

REVIEW

Autocorrelation-informed home range estimation: A review and practical guide

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Abstract

1. Modern tracking devices allow for the collection of high-volume animal tracking data at improved sampling rates over very-high-frequency radiotelemetry. Home range estimation is a key output from these tracking datasets, but the inherent properties of animal movement can lead traditional statistical methods to under- or overestimate home range areas.
2. The autocorrelated kernel density estimation (AKDE) family of estimators was designed to be statistically efficient while explicitly dealing with the complexities of modern movement data: autocorrelation, small sample sizes and missing or irregularly sampled data. Although each of these estimators has been described in separate technical papers, here we review how these estimators work and provide a user-friendly guide on how they may be combined to reduce multiple biases simultaneously.
3. We describe the magnitude of the improvements offered by these estimators and their impact on home range area estimates, using both empirical case studies and simulations, contrasting their computational costs.
4. Finally, we provide guidelines for researchers to choose among alternative estimators and an R script to facilitate the application and interpretation of AKDE home range estimates.

KEYWORDS

home range, kernel density estimation, movement process, telemetry, tracking data

1 | INTRODUCTION

An animal's *home range* was first defined in Burt (1943) as 'the area traversed by the individual in its normal activities of food gathering,

mating, and caring for young'. Although this definition does not provide a mathematical description or statistical method for estimation, it highlights how behaviour drives animal movement: areas selected by individual animals are usually distinct from the larger

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areas an animal could explore given their movement abilities. Early translations into a statistical definition include quantifying an animal's probability of using a given location (i.e. utilization distribution; Jennrich & Turner, 1969; Worton, 1989). The concept of *home range* has been redefined by many authors over the years (Harris et al., 1990); here, we follow the definition of *home range* as the area repeatedly used throughout an animal's lifetime for all its normal behaviours and activities, excluding occasional exploratory excursions outside of home range boundaries. The characteristic temporal stability of a home range also highlights additional concepts: *range residency*, defined as the tendency of an animal to remain within its home range; and time-scale parameters that quantify the weakness of this tendency, including the *home range crossing time-scale* (τ), defined as the average time required for an animal to cross the linear extent of its home range.

Home range area estimates are used to inform conservation practitioners and wildlife managers about protected area sizes and to advocate for conservation policy changes (Bartoń et al., 2019; Lambertucci et al., 2014; Linnell et al., 1997). It is thus crucial to provide a reliable and statistically robust metric that is comparable across individuals, species and sites. Natural landscapes are becoming increasingly fragmented (Curtis et al., 2018; Hansen et al., 2020), imposing new challenges at local, regional and global scales, and unreliable estimations may hinder area-based conservation. Reliable estimates of home ranges, however, have proven to be deceptively difficult to achieve, and have occupied generations of ecologists (Fieberg & Börger, 2012; Horne et al., 2020; Jennrich & Turner, 1969; Worton, 1989). The inherent properties of animal tracking data create unique analytical challenges. Specifically, animal movement data frequently feature some combination of autocorrelation, small sample sizes, missing observations or irregular sampling, and home range estimators that are not designed to handle these issues can both under- and overestimate the sizes of home ranges.

Although many home range estimators exist (Horne et al., 2020), autocorrelated kernel density estimation (AKDE) was the first to explicitly account for temporal autocorrelation in the data (Fleming et al., 2015). Since its introduction, AKDE has grown into a family of related techniques, each aimed at mitigating a different source of bias that can affect home range estimates, including *unmodelled autocorrelation* (Hemson et al., 2005; Kie et al., 2010; Swihart & Slade, 1997), *oversmoothing* (Seaman & Powell, 1996; Worton, 1995), *autocorrelation estimation bias* (Cressie, 2015) and *unrepresentative sampling in time* (Frair et al., 2004; Horne, Garton, & Sager-Fradkin, et al., 2007; Katajisto & Moilanen, 2006). These biases are mitigated, respectively, by the original AKDE (Fleming et al., 2015), the area-corrected AKDE (Fleming & Calabrese, 2017), the perturbative hybrid residual maximum likelihood (REML) parameter estimation and parametric bootstrapping (Fleming et al., 2019) and weighted AKDE (Fleming et al., 2018). REML is a form of maximum likelihood estimation that reduces biases in variance/covariance estimation. AKDE and associated corrections have been shown to outperform traditional home range estimators across species, degrees of autocorrelation and sample size (Noonan et al., 2019). The `ctmm` workflow

also allows researchers to partially account for the location errors associated with their tracking datasets (Fleming et al., 2021). These methods can be run using the programming language R (www.r-project.org) and the `ctmm` or `amt` packages (Calabrese et al., 2016; Signer & Fieberg, 2021), or the `ctmmweb` graphical user interface (<https://ctmm.shinyapps.io/ctmmweb>; Calabrese et al., 2021). In addition to offering flexible and open-source tools for home range estimation, these software programs allow easy documentation and implementation of new methods by sharing code and workflows. Such reproducible methods can increase reliability and transparency in ecology (Alston & Rick, 2021; Culina et al., 2020; Powers & Hampton, 2019; Signer & Fieberg, 2021).

Because movement data often violate multiple assumptions of traditional methods, the individual methodological advances offered by the AKDE family of home range estimators can and often should be combined. The costs and benefits of each estimator have previously been described in separate technical papers, so in this paper, we bring all of these estimation methods together in one document. We describe their effects on the quality of home range estimates, both in isolation and in combination, while evaluating how sample size interacts with multiple different sources of bias. We use tracking data from African buffalo (*Syncerus caffer*; Cross et al., 2009), lowland tapir (*Tapirus terrestris*; Fleming et al., 2019) and jaguar (*Panthera onca*; Morato et al., 2018) as empirical case studies to guide researchers through the application and value of these analyses. Finally, we use simulations to show the improvements offered by combining these techniques and demonstrate their application in real-world problems. We conclude by giving clear guidance on how ecologists can choose among these alternatives to best achieve their study goals. We hope that this review provides a practical guide to *why* and *how* to use AKDE methods to estimate home ranges that will be useful for both researchers and practitioners who are unfamiliar with these methods.

2 | SOURCES OF BIAS AND MITIGATION MEASURES

Many biases, including most that affect home range estimates, are exacerbated by small sample sizes. Conversely, large sample sizes in modern tracking datasets are typically achieved through higher sampling frequencies, which exacerbate autocorrelation. Autocorrelation is a general statistical property of variables measured across geographic and temporal space (Dale & Fortin, 2002; Legendre, 1993), as observations sampled more closely in space or time tend to be more similar. In these conditions, it is thus important to distinguish between two different measures of sample size: *absolute sample size* (n) and *effective sample size* (N). *Absolute sample size* is simply the total number of observations in a dataset. More relevant for home range estimation, however, is the *effective sample size*. Specifically, the amount of information available to home range estimators is governed not simply by the total number of observations, but by the number of *range crossings* that

occurred during the observation period (i.e. how many times an animal traversed the linear extent of its home range). The *effective sample size* can be roughly estimated as T/τ , where T is the temporal duration of the tracking dataset, and τ is the average *home range crossing time parameter*. Increasing sampling frequency leads to larger *absolute sample sizes*, but does not increase the *effective sample size* commensurately. For autocorrelated data, the *effective sample size* is necessarily smaller than the *absolute sample size* and, very frequently in practice, orders of magnitude smaller (Fleming et al., 2019). In contrast, small *absolute sample sizes* commonly occur in very-high-frequency (VHF) tracking data but are becoming rarer in modern GPS tracking data.

We now describe each source of bias and the mitigation measure available to correct it, highlighting the difference each correction makes with real data from multiple case studies. We present the bias sources in order of their general importance, from the largest bias to the smallest. Note that this ranking refers to the typical magnitude of each type of bias, but the order may be different under some conditions.

3 | BIAS I: UNMODELLED AUTOCORRELATION

Traditional home range estimators such as minimum convex polygons (MCPs) and kernel density estimators (KDEs) assume *independently and identically distributed* (IID) data. When these techniques came into common use in the 1980s, the sheer difficulty of obtaining VHF location fixes ensured that the time interval between successive observations was typically long enough for most of the autocorrelation among observations to have decayed (Swihart & Slade, 1997; Worton, 1989). The IID assumption at the heart of these techniques was therefore usually satisfied by VHF-quality data (Harris et al., 1990). The situation began to change with the arrival of new technologies, most notably GPS tracking systems (Rempel et al., 1995), which now routinely feature large volumes of data with much more frequent temporal sampling than is feasible for VHF-based animal tracking. As autocorrelation arises from observations sampled closely in time also being located closely in space, increasing sampling frequencies inevitably leads to more strongly autocorrelated tracking data (De Solla et al., 1999). Automated, high-sampling frequency tracking data have undoubtedly revolutionized movement ecology (Kays et al., 2015), but these advances have broken the armistice between the statistical assumptions of traditional home range estimators and the reality of the datasets now used to study animal movement (Boyce et al., 2010).

Specifically, feeding autocorrelated data into a home range estimator based on the IID assumption yields negatively biased estimates (Noonan et al., 2019). Autocorrelation-induced underestimation of home range areas is particularly pronounced when the *effective sample size* is small. In the recent comparative study of Noonan et al. (2019), 368 of 369 tracking datasets featured strong autocorrelation, and roughly half were also plagued by small *effective*

sample size. In these conditions, conventional estimators—such as MCPs, KDEs and local convex hull polygons—underestimate home range areas by a factor of ~2 to 13 (on average), depending on the method and bandwidth optimizer, which is what determines how tightly KDEs conform to the data. Accordingly, published estimates featuring these traditional methods may severely underestimate animal space-use requirements, hindering conservation and management decisions.

4 | MITIGATION MEASURE I: AKDE

Fortunately, it is not autocorrelation per se that causes errors in home range estimation, but rather autocorrelation that is statistically ‘unmodelled’ (Calabrese et al., 2021). Home range estimators that account for autocorrelation can therefore avoid the biases and violated assumptions of traditional methods. Autocorrelated kernel density estimation (AKDE) explicitly requires a movement model that accounts for the autocorrelation in the tracking data (Figure 1) and then estimates the home range while conditioned on the same movement model (Fleming et al., 2015). This model is identified via formal model selection among a range of plausible alternatives, currently spanning from uncorrelated data (IID), correlated positions but uncorrelated velocities (Ornstein–Uhlenbeck or OU; Uhlenbeck & Ornstein, 1930), to correlated positions and correlated velocities (Ornstein–Uhlenbeck foraging process or OUF; Fleming et al., 2014). In this framework, IID is both a candidate model and one limit of a continuum of possibilities, rather than an a priori assumption. These models are ranked based on Akaike’s information criterion adjusted for small sample sizes (AICc) by default, although the `ctmm` package also offers AIC, Bayesian information criterion (BIC), leave-one-out cross-validation (LOOCV) and half-sample cross-validation (HSCV).

Ad hoc measures such as data thinning (Harris et al., 1990; Rooney et al., 1998) are not necessary, as AKDE allows model assumptions to conform as closely as possible to empirical reality, instead of coercing the data to fit a model with unrealistic assumptions. Feeding IID data into AKDE will not have any adverse effects, as it will simply result in a conventional KDE estimate. This workflow also allows reliable confidence intervals to be determined for home range area estimates, which historically have not been applied to home range estimates. This measure of confidence is fundamental for any statistical estimate (Pawitan, 2001), increasing the comparability of AKDE and its relevance for biogeographical and conservation applications.

5 | BIAS II: OVERSMOOTHING

Kernel density estimators are best-in-class tools for estimating unknown probability distributions and are used in this capacity across the sciences (Chen, 2017; Silverman, 1986; Wang et al., 2013). In the context of tracking data, KDEs estimate the probability distribution of locations, which is then used to estimate the area of a home range

FIGURE 1 An example of autocorrelated data (individual six from the African buffalo dataset, available within the `ctmm` package), and the same data when it achieves independence (IID) after data thinning (from one fix per hour to one fix per week). We calculated the 95% contour of an autocorrelated kernel density estimation (AKDE) and a Gaussian reference function KDE (GRF-KDE). Displayed errors correspond to % bias of full dataset KDE and subset KDE against full dataset AKDE. N : effective sample size, n : absolute sample size

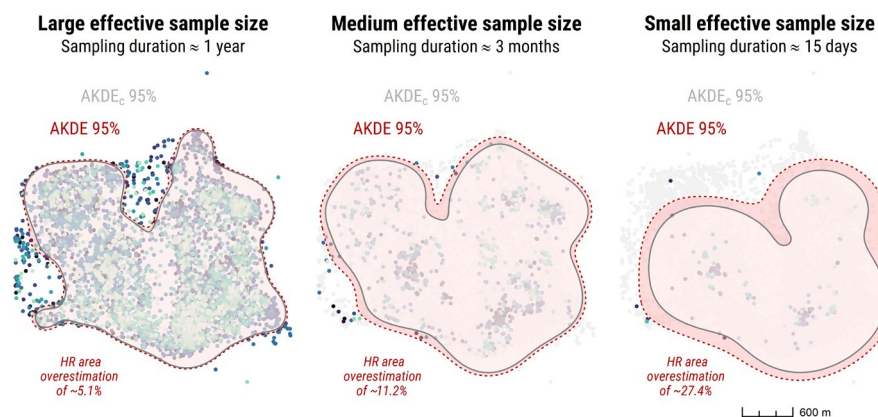
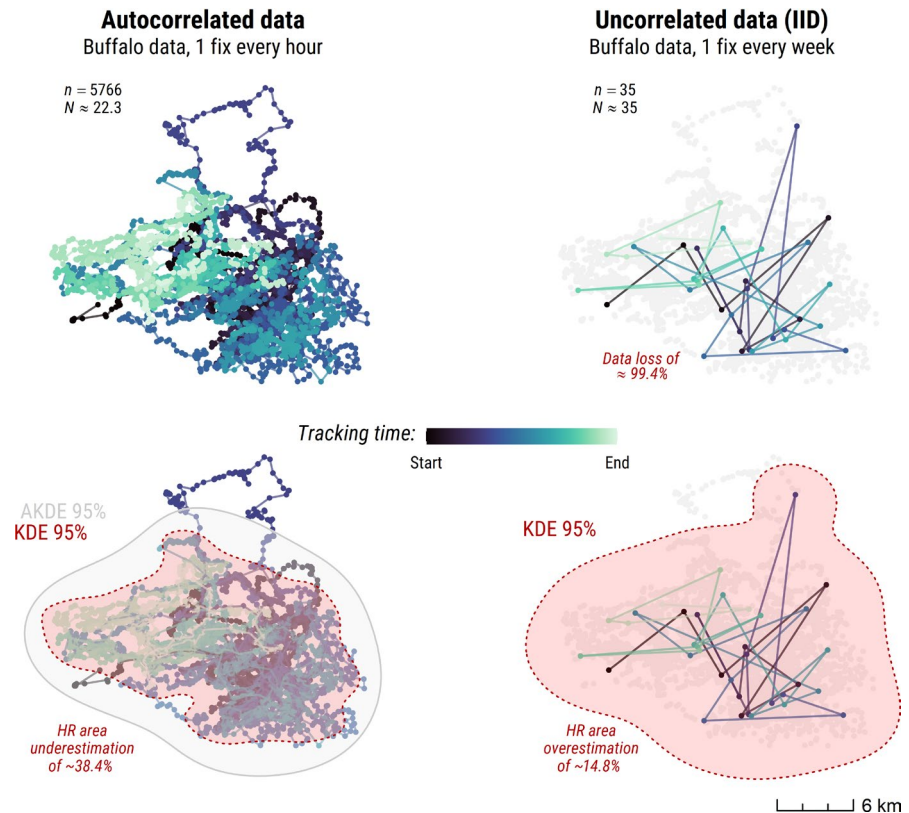


FIGURE 2 Autocorrelated kernel density estimation (AKDE) and area-corrected AKDE ($AKDE_c$) calculated for one individual from the lowland tapir tracking dataset with: large effective sample size ($N \approx 1,566$), medium effective sample size ($N \approx 261$) and small effective sample size ($N \approx 30$). Displayed errors correspond to % bias of AKDE against $AKDE_c$ of the same individual. Note that for large N values the estimates from AKDE and $AKDE_c$ overlap considerably

(Powell, 2000; Worton, 1989). Typically, ecologists are more interested in this area estimate than in the distribution itself.

Even when we account for autocorrelation (AKDE), kernel density estimators based on the Gaussian reference function (GRF) remain biased owing to the natural tendency of the GRF approximation to oversmooth (yielding a more spread-out distribution). This bias is estimator specific, and may be either positive or negative (Kie et al., 2010; Worton, 1995): for GRF-KDEs—such as AKDE and h_{ref} (Silverman, 1986)—this bias is positive and, all else being equal, leads to an overestimated home range (Seaman & Powell, 1996). Importantly, for estimators that do not account for autocorrelation, like h_{ref} but unlike AKDE, this positive bias can be masked by the often stronger negative bias caused by unmodelled autocorrelation. For KDEs based on least-squares cross-validation, h_{LSCV} , this bias is typically

negative (Blundell et al., 2001; Hemson et al., 2005) and exacerbates the autocorrelation-induced underestimation of home range areas.

6 | MITIGATION MEASURE II: KDE_c or $AKDE_c$

Fleming and Calabrese (2017) derived an improved KDE by calculating the bias in area estimation under a GRF approximation and applying a correction in an area-based coordinate system. By pulling the contours of the location distribution estimate inward towards the data without distorting its shape, this correction removes the tendency of GRF-based methods (including AKDE) to overestimate the area of home ranges, particularly at small effective sample sizes

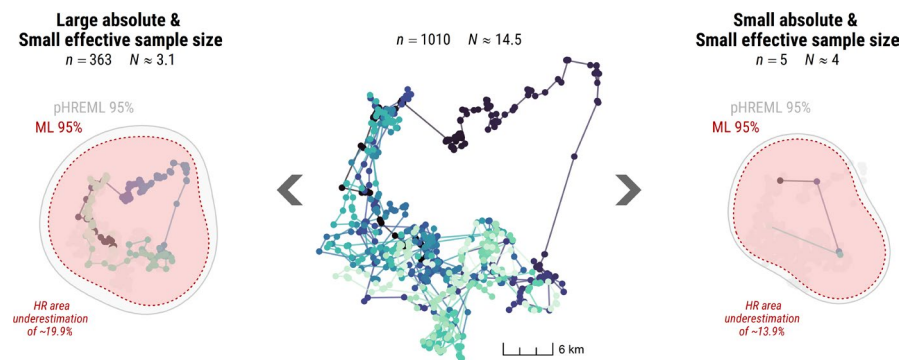


FIGURE 3 AKDE_c calculated with maximum likelihood (ML) and with perturbative Hybrid REML (pHREML) for an individual within the jaguar dataset, showcasing its effect on large *absolute* but small *effective sample size* (reduce to a sampling duration of 3 months: $n = 363$ locations, $N \approx 3.1$), and both *small absolute* and *small effective sample size* (3 months thinned to $n = 5$ locations, $N \approx 4$). Displayed errors correspond to % bias of ML-fitted AKDE against pHREML-fitted AKDE

(Figure 2). Formally correcting the density function estimate allows us to calculate a more reliable home range area and confidence intervals. This correction can be applied to both conventional and autocorrelated GRF-KDEs (then termed KDE_c and AKDE_c respectively), and is the default method within the `ctmm` package. As this source of bias is estimator specific, the mitigation must also be estimator specific, so this correction cannot be applied to non-GRF KDE approaches such as h_{LSCV} .

7 | BIAS III: AUTOCORRELATION ESTIMATION BIAS

The main advantage of AKDE is that it accounts for the autocorrelated structure of animal movement data; for optimal performance, we need to estimate this autocorrelation correctly. Maximum likelihood (ML) estimation is the standard approach to fitting movement models to animal tracking data (Horne Garton, Krone, et al., 2007; Michelot et al., 2016) due to its versatility, widespread use and relatively good performance (Pawitan, 2001). However, ML performs best at large sample sizes, while parameters related to variances and covariances tend to be underestimated in small sample size conditions (Cressie, 2015). As variance-associated parameters are closely related to home range size, their underestimation propagates into underestimated home range areas (Noonan et al., 2019).

8 | MITIGATION MEASURE III: pHREML AND PARAMETRIC BOOTSTRAPPING

Residual ML estimation is often used to improve (co)variance parameter estimation with small sample sizes, but it can perform poorly for the class of movement models on which AKDE depends (Fleming et al., 2019). To mitigate the small sample size bias in autocorrelation model parameter estimates, Fleming et al. (2019) developed a series of REML-based estimators that focus on small *effective sample sizes* (perturbative REML; pHREML), small *absolute sample sizes* (Hybrid REML; HREML), or both *small absolute* and *small effective sample sizes* (perturbative Hybrid REML; pHREML). We focus on pHREML here (Figure 3) as it is the most broadly applicable of these methods and has no serious disadvantages relative to the others, because it combines the bias

correction of REML and the stability of ML. It is currently the default parameter estimation method in the `ctmm` package.

The parametric bootstrap method (Efron, 1982) is another standard solution for the biases caused by ML estimation and can be applied on top of REML-based estimations to further reduce biases. In extreme cases where *effective sample sizes* are ~ 5 or less, parametric bootstrapping may result in substantial improvements. However, the high computational cost incurred by bootstrapped pHREML (Supporting Information File 1), coupled with the usually modest improvements it provides, reinforce its use only as a last resort.

9 | BIAS IV: UNREPRESENTATIVE SAMPLING IN TIME

From a statistical perspective, evenly spaced temporal sampling of tracking data ensures the widest possible range of analytical options. In practice, however, many real-world issues can lead to animal locations being sampled irregularly in time: duty-cycling tags to avoid wasting battery during periods of inactivity, acceleration-informed sampling, device malfunction, habitat-related signal loss and many other causes (DeCesare et al., 2005; Frair et al., 2004; Horne, Garton, & Sager-Fradkin, et al., 2007). When unaccounted for, such cases can yield biased datasets, causing area estimates associated with over-sampled portions of home ranges to be too large and those associated with under-sampled parts of home ranges to be too small (Fieberg, 2007). There is no guarantee that these contrasting biases cancel each other out, so the overall home range area estimate may be either positively or negatively biased.

10 | MITIGATION MEASURE IV: wAKDE

Weighted AKDE (or wAKDE) corrects for unrepresentative sampling in time (Fleming et al., 2018) through the larger bias addressed is *where* the area is distributed: it optimally upweights observations that occur during under-sampled times, while optimally downweighting observations occurring during over-sampled times. In IID data, optimal weights are uniform (i.e. there is no temporal sampling bias, as all times are equally important) so there is no advantage to weighting. For autocorrelated data with highly irregular sampling, however, the difference between weighted and unweighted AKDE can be considerable (Figure 4).

In practice, very few tracking datasets are perfectly regular, so it is essential to handle data irregularity appropriately. Missing data equate to a loss of information, and these errors can propagate into biases in habitat selection or area-based conservation outputs (Frair et al., 2004). For example, areas with good satellite reception (e.g. open flat landscapes) may appear over-used even when animals did not spend more time in them compared to areas with poorer reception. Shifting sampling schedules (based on behavioural or seasonal patterns) is a common strategy employed in animal tracking projects, due to the trade-off between sampling intensity and battery life (Brown et al., 2012); in these circumstances, weight optimization via wAKDE is critical for comparisons between individuals or populations.

11 | COMBINATION OF MITIGATION MEASURES

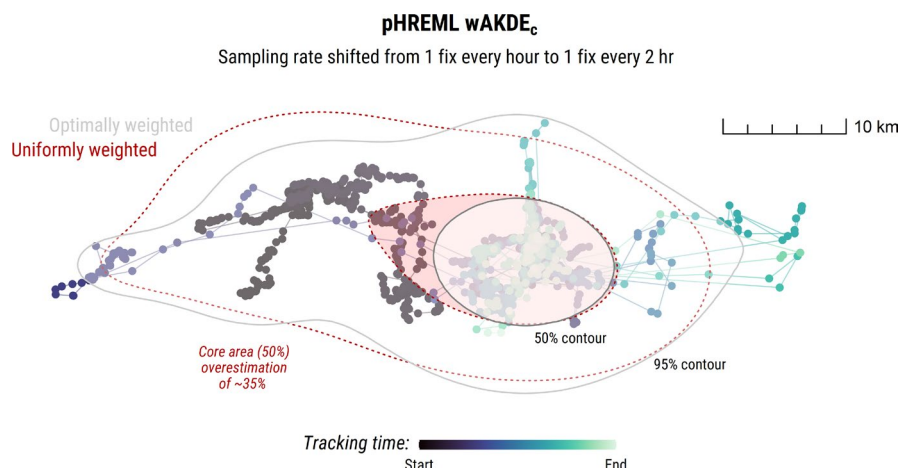
In practice, different sources of bias frequently occur together in the same datasets. This is a key reason why home ranges are so difficult to estimate accurately. However, the mitigation measures described above can be implemented simultaneously when necessary to combat multiple biases. For example, if a tracking dataset features autocorrelation, small *effective sample size* and irregular temporal sampling, we can use pHREML to estimate and select the underlying movement model, and then pass the selected model to an optimally weighted area-corrected AKDE (wAKDE_c) to properly estimate home range area. The default settings in the `ctmm` package have been carefully chosen to balance performance against computational cost, so in this example, only optimal weighting would need to be manually selected by the user. Default values and alternative options are discussed in more detail in the `ctmm` documentation (Fleming & Calabrese, 2021).

To quantify the level of improvement offered by each mitigation measure and to explore the trade-off between accuracy and computational cost, we performed a detailed simulation study. Our simulations are based on an OUF movement model, which features both correlated velocities (i.e. directional persistence), correlated positions and restricted space use. We chose the OUF model because it was the most frequently selected across all empirical GPS datasets in the

Noonan et al. (2019) study, with 240 of 369 datasets. We set both the directional persistence and range crossing time-scales to 1 day, and varied the duration of the simulated datasets from 1 to 4,096 days in a doubling series, sampled hourly (except for bootstrapped pHREML wAKDE_c which was significantly more computationally intensive and impractical to simulate over the whole sampling duration). This setup results in *effective sample sizes* that approximate the duration of each simulated dataset. We then sequentially fit home range estimators in the `ctmm` package to each simulated dataset in the following order: KDE, AKDE, AKDE_c, pHREML AKDE_c, pHREML wAKDE_c and bootstrapped pHREML wAKDE_c. This represents a progression from no bias corrections (KDE) through all possible bias corrections applied simultaneously, in order of the typical importance of the corrections. Each simulation was repeated 400 times. We calculated bias as the 95% area estimate of the method in question divided by the exact expectation value of the true 95% area (under the model from which the data were simulated), while the computational cost was the time the simulation took to complete in seconds. All simulations were performed in the R environment (version 3.5.2; R Core Team, 2018) using the `ctmm` package (version 0.5.2; Calabrese et al., 2016) and conducted on the University of Maryland High Performance Cluster.

Compared to conventional KDE, the original AKDE offered clear advantages for small *effective sample sizes*, but failed to improve area estimation for medium and large *effective sample sizes* ($N > 32$; Table 1). By solving the oversmoothing bias, AKDE_c improved over KDE for all effective sample sizes. The next technique, pHREML-fitted AKDE_c (`ctmm` default settings) further improved over conventional KDE and all previous measures, and stabilized the closest to 0% relative error after only eight sampling days (Figure 5a). Additional mitigation measures do lead to an increasingly higher computational cost: for the full sampling duration (4,096 days), pHREML-fitted wAKDE_c ran on average 2.7 times longer than the original AKDE, and 230 times longer than a conventional KDE (Figure 5b, Supporting Information File 1). With an Intel i7 3.9GHz processor using a single core, and an hourly tracking dataset collected for a year, this could correspond to an increase from a few seconds to approximately 45 min. However, unlike AKDE, conventional KDE does not run any autocorrelation model selection, or numerical optimization of parameter estimates.

FIGURE 4 A uniformly weighted AKDE_c and an optimally weighted AKDE_c (wAKDE_c), calculated from an individual from the African buffalo dataset with an irregular sampling schedule likely due to a device malfunction (nicknamed 'Pepper'; available within the `ctmm` package). Displayed errors correspond to % bias of AKDE_c core area (50%) against wAKDE_c core area (50%)



12 | DISCUSSION

The techniques presented in this paper represent a family of home range estimators starting with conventional GRF-KDE and progressing through a series of estimation methods designed to mitigate bias arising when the core assumption of IID data is not met.

TABLE 1 Mean improvement (%) in area estimation for each AKDE method compared to baseline KDE, over small ($N < 32$), medium ($32 > N < 512$) and large *effective sample sizes* ($N > 512$). Negative values denote underperformance

Methods	Improvement over KDE		
	Small N	Medium N	Large N
AKDE	51.3%	-31.3%	-78.4%
AKDE _c	42.6%	48.3%	36.4%
pHREML AKDE _c	59.8%	52.9%	40.4%
pHREML wAKDE _c	59.4%	52.9%	43.1%
Bootstrapped pHREML wAKDE _c	72.0%	NA	NA

These methods are implemented with efficient computational algorithms that work with both small and large animal tracking datasets. We have brought these techniques together in a single document to demonstrate when each correction is applicable, the degree to which home range estimates can be improved, and when and how they can be combined to handle the unique quirks of each tracking dataset to yield accurate home range estimates.

The AKDE family of estimators are all implemented in the `ctmm` R package (Calabrese et al., 2016), so we provide an annotated R script in the supplementary material of this paper to guide users through the applications of these techniques (Supporting Information File 2). The current default settings are pHREML, for estimating movement model parameters, and (A)KDE_c for estimating home ranges. The decision between KDE_c and AKDE_c is determined using model selection, and dependent on whether the data are independently distributed or autocorrelated respectively. We recommend that users keep pHREML and (A)KDE_c as the default settings and especially caution against changing these settings for any *effective sample sizes* below 20. When working with legacy data where small *effective sample sizes*

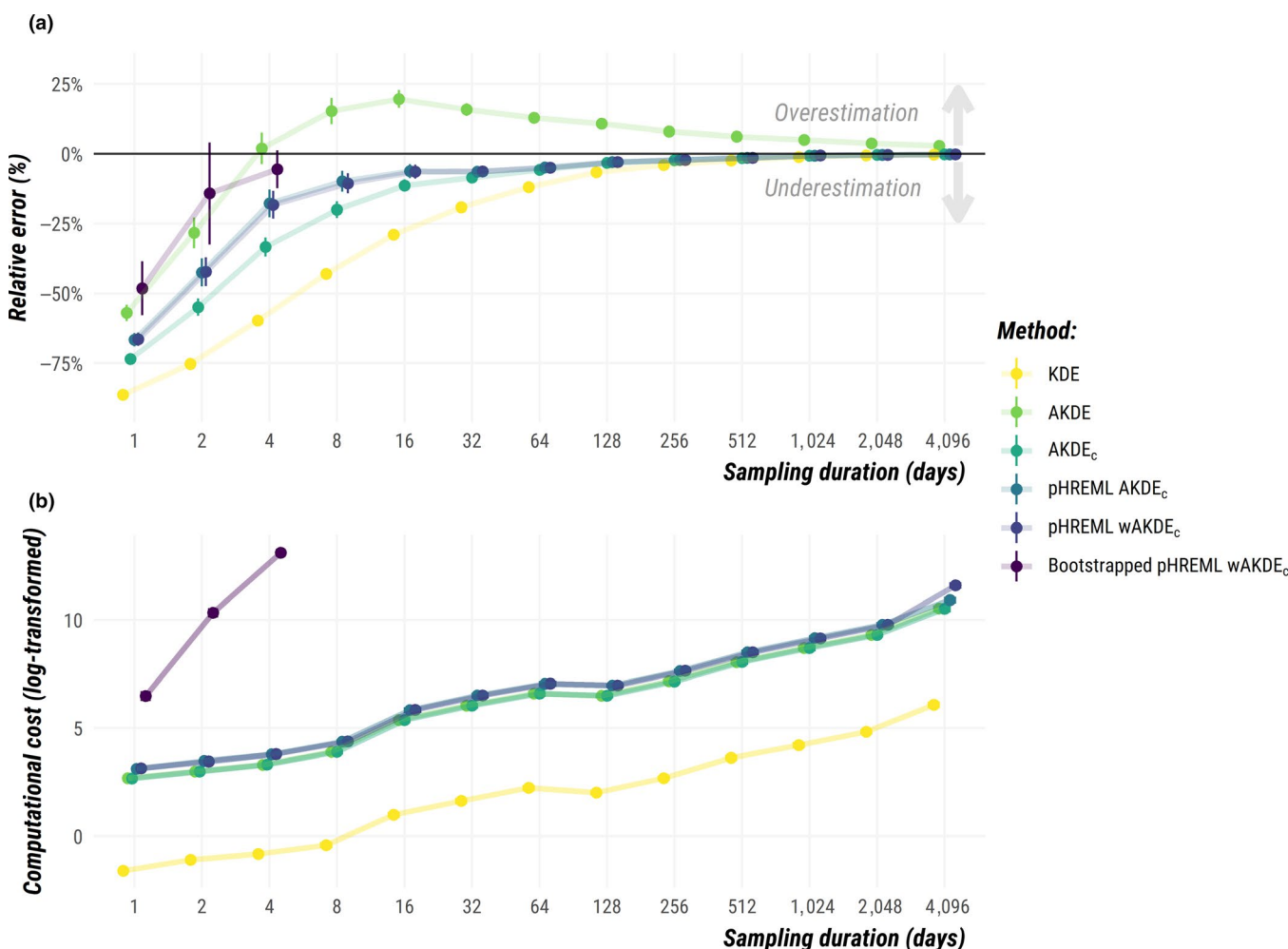


FIGURE 5 (a) Mean relative error (%) of the home range area estimation and (b) computational cost (log-transformed) for each method, by sampling duration (in days). Based on simulations (repeated 400 times) where the position and velocity autocorrelations were kept constant at 1 day and 1 hr respectively. Error bars represent 95% confidence intervals. AKDE and AKDE_c have almost overlapping performances, as well as pHREML-fitted AKDE_c and pHREML wAKDE_c

are a serious concern, but additional data collection is not an option, bootstrapped pHREML may be used as a method of last resort to obtain the best possible home range estimates. However, due to the high computational cost of using bootstrapped pHREML, users should decide on a bias threshold (typically >1%–5% with an initial pHREML estimate) before applying this measure (see Supporting Information File 2 for how to determine this bias threshold). Finally, wAKDE_c can account for temporal sampling bias (i.e. missing or irregular tracking data), but is switched off by default due to its considerable computational cost (approximately 200 times longer than KDE).

Most mitigation measures we have discussed here become increasingly valuable at small sample sizes (absolute and/or effective), allowing researchers to maximize the value of legacy datasets or to handle situations where larger *effective sample sizes* are impossible to obtain (e.g. on smaller animals for which battery size limits the temporal duration of GPS life spans). Nevertheless, the application of these analytical methods should not replace careful study design before data collection, tailored to address specific research questions (Fieberg & Börger, 2012). When the main goal of a study is home range estimation, the sampling duration should be many times larger than the average *range crossing time* of the focal species. This ensures that the *effective sample size* will be large enough to facilitate reliable estimation of the area of home ranges. Achieving this goal may require researchers to decrease the sampling rate of their devices to save battery power, although small *effective sample sizes* may be inevitable even in these conditions due to battery constraints, specific ranging behaviours or short life spans.

Although AKDEs provide reliable home range area estimations in the conditions presented in this manuscript, there are scenarios in which they fail. A known issue of KDE methods is that their estimates can spill over discontinuities, such as hard boundaries (e.g. coastal lines and water sources for terrestrial species, land for aquatic species) or three-dimensional features (e.g. steep terrain, impermeable barriers), and have difficulties resolving narrow movement corridors (Guo et al., 2019; Péron, 2019; Silverman, 1986; Worton, 1995). The positive bias from boundary spillover is likely less influential than the negative bias due to unmodelled autocorrelation; nevertheless, it is possible to correct for hard boundaries by following the workflow presented in appendix 3 of Noonan et al. (2019). Kernel density methods also fail to adequately resolve non-stationary behaviour and nomadism (Lichti & Swihart, 2011; Nandintsetseg et al., 2019), as nomadic species lack site fidelity to movement pathways or key sites (e.g. breeding or wintering areas). Addressing non-stationarity requires home range estimates that accommodate multiple centres and allow for variation in use patterns (Breed et al., 2017). In addition, a misspecified model due to migratory behaviours will affect the accuracy of AKDE area outputs due to the stationary movement models being leveraged (OU, OUF and IID). However, if an animal is not range resident, then the data are not appropriate for any home range estimation method.

Moving forward, we hope to address two remaining challenges in home range estimation: location error and resource selection

(which includes boundary interactions). Home range estimation is not as sensitive to location error as fine-scale quantities, such as speed estimation (Noonan et al., 2019). However, any biological inferences can become compromised if location errors are comparable to the relevant movement scales. At present, location errors can be partially accounted for in the autocorrelation modelling stage of the `ctmm` workflow (Fleming et al., 2021). First, the autocorrelation and bandwidth calculations are error-informed, which mitigates various biases in autocorrelation and bandwidth estimates that would otherwise occur had location error been ignored. Second, location estimates are fed through a Kalman smoother before kernel placement, which counteracts overdispersal. However, there are two adjustments that could provide further improvements. First, more erroneous location estimates could be optimally downweighted in the sense of Fleming et al. (2018), which would increase statistical efficiency. Second, instead of employing a Kalman smoother that is only consistent with normal distributions, the data could be nonlinearly smoothed via iteration. Finally, the inclusion of resource selection parameters into KDE has been considered by Guo et al. (2019) and Péron (2019). Resource selection can include the respecting of hard boundaries, as well as softer habitat preferences. The influence of resource selection on AKDE can be considered at various stages, including autocorrelation modelling, bandwidth optimization and kernel shape, and will likely take multiple research efforts to fully implement in a general use software solution.

Only by estimating home ranges in a comparable way across sampling schedules, study designs and behavioural idiosyncrasies can wildlife researchers provide wildlife managers and practitioners with accurate information for conservation planning and land-use decision-making. Movement ecology has reached an inflection point where it is no longer possible to ignore autocorrelation: using autocorrelated tracking datasets with estimators that assume IID data will result in underestimated home range areas (Noonan et al., 2019). Although further technological advances will only increase the amount of autocorrelation present in tracking data, autocorrelation is often still present even in VHF data and should not be overlooked. We have provided guidelines to obtain accurate home range area estimates with the AKDE family of home range estimators which, in their current form, provide the most reliable and flexible solution for home range area estimation. These methods were explicitly designed to work synergistically, eliminating discrepancies between empirical reality and estimator assumptions that drive home range under- or overestimation with conventional techniques. Furthermore, these techniques can be implemented with open-source software and code (Calabrese et al., 2016, 2021), and new movement processes can be easily added into the AKDE workflow as they are developed. This flexibility ‘future proofs’ the AKDE family of analyses by allowing it to be tailored to new datasets, movement behaviours and species as necessary.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

C.H.F., M.J.N., W.F.F. and J.M.C. conceived the ideas; C.F. and I.S. conducted the simulations; I.S. led the analyses for the empirical examples and the data visualization; J.M.C. and I.S. led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All empirical datasets used in the manuscript are currently openly accessible: the African buffalo tracking data are archived in the MoveBank Data Repository (Cross et al., 2016) and partially included in the `ctmm` package (Fleming & Calabrese, 2021); lowland tapir tracking data are archived in the Dryad Digital Repository (Fleming et al., 2019); jaguar tracking data are available as a data paper (Morato et al., 2018) and partially included in the `ctmm` package (Fleming & Calabrese, 2021). R scripts, tutorials and outputs are available on GitHub (https://github.com/ecoisilva/AKDE_minirview) and archived on Zenodo (Silva et al., 2021).

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