i.e., the method became less precise with better data.

*Sampling frequency.*—For IID data collected over a fixed sampling duration, KDEc and AKDEc 95% area estimates produced identical range estimates, and converged to the true 95% area as the sampling frequency increased (Fig. 8b). Similar convergence was also observed for Srt- and lscv-KDE estimates, and again convergence was slower for the MCP and $k$-LoCoH methods. As observed when sampling duration was manipulated, the variance of all estimators decreased as the sampling frequency was increased for IID data.

For autocorrelated data, however, despite a constant $\hat{N}_{area}$ across the range of frequency manipulations, all
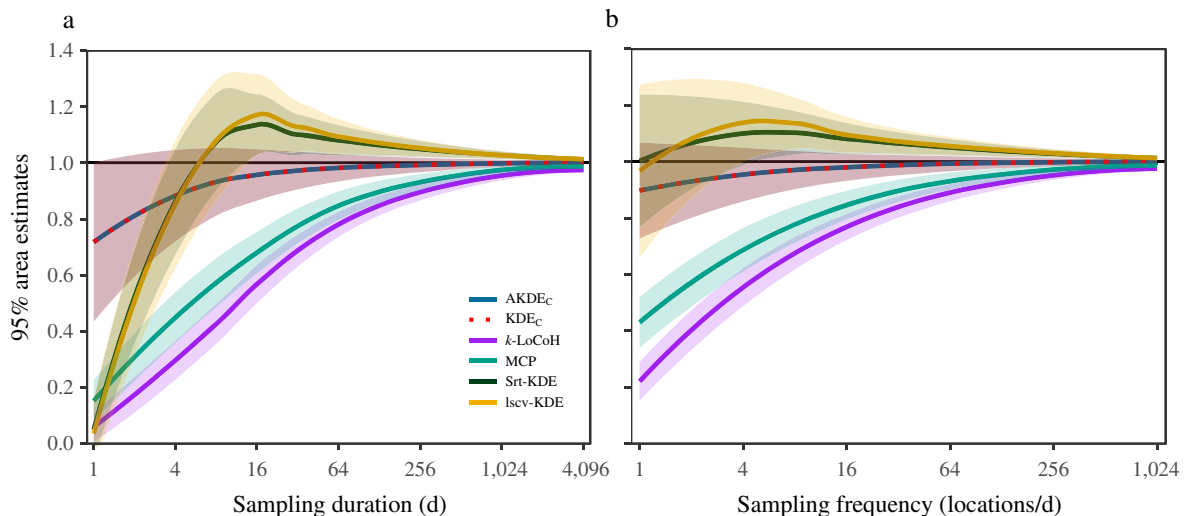


FIG. 8. Results of simulations demonstrating the relationship between the bias and sampling variance of 95% area estimates and (a) sampling duration; and (b) sampling frequency for independent and identically distributed (IID) data. In all panels the x-axis is log-scaled, and the horizontal black line depicts the true area. Note how, for IID data, AKDEc and KDEc estimates are indistinguishable (the maroon color is coming from the complete overlap of the KDEc [red] and AKDEc [blue] standard errors) and the bias and variance of all estimators benefited from an increase in the number of locations by either extending the sampling duration or increasing the sampling frequency.
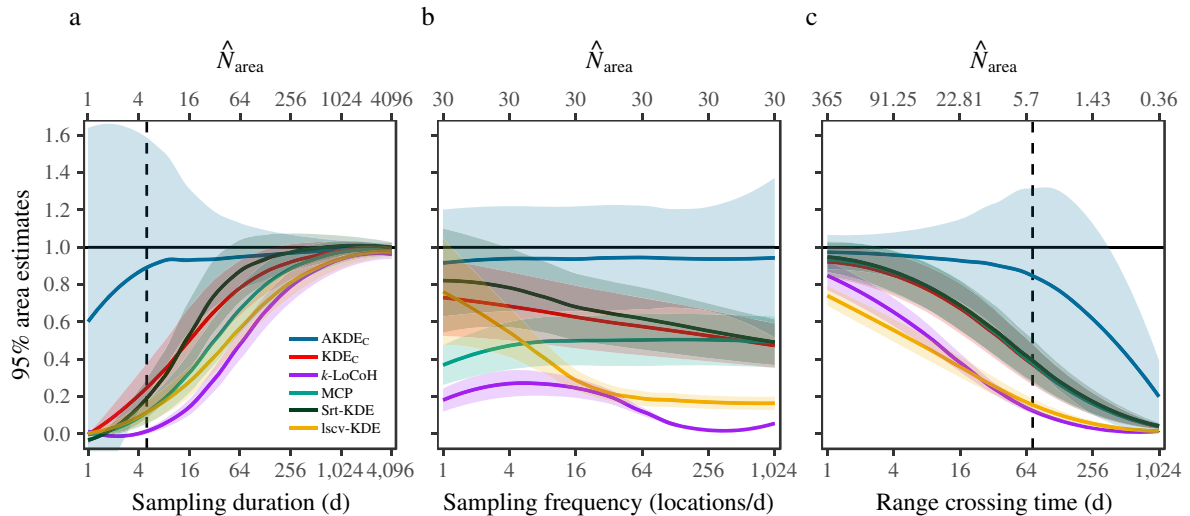
F<small>IG</small>. 9.    Results of simulations demonstrating the relationship between the bias and sampling variance of 95% area estimates for an autocorrelated Ornstein-Uhlenbeck Foraging (OUF) process and (a) sampling duration, (b) sampling frequency, and (c) an individual's range crossing time. Note the upper x-axis indicating the effective sample size ($\hat{N}_{area}$). In all panels, the x-axes are log-scaled, the horizontal black line depicts the true area, and the dashed vertical lines an $\hat{N}_{area}$ of 5, included as a visual aid. In panel a, the sampling duration exhibits a 1:1 relationship with $\hat{N}_{area}$; in panel b, $\hat{N}_{area}$ is fixed at 30; and in panel c, the range crossing time exhibits a negative relationship with $\hat{N}_{area}$. We note that deviations between AKDEc and the truth at $\hat{N}_{area} < 5$ represent ordinary small sample size bias.

conventional kernel estimators became increasingly negatively biased as the sampling frequency increased (all $P < 0.001$; Fig. 9b). Furthermore, while the bias of conventional kernel estimators increased with increasing sampling frequency, their variance actually decreased (all $P < 0.001$). Notably, although MCP and $k$-LoCoH methods were not negatively biased by an increase in the sampling frequency, the bias of these estimators was always >50% and >85% respectively. In contrast, both the bias and variance of AKDEc 95% area estimates were unaffected by an increase in the sampling frequency ($F_{1,9} = 0.73$, $P = 0.42$; $F_{1,9} = 2.14$, $P = 0.18$, respectively).

*Range crossing time.*—Despite a year of sampling at regular intervals, as an individual's home range crossing time increased, all home range estimators became increasingly biased (Fig. 9c). However, the increase in bias occurred more rapidly for MCP, $k$-LoCoH, Srt-KDE, lscv-KDE, and KDEc than for AKDEc, and conventional methods that did not account for autocorrelation were not robust to variation in the range crossing time. Crucially, the increased range crossing time, and resultant decrease in $\hat{N}_{area}$, was correctly accompanied by an increase in variance for AKDEc ($F_{1,9} = 13.2$, $P = 0.005$), but the variance of conventional methods estimates actually decreased (all $P < 0.02$).

## DISCUSSION

Quantifying the size of a home range is an attempt at answering the question "how much space does an animal use?" (Burt 1943, Fieberg and Börger 2012, Fleming et al.

2015a). The answer can have important implications for ecological theory (e.g., Jetz 2004, Buchmann et al. 2011), and/or species management (e.g., Law and Dickman 1998, Macdonald 2016), but only if differences are truly the result of ecological processes and not bias in the estimates. Although the issue of autocorrelation has been termed a "red herring" (Fieberg 2007, Kie et al. 2010), from both empirical and simulated data, we demonstrated conventional home range estimators to be significantly and often massively negatively biased when used on autocorrelated data. Cross-validation of home range estimators demonstrated that, when autocorrelation in animal tracking data was accounted for, the ability to capture future space use (assuming no change in movement process) was improved dramatically, whereas conventional estimators regularly underestimated an individual's future space use. Additionally, not only was the extent of this bias influenced by the effective sample size and sampling frequency, but also by variation in an individuals' average home range crossing time. In contrast, when autocorrelation was accounted for, home range estimates were reliably accurate, even with an $\hat{N}_{area}$ as low as 5, were not biased by increased sampling frequency (i.e., an increase in the amount of autocorrelation), and were consistent across different range crossing times.

### Autocorrelation, sample size and asymptotic consistency

For simulated IID data, consistent with standard advice from the literature (e.g., Seaman et al. 1999, Girard et al. 2002, Börger et al. 2006, Fieberg 2007), the accuracy of all estimators benefited from an increase in

the total number of locations by either extending the sampling duration, or by increasing the sampling frequency. For simulated autocorrelated data, we found that conventional kernel methods did eventually converge to the true area, but required extremely large effective sample sizes to do so. This finding was also consistent with previous work in the statistical literature (Hall and Hart 1990, Butucea and Neumann 2005, Wu et al. 2010). As noted by Fleming et al. (2015a), conventional KDE is only statistically optimal when tracking data are sampled so coarsely that the data appear uncorrelated in time, or for a far longer period than the time scale over which any autocorrelation persists. Even more extreme negative biases were found with geometric MCP and $k$-LoCoH estimates on autocorrelated data. Conversely, AKDEc estimates were the most accurate on autocorrelated data. This is not surprising, as the autocorrelation structure was accounted for in the fitted movement model, and conditioned on during the bandwidth optimization.

Given that ecologists are increasingly taking advantage of advances in animal tracking technologies to uncover hidden facets of animal behavior (Tomkiewicz et al. 2010, Kays et al. 2015, Noonan et al. 2015), and/or better resolve the autocorrelation structure of animal movement data (Cushman et al. 2005), modern data sets are unlikely to meet the critical assumption of independence necessary for accurate home range analysis with estimators that assume IID data (Fleming et al. 2015a, Walter et al. 2015; see also Fig. 1). Although conventional methods can produce accurate estimates from autocorrelated data, the effective sample size required to do so is unrealistically large: on the order of hundreds to thousands of times larger than for AKDE. Because of limitations on both battery life and animal lifespans, there is often no option to collect more tracking data from the same individual and so the consistently poor performance of conventional estimators at realistic $\hat{N}_{area}$ is not very practical for animal tracking applications. When faced with autocorrelated data collected over a realistic period of time, conventional methods are therefore likely to significantly underestimate the size of an individual's home range (see also Fleming et al. 2014b, 2015a). Accordingly, we found empirical AKDEc 95% area estimates to be larger than those produced by conventional methods, with this difference being greatest for data sets with mid to low $\hat{N}_{area}$. These were not overly large however, as evidenced by AKDEc's consistent cross-validation at the appropriate quantile, vs. conventional estimators' failure to do so. Interestingly, Signer et al. (2015) used individual based models to simulate tracking data, and found that Srt-KDE tended to produce the largest estimates, followed by MCP, lscv-KDE, and $k$-LoCoH estimates respectively. This ordering was identical to that found in the present study, with the caveat that Signer et al. (2015) did not include an evaluation of AKDE, and did not quantify the amount of autocorrelation in their data. The results in Signer et al.

(2015) serve as further indication that the results of our study are not a by-product of the methods used to simulate the data, but rather an accurate depiction of how the home range estimators we evaluated can be expected to perform on real data sets.

### Common issues with home range estimation in ecology

Because of the ubiquitous nature of home range estimation in the field of movement ecology (Laver and Kelly 2008), it is not commonly recognized that this analysis may not be appropriate for every tracking data set. A crucial first step for home range analysis is ensuring that there is clear evidence of range residency in the data. When a tracked animal does not show evidence of range residency, home range estimation is not appropriate (Calabrese et al. 2016, Morato et al. 2016, Fleming and Calabrese 2017). We therefore strongly recommend starting with visual verification of range residency in each tracking data set via variogram analysis (Fleming et al. 2014b), prior to estimating home ranges. Specifically, the variogram of a range resident individual should show a clear asymptote, indicating asymptotic space use over time. Beyond checking for range residency, we also strongly recommend home range analysis be performed conditionally on an appropriate movement model for the data, as opposed to relying on the assumption of independence. The best model for each data set should be identified via model selection, and not imposed a priori. It should also be confirmed that all modeling assumptions are satisfied, and that the resulting model fits are reasonable. While AKDEc is, by itself, very general, it relies on a fitted movement model that adequately captures the autocorrelation structure of the data (Calabrese et al. 2016). In our experience, the generic range resident models currently implemented in the R package ctmm (Fleming et al. 2015b) are useful for a broad array of range resident species (Fleming et al. 2014b). However, in cases where no appropriate model exists, even AKDEc will not be able to provide good range estimates. The library of continuous-time movement models on which AKDE can be based is expanding rapidly (Blackwell et al. 2015, Breed et al. 2017, Fleming et al. 2017, Gurarie et al. 2017, Péron et al. 2017), so the range of data sets to which AKDE can be applied will only expand going forward.

There is also a common misconception in the home range literature that once a threshold number of locations, or days, has been reached, KDE will produce an accurate estimate (e.g., Seaman et al. 1999, Girard et al. 2002, Börger et al. 2006). In reality, this is only partly true. As we demonstrated with simulated data, conventional methods were asymptotically consistent when the data were IID, and increasing the total number of locations in such cases by increasing the sampling duration and/or frequency did indeed result in a more accurate estimate. This relationship broke down, however, when data were autocorrelated (see also Fleming et al. 2014b, 2015a, Calabrese

et al. 2016, Fleming and Calabrese 2017). For instance, and perhaps counterintuitively, unless autocorrelation was accounted for, getting more locations by increasing the sampling frequency will actually decrease the accuracy of a home range estimate. This occurs because, all else being equal, the degree of autocorrelation in the data increases as sampled locations become closer together in time, and home ranges are not resolved by the total number of locations, but rather by the effective number of statistically independent locations (i.e., $\hat{N}_{area}$; Calabrese et al. 2016, Fleming and Calabrese 2017). This was confirmed using an extensive set of empirical data, where we demonstrated no relationship between the sampling duration, or number of locations, and the ratio between KDEc and AKDEc 95% area estimates. In contrast, this ratio exhibited a clear and highly significant relationship with $\hat{N}_{area}$. While we have demonstrated that AKDEc performs well down to $\hat{N}_{area} \sim 5$, we recommend extreme caution when working with low $\hat{N}_{area}$ data for home range analysis. We therefore further recommend that data collection be carried out such that $\hat{N}_{area}$ is as large as possible if home range analysis is the goal of the study. In this respect, the median $\hat{N}_{area}$ across all 369 individuals was 91, a sample size where we found conventional geometric and kernel methods to produce severely biased estimates. As such, the broad range of studies used in our analyses suggest that typical tracking data sets are unlikely to have effective sample sizes large enough for accurate home range estimation via conventional methods that assume independence.

Although we found that AKDE was the most accurate estimator on autocorrelated data, a known issue with all kernel methods is that their estimates tend to spill over beyond hard boundaries (Worton 1995, Getz and Wilmers 2004). In Appendix S3, we evaluated the bias and sampling variance of home range estimators on simulated data with a hard boundary and a movement process that tended to hug the boundary. For both IID data and autocorrelated data, all of the kernel methods resulted in faster convergence to the truth within the accessible region compared to geometric methods, but with the trade-off that the estimates spilled over the boundary by an amount proportional to the bandwidth. In contrast, geometric methods traded off the ability to respect simple (i.e., convex) boundaries against negative bias within the accessible region, and slower convergence therein. We also compared the cross-validation performance of AKDE and $k$-LoCoH on four individual empirical data sets that featured particularly apparent boundaries. On average across these data sets, AKDE 95% estimates cross-validated at 84.8%, while $k$-LoCoH 95% estimates cross-validated at only 53.4%. In none of these individual cases did $k$-LoCoH's ability to respect boundaries outweigh its inherent tendency to underestimate home range area in unbounded regions. We also note that, in compiling our empirical database, we did not specifically seek out data sets that featured boundaries, nor did we reject data sets where boundaries were present. Thus, our unparalleled database can be considered representative of

the degree to which boundaries might influence home range estimates in real tracking data. AKDE was the only estimator with consistently appropriate cross-validation across all of the data sets we examined, which suggests that, in practice, the positive bias associated with boundary spillover is less influential than the negative bias incurred by ignoring autocorrelation in the data. While we do not doubt the existence of situations where movement is completely hemmed in by hard boundaries, we do not think such cases are representative of real world tracking data in general. For such more extreme cases, we suggest that efforts aimed at developing an estimator combining AKDE's accuracy on autocorrelated data with $k$-LoCoH's ability to respect hard boundaries might be particularly fruitful.

Finally, a statistical estimate derived from data should also be accompanied by some measure of the confidence level associated with said estimate (Pawitan 2001). Although confidence interval estimation is commonplace in nearly all other aspects of ecological research, except for recent implementations in the R package ctmm (Calabrese et al. 2016), the field of home range estimation has yet to cover this fundamental statistical tenet. Indeed, no other home range estimator we tested provided a measure of error along with home range estimates. This is particularly problematic for conventional estimators, where, despite routine use (e.g., Börger et al. 2006, Signer et al. 2015), we found that sampling variance was not reliably related to either the accuracy of an estimate or the information content of the data (i.e., $\hat{N}_{area}$). When KDEc estimates were accompanied by CIs, the width of those CIs was unrelated to $\hat{N}_{area}$. These inappropriately narrow confidence intervals are an artefact of conventional KDE using the total number of observations, $n$, as the relevant sample size, which is valid only for IID data, instead of $\hat{N}_{area}$ (Fleming and Calabrese 2017). To see this, consider a Cape Vulture (*Gyps coprotheres*) we analyzed that had >45,000 locations collected at 5-min intervals. For this individual, the KDE CIs were far too narrow because KDE assumed that each of these 45,000 locations were independent data points, when in reality, the autocorrelation in the data caused most of the locations to be quite similar to each other, resulting in the vastly smaller $\hat{N}_{area}$ of 7.3. In contrast, AKDEc's CIs were appropriately large when few range crossing events were observed, and narrowed only as $\hat{N}_{area}$ increased. Unfortunately, ecologists have been conditioned by severely biased methods to expect a home range estimate that tightly conforms to the tracking data, with high confidence, even when the amount of data is insufficient to produce an accurate range estimate with conventional estimators.

### *Capturing future space use*

Unlike occurrence estimation, which attempts to answer the question 'where did the animal go during the study period?' (e.g., Fleming et al. 2016), home range estimation is an attempt at predicting the area that an

individual is likely to use over its lifetime, though excluding dispersal events and range shifts (sensu Burt 1943, see also Powell 2000, Kie et al. 2010, Fleming et al. 2015a). Indeed, all proper home range estimators, whether conventional or autocorrelation-informed, attempt this kind of extrapolation. In this respect, our cross-validation study revealed that, when estimators fail to account for the autocorrelation structure present in animal movement data, the ability to capture future space use decays significantly, and especially so at low $\hat{N}_{area}$. For instance, when species with small ranges and/or short range crossing times were tracked for extended durations (i.e., $\hat{N}_{area}$ was high), KDEc and AKDEc resulted in nearly identical range estimates, and both methods provided good cross-validation at both the 95% and 50% quantiles. In contrast, when few range crossing events were observed, AKDEc estimates tended to be large, and often included areas not occupied by the animal during the study period, while KDEc still produced range estimates that tightly conformed to the data, with narrow CIs. Cross-validation, however, demonstrated that AKDEc's larger range estimates were appropriate, with previously vacant areas becoming occupied over time (e.g., Fig. 4), whereas KDEc estimates regularly failed to capture future space use (see also Fleming et al. 2015a). Importantly, the median number of subsequent locations included in AKDEc 95% (or 50%) area estimates was 95.3% (or 50.1%), highlighting that AKDEc's improved cross-validation was not a factor of range estimates simply being overly large such that they inevitably captured all future space use, but rather because AKDEc was appropriately selective at the specified quantile. AKDEc's improved cross-validation was also consistent across all the data sets we examined. This included species with a wide range of life history strategies and movement processes, as well as including both volant and cursorial species. Consistency across such a broad range of taxa confirmed the versatility of AKDEc (Fleming et al. 2014b, 2015a).

### Implications for ecology and conservation

Home range estimation is a routine analysis across the fields of movement ecology and animal conservation, with most estimates being based off of conventional MCP and KDE methods (Laver and Kelly 2008). With this in mind, we analyzed a broad taxonomic, and geographic range of tracking data that are likely to be representative of the forms of animal tracking data most ecologists are collecting (Tomkiewicz et al. 2010, Kays et al. 2015). Worryingly, we found that conventional KDEc, Srt-KDE, and MCP estimates were, on average, smaller than AKDEc's estimates by a factor of $\sim 2$, and by a factor of $\sim 13$ for lscv-KDE and $k$-LoCoH. This suggests that many published estimates may be significantly underestimating animal space requirements, particularly those based on modern GPS data with high-frequency sampling.

Researchers regularly make recommendations on park/reserve size based on the results of conventional home range analysis (Kramer and Chapman 1999, Linnell et al. 2001, Rechetelo et al. 2016) as a means of mitigating the negative impact of habitat loss and fragmentation on biodiversity (Wilcove et al. 1998, Fahrig 2003, Venter et al. 2006, Monastersky 2014). If management decisions were to be informed by conventional estimates, the severe negative bias in these would likely result in less effective initiatives (e.g., Brashares et al. 2001). Human wildlife conflict also presents a serious challenge for wildlife management, which is particularly acute for large carnivores living on, or near, park boundaries (Brashares et al. 2001, Macdonald 2016, Van Eeden et al. 2017). Under these circumstances, the translocation of problem animals is often used as a management tool (Linnell et al. 1997, Dickman 2010). Related to this, we found that because of the negative bias in conventional KDEc estimates, these home ranges regularly failed to capture future patterns of space use, for example, the 95% KDEc home range of a black bear (*Ursus americanus*) presented in Fig. 4 captured only 50% of that individual's future locations. Again, if home range analysis is the basis of identifying problem animals (e.g., Bauer and Iongh 2005), and used as a guideline for removal distance of these individuals, the negative bias of conventional methods may result in ineffective management operations in general. Although the importance of accurate area estimates for the scenarios detailed above is clear, these represent only a subset of common home range applications (e.g., Boyce 1992, Powell 2000, Jetz 2004).

### Conclusions

In summary, using an extensive empirical data set and carefully tailored simulations, we provide clear evidence that autocorrelation is not a red herring (Fieberg 2007, Kie et al. 2010), and ignoring it can produce severely negatively biased range estimates, with deceivingly narrow confidence intervals, resulting in erroneous conclusions. The high degree of autocorrelation in most modern animal tracking data sets (Fig. 1) strongly violates the key assumption of independence required for conventional home range estimators to generate accurate estimates. Furthermore, the amount of autocorrelation in tracking data sets will only continue to increase as technological advances facilitate ever-finer sampling of movement paths (Kays et al. 2015). In contrast, accounting for autocorrelation during the home range estimation process, results in reliably accurate home range estimates that will not merely cover past occurrences, but adequately capture future space use, assuming the movement process doesn't change. While the requirement of similar movement behavior may sound overly restrictive, we found that an average of $\sim 90\%$ of the individuals from each study satisfied this assumption. Crucially, in the frequently-encountered scenario of small $\hat{N}_{area}$, AKDEc was the only method capable of producing a relatively unbiased home range estimate on autocorrelated data. Based on these findings, we suggest use of AKDEc for home range

estimation, particularly for cases where $\hat{N}_{area} \ll n$. We also suggest that when designing a tracking study aimed at quantifying an individual's home range, the focus should be on maximizing the effective sample size (Fleming and Calabrese 2017). This can be achieved by tailoring the study design such that the duration of data collection is $\gg$ than the average range crossing time.

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DATA AVAILABILITY

Tracking data on *Aepyceros melampus*, *Beatragus hunteri*, *Bycanistes bucinator*, *Cerdocyon thous*, *Eulemur rufifrons*, *Glyptemys insculpta*, *Gyps coprotheres*, *Madoqua guentheri*, *Ovis canadensis*, *Propithecus verreauxi*, *Sus scrofa*, and *Ursus arctos* are publicly archived in the Dryad repository (Noonan et al. 2018; https://doi.org/10.5061/dryad.v5051j2), as are data from *Procapra gutturosa* (Fleming et al. 2014a; https://doi.org/10.5061/dryad.45157). Data on *Panthera onca* were taken from (Morato et al. 2018). Additional data are publicly archived in the Movebank repository under the following identifiers: *Canis latrans*, 8159699; *Canis lupus*, 8159399; *Chrysocyon brachyurus*, 18156143; *Felis silvestris*, 40386102; *Gyps africanus*, 2919708; *Lepus europaeus*, 25727477; *Martes pennanti*, 2964494; *Panthera leo*, 220229; *Papio cynocephalus*, 222027; *Syncerus caffer*, 1764627; *Tapirus terrestris*, 443607536; *Torgos tracheliotus*, 2919708; and *Ursus americanus*, 8170674. The R code necessary to reproduce the analyses are provided in the appendix material.