

## Effects of body size on estimation of mammalian area requirements

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## **Abstract**

Accurately quantifying species' area requirements is a prerequisite for effective area-based conservation. This typically involves collecting tracking data on species of interest and then conducting home-range analyses. Problematically, autocorrelation in tracking data can result in space needs being severely underestimated. Based on previous work, we hypothesized the magnitude of underestimation varies with body mass, a relationship that could have serious conservation implications. To evaluate this hypothesis for terrestrial mammals, we estimated home-range areas with GPS locations from 757 individuals across 61 globally distributed mammalian species with body masses ranging from 0.4 to 4,000 kg. We then applied block cross-validation to quantify bias in empirical home-range estimates. Area requirements of mammals <10 kg were underestimated by a mean ~15%, and species weighing ~100 kg were underestimated by ~50% on average. Thus, we found area estimation was subject to autocorrelation-induced bias that was worse for large species. Combined with the fact that extinction risk increases as body mass increases, the allometric scaling of bias we observed suggests the most threatened species are also likely to be those with the least accurate home-range estimates. As a correction, we tested whether data thinning or autocorrelation-informed home-range estimation minimized the scaling effect of autocorrelation on area estimates. Data thinning required a ~93% data loss to achieve statistical independence with 95% confidence and was therefore not a viable solution. In contrast, autocorrelation-informed home-range estimation resulted in consistently accurate estimates irrespective of mass. When relating body mass to home range size, we detected that correcting for autocorrelation resulted in a scaling exponent significantly >1, meaning the scaling of the relationship changed substantially at the upper end of the mass spectrum.

## Introduction

Globally, human-altered landscapes are restricting animal movement (Fahrig 2007; Tucker et al. 2018), and habitat loss and fragmentation are the principal threats to terrestrial biodiversity (Brooks et al., 2002; Wilson et al., 2016). A key component to conserving species in increasingly human-dominated landscapes is understanding how much space is required to maintain stable, interconnected populations (Brashares et al., 2001; Pe'er et al., 2014). Area requirements are typically quantified via home-range analysis (Burt, 1943). This routinely involves collecting tracking data on species of interest (Kays et al., 2015) and then applying a home-range estimator to these data (Fleming et al., 2015; Noonan et al., 2019). These range estimates can then be used to inform recommendations on reserve sizes (Linnell et al., 2001), to advocate for specific land-tenure systems (Johansson et al., 2016; Farhadinia et al., 2018), and to make conservation policy recommendations (Bartoń et al., 2019). However, tracking data are often strongly autocorrelated, whereas conventional home-range estimators are based on the assumption of independent and identically distributed data (Noonan et al., 2019).

When data are autocorrelated, the total number of data points does not reflect the total amount of information in the data set (i.e., effective sample size) (Fleming & Calabrese, 2017). Although the idea that autocorrelation may affect home-range estimates is not new (e.g., Swihart & Slade, 1985; Fieberg, 2007; Fleming et al., 2015), only recent analyses have demonstrated the seriousness of the problem. Using the largest empirical tracking data set assembled to date, Noonan et al. (2019) found conventional estimators significantly negatively biased when used on autocorrelated data. While any form of bias is undesirable, the systematic underestimation of home-range areas is a worst-case scenario from a conservation perspective. Any policy or management

decisions informed by underestimated home-range estimates could result in failed conservation initiatives (Brashares et al., 2001; Gaston et al., 2008) or exacerbate negative human-wildlife interactions at reserve boundaries (Van Eeden et al., 2018).

Noonan et al. (2019) noticed that large-bodied species tended to exhibit more negatively biased conventional home-range estimates than small-bodied species. However, the species included in their study were not selected to provide the broad range of body masses required to investigate allometric trends. We compiled an extensive empirical data set of GPS locations from 757 individuals across 61 terrestrial mammalian species with body masses ranging from 0.4 to 4,000 kg. We used these data to investigate whether the underestimation of home-range size scales with body mass. To see the potential for this, consider that large species have large home ranges (Jetz et al., 2004) that tend to take longer to cross than smaller home ranges (Calder, 1983). In addition, range crossing time ( $\tau_p$ ) interacts with the sampling interval ( $dt$ ) in determining the amount of autocorrelation in tracking data (Fleming & Calabrese, 2017; Noonan et al., 2019). When  $dt \lesssim \tau_p$ , the resulting data are autocorrelated, while  $dt \gg \tau_p$  results in effectively independent data. Finally, the magnitude of the negative biases in conventional home-range estimates increases in proportion to the strength of autocorrelation in the data (Noonan et al., 2019). Combining these facts, we arrived at the hypothesis that an allometry in  $\tau_p$  drives autocorrelation and negative estimation bias to scale with body size.

We examined this hypothesis in two ways. First, we tested whether the chain of relationships that would drive bias to scale with mass holds for empirical tracking data. Second, we explored how well 2 methods of home-range estimation for autocorrelated data eliminate the scaling of home-range estimation bias. These methods were model-informed data thinning, which removes autocorrelation from the data prior to home-

range estimation, and autocorrelation-informed home-range estimation, which statistically accounts for autocorrelation in movement data. We then used model selection to determine whether significant allometry bias remains in the data for each approach and identified whether one of these corrections offers improved performance over the other. Finally, in light of our findings, we revisited the concept of home-range allometry (e.g., McNab, 1963; Jetz et al., 2004; Tucker et al., 2014). Mammalian home-range area ( $H$ ) scales positively with body mass ( $M$ ) as  $H = B_0M^b$ , where  $B_0$  is a normalization constant and  $b$  the scaling exponent (McNab, 1963). Despite decades of research, however, there has been little consensus on whether the allometry is linear (i.e.,  $M^1$ ), or superlinear (i.e.,  $M^{>1}$ ). Historically, this scaling relationship has been calculated by compiling home-range areas estimated via conventional estimators, which are subject to varying levels of autocorrelation-induced bias (Noonan et al., 2019), whereas no one has assessed this relationship directly from tracking data. While consistent bias across the mass spectrum would lead only to a change in the normalization constant, differential bias across the mass spectrum could alter the scaling exponent, fundamentally changing the properties of the relationship. As such, we tested for any significant deviations from linear ( $M^1$ ) scaling.

## **Methods**

All analyses were based on precollected tracking data sets obtained under appropriate permits and that were based on Institutional Animal Care and Use Committee (IACUC) approved protocols.

### *Data compilation*

To investigate whether biases in home-range estimation scale with body size, we compiled GPS tracking data for 61 globally distributed terrestrial mammalian species, comprising  $6.94 \times 10^6$  locations for 757 individuals collected from 2000 to 2019 (Fig. 1). Individual data sets were selected based on the criterion of range resident behavior (i.e., area-restricted space use), as evidenced by plots of the semivariance in positions as a function of the time lag separating observations (i.e., variograms) with a clear asymptote at large lags (Calabrese et al., 2016). When data do not indicate evidence of range residency, home-range estimation is not appropriate (Calabrese et al., 2016; Fleming & Calabrese, 2017), so we excluded data from migratory or non-range resident individuals. The visual verification of range residency via variogram analysis was conducted using the R package *ctmm* (version 0.5.3) (Calabrese et al., 2016). Further details on these data are in Supporting Information.

For each of the species in our data set, we compiled covariate data on that species' mean adult mass in kilograms. We also identified the main food source for each species and classified them as carnivorous or omnivorous or frugivorous or herbivorous. Data from these two dietary classes were analyzed separately. Mass and dietary data were from the EltonTraits database (Wilman et al., 2014).

### *Tracking-data analyses*

Our conjecture that the underestimation of home-range areas increases as body size increases was based on two well-established biological and one methodological relationship: the positive correlation between body mass and home-range area (Jetz et al., 2004); the positive correlation between home-range area and range crossing time,  $\tau_p$  (Calder, 1983); and the negative correlation between range crossing time and the effective sample size for area estimation,

$N_{\text{area}}$  (i.e., equivalent number of statistically independent locations [Noonan et al., 2019]). We hypothesized that these conspired to drive 2 previously untested relationships: a potential negative correlation between body mass and  $N_{\text{area}}$  and a potential negative correlation between body mass and home-range estimator accuracy.

Testing for these relationships first required estimating the autocorrelation structure in each of the individual tracking data sets. To accomplish this, we fitted a series of range-resident, continuous-time movement models to the data with the estimation methods developed by Fleming et al. (2019). The fitted models included the independent and identically distributed process, which features uncorrelated positions and velocities; the Ornstein-Uhlenbeck (OU) process, which features correlated positions but uncorrelated velocities (Uhlenbeck & Ornstein, 1930); and an OU-foraging (OUF) process, featuring both correlated positions and velocities (Fleming et al., 2014). We used model selection to identify the best fitting model given the data (Fleming et al., 2014) from which  $\tau_p$  and  $N_{\text{area}}$  were extracted. To fit and select the movement models, we used the R package *ctmm* and applied the workflow described by Calabrese et al. (2016).

We estimated home-range areas for each of the 757 individuals in our tracking database via kernel density estimation (KDE) with Gaussian reference function bandwidth optimization because this is one of the most commonly applied home-range estimators in ecological research (Noonan et al., 2019). The KDE home ranges were estimated via the methods implemented in *ctmm*, and the further small-sample-size bias correction that was introduced in area-corrected KDE (Fleming & Calabrese, 2017).

Our primary aim was to determine the extent to which autocorrelation-induced bias in conventional home-range estimation might increase with body size. This required an objective and statistically sound measure of bias. We applied the well-established

technique of block cross-validation (Noonan et al., 2019) to quantify bias in empirical home-range estimates. By determining the extent to which the results of an analysis generalize to a statistically independent data set, cross-validation is an effective tool for quantifying bias (Pawitan, 2001). For this approach, each individual data set was split in half, and a home-range area was estimated from the first half of the data only (i.e., training set). Next, the percentage of observations in the second half of the data (i.e., held-out set) that fell within the specified contour (here 50% and 95%) of the estimated home range was calculated. If the percentage of points included came out consistently higher or lower than the specified contour, then it would suggest positive or negative bias respectively. As a further measure of bias, we identified the contour of the home range estimated from the training set that contained the desired percentage of locations in the held-out set (i.e., 50% and 95%) and compared the area within that contour to the estimated area at the specified quantile. For example, consider that the 95% area estimated on the training data contained only 90% of the locations in the held-out set, whereas the 97% contour contained 95% of the locations. To measure bias, we would take the ratio between the 97% area and the 95% area. Cross-validating home-range estimates in this way can also be seen as providing a measure of how well a home-range estimate can be expected to capture an animal's future space use, assuming no substantial changes in movement behavior.

Block cross-validation is based on the assumption that data from the training and held-out sets are generated from the same processes. To confirm this assumption, we used the Battacharryya distance implementation in *ctmm* (Winner et al., 2018) as a measure of similarity (range  $0 - \infty$ ) between the mean area and covariance parameters of movement models fitted to the training and held-out data sets and determined whether

the confidence intervals on this distance contained 0 (details in Appendix S1 in Noonan et al. [2019]). Using this method, we determined that 160 of 757 individuals had movement models with significantly different parameter estimates between the first and second halves of the data, so we excluded these from our cross-validation analyses. We found no significant relationship between whether or not a data set was excluded from our analyses and which species the data were from ( $p = 0.52$ ) or between exclusion and how long an individual was tracked ( $p = 0.39$ ). This confirmed that the subsampling required to meet the assumptions of half-sample cross-validation did not bias our sample.

### *Correction factors*

We explored two potential solutions to the allometric scaling of autocorrelation and home-range estimation bias: thinning data to minimize autocorrelation and using autocorrelation-informed home-range estimation.

Conventional kernel methods are based on an assumption of independence; however, they can provide accurate estimates for autocorrelated processes when the sampling is coarse enough that the data appear uncorrelated over time (Hall & Hart, 1990). Thus, data thinning presents a potentially straightforward solution to autocorrelation-induced bias, but requires a balance between reducing autocorrelation and retaining sample size. We therefore explored model-informed data thinning as a means of mitigating size-dependent home-range bias. As noted above, the parameter  $\tau_p$  relates to an individual's range-crossing time and quantifies the timescale over which positional autocorrelation decays to insignificance. More specifically, because positional autocorrelation decays exponentially at rate  $1/\tau_p$ , the time required for the percentage of

the original velocity autocorrelation to decay to  $\alpha$  is  $\tau_\alpha = \tau_p \ln(1/\alpha)$ . Conventionally, data are thinned to independence with a 95% level of confidence, and  $\sim 3\tau_p$  is the time it takes for 95% of the positional autocorrelation to decay. Consequently, we thinned each individual's tracking data to a sampling frequency of  $dt = 3\tau_p$ . We then used autocorrelation functions to quantify how much autocorrelation remained in the thinned data and evaluated the performance of KDEs on these thinned data.

As opposed to manipulating the data to meet the assumptions of the estimator, the second potential solution was to use an estimator that explicitly modeled the autocorrelation in the data. Autocorrelated-KDE (AKDE) is a generalization of Gaussian reference function KDE that conditions upon the autocorrelation structure of the data when optimizing the bandwidth (Fleming et al., 2015). Following the workflow described by Calabrese et al. (2016), AKDE home-range areas were estimated conditioned on the selected movement model for each data set, via the methods implemented in *ctmm*, with the same small-sample-size bias correction applied to the conventional KDE area estimates (Fleming & Calabrese, 2017). The AKDE is available via the web-based graphical user interface at [ctmm.shinyapps.io/ctmmweb/](http://ctmm.shinyapps.io/ctmmweb/) (Dong et al., 2017).

### *Correction factor performance*

To test for body-size-dependent biases in cross-validation success, we fitted three regression models to the cross-validation results as a function of  $\log_{10}$ -scaled mass. The models included an intercept only model (i.e., no change in bias with mass); linear model; and logistic model. We then identified the best model for the data via small-sample-size corrected quasi-Akaike information criterion (QAICc) (Burnham et al., 2011).

Species may exhibit similarities in traits due to phylogenetic inertia and the constraints of common ancestry; thus, controlled comparisons are required (Harvey & Pagel, 1991). Accordingly, we did not treat species data records as independent; rather, we used the phylogenetic distances among species to construct a variance-covariance matrix and defined the correlation structure in our allometric regressions with the R package nlme (version 3.1-137) (Pinheiro et al., 2018). Phylogenetic relationships between eutherian mammalian orders were based on genetic differences and taken from Liu et al. (2001). Intraorder relationships were taken from more targeted studies aimed at resolving species-level relationships, including Price et al. (2005) for Artiodactyla, Matthee et al. (2004) for Lagomorpha, Steiner and Ryder (2011) for Perissodactyla, Barriel et al. (1999) for Proboscidea, Perelman et al. (2011) for Primates, and Agnarsson et al. (2010) for Carnivora. For Canidae, however, we took relationships from Lindblad-Toh et al. (2005), due to better coverage of the species in our data set. The phylogenetic tree was built with the R package ape (version 5.2) (Paradis & Schliep, 2019), and branch lengths were computed following Grafen (1989). Phylogenies are in Supporting Information.

## **Results**

### *Allometric scaling of bias*

Out of 757 data sets, only one was independent and identically distributed and free from significant autocorrelation. Conventional KDE 95% home-range areas cross-validated at a median rate of 88.3% (95% CI 87.2% – 90.1%), which was below the target 95% quantile and demonstrated a tendency to underestimate home-range areas on average. Similarly, KDE 50% home-range areas cross-validated at a median rate of 41.5% (95% CI 39.4% – 43.3%), which was again below the target 50% quantile. The magnitude of KDE's

underestimation worsened as body mass increased ( $t = 2.30$ ,  $p = 0.02$ ) (Fig. 2a) carnivores and herbivores did not differ significantly ( $t = 0.31$ ;  $p = 0.75$ ). Cross-validation success of 50% home-range areas across the mass spectrum was best described by a linear decay model with an intercept of 47.2 (95% CI 39.9 – 54.5) and a slope of -3.9 (95% CI -7.0 – -0.8). In other words, for every order of magnitude increase in body mass, home-range estimates captured ~4% less of an individual’s future space use.

When comparing the 95% area estimates with the area estimates for the contours that contained 95% of locations, KDE accuracy across the mass spectrum was best described by linear decay (Fig. 2b). Consequently, whereas the home-range areas of mammals weighing <10 kg were underestimated by 13.6% (95% CI: 6.3% – 18.6%), those of species weighing >100kg were underestimated by 46.0% on average (95% CI: 36.7% – 51.4%).

#### *Mechanisms driving body size-dependent estimation bias*

We found significant positive relationships between body mass and home-range area (regression parameter:  $\beta = 1.18$ , 95% CI = 0.92 – 1.43,  $t = 9.09$ ;  $p < 0.0001$ ) (Fig. 3a) and between home-range area and range crossing time,  $\tau_p$  ( $\beta = 7.09$ , 95% CI = 4.78 – 9.41,  $t = 6.00$ ;  $p < 0.0001$ ) (Fig. 3b) and a negative relationship between  $\tau_p$  and the effective sample size,  $N_{\text{area}}$  ( $\beta = -0.65$ , 95% CI = -0.70 – -0.60,  $t = 25.46$ ,  $p < 0.0001$ ) (Fig. 3c). The former two scaling relationships differed significantly between carnivorous and herbivorous mammals ( $t = 3.08$ ,  $p < 0.005$  and  $t = 2.37$ ,  $p = 0.02$ , respectively). Carnivores tended to have larger home ranges and shorter range crossing times than comparably sized herbivores, and herbivores tended to have longer range crossing times. The relationship between  $N_{\text{area}}$  and mass did not differ between dietary classes ( $t = 0.82$ ;  $p = 0.06$ ). The  $N_{\text{area}}$  was governed by both  $\tau_p$  and sampling duration,  $T$ ,

such that  $N_{\text{area}} \approx T/\tau_p$ . Although we noted a positive correlation between body mass and  $T$  in the studies we sampled ( $\beta = 0.24$ , 95% CI = 0.09 – 0.39,  $t = 3.17$ ;  $p < 0.005$ ), this was not enough to counter the positive correlation between mass and  $\tau_p$ . Consequently, the net result was a negative relationship between body mass and  $N_{\text{area}}$  ( $\beta = -0.23$ , 95% CI = -0.39 – -0.08,  $t = 2.98$ ;  $p < 0.005$ ) (Fig. 3d).

### *Correction factors*

Model-informed data thinning served to reduce the mean autocorrelation at lag 1 from 0.96 (95% CI: 0.96– 0.97) to 0.32 (CI: 0.30 – 0.35) (Fig. 4). Hence, an independent and identically distributed model was the best fit for 167 of the 463 individuals for which sufficient data (>2 locations) remained after data thinning. The remaining individuals were best described by OU and OUF processes whose autocorrelation parameters were not significant. Although thinning mitigated the correlation between bias and body mass ( $\beta = -2.41$ , 95% CI -6.08 – 1.26,  $t = 1.29$ ;  $p = 0.20$ ), the median cross-validation rate of 95% home ranges estimated using the thinned data was only 85.1% (95% CI: 83.6% – 86.5%). This ~3% decrease in performance, as compared with conventional KDE on the full data, was likely the result of the small sample size. Model-informed data thinning resulted in a mean data loss of 93.2% (95% CI: 92.1%– 94.3%), and the median number of approximately independent locations left in each data set after thinning was only 23 (95% CI: 18 – 26). Furthermore, in ~20% of the individuals  $\leq 2$  locations remained after thinning, making it impossible to estimate a home-range area on the thinned data.

### *Autocorrelation-informed home-range estimation*

Like model-informed data thinning, autocorrelation-informed home-range estimation via

AKDE also eliminated the correlation between cross-validation success and body mass ( $\beta = -0.51$ , 95% CI =  $-1.88 - 0.86$ ,  $t = 0.73$ ;  $p = 0.47$ ). However, without the data loss required by the thinning approach, AKDE resulted in a median cross-validation rate of 95.2% (95% CI: 94.2% – 95.9%) for 95% home ranges and 51.3% (95% CI 49.26% – 54.36%) for 50% home ranges. In other words, AKDE exhibited consistent accuracy across species, irrespective of the allometries in autocorrelation timescales and effective sample sizes.

### *Scaling of mammalian space use*

When regressing home-range area against mass with conventional KDE estimates, we documented no significant difference from linear scaling for either herbivores or carnivores (Table 1). For AKDE derived area estimates, however, we detected that the scaling exponent was significantly  $>1$  for both taxonomic groups, suggesting home-range area scales with mass according to a power function.

## **Discussion**

The importance of autocorrelation in animal-tracking data has been an active area of research for decades (Swihart & Slade, 1985; Fieberg, 2007; Fleming et al., 2015). We, however, are the first to demonstrate that mass-specific space requirements driven by autocorrelation-induced underestimation of home-range areas is worse for larger species. From a fundamental perspective, the continuous nature of animal movement means quantities such as positions, velocities, and accelerations are necessarily autocorrelated (Fleming et al., 2014). Autocorrelation timescales ( $\tau$ ) should therefore be viewed as explicit attributes of an animal's movement process (Gurarie & Ovaskainen,

2015) that are revealed when the temporal resolution of measurement becomes  $\lesssim \tau$ . As technological advances continue to permit ever-finer sampling (Kays et al., 2015), persistent autocorrelation is likely to become the norm in animal-tracking data. Pairing data from inherently autocorrelated processes with statistical approaches that ignore autocorrelation not only risks biasing any derived quantities, but also effectively negates the technological advances that are improving data quality. Unless analyses that are informed by autocorrelation become adopted by movement ecologists and conservationists, the issue of autocorrelation-induced bias will only worsen. Conversely, properly harnessing the wealth of information provided by autocorrelation can dramatically improve the accuracy of tracking-data derived measures (see also Fleming & Calabrese, 2017; Winner et al., 2018; Noonan et al., 2019). Our findings therefore highlight the need for more statistical estimators that can handle biologically induced variance without introducing bias.

#### *Implications of size-dependent bias*

From a conservation perspective, the underestimation of home-range areas is a worst-case scenario. When reserves are too small, relative to their target species' area requirements, the probability of local populations undergoing declines or extirpations increases significantly (Brashares et al., 2001; Gaston et al., 2008). Undersized protected areas resulting from poorly estimated space needs also risk exacerbating the issue of negative human wildlife interactions at reserve boundaries (Van Eeden et al., 2018) as animals move beyond reserve boundaries to meet their energetic requirements (Farhadinia et al., 2018). It is thus of critical importance that policy actions be well informed about species' spatial requirements. To this end, we analyzed a broad

taxonomic and geographic range of data and identified a strong correlation between home-range underestimation and body size when autocorrelation was ignored; average bias was ~50% at the upper end of the mass spectrum. In this regard, the majority of home ranges are estimated via methods based on the assumption of statistically independent data (Noonan et al., 2019). Combined with the facts that humans are the dominant mortality source for terrestrial vertebrates globally (Hill et al., 2019), that this mortality is higher for larger-bodied species (Hill et al., 2020), and that megafauna are experiencing more severe range contractions (Tucker et al., 2018) and extinction risk (Cardillo et al., 2005), the most threatened species are also likely to be those with the least accurate home-range estimates, a worrying combination.

Based on these findings, we suggest that any conservation initiatives or policy based on home-range estimates derived from estimators based on the assumption of statistically independent data be revisited, especially where large-bodied species are involved. To facilitate this, we developed HRcorrect, an open-access application that allows users to correct a home-range area estimate for their focal species' body-mass-specific-bias with a correction factor calculated from our cross-validation regression models. The current version of HRcorrect is freely available from <https://hrcorrect.shinyapps.io/HRcorrect/>. However, there are numerous factors beyond body mass that influence an individual's home-range size. For instance, mammalian home-range areas are well known to covary with the spatial distribution of resources (Litvaitis et al., 1986; Boutin, 1990), social structure (Lukas & Clutton-Brock, 2013), sex (Cederlund & Sand, 1994; Lukas & Clutton-Brock, 2013; Noonan et al., 2018), age (Cederlund & Sand, 1994), population density (Adler et al., 1997), and reproductive status (Rootes & Chabreck, 1993; Noonan et al., 2018). Furthermore, if an individual's

space use changes over time (e.g., interseasonal, -annual variation), a home-range area estimated from a single observation period may not be representative of its long-term area requirements. As such, the deterministic trend-based correction provided by HRcorrect is not a substitute for more rigorous data collection and home-range estimation and should only be used for cases where the underlying tracking data are not accessible.

### *Allometries and conservation theory*

The metabolic theory of ecology (West et al., 1997) suggests body mass represents a super trait that governs a wide range of ecological processes. Prime among these is the relationship between body mass and home-range area, an allometry that has guided ecological theory for more than 50 years (McNab, 1963; Calder, 1983; Jetz et al., 2004). More recently, attempts have been made to integrate this allometry into conservation theory. For instance, Hilbers et al. (2016) incorporated the home-range allometry into a method for quantifying mass-specific extinction vulnerability, and Hirt et al. (2018) highlighted how allometries in movement and space use can be used to make testable predictions of movement and biodiversity patterns at the landscape scale. Similarly, Pereira et al. (2004) used allometries of space use and movement rates to predict species level vulnerability to land-use change. If the underlying allometries are biased, however, hypothesis testing and conservation planning in this context can fail even if the logic behind the experimental design is perfectly sound. While the earliest derivation of the home-range allometry proposed a metabolically determined  $M^{0.75}$  allometry (McNab, 1963), subsequent revisions showed no support for a purely energetic basis for home-range scaling (Calder, 1983; Kelt & Van Vuren, 2001; Jetz et al., 2004; Tucker et al.,

2014; Tamburello et al., 2015). Although all these studies concluded that home-range area should scale with an exponent greater than the 0.75 predicted by metabolic requirements alone, there has been little consensus on whether the allometry is linear ( $M^1$ ) or superlinear ( $M^{>1}$ ). Our results suggest that at least part of the confusion can be attributed to the increasing bias in underestimating home ranges with increasing body size. Ours is the first study to estimate this relationship directly from tracking data by applying a consistent estimator across all individuals and, crucially, correcting for any potential autocorrelation-induced bias (Noonan et al., 2019). In doing so, we documented a super-linear relationship between body mass and home-range area (exponent of  $\sim 1.25$  for  $M$ ). This shift from linear to power-law scaling fundamentally changes the behavior of the relationship, particularly at the upper end of the mass spectrum. Although we did not investigate the mechanisms behind the deviation from the metabolically determined  $M^{0.75}$ , we encourage future work on this subject be based on the assumption of a superallometry, as opposed to linear allometry. Accurately quantifying species' area requirements is a prerequisite for successful, area-based conservation planning. Our results highlight an important yet hitherto unrecognized aspect of home-range estimation: autocorrelation-induced negative bias in home-range estimation that is systematically worse for large species. Crucially, however, our findings also outline a readily applicable solution to the problem of size-dependent bias. We demonstrated that home-range estimation that properly accounts for the autocorrelation structure of the data is currently the only consistently reliable solution for eliminating allometric biases in home-range estimation (see also Noonan et al., 2019). We emphasize that the differential scaling of autocorrelation across the mass spectrum be a key consideration for movement ecologists and conservation practitioners and suggest

avoiding home-range estimators that assume statistically independent data.

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## **Supporting Information**

Data set summary statistics (Appendix S1), individual tracking data set summaries (Appendix S2), and mammalian phylogenetic relationships (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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**Table 1:** Estimates of the scaling exponent ( $b$ ) of mass to home-range area relationship.\*

	KDE (95% CI)	AKDE (95% CI)
All mammals	1.20 (0.95 – 1.45)	1.28 (1.01 – 1.54)
Herbivores and frugivores	1.26 (0.99 – 1.52)	1.38 (1.09 – 1.66)
Carnivores and omnivores	1.23 (0.95 – 1.50)	1.27 (1.01 – 1.56)

\*Abbreviations: KDE, Kernel Density Estimation; AKDE, autocorrelated-Kernel Density Estimation.

**Figure 1:** Distribution of study sites for the empirical GPS tracking data set spanning 757 individuals across 61 mammalian species.

**Figure 2:** Cross-validation of conventional Kernel Density Estimation (KDE) across the mammalian body-mass spectrum: (a) percentage of locations from the second half of the data (held-out set) included in KDE 50% home ranges estimated from the first half of the data (training set) as a function of body mass (dashed line, target 50% quantile; solid line, phylogenetically controlled regression model fit to cross-validation results; shading, 95% CI of the fit) and (b) regression model describing the accuracy of 95% KDE area estimates across the mass spectrum. Accuracy was quantified as the ratio between estimated 95% area of the training set and the area contained within the contour that encompassed 95% of locations in the held-out set. The horizontal dashed line represents an unbiased area estimate. The x-axes in (a) and (b) are log scaled.

**Figure 3:** Mechanisms driving body-size-dependent estimation bias: (a) positive allometry of home-range areas, (b) correlation between home-range area and range-crossing time ( $\tau_p$ ), (c) negative correlation between  $\tau_p$  and effective sample size ( $N_{\text{area}}$ ) governed by duration of observation period ( $T$ ) and  $\tau_p$  such that  $N_{\text{area}} \approx T/\tau_p$ , and (d) resulting negative allometry of  $N_{\text{area}}$  (axes, log scaled; lines, phylogenetically controlled fitted regression models). From (a) to (d), 1 axis is preserved from the previous panel to demonstrate the inherent link between each of these relationships (arrows, visual aid of link; top-left arrow, end of the chain).

**Figure 4:** Frequency of amounts of autocorrelation at lag 1 in the full tracking data sets for each of the 757 individuals used to estimate home ranges via conventional Kernel Density Estimation (KDE), compared with the thinned data sets for individuals for which sufficient data remained after thinning to apply KDE.