The Importance of Representative Sampling for Home Range Estimation in Field Primatology

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Abstract

Understanding the amount of space required by animals to fulfill their biological needs is essential for comprehending their behavior, their ecological role within their community, and for effective conservation planning and resource management. Habituated primates are often studied using handheld GPS data, which provides detailed movement information that can link patterns of ranging and space-use to the behavioral decisions that generate these patterns. However, this data may not accurately represent an animal's total movements, posing challenges when the desired inference is at the home range scale. To address this, we used a rich 13-year dataset from 11 groups of white-faced capuchins (*Cebus imitator*) to examine the impact of sampling elements, such as sample size and regularity, on home range estimation accuracy. We found that accurate home range estimation is feasible with relatively small sample sizes and irregular sampling, as long as the data are collected over extended time periods. Concentrated sampling can lead to bias and overconfidence due to uncaptured variations in space-use and underlying movement behaviors. Therefore, it is crucial to develop sampling protocols that provide adequate temporal coverage and consider the movement behaviors of the study species.

Keywords: capuchin, movement, spatial ecology, autocorrelated kernel density, handheld GPS

Resumen

Entender la cantidad de espacio necesario para satisfacer las necesidades biológicas de los animales es esencial para comprender su comportamiento, su papel ecológico dentro de su comunidad y para una planificación efectiva de la conservación y gestión de recursos. Los primates habituados a menudo son estudiados utilizando datos de GPS portátil, lo que proporciona información detallada sobre los movimientos y puede vincular los patrones de rango a las decisiones comportamentales. Sin embargo, estos datos pueden no representar con precisión los movimientos totales del animal, lo que plantea desafíos para inferir patrones de rango de hogar. Para abordar esto, utilizamos un rico conjunto de datos de 13 años de 11 grupos de monos cara blanca (*Cebus imitator*) para examinar el impacto de los elementos de muestreo, como el tamaño y la regularidad de la muestra, en la precisión de la estimación del rango de hogar. Encontramos que la estimación precisa del rango de hogar es factible con tamaños de muestra relativamente pequeños y muestreo irregular, siempre que los datos se recolecten durante períodos prolongados. El muestreo concentrado puede conducir a sesgos y sobreconfianza debido a variaciones no capturadas en el uso del espacio y los comportamientos subyacentes del movimiento. Por lo tanto, es crucial desarrollar protocolos de muestreo que proporcionen una cobertura temporal adecuada y consideren los comportamientos de movimiento de la especie estudiada.

Introduction

Animal space-use is often described using the home range concept, developed by Burt (1943), who defined the home range as ‘the area traversed by the individual in its normal activities of food gathering, mating and caring for young’. The home range concept is integral to primate research, helping us understand how individuals - and social groups - interact with one another and their environment. Measuring home ranges provides insights into elements of behavioral ecology, such as habitat selection, species abundance and distribution (Gautestad & Mysterud, 2005), metabolism (Harvey & Clutton-Brock, 1981), learning and cognition (Spencer, 2012), resource competition (Crofoot et al., 2008), predator-prey dynamics (Suraci et al., 2022), and the roles species play in their ecological communities (e.g. seed dispersal (Gelmi-Candusso et al., 2019) and pollination (Abe et al., 2011)). Home range estimates are also frequently used to inform species’ minimum area requirements (Pe’er et al., 2014), size recommendations for protected areas (Brashares et al., 2001), land-use decisions (Johansson et al., 2016), and other aspects of conservation policy and initiative.

Overview of Home Range Estimation

While home range estimation is a simple concept, in practice, it is a logistically and statistically challenging endeavor (C. H. Fleming et al., 2015a). Recent research has identified three key elements required to estimate an accurate home range: 1) a quantitative definition of the home range (Börger et al., 2020), 2) sufficient sampling across the home range, which generally scales with time rather than number of recorded locations (C. H. Fleming et al., 2018), and 3) a robust estimator that extrapolates future space-use and provides a workflow to overcome the numerous possible sources of bias in home range estimation (C. H. Fleming et al., 2015a). Further, having a home range requires *site fidelity*, the tendency to remain or return to previously occupied areas (Switzer, 1993). Thus, most approaches assume home ranges are stationary, and the data themselves must show clear evidence of range residency, otherwise home range analysis is not appropriate (C. H. Fleming & Calabrese, 2017).

Burt's definition (1943) provides a conceptual framework for the home range, but it lacks a statistical basis needed to quantify it (Silva et al., 2021). Early efforts used the Minimum Convex Polygon (MCP), but joining the outermost points is problematic as it leads to estimates that are highly sensitive to sampling and assume uniform space-use (Burt, 1943; Kernohan et al., 2001; Worton, 1995). Efforts have since focused on measuring the *utilization distribution* (hereafter UD) (Worton, 1989). The UD is a density function describing the probability distribution of an animal being at any point in space within a particular area (Börger et al., 2020; Calhoun & Casby, 1958; Jennrich & Turner, 1969). The 95% UD - or 'the smallest area associated with a 95% probability of finding the animal' (Fieberg & Kochanny, 2005; White & Garrott, 1990) is the widely adopted – although somewhat arbitrary - quantitative formulation, as Burt's original home range concept excludes 'occasional sallies outside the area used for normal activities' that are 'perhaps exploratory by nature' (Burt, 1943).

Constructing UDs generally involves kernel density estimation (hereafter KDE), which works by placing kernels, or small probability density functions, over each location data point and averaging them to acquire a total probability density function across all the points (Börger et al., 2020; Worton, 1989). The resulting probability density function has the highest density where the points are the most concentrated (Worton, 1989). The conventional KDE method was developed for home range estimation when movement data were generally collected at relatively low sampling rates using VHF radio-telemetry (Börger et al., 2020). Consequently, the underlying statistics of the KDE assumes that the data have no autocorrelation (Worton, 1989), meaning the observed locations are independent of previously, or subsequently, observed locations. This is a false assumption with most current GPS-based sampling regimes, as the ability of these devices to collect movement data at higher frequencies results in greater degrees of autocorrelation in movement datasets (C. H. Fleming et al., 2015a). When the data are sampled at intervals short enough that the recorded locations are correlated in space and time, which can even be as coarse as one fix per day (Calabrese et al., 2016)), the assumptions of the conventional KDE are violated (C. H. Fleming et al., 2015a).

In the context of autocorrelated data, traditional KDE methods yield UDs that are better suited to reflecting an animal's space-use during the observation period (i.e., occurrence distribution), rather than providing a home range estimate that extrapolates beyond the observed data to encompass future space use (i.e., range distribution) (Börger et al., 2020). The range distribution aligns with Burt's initial description of the home range by measuring an animal's long-term space use, making it relatively resilient to variations in sampling effort (C. H. Fleming et al., 2015a). Conversely, the occurrence distribution focuses on space-use during the observation period, making it highly sensitive to sampling and conforming closely to the observed data (J. Alston et al., 2022).

Calculating the occurrence distribution can be beneficial for various analytical purposes not related to home range estimation, such as path reconstruction (C. H. Fleming et al., 2015b), and determining the times and locations of animal interactions or crossings over landscape features (J. Alston et al., 2022). There are several methods that explicitly estimate the occurrence distribution including Brownian bridge approaches (Horne et al., 2007), the continuous-time correlated random walk (Johnson et al., 2008), time-dependent LocoH (Lyons et al., 2013), and time-series Kriging (C. H. Fleming et al., 2015b). Nevertheless, the KDE is widely used to estimate the home range (hereafter referred to as the range distribution), instead of the occurrence distribution (C. H. Fleming et al., 2015a), which is only suitable when the recorded location data are independent and not autocorrelated (Börger et al., 2020). As almost all modern movement data are autocorrelated (C. H. Fleming et al., 2015a), using the KDE method typically generates UDs that more closely resemble the occurrence distribution. Therefore, if the intended goal is to estimate the home range, the KDE approach will provide negatively-biased results that are potentially misleading (C. Fleming et al., 2014).

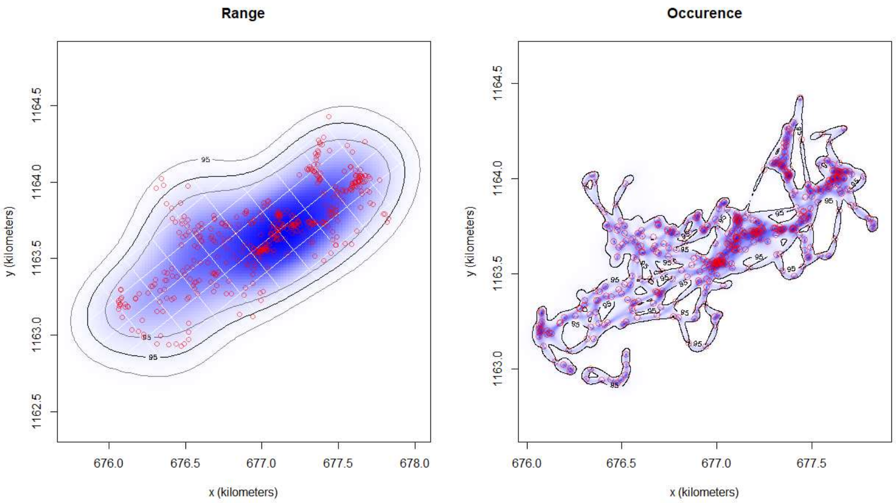

Figure 1: Comparison of the range distribution using auto-correlated kernel density estimation versus the occurrence distribution using time-series Kriging over the same autocorrelated data. Red points are recorded locations of capuchin movements, blue represents the estimated utilization distribution, and black lines show the mean and 95% confidence interval boundary of the 95% level utilization distribution.

Recently, new home range estimation methods have been developed that account for the fact that animals' paths result from movement processes that are, by definition, spatio-temporally autocorrelated. These methods therefore explicitly treat movement data as a sample of location estimates taken along an animal's mostly unobserved continuous movement path (C. H. Fleming et al., 2015a). Improving upon the KDE, the auto-correlated kernel density estimate (hereafter AKDE) models the underlying continuous-time movement process of the animal, generating home range estimates that are informed by autocorrelated data, rather than hindered by it (Calabrese et al., 2016). The AKDE is a flexible approach that provides the analytical toolkit to handle several other obstacles, such as satellite error, irregular sampling, bandwidth optimization, and estimation uncertainty (C. Fleming et al., 2020; C. H. Fleming et al., 2018; C. H. Fleming & Calabrese, 2017).

A comprehensive analysis by Noonan et al. (2019), showed that the AKDE outperformed all conventional estimators, and was the only estimator capable of producing unbiased estimates with low effective sample sizes. While the AKDE is increasingly being adopted in studies of animal ranging behavior (Crabb et al., 2022; Desbiez et al., 2020; Lenske & Nocera, 2018; McEvoy et al., 2019; Montano et al., 2021; Naveda-Rodríguez et al., 2022; Poessel et al., 2022), the overwhelming majority of primatology studies still use methods such as the MCP and conventional KDE. In a Google Scholar search, we found only five published articles using the AKDE for home range estimation on primate species (Havmøller et al., 2021; Kalbitzer et al., 2023; Oliveras, 2021; Teichroeb et al., 2022), only one of which is in a major primatology journal (e.g. AJP, IJP, Primates, Folia Primatologica) (Tórrez-Herrera et al., 2020). The potential presence of significant, systematic biases in home range estimates is concerning, as it can lead to erroneous conservation decision-making (Gaston et al., 2008) or inaccurate meta-analyses that influence public opinion and theoretical frameworks (as noted by Noonan et al., 2020). Also, particularly worrying is that the methods used to record primate movement (e.g. handheld GPS) are fundamentally different than those used on studies of most other species (e.g. GPS tags), introducing additional bias into any comparative work.

Collection of Movement Data in Field Primatology

Due to technological advances in satellite acquisition, position accuracy, and battery conservation (Markham & Altmann, 2008; Sprague et al., 2004), the use of GPS devices became feasible in dense tropical forests around the year 2000 (Dominy & Duncan, 2002; Phillips et al., 1998; Singleton & van Schaik, 2001). Handheld GPS devices allow researchers to collect high-resolution movement data in conjunction with behavioral observations without applying expensive and potentially risky GPS tags directly on habituated animals. On the other hand, using GPS tags negates the need to continuously monitor primates via on-the-ground personnel, allowing movement data to be collected in areas that are inaccessible to humans, and avoiding any potential disturbance introduced from human presence that may change behaviors or community interactions (Crofoot, 2021). Although GPS tags are becoming increasingly common in primate studies (Dore et al., 2020; Markham & Altmann, 2008; Strandburg-

Peshkin et al., 2015; Tórrez-Herrera et al., 2020), most longitudinal studies continue to use handheld devices (Irwin & Raharison, 2021; Janmaat et al., 2021; Seiler & Robbins, 2020).

There is vast potential in the datasets generated by handheld GPS devices from longitudinal studies, as they span several years or decades and have corresponding data on demography, behavior, and environmental variables (Campos et al., 2014; Gibson & Koenig, 2012; Irwin & Raharison, 2021; Seiler & Robbins, 2020). Thus, these data can give rise to novel and important investigations that are not feasible for most tracking studies, including how movement and space-use are influenced by demography, memory and learning, climate change, and human disturbance. Yet the accumulated handheld GPS data from longitudinal studies is often underutilized, with inquiries on social behavior and life history taking precedence. Thus, there is generally a lack of understanding of what drives long-term movement and space-use patterns of primates and how these patterns link with fitness.

Another key issue is that most modern approaches for estimating the home range, including the AKDE, have been designed to handle movement data sampled continuously at discrete intervals over predetermined time periods (e.g., GPS tag datasets). Challenges arise when applying these approaches to the extensive, but often discontinuous and opportunistic datasets produced by tracking the movements of habituated animals using handheld GPS devices. When animal movement data are collected by tracking the movements of human observers (e.g. handheld GPS datasets), sampling bias is introduced from several sources. For instance, data can only be collected when observers are present, causing missing data when rotating between multiple groups or during vacation periods. Bias is also introduced when some areas are less accessible to observers, for example over cliffs or flooded rivers. Sampling disruptions can also be non-random in time and across behaviors, as groups can be more easily 'lost' in rainy seasons where visibility and audibility are limited, or when groups are moving rapidly.

For primatologists, handheld GPS data remain an exceedingly valuable input for estimating space-use. Nevertheless, it remains unclear whether common sampling protocols in field primatology produce home range estimates that are truly accurate. Here, we address this concern by answering the following questions:

1. How much movement data from handheld GPS are necessary to maximize estimation accuracy?
2. At what temporal scales should we measure home ranges?
3. What are the most important considerations for obtaining representative samples?

Our aim is to understand how to maximize the potential of long-term, handheld GPS data for accurate home range estimation and to make recommendations for robust home-range estimation using such datasets. We used a longitudinal dataset from the Lomas Barbudal Monkey Project – comprising 13 years of handheld GPS data collected over 11 groups of white-faced capuchin monkeys (*Cebus imitator*) in Guanacaste, Costa Rica. We thinned continuous segments of data into alternative sampling regimes of varying temporal scales and levels of consistency, and assessed the home range estimation performance using cross validation from the total samples. This approach allows us to better understand how key features of movement datasets collected by on-the-ground observers - namely small sample sizes and gaps in sampling time frames - affect the accuracy of home range estimates.

Methods

Study site

Our field work was carried out at the Lomas Barbudal Monkey Project which was established by Prof. Dr. Susan Perry in 1990. Her ongoing longitudinal study aims to monitor the social behavior and life history of white-faced capuchins (Perry et al., 2012). The Lomas Barbudal Monkey Project is centered around the neotropical dry forests of Reserva Biologica Lomas Barbudal (10°29–32′N, 85°21–

24′W) in Guanacaste, Costa Rica (aka “Lomas”). However, the capuchin groups also venture outside the reserve into land owned by Finca El Pelón de la Bajura and other nearby private and public lands.

The landscape at Lomas is rugged and highly heterogeneous, consisting of various distinct forest types, including dry deciduous, riparian, savanna, mesic, extreme deciduous, and regenerative – as well as large patches cleared for cattle ranching (Frankie et al., 1988). Lomas experiences extreme seasonality with virtually all of the annual rainfall (1000-2200 mm) occurring between May - November (Frankie et al., 1988). During the dry season, most animal life seeks refuge in riparian areas as they provide the primary means of shade and food resources (Frankie et al., 1974). Fires are also common in the dry season, and increasingly so with stronger and more frequent El Niño events due to climate change (Perry et al., 2012); Perry *pers. obs*). Additionally, human disturbance persists year-round at Lomas through agriculture, mining, poaching, and logging (Quesada & Stoner, 2004; Stoner & Timm, 2004; *pers. obs*).

Study Species

White-faced capuchin monkeys (*Cebus imitator*) are arboreal platyrrhine primates that live in multi-male, multi-female groups ranging anywhere from 5-40 (average 18.8) individuals at Lomas Barbudal (Perry, 2012). Females typically remain in their natal group for life, while males disperse as adolescents (mean 7.6 years old) to join other groups and avoid inbreeding (Perry et al., 2012). Fruit and arthropods comprise most of their diet (McCabe & Fedigan, 2007; Perry & Ordoñez J., 2006); however, they are dietary generalists and also eat flowers, eggs, pith, and small vertebrates. Groups are generally cohesive and move collectively, with each individual remaining within audio-visual contact with at least one other group member (Campos et al., 2014). Home ranges can overlap extensively with neighboring groups, and although they don’t defend strict territorial borders, interactions between groups are aggressive and sometimes even deadly (Crofoot, 2007; Gros-Louis et al., 2003; Perry, 1996). Over the course of the study, we monitored 11 neighboring groups that are habituated to human observation. Several of these formed as a result of fissions from existing study groups.

Data collection

We collected data on the movement trajectories of capuchin groups from September 2009 to March 2020 using handheld Garmin GPSmap Series units (62s, 64, 64s, 66sr) clipped on or placed in researcher backpacks. Researchers followed capuchin groups from dawn until dusk (switching between groups when behavioral data collection was completed (i.e., ~3-10 days)), recording the groups' trajectory over the period when capuchins are expected to be active. On search days, GPS recording began upon encountering groups and continued until groups reached their sleeping site; recording terminated early in cases of losing contact due to challenging conditions or alternating study groups. Inefficiency of early GPS models and satellite disconnection due to cloud cover, cliff topography, or dense canopy also disrupted GPS data collection. In our dataset, 55% of tracks are at least 10 hours in duration and 78% of tracks are at least 5 hours. GPS units were programmed to collect locations at one fix per 5 minutes between 2009-2012. When GPSs were upgraded in 2013 they began collecting at one fix per 30 seconds, which remains the same today. It should be noted that we rediscretize the sampling rate to one fix per 30 minutes to manage computational costs during home range estimation.

As is common in field primatology studies, movement data collection is somewhat opportunistic, as behavioral data collection protocols determine which group to follow, as well as when and how frequently. Once the behavioral data collection priorities were fulfilled for one group, data collection teams switched to another group. The time spent consecutively with any one group ranged between 1 and 22 days (mean 2.49) depending on the amount of behavioral data needed, visibility, and whether or not the researchers lost contact with the monkeys. We cleaned all tracking data in the software environment R (R Core Team, 2022) by visualizing tracks with the mapview package (Appelhans et al., 2022), and then flagging and removing erroneous points caused by satellite error or researchers forgetting to turn off their GPS units once they finished behavioral follows and left a focal group.

The dataset is exceptional in that it covers a large number of groups (11) over a long timeframe (13 years--see Figure 2). It represents a high-quality example of the data collected during primate field studies and showcases key challenges in using such data to infer space use: varying temporal coverage and large and irregular gaps between consecutive sampling periods. There were six cases where specific groups were followed almost continuously for long periods of two to four months because of concurrent research projects. These intervals provide ideal subsets of the data to explore the impact of irregular sampling and small sample sizes on home range estimation. We subsampled these data to emulate sampling regimes that varied in total duration, regularity of sampling effort, and volume of data.

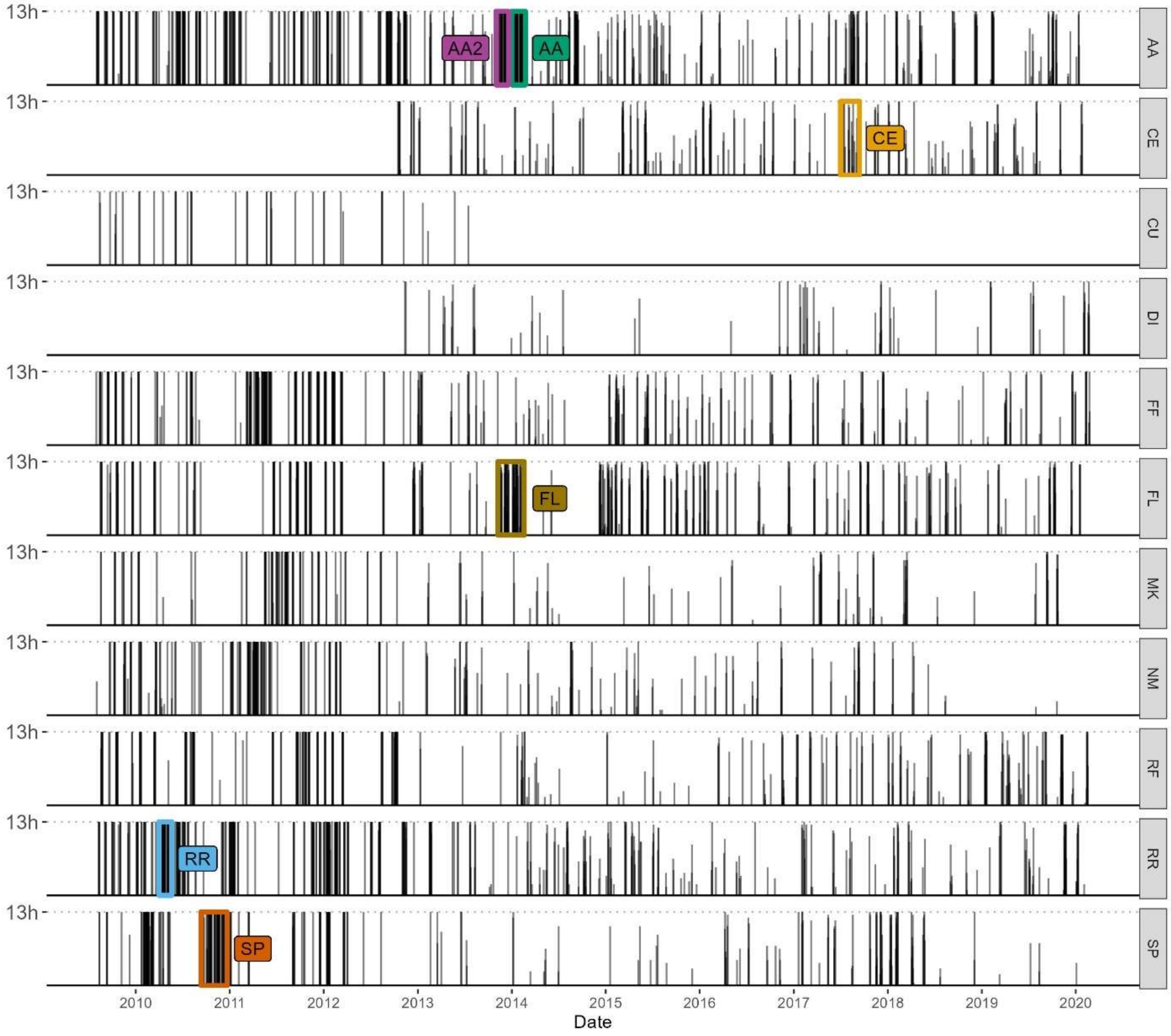

Figure 2: *The six complete segments of data selected from the total handheld GPS dataset with the group name provided on the right side.* Each line shows the time sampled in a single day, with a maximum of 13 possible tracking hours (or 26 locations collected at a 30-minute sampling rate) in a day as the monkeys very rarely move at night. The selected segments were thinned to emulate the varying sampling regimes shown in Figure 3.

Emulating Sampling Regimes

We chose six high-quality segments (hereafter referred as "complete segments") from five different capuchin groups (two of the segments came from one group; the rest were from different groups), in which the data were collected almost continuously over multiple months. The movement data from these segments were collected over at least 50 (max = 102 days) nearly consecutive full tracking days (~13 hours). We thinned each complete segment to generate ten alternative sampling regimes per complete segment, totaling 60 different sampling regimes. Out of the ten sampling regimes created from each complete segment, five were thinned by removing days from either the beginning, the end, or both, and thus these regimes retained nearly continuous monitoring effort (hereafter, "concentrated sampling regimes"). The other five regimes were thinned by randomly removing days to create irregular sampling gaps (hereafter, "spread sampling regimes"). Across the 60 sampling regimes, 30 were concentrated and 30 were spread. The number of days (and approximately the amount of locations) were held constant across concentrated and spread sampling regimes so that both spread and concentrated regimes have either 30, 20, 10, 6 or 3 days, corresponding to approximetely 780, 520, 260, 156 and 78 recorded locations respectively. Each sampling regime is given a sampling regime ID denoting whether it is concentrated (C) or spread (S) followed by the number of days in the sampling regimes (e.g. S20).

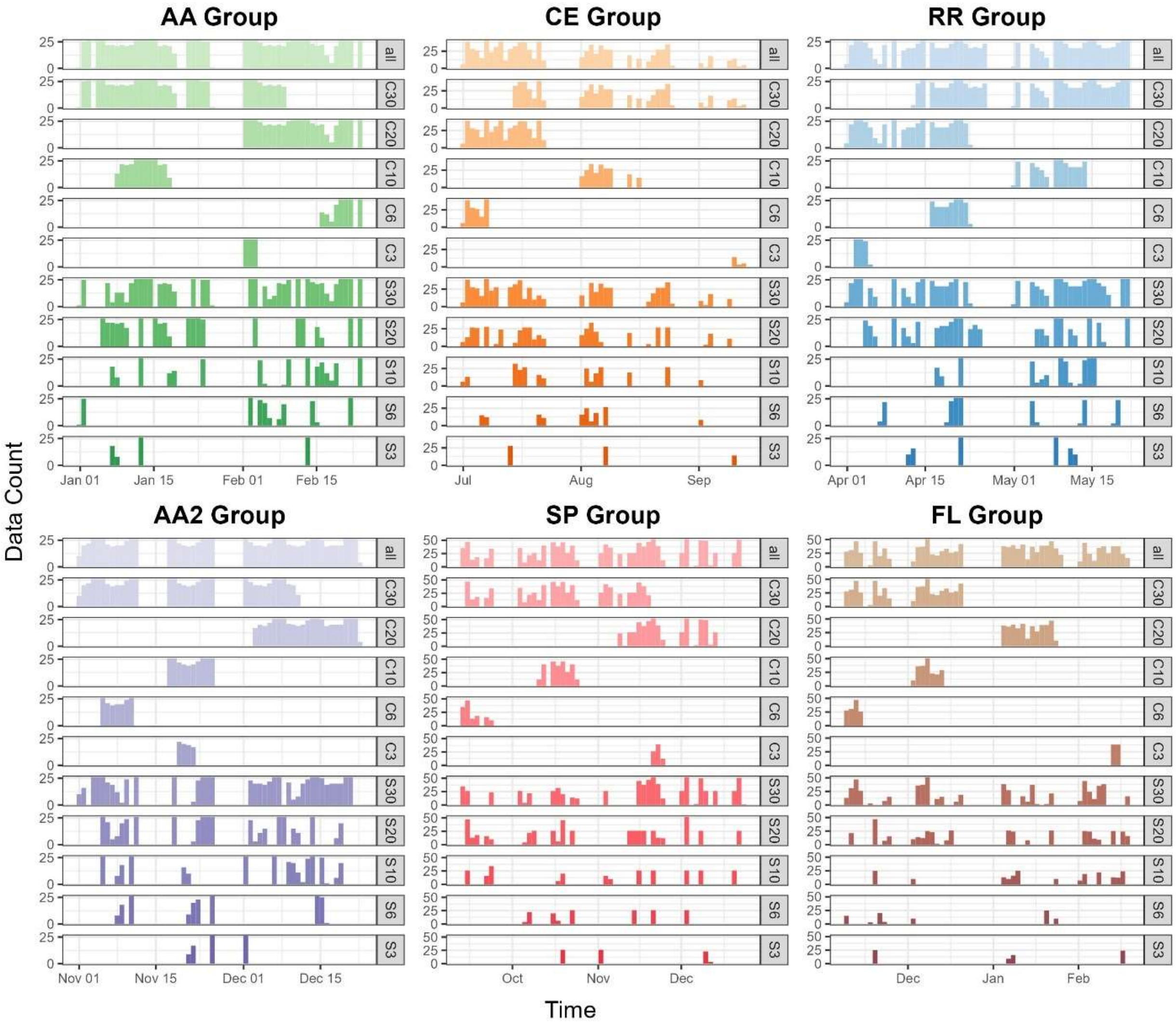

Figure 3: *Emulated sampling regimes thinned from the six high-quality complete segments*. The x-axis shows the temporal scale, while the y-axis shows the number of recorded locations. For plot aesthetic purposes, the maximum value each bar can take is variable depending on the temporal scale of the complete segment (unlike Figure 2 where the maximum was always 26 locations or one full day). The top row of each segment (labelled as "all") shows the total data from the complete segment. The following 10 rows indicate the different sampling regimes, which are labelled with a sampling regime ID. The "C" labels indicate concentrated data, while "S" indicates spread data. The numbers indicate the number of days in the sampling regime.

Home Range Estimation

We computed home range estimates for the 60 emulated datasets using the AKDE method implemented in the ctmm package (Calabrese et al., 2016) in the R Environment for Statistical Computing (R Core Team, 2022). The ctmm package leverages advances in continuous-time movement models to provide a suite of tools for generating UDs (among other downstream analyses) while accounting for the wide range of autocorrelation structures present in most modern tracking datasets as well as the option to model GPS error. We detail ctmm analysis for home range estimation and provide an example workflow to make it easy to replicate the analyses with one's own data in Appendix 1. Then we demonstrate how we applied this method to the 60 sampling regimes for this study in Appendix 2.

Performance of Home Range Estimates

To evaluate the performance of the 60 emulated regimes—and thus the impact of different aspects of sampling design—we compared each home range estimate against the data from the full time period (i.e., complete segments), assuming that estimates that accurately represent these data are more likely to be closer to the "true" home range. We defined performance as the proportion of the recorded GPS locations from the complete segments that fall within the boundaries of the 95% UD home range estimates calculated from the emulated sampling regimes. For simplicity, this measure is hereafter referred to as simply "performance" or "performance score". Because the 95% UD is an estimate of the area in which there is a 95% probability of finding the animal, a perfect performance score is 0.95, indicating that 95% of the total locations from the complete segment fell within the HR estimate. It is important to note that because the data from the sampling regimes also represents a portion of the data within the complete segments, it is expected that performance scores should not deviate substantially from the optimal value of 0.95. Thus, performance scores that deviate below 0.90 can be viewed as exceedingly poor.

Statistical Analysis

The goal of our statistical analysis is to predict home range performance in relation to key sampling characteristics using binomial generalized linear mixed models (GLMMs) in the *brms* package (Bürkner et al., 2023). Our initial model uses a binary predictor variable that indicates whether the data is concentrated or spread, to predict the performance score as the response variable. In contrast, our second model predicts the performance score based on the *absolute sample size*, which is indicated by the number of recorded locations (collected at a sampling rate of 30 minutes per location). Finally, our third model predicts performance based on the number of unique weeks, which is a measure of *temporal coverage*, quantifying both the length of the sampling window and the number of unique time periods represented within it. However, the number of unique weeks does not indicate the amount of data collected within each week. We included an interaction between the predictors and the binary variable indicating spread or concentrated data in the last two models, and all models have varying slopes and intercepts per group.

Finally, we compared the effects of increasing unique weeks versus increasing locations on the performance score. We did this by first z-score standardizing (by subtracting the mean and dividing by the standard deviation) the number of weeks and locations in each regime. This method centers the range of these predictors on zero so that they are on the same scale and can be more easily compared across models. Thus, one standardized unit is equivalent to one standard deviation away from zero. Next, we calculated the instantaneous slopes (or first derivatives) of the model predictions across various standardized units of weeks and locations. This is a way of measuring the rate of increase (or effect of increasing one standardized unit of weeks or locations on the performance score) at different levels along the posterior prediction curve. We chose three different standardized numbers (-1.30, -0.55, and 0.20) that designate three levels (low, medium, and high) and are meant to be representative points across the possible values of standardized weeks and locations. These three standardized numbers correspond to 21, 203, and 385 locations, and 1, 3 and 6 weeks.

Effective Sample Size

We analyzed estimates of the effective sample size, which is measured as the number of statistically independent locations within the sample (C. H. Fleming et al., 2019). The effective sample size is proportional to the mean number of times the animal reverted back toward the center of its home range (C. H. Fleming et al., 2019), or the mean number of times the animal crossed the linear extent of its home range (C. H. Fleming & Calabrese, 2017). It is estimated by dividing the sampling time (T) by the time-lag between locations required for independence (τ) (which is also roughly the average home range crossing timescale) (C. H. Fleming & Calabrese, 2017; Silva et al., 2021). The effective sample size provides more information on spatial variance than the number of observed locations (i.e., absolute sample size) (Silva et al., 2021), and is therefore a better indicator of the reliability of home range estimates (C. H. Fleming et al., 2019; Noonan et al., 2019).

As τ (i.e. the average home range crossing timescale) is integral to the calculation of the effective sample size, we compared estimates of τ from the movement models fitted to the 60 different sampling regimes to those estimated from the movement models fitted to the six complete segments. This procedure gives us a better understanding of how estimates of the effective sample size may be biased by missing data, which has important implications for the shape of the home range contours and the certainty of area estimates. If τ is underestimated, effective sample sizes will be positively-biased, which results in overconfident and misleading home range estimates. On the other hand, overestimating τ will result in negatively-biased effective sample sizes, leading to exceedingly large uncertainties.

For all practical purposes, we assumed values of τ taken from the movement models fit to the complete segments were the "true" home range crossing timescales. We used these values to estimate the "true" effective sample size for each sampling regime (i.e., what the effective sample sizes should be if the home range crossing timescales were accurately estimated), by dividing the sampling times (T) of the sampling regimes by the "true" τ values. Then we calculated the "estimated" effective sample size for each sampling regime by dividing T by the “estimated” τ values, which were instead taken from the movement models fit to the sampling regimes. Finally, we compared the “estimated” and the “true” effective sample sizes to evaluate any potential biases caused by the different sampling regimes.

It should be noted that the outputs of the fitted movement models already provide an estimate of the effective sample size which negates the need to manually calculate it. However, we chose to calculate the effective sample size as described above because it permits comparison across different models.

Ethical Note

The study was entirely observational; GPS devices were carried by observers instead of attached to the animals. All protocols were approved by UCLA's Animal Care Committee (protocol 2016–022), and all necessary permits were obtained from SINAC and MINAE (the Costa Rican government bodies responsible for research on wildlife) and renewed every 6 months over the course of the study; the most recent scientific passport number being #117-2019-ACAT and the most recent permit being Resolución # M-P-SINAC-PNI-ACAT-072-2019. This research follows the Animal Behavior Society’s Guidelines for the Use of Animals in Research.

Results

Spread Sampling Outperforms Concentrated Sampling

Spread sampling regimes were on average more accurate, estimating home ranges that more closely approximated the target performance score of 0.95 (posterior median = 0.93, 95% quantile interval: 0.87-0.96). Concentrated sampling regimes estimated home ranges that were more consistently negatively-biased (posterior median = 0.85, 95% quantile range: 0.61-0.91) (see Figure 4a). Additionally, spread sampling regimes were more robust than concentrated sampling regimes to low quantities of recorded locations and unique weeks (see Figure 4b and 4c). Generally, home range estimates for concentrated sampling regimes performed worse with fewer locations and weeks, but their confidence intervals remained consistently narrow. On the other hand, the performances for spread sampling regimes did not substantially decrease with fewer locations and weeks, but the confidence intervals around their home range estimates widened (see Figure 7).

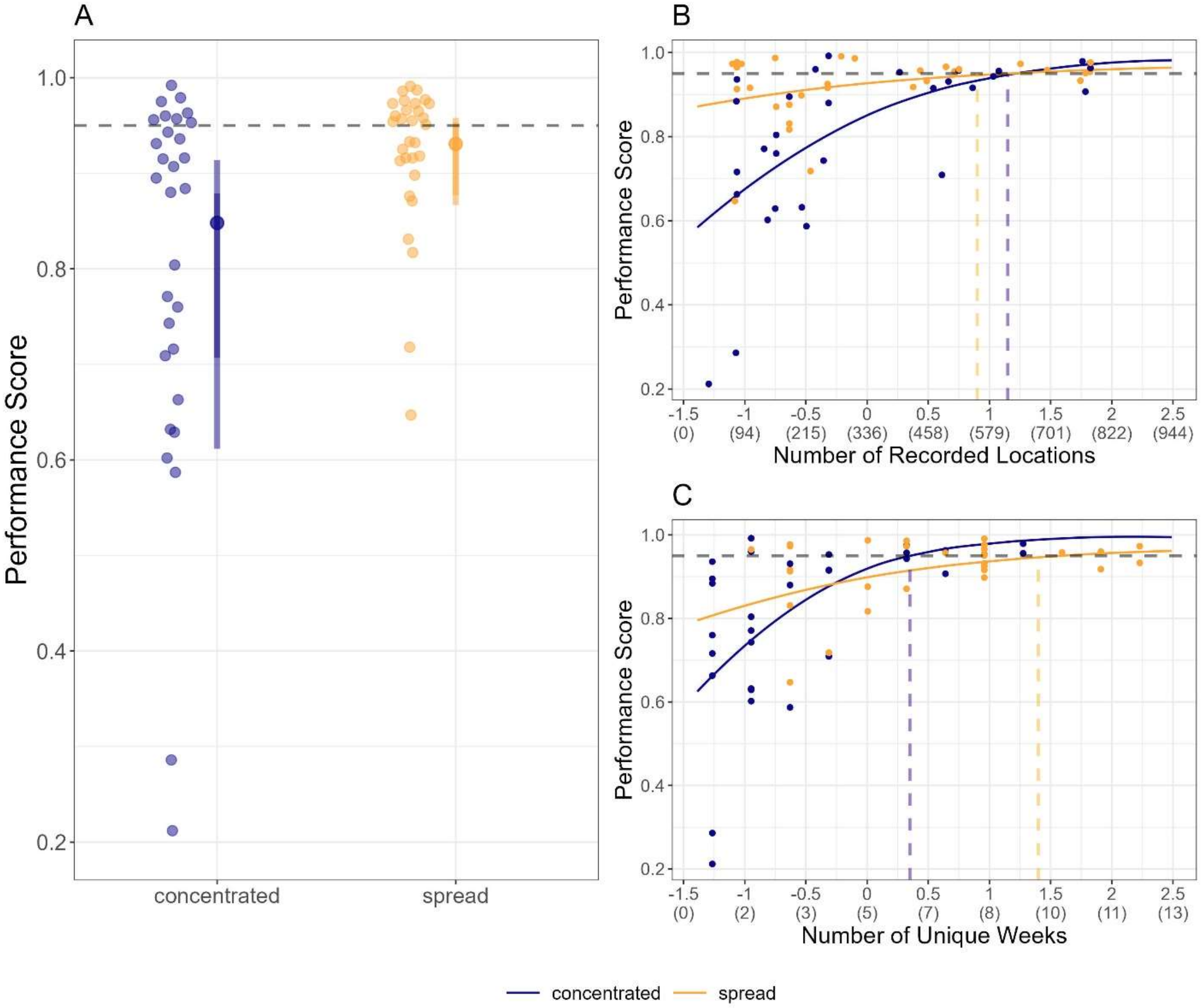

Figure 4: *Home range estimation performance predicted by characteristics of sampling*. A: Plot showing the home range estimation performance score predicted by whether the data was concentrated (blue) or spread (orange). Within these two categories, the raw data are shown on the left, and posterior point intervals are shown on the right. The posterior point intervals describe the median and 66% and 95% quantile intervals of the posterior distribution. B and C: Plots showing the model predictions for the effect

of number of locations (B) and number of unique weeks (C) within the sampling regimes on the performance score. Horizontal dashed line shows the optimal performance score of 0.95. The x-axis shows the z-score standardized locations and/or weeks, and the real-scale locations and/or weeks in parentheses. The dark solid lines are the mean posterior predictions; lighter lines (although difficult to see because they are very close to the mean) are 200 randomly sampled posterior predictions. The vertical dashed lines show the number of locations or weeks to achieve the optimum performance according to the posterior predictions. The plots showing the varying effects per group are shown on Figures 1, 3, and 5 in Appendix 3.

More Data is Not Always Better

We show that, when data are lacking, increasing the temporal coverage (measured by the number of unique weeks) in sampling regimes improves home range estimation performance more than increasing the absolute sample size (measured by the number of recorded locations). When concentrated sampling regimes had *low* absolute sample sizes and temporal coverages (*low* = -1.3 SD corresponding to 21 locations or one week), a +1 SD increase in locations (243 locations) improved performance of home range estimates by about 23% (Figure 5a). Meanwhile, a +1 SD increase in weeks (three weeks) boosted estimation performance by approximately 30% (Figure 5c). This implies that collecting as few as three locations on a weekly or less frequent sampling schedule can lead to better performance improvements than collecting 243 locations at a continuous 30-minute sampling rate.

With larger quantities of data already present in sampling regimes, adding more weeks and/or locations had less impact because the rate of improvement slowed down as it approached optimal performance. For instance, when concentrated sampling regimes had *medium* quantities of locations and weeks (*medium* = -0.55 SD corresponding to three weeks or 203 locations), a +1 SD in weeks and +1 SD in locations both improved performance by around 17%. At *high* quantities (*high* = 0.2 SD corresponding to six weeks or 385 locations), a +1 SD increase in weeks improved performance by about 8% and a +1 SD increase in locations improved performance by about 10%.

We found a similar trend for spread sampling regimes: increasing the number of weeks improved performance more than increasing the number of locations (Figure 5b and 5d). However, the effects of increasing both weeks and locations were much smaller compared to concentrated sampling regimes because spread sampling regimes already had performance scores relatively close to optimal even with *low* quantities of locations and weeks.

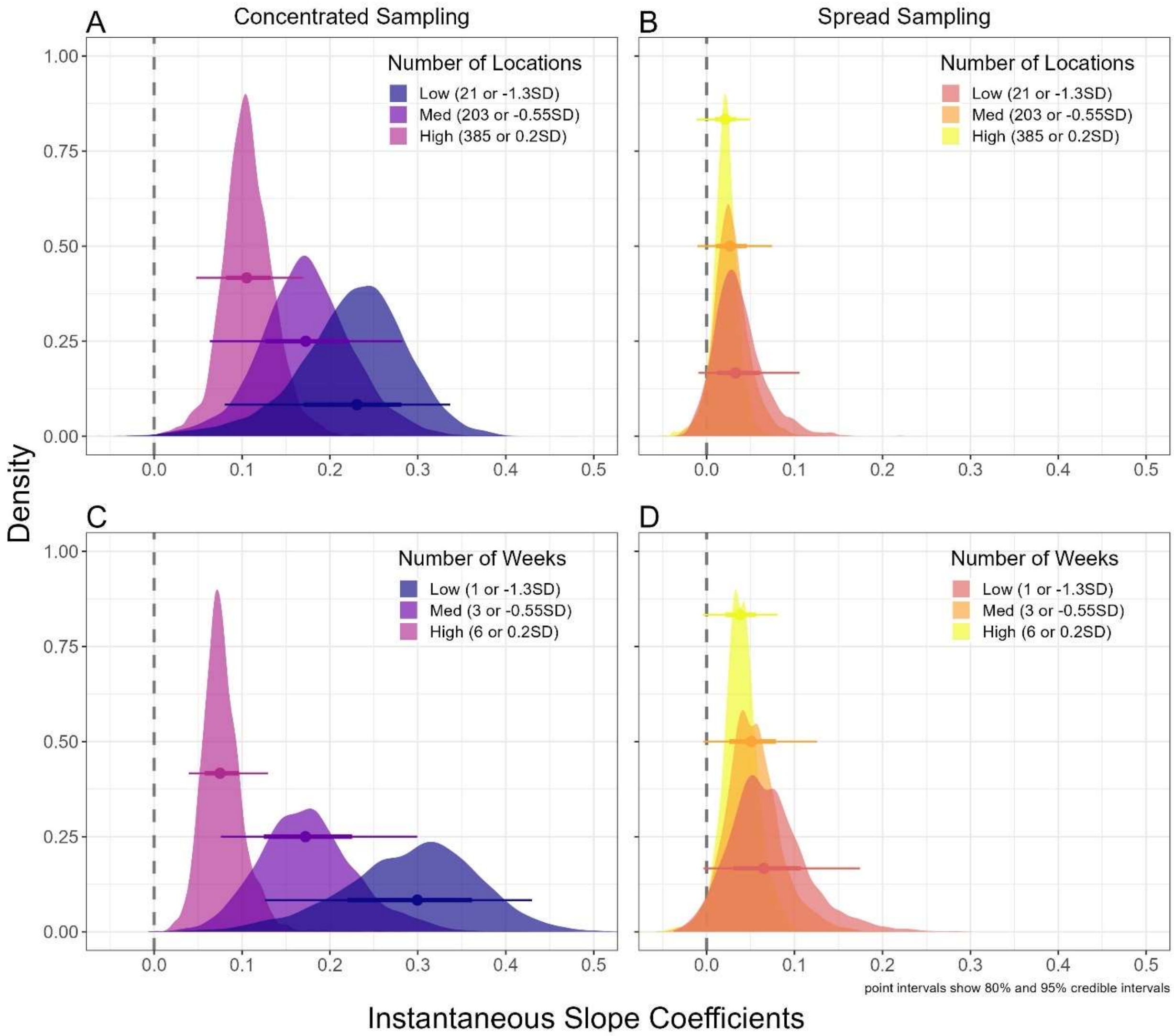

Figure 5: *Effects of increasing the number of locations and/or weeks on performance of home range estimates.* Half-eye plots showing the estimates and uncertainties of the instantaneous slope coefficients (or first derivatives) across a representative spectrum of standardized weeks and recorded locations. The instantaneous slope coefficients represent the effect of increasing one standard deviation in weeks or locations on the home range estimation performance score. Plots A and C (Blue-purple colors) represent concentrated sampling regimes, and plots B and D (orange-yellow) represent spread sampling regimes. Darker colors represent smaller units, and lighter colors represent greater units of weeks or locations.

Concentrated Sampling is Prone to Bias in the Effective Sample Size

We found that missing data can result in biased effective sample size estimates, particularly for concentrated sampling regimes. Differences between the "estimated" and the "true" effective sample size for most sampling regimes were within a relatively reasonable range (~20). Even so, several concentrated sampling regimes with seemingly adequate absolute sample sizes (~300-500 locations) and total time sampled (~10-20 full tracking days) had substantially positively-biased (e.g. by ~50-220) effective sample sizes (within Figure 6, see sampling regime IDs C2, C3, and C4 in CE group and C2 in FL group). The effective sample size biases resulted in home range estimates with high levels of certainty, but very low performance scores (see Figure 7).

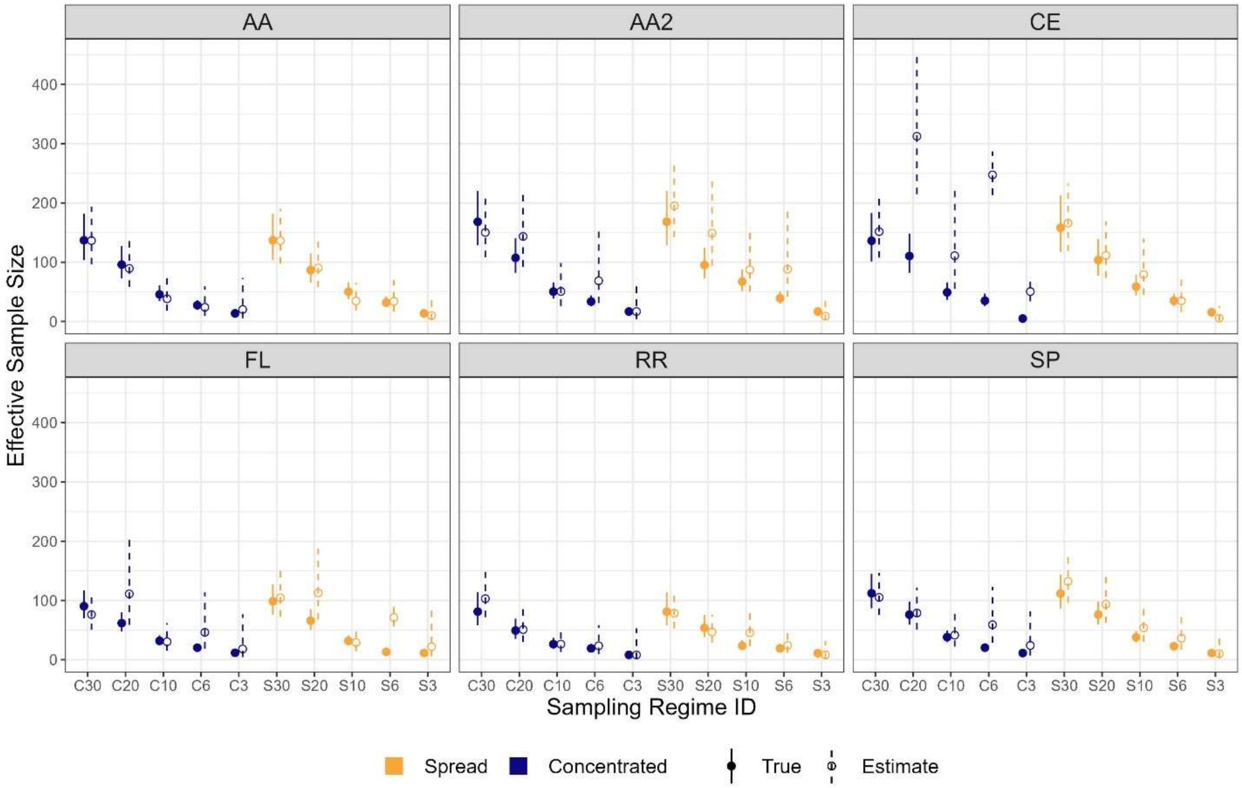

Figure 6: *Bias in effective sample size estimates.* Plot showing the comparison between the "estimated" effective sample size (open circles indicate the means; dashed lines indicates 95% confidence intervals) and the "true" effective sample size (closed circles indicate the means; solid lines indicate the 95% confidence intervals) across all 60 sampling regimes (6 groups with 10 sampling regimes each). Colors indicate whether the sampling regime had concentrated (blue) or spread (yellow) data.

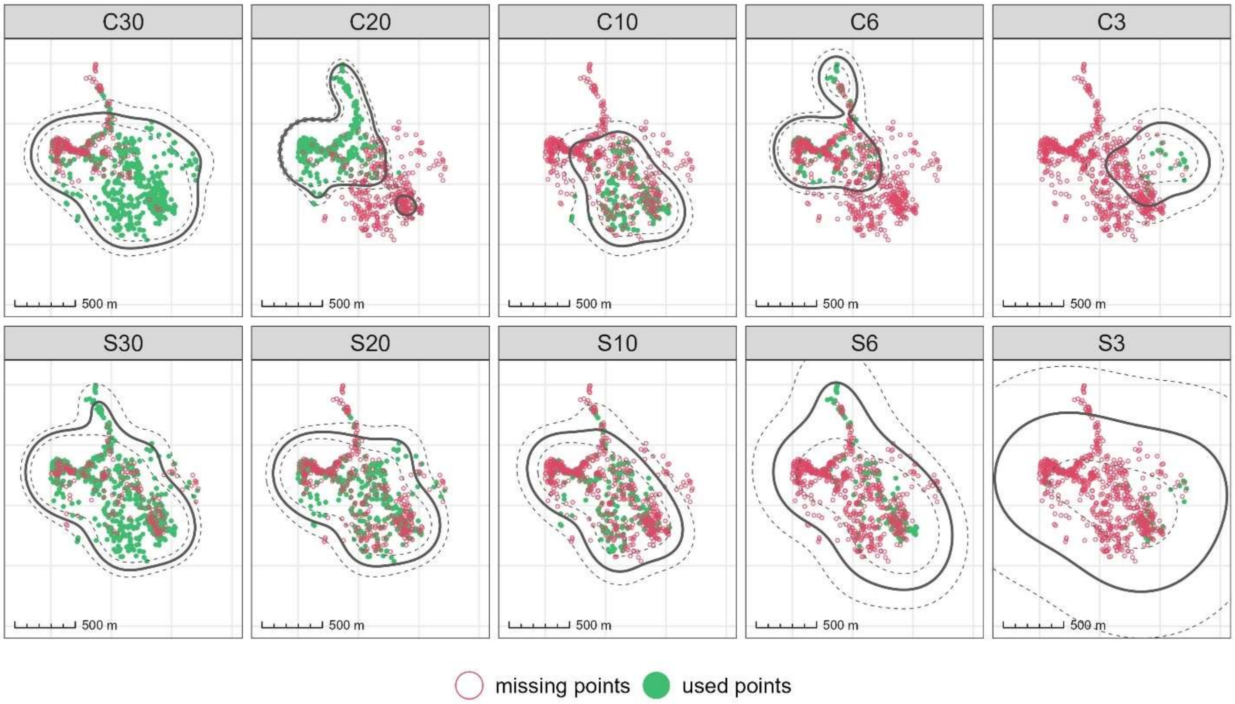

Figure 7: *Impact of biased effective sample sizes on home range estimation confidence and performance***.** This plot shows an example from CE group of the 10 home range estimates from the sampling regimes plotted over the total data of the complete segment (see Appendix 2 for all groups). The dark lines indicate the mean 95% UD contour and the dotted lines indicate the 95% confidence intervals. The open pink points indicate the locations that were thinned and the filled green points indicate the locations that remain in the emulated sampling regimes. The top row shows the concentrated sampling regimes and the bottom row shows the spread sampling regimes. Sampling Regime IDs C20, C10, C6 and C3 produced home range estimates with poor performances, but also positively-biased effective sample sizes which resulted in misleading confidence intervals.

Discussion

Our study demonstrates that temporal coverage is a more important factor than the quantity of data for home range estimation. Advances in GPS technology are allowing researchers to collect data at increasingly high frequencies, but our results suggest that this does not necessarily translate into more accurate home range estimates. This is in line with other recent studies (Noonan et al., 2019) which caution that increasing the sampling rate often does little to improve the accuracy of home range estimates due to the high level of redundancy in information when locations are close together in time. Researchers are encouraged instead to focus on sampling regimes that will increase the “effective” sample size – which is approximately the number of times the animal crossed the linear extent of its home range during sampling (C. H. Fleming & Calabrese, 2017)(see Methods section for a more detailed explanation).

Encouragingly for researchers who use handheld GPS data for home range estimation, our study highlighted that random gaps in data collection are not inherently detrimental for home range estimation accuracy. In fact, sampling regimes that sacrificed continuous observation for greater temporal coverage vastly outperformed sampling regimes that were continuous but concentrated into short time periods, even when effective sample sizes were equal. While this may not be an intuitive finding, consider that wider sampling windows provide more time for animals to use the full extents of their home range. Even if sampling gaps result in unobserved home range crossings (thus reducing effective sample sizes), spread-out data will capture more variation in space-use. Therefore, sampling regimes with longer durations should be more representative of an animal’s total space-use, provided that sampling gaps do not cause important variation to go uncaptured.

Another key finding was that concentrated sampling sometimes lead to positively-biased effective sample sizes, resulting in over-confident home range estimates. To explain this, we can again consider the biological processes behind home range use. Species that forage on ephemeral and patchily distributed resources, such as fruit-eating primates, must allocate time differentially across their home range so that search efforts align with when and where resources are most productive (Altmann, 1974; Janson, 2019). White-faced capuchins are known to do this by foraging for extended time periods in small areas (Oppenheimer, 1968), and then shifting within their home range in response to changes in resource availability (Campos et al., 2014). We observed this in our study, as some groups remained within one side of their home range for up to several weeks before moving to the other side, which was surprising given that the average home range crossing time across all groups was about one day. These movement patterns are difficult to predict relative to those of most leaf-eating primates, which tend to move in constant patterns, as their food resources are more evenly distributed (Reyna-Hurtado et al., 2018).

As a consequence of capuchin groups temporarily confining their movements within sub-areas of the home range, movement models fitted to data concentrated within these periods overestimated the effective sample size. This is because the capuchin groups repeatedly traversed this smaller area, which lead to underestimated home range crossing times, and therefore overestimated observed home range crossings. Subsequently, the large effective sample sizes from these samples suggested high quality home range estimates, although in reality they were too small (see Figure 7 – C20, C10, C6, and C3). This highlights the importance of examining home range estimate outputs in the context of the biology of the species, and not relying on statistical criteria alone.

Linking Biology to Temporal Scale

It is common practice to report home range estimates at several standardized temporal scales (e.g. monthly, quarterly, half-annually, annually), as the results are thought to change depending on the length of the sampling window (Börger et al., 2008; Campos et al., 2014; White & Garrott, 1990). This is particularly true up until a sufficient effective sample size is reached, or when home ranges are non-stationary, such as for groups of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), which shift their home ranges over time (Li et al., 2001). However, when home ranges are relatively stable, which is the case for many primate species (Janmaat et al., 2009; Jolly & Pride, 1998; Poirier, 1968; Singleton & van Schaik, 2001), widening the sampling window should have little effect after a sufficient effective sample size is reached (C. Fleming et al., 2014). At this point, the estimated home range area should have reached a plateau, ceasing to increase with more sampling. The amount of sampling time it takes to reach this plateau depends upon the home range crossing timescale of the animal.

Applying standardized sampling schedules to species with different home range crossing times can introduce bias in cross-species comparisons (C. H. Fleming & Calabrese, 2017). Additionally, when an animal's home range crossing time is relatively long, shorter time scales such as monthly or quarterly may not be sufficient to estimate their home range accurately. If not reported correctly, these results may misinform metanalyses or conservation plans. A more justifiable approach is to design the sampling window corresponding to how long it takes for the animal to cross its home range. With this practice, researchers can make well-founded comparisons across different species and sampling designs, and avoid potential biases introduced from applying standardized sampling routines to species with different home range crossing times (C. H. Fleming & Calabrese, 2017).

When designing sampling regimes, it is important to note that the time it takes to cover the home range varies widely across species. Broadly speaking, home ranges tend to be larger for frugivores (compared to folivores) (Milton & May, 1976) and large-bodied species (compared to small-bodied species) (Terborgh & Janson, 1986) - which usually translates into longer home range crossing times, assuming that movement speeds are approximately the same. Group-living species, such as gray langurs (*Presbytis entellus*)(Jay, 1965), chimpanzees (Pan troglodytes)(Nishida, 1968), and yellow baboons (*Papio cynocephalus*) (Altmann & Altmann, 1970) tend to have much longer home range crossing times than solitary species (Milton & May, 1976). Meanwhile, territorial species, such as gibbons (*Hylobatidae*) (Cheney, 1986), red-bellied titi monkeys (*Callicebus moloch*) (Mason, 1968), and vervet monkeys (*Chlorocebus pygerythrus*) (Reyna-Hurtado et al., 2018) generally have much shorter home range crossing times than non-territorial species as they must traverse across their home range rapidly to defend their borders against neighboring conspecific groups (Mitani & Rodman, 1979). However, some non-territorial species may also move rapidly across their range, such as the highly mobile squirrel monkey (*Saimiri oerstedi*), which can use 75-90% of its home range in a single day (Baldwin & Baldwin, 1972).

To ensure that sampling regimes are sufficient to estimate accurate home ranges, they should be designed so that the sampling window is much longer than the average home range crossing time

(Noonan et al., 2019). Nonetheless, the average home range crossing time differs across species and ecological contexts. Also, as we have demonstrated, home range crossing times can be underestimated fairly easily depending on the underlying movement behavior of the animal. To avoid these potential biases and determine the appropriate temporal scale for sampling regimes, it can be extremely valuable to have a field-based approximation of the home range crossing time for the species of interest.

For reference, the capuchin groups in our study had a mean home range crossing timescale of 12.5 (95% CI: 9.4-16.7) hours, which is about one day considering that they very rarely move at night. Given this, sampling regimes required ~100-600 locations spread over ~5-7 unique weeks to optimize home range estimation performance. A relatively similar sampling time (45 to 136 days) was required for a study on giant anteaters (*Myrmecophaga tridactyla*), who found that they had a home range crossing time of about 2 days on average (Giroux et al., 2021). By comparison, a study on elongated tortoises (*Indotestudo elongata*) found that they crossed their home range once every 17 days on average (although sometimes much longer), and even with up to one year of consistent sampling, were not able to achieve adequate effective sample sizes for several of their focal animals (Montano et al., 2021).

Relevance of Sampling Regime for Conservation

It is notable that, in our study, effective sample size bias was most problematic for groups that have the most fragmented habitats from roads and pastures (see CE and FL group in Figure 6). Sampling regimes for these groups also required more locations and unique weeks to accurately estimate the home range compared to other groups (see Figure 3 and 5 in Appendix 3). This may be because individuals in these groups perceive crossing the home range as riskier (Frid & Dill, 2002) or more energetically expensive (Huang et al., 2017). Thus, it may be favorable to deplete local resources before commuting long distances. Indeed, human-related disturbances have restricted and reduced the movements of mammals (Tucker et al., 2018), including primates (Pereira et al., 2022), across the globe. However, such disturbances may only delay movements until individuals are desperate, and moving between fragmented habitats becomes essential to find certain resources (Bonelli et al., 2013; Lens & Dhondt, 1994; Panzacchi et al., 2013; Schtickzelle et al., 2006). If habitat fragmentation delays movements across animal home ranges, then gathering sufficient data for home range estimation may take more time than expected. Sampling regimes that don't provide enough time for the animals to cross between fragments will underestimate their home range crossing time, and therefore will have highly biased effective sample sizes.

It is particularly worrying that species that are of the greatest conservation concern are perhaps the most prone to biased home range estimates. For instance, large-bodied species with long home range crossing times, which are the species most vulnerable to extinction (Cardillo et al., 2005), have been found to be the most likely to have underestimated home range areas (Noonan et al., 2020). Similarly, our findings suggest that animals that live in fragmented habitats are prone to effective sample size bias. As we have demonstrated, this bias can lead to both overconfident and underestimated home range estimates. This is highly concerning from a conservation standpoint given that underestimated home range estimates may lead to the establishment of protected areas which don't accommodate enough space for populations to survive and reproduce (Brashares et al., 2001; Gaston et al., 2008). Therefore, it is crucial that sampling for home range estimation be designed carefully around the ecological context and behavior of the study species, especially when conservation initiatives use these results to inform management decisions.

Conclusions and Recommendations for Sampling Design

GPS data collection is a component of almost all modern primate field studies (Janmaat et al., 2021), and home range estimates are one of the most sought-after outputs of these data. However, reliable home range estimates can be compromised when sampling is insufficient to adequately capture the biological home range, or through inappropriate application of statistical approaches, which is a concern given that home range estimates are key elements of ecological inference and conservation guidance.

To ensure that biologists design appropriate sampling regimes (balancing effort with temporal coverage), it is important to understand (a) the target distribution we are aiming to estimate, (b) what we should be aiming for in terms of "good quality" data and (c) how we can tell 'how much is enough?'.

When we are aiming to estimate the home range according to Burt's original definition, we are targeting the range distribution. This is the space needed by the animal to survive and reproduce, which includes both the space used during the sampling period and the space that will eventually be used in the future (J. Alston et al., 2022). If we are targeting the occurrence distribution, then we are only interested in the space used during the sampling period, which essentially is an attempt to fill in the gaps between observed locations. The best quality data for the occurrence distribution is therefore when the sampling rate is at the highest possible, as this will produce estimates closest to the animals' actual movement path (Börger et al., 2020). When the range distribution is the target, the best quality data is when the effective sample size, or number of observed home range crossings, is maximized (C. H. Fleming & Calabrese, 2017). As we have demonstrated, this is best accomplished by increasing the temporal coverage of sampling, rather than the sampling rate. With this in mind, we recommend the following guidelines for estimating the range distribution from handheld GPS data:

1. Design sampling protocols based on an informed understanding of the study species. One should consider their home range crossing time and whether they are prone to changes in space-use patterns over time. Conducting a pilot study may be necessary to gather this information. Alternatively, researchers can utilize a new application called *Movedesign*, which employs continuous-time movement modeling principles to help identify the most suitable sampling design for their specific data and study species (Silva et al., 2023).

2. Aim to maximize the effective sample size by designing the sampling window to be considerably longer than the average home range crossing time. Anything lower than 10 observed home range crossings tends to be problematic (C. H. Fleming et al., 2018), and

researchers should aim for even higher sample sizes to ensure that home range estimates are robust.

3. When missing data cannot be avoided, aim to sample over longer time periods at regular intervals rather than concentrating sampling efforts into short periods.

4. If it is necessary to use standardized sampling schedules (e.g. weekly, monthly, quarterly, seasonally, annually, etc.) it is advisable to avoid short temporal scales, especially when the species has a long home range crossing time. Opting for sampling time scales that either align with the biology of the species, such as seasonal sampling, or are sufficiently long and comparable across studies, such as annual sampling, is preferable.

5. Consider reevaluating data collection priorities that could lead to missing movement data, such as collecting behavioral data from more groups than can be observed at a single time. Determine whether the temporal coverage or number of individuals/groups is more critical. Develop adaptable protocols that reduce bias in home range estimation for the focal individuals or groups while having minimal or no impact on other aspects of data collection.

6. Be explicit with the limitations of handheld GPS data. If missing data are caused by the inability of researchers to follow primates in particular areas or at particular times, then home range analysis may not be appropriate.

7. After data collection, it is important to check if there are enough data for home range analysis. One way to do this is by using variogram regression (see Appendix 1), which visually evaluates whether diffusion rates have stabilized (C. Fleming et al., 2014). If the sampling time is significantly longer than the time-lag required for the variogram curve to plateau, then there is likely sufficient data for home range analysis. Another approach is to plot home range area over time to see if it has reached a plateau.

8. If the data meets the requirements for home range estimation, utilize an estimator that considers autocorrelation and other potential biases. Our suggestion is to use the AKDE method (see Appendix 1 for a detailed walkthrough). In addition, recent advancements in this technique have enabled the integration of habitat components to refine the home range estimate (J. M. Alston et al., 2023). This is particularly beneficial as it reduces the importance of areas that are less likely to be utilized by the animal, such as bodies of water or pastures.

In general, we acknowledge the immense potential of longitudinal movement data in shedding light on important ecological questions. At present, we lack an understanding of how ranging patterns are influenced by enduring factors such as climate change, environmental disturbance, demographics, and social learning. Given that primate studies regularly gather longitudinal data on movement, environmental variables, behavior, and demographics, they may be in a unique position to address these inquiries and connect them to fitness. Nonetheless, our study has revealed that the usefulness of movement data in estimating home ranges depends on whether the sampling regimes have adequate temporal coverage for the focal animals to utilize their entire home range. Therefore, primatologists should be cautious in designing their sampling protocols to ensure that they accurately represent the biological home range of the species under investigation.

Supplementary Information

Supporting information detailing home range estimation using AKDE (Appendix 1), the results of home range analysis from every sampling regime in our study (Appendix 2), and additional information on the statistical analysis (Appendix 3) are available online.

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Conflict of Interest

The authors declare no financial or non-financial conflicts of interest.

Data Availability Statement

The datasets generated and/or analyzed during the current study are available in a public anonymized github repository found here: https://anonymous.4open.science/r/CH1_Sampling-CEB3/README.md. We will deposit them in Zenodo or Movebank in a DOIed repository upon acceptance.

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Appendix 1: Home Range Estimation using Autocorrelated Kernel Density Estimation

April 19, 2023

I. Background

The purpose of this appendix is to detail the steps to estimating a home range (HR) using continuous-time movement modelling and the *ctmm* package. This document can be used as a practical guide, where one can use our practice dataset or one's own data to walk-through the analytical process.

Accounting for autocorrelation is important so that we avoid biases in our results. However, it requires some additional steps compared to most conventional estimators, which is why we describe the process and provide an example workflow. We strongly recommend going through the *ctmm* vignettes (see https://ctmm-initiative.github.io/ctmm/index.html) for a more detailed review.

Generating a home range estimate from movement data using continuous-time movement modelling involves three main steps: 1) variogram inspection, 2) model fitting and selection, and 3) Autocorrelated Kernel Density Estimation (AKDE). This process can either be done using the *ctmm* package in the R environment for statistical computing (R Core Team 2022), or using the *ctmmweb* point-and-click graphical user interface (Calabrese et al. 2021), which streamlines the modelling steps, helping users conduct home range analysis without the need to know the R programming language. We describe the process using R below:

The first step is to load the necessary packages and prepare the data

```r
# you can install ctmm from CRAN, but better to get the development version for recent
 ↪  updates
devtools::install_github("ctmm-initiative/ctmm")

# load packages
library(tidyverse)
library(ctmm)
```

II. Prepare Data

The data must have the same format as the following dataframe with the same column names. These are the same format required by *Movebank*. Either you can manually edit the dataframe and then convert to a telemetry object, or put data on Movebank and import from there, which will automatically put the data in the correct format.

Note: `individual.local.identifier` (ILI) specifies the unique ID (usually individual or group) that you want the home range estimate for. At the bottom of the document, we also include some example code of how to do all of the below analysis in a single step for a list of several ILIs.

In our study, the ILI indicated the different sampling regimes. "All" was the ILI for the complete segments. For this walkthrough, we will use the data from the complete segment of SP group, and change the ILI to the group.

```
# read in data frame
# filtering data from SP group, and taking the data from the complete segment - denoted
 ↪  as "all"
DATA <- read.csv("Data/CH1_GPS_data.csv", row.names = NULL) %>%
  filter(group == "SP" & individual.local.identifier == "all") %>%   #select the complete
   ↪  segment from SP group (could pick any group)
  dplyr::select(-individual.local.identifier) %>% # remove prev ILI column
  rename(individual.local.identifier = group) # make group the new ILI
```

The data should should look like this (these are the first six rows):

```
head(DATA)
```

```
##   individual.local.identifier           timestamp location.long location.lat
## 1                          SP 2010-09-12 05:00:00     -85.37901     10.50080
## 2                          SP 2010-09-12 05:30:00     -85.37907     10.50041
## 3                          SP 2010-09-12 06:00:00     -85.37932     10.49956
## 4                          SP 2010-09-12 06:30:00     -85.37947     10.49877
## 5                          SP 2010-09-12 07:00:00     -85.37920     10.49790
## 6                          SP 2010-09-12 07:30:00     -85.37858     10.49784
```

Once the dataframe is in the correct format, convert it to a telemetry object and specify the UTM projection:

```
# convert data to telemetry object
DATA <- DATA %>%
  as.telemetry(projection = "+proj=utm +zone=16 +north +datum=WGS84 +units=m +no_defs
   ↪  +ellps=WGS84 +towgs84=0,0,0")
```

Plot the data:

```
# plot location data
plot(DATA, main = "Location Data")
```

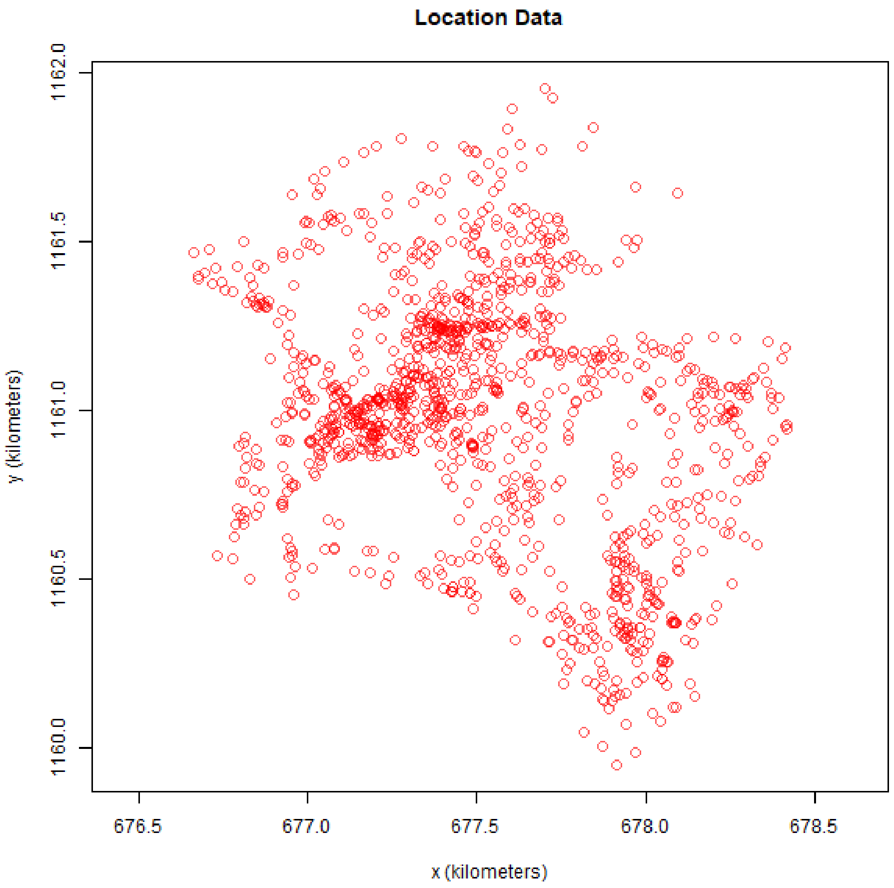

Figure 1: Location data from the complete segment of SP group

III. Variogram Inspection

Variograms plot the semi-variance (y-axis), which is a measure of the average squared displacement, as a function of the time-lag that separates any pair of observed locations (Diggle and Ribeiro 2007; Silva et al. 2021). Variograms play two major roles in the *ctmm* workflow: first, they provide an unbiased visual diagnostic to assess the autocorrelation structure present in the data, and second, they inform whether the data shows evidence of range residency (Silva et al. 2021). Asymptoting curves in a variogram indicate range residency. Where the asymptote aligns with the x-axis is a measure of the necessary time-lag between positions to assume independence (Silva et al. 2021). It is also a rough estimate of the home range crossing time (Christen H. Fleming and Calabrese 2017). If the curve continues to increase without flattening, the animals are either non-resident (i.e. home range drift or migration), or not tracked long enough to capture the full extent of their home range (Calabrese, Fleming, and Gurarie 2016).

Once the data are confirmed to represented range-restricted movement, we can proceeded with model fitting and selection. It is necessary to confirm range-residency before conducting home range estimation because, while ctmm is capable of fitting both range-resident (the default) and endlessly diffusing movement models, only the first set are appropriate for home range estimation.

```
SVF <- variogram(DATA, dt = c(1,10) %#% "hour") # dt argument changes the width of the
↪  time-lag bins (makes variogram smoother)
plot(SVF, main = "Empirical Variogram")
```

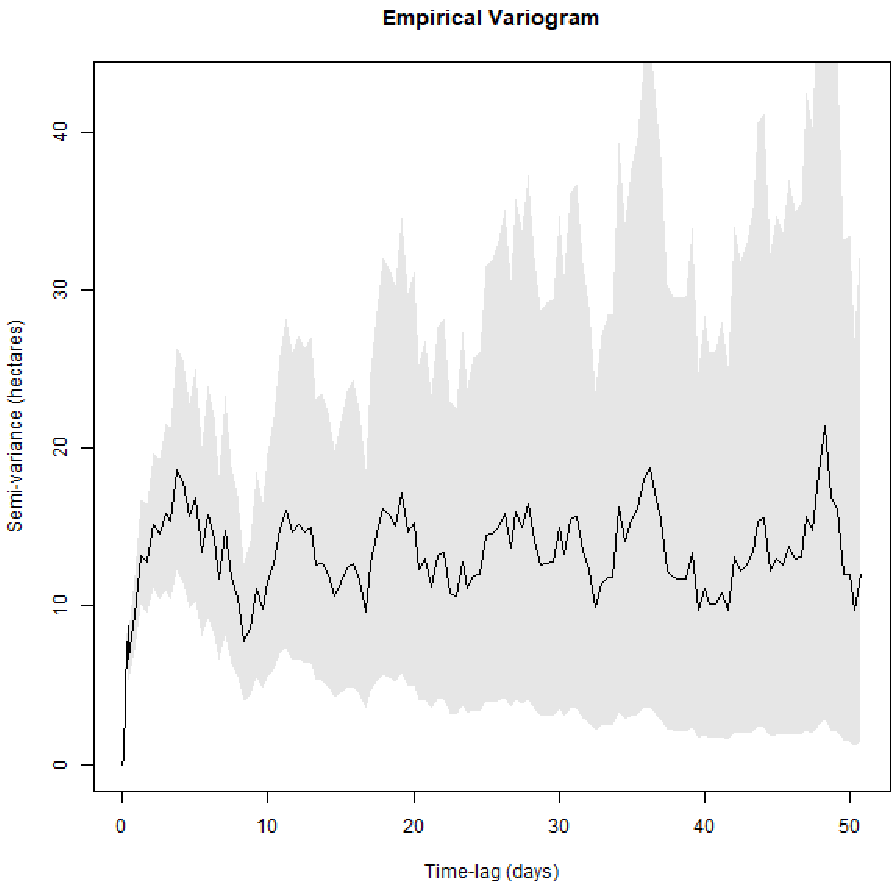

Figure 2: Empirical variogram from the complete segment of SP group

This is a plot of the empricial varigram. The line asymptotes at approximately three days. This is roughly the average home range crossing time. This is also approximately how far apart locations need to be in time for them to be independent (https://ctmm-initiative.github.io/ctmm/articles/variogram.html).

IV. Movement Model Selection

Model fitting also involves two steps: first the `ctmm.guess` function uses the shape of the empirical variogram to generate starting values required for the non-linear models, and second, the `ctmm.select` function uses the values calculated from `ctmm.guess` to fit a range of alternative stationary (and range-restricted) movement models using Maximum Likelihood (Christen H. Fleming et al. 2014). Models are ranked by AICc (Akaike information criterion) allowing us to evaluate which model or models best predict the data. This process permits identification and fit of a stationary movement model that corresponds to the observed movement behavior of the animal (Christen H. Fleming et al. 2014).

It is worth noting that here, stationary means that the underlying movement processes are assumed to be consistent throughout the duration of the data. Movement model parameters represent time-averaged values, which has important implications on how data should be segmented for home range analysis. If the underlying parameters change drastically within the sample—particularly the mean location—then the stationary assumption has been violated. Therefore, it is common practice to segment the data when the parameters change and estimate separate ranges. This is consistent with Burt's original concept of the home range where, for example, he stated winter and summer ranges for migratory species should be considered separately with the travel between as transit (Burt 1943). In our case, all sampling regimes were from single, stationary ranges which negated any need for further segmentation.

The pool of potential movement models which involve home range behavior include:

1) *Independent and Identically Distributed* (IID) – location data has uncorrelated positions and velocities.
2) *Ornstein–Uhlenbeck* (OU) – location data has autocorrelated positions and uncorrelated velocities.
3) *OU Foraging* (OUF) – location data has autocorrelated positions and velocities (Calabrese, Fleming, and Gurarie 2016; C. Fleming et al. 2014; Christen H. Fleming et al. 2014)

OU and OUF can be further specified with isotropic or anisotropic versions of each. Isotropic means diffusion is equal on every extent of the home range, while anisotropic means diffusion is asymmetrical (Silva et al. 2021).

Endlessly diffusing movement models (non-HR models) such as *brownian motion* (BM) or *integrated OU* (IOU) cannot be statistically compared to HR models using maximum likelihood (see `?ctmm.select`). To fit these movement models, one must manually specify them.

```
# get starting values for models
GUESS <- ctmm.guess(DATA,interactive=FALSE, variogram = SVF)

# fit models and select top one, trace = 2 allows you to see progress
FIT <- ctmm.select(DATA,GUESS,trace=2)
```

```
# see model summary for top model
summary(FIT)
```

```
## $name
## [1] "OUF anisotropic"
##
## $DOF
##       mean       area  diffusion      speed
##   49.56111   81.16699  346.58408 1183.63214
##
## $CI
##                                   low       est      high
## area (square kilometers)  2.054622  2.586565  3.178821
##  [position] (hours)      10.561126 13.624460 17.576337
##  [velocity] (minutes)    21.251008 23.651631 26.323441
## speed (kilometers/day)    5.282984  5.437900  5.592755
## diffusion (hectares/day) 39.214897 43.694482 48.412835
```

The top model selected for our practice dataset was *OUF anisotropic*. Above is the summary information for that model. The `$DOF` specifies the effective sample sizes. The most important one for home range estimation being under `area` which indicates the number of statistically independent points (or approximately the number of home range crossings – see Methods in the main text).

The `area (square kilometers)` slot indicates the Gaussian area, which is an estimate of spatial variance, but is not our AKDE area. `tau[position] (hours)` is the tau referenced in the main text. This is time necessary between locations for them to be independent, or approximately the home range crossing timescale. `tau[velocity] (minutes)` is the timescale necessary for the velocities to be independent. Estimates of speed (i.e. proportional to average daily travel distance) and diffusion rate are also included.

```
# plot empirical variogram with best model
plot(SVF, CTMM = FIT, main = "Variogram and Fitted Model")
```

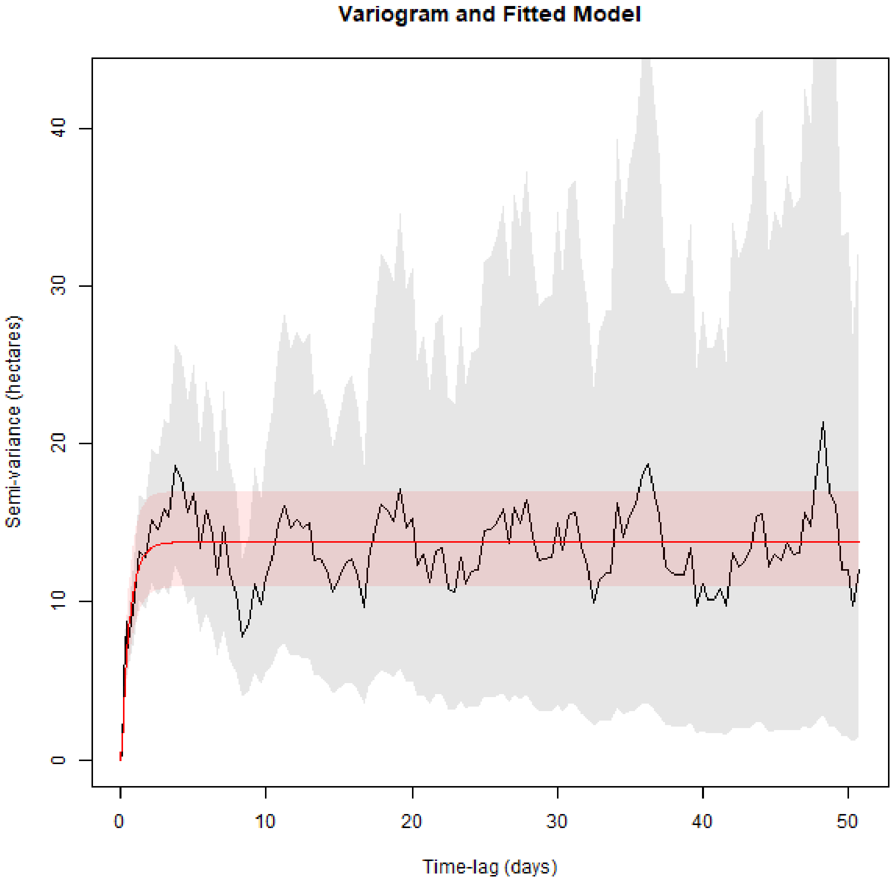

Figure 3: Top movement model fitted to the empirical variogram

V. AKDE Home Range Estimation

The final step is to calculate an autocorrelated kernel density home-range estimate (AKDE) using the eponymously named `akde` function (Calabrese, Fleming, and Gurarie 2016). This function takes the movement data and the corresponding fitted model and returns: a utilization distribution (UD) object corresponding to the range distribution, information on the optimal bandwidth, point estimates and confidence intervals for HR area, and a measure of the effective sample size of the data for home range estimation. For the sampling regimes in our study, we also included the `weights = TRUE` option, which helps correct for irregular and missing data by down-weighting over-sampled portions of the data and up-weighting under-sampled portions (C. H. Fleming et al. 2018). This helps to offset sampling bias, but is not sufficient if large portions of the true range are missing from the sampled data.

```
# get UD using AKDE
UD <- akde(DATA, FIT, weights = TRUE)
```

```
# plot UD over location data
plot(DATA,UD = UD, main = "AKDE Home Range Estimate")
```

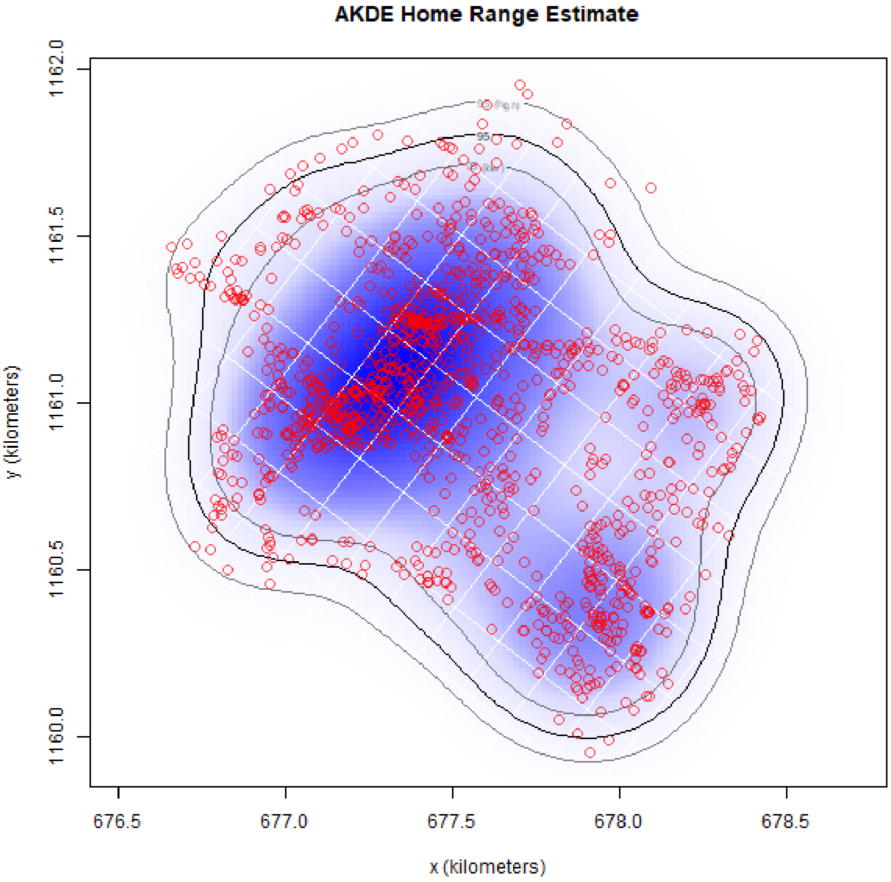

Figure 4: Home range estimate (95% utilization distribution) mean contour and 95% confidence intervals plotted over location data

Below is the summary information:

```
summary(UD)
```

```
## $DOF
##      area bandwidth
##  81.16699 145.73448
##
## $CI
##                                  low      est     high
## area (square kilometers) 1.745174 2.197001 2.700057
##
## attr(,"class")
## [1] "area"
```

The effective sample size (DOF area) is the same as from the fitted model. In this case, there was about 81 observed home range crossings in the data. The `area (square kilometers)` slot shows the estimated home range area and 95% confidence intervals.

VI. Bulk analysis for several individuals or groups

Below is code to demonstrate how to perform the above analysis with multiple individuals or groups in one step using a loop (may take a little while to run, ~20min).

```
## PREPARE DATA
# take only complete segments (all)
# make group the new individual.local.identifer (ILI)
# change to tele object
DATA_bulk <- read.csv("Data/CH1_GPS_data.csv", row.names = NULL) %>%
  filter(individual.local.identifier == "all") %>% # take only complete segments
  dplyr::select(-individual.local.identifier) %>% # remove prev ILI column
  rename(individual.local.identifier = group) %>% # make group the new ILI
  as.telemetry(projection = "+proj=utm +zone=16 +north +datum=WGS84 +units=m +no_defs
   ↪  +ellps=WGS84 +towgs84=0,0,0")

# note: when there are multiple individual.local.identifiers, as.telemetry makes a list,
 ↪  with each
# individual.local.identifier being an element in the list
# variograms, model fits, and UDs follow the same list format

# make empty lists to be filled by below loop
UDs <- FITs <- SVFs <- list()

## BULK CALCULATIONS
# for every ILI, make a variogram (SVF), get starter values (GUESS), select model (FIT),
 ↪  and calculate AKDE (UD)
# grid argument in akde aligns UDs so that overlap function is possible if desired later
 ↪  on
for(i in 1:length(DATA_bulk)){
  SVFs[[i]] <- variogram(DATA_bulk[[i]])
  GUESS <- ctmm.guess(DATA_bulk[[i]],interactive=FALSE, variogram = SVFs[[i]])
  FITs[[i]] <- ctmm.select(DATA_bulk[[i]],GUESS,trace=2)
  UDs[[i]] <- akde(DATA_bulk[[i]],FITs[[i]], weights = TRUE,
 ↪  grid=list(dr=10,align.to.origin=TRUE))
}

# make names of variograms, fits, and UDs the same as data
names(UDs) <- names(FITs) <- names(SVFs) <- names(DATA_bulk)
```

```
# make color blind pallette
colorblind_pal <- c("#E69F00", "#56B4E9", "#009E73", "#F0E442", "#D55E00", "#CC79A7")

# plot together
plot(UDs, col.DF=colorblind_pal)
```

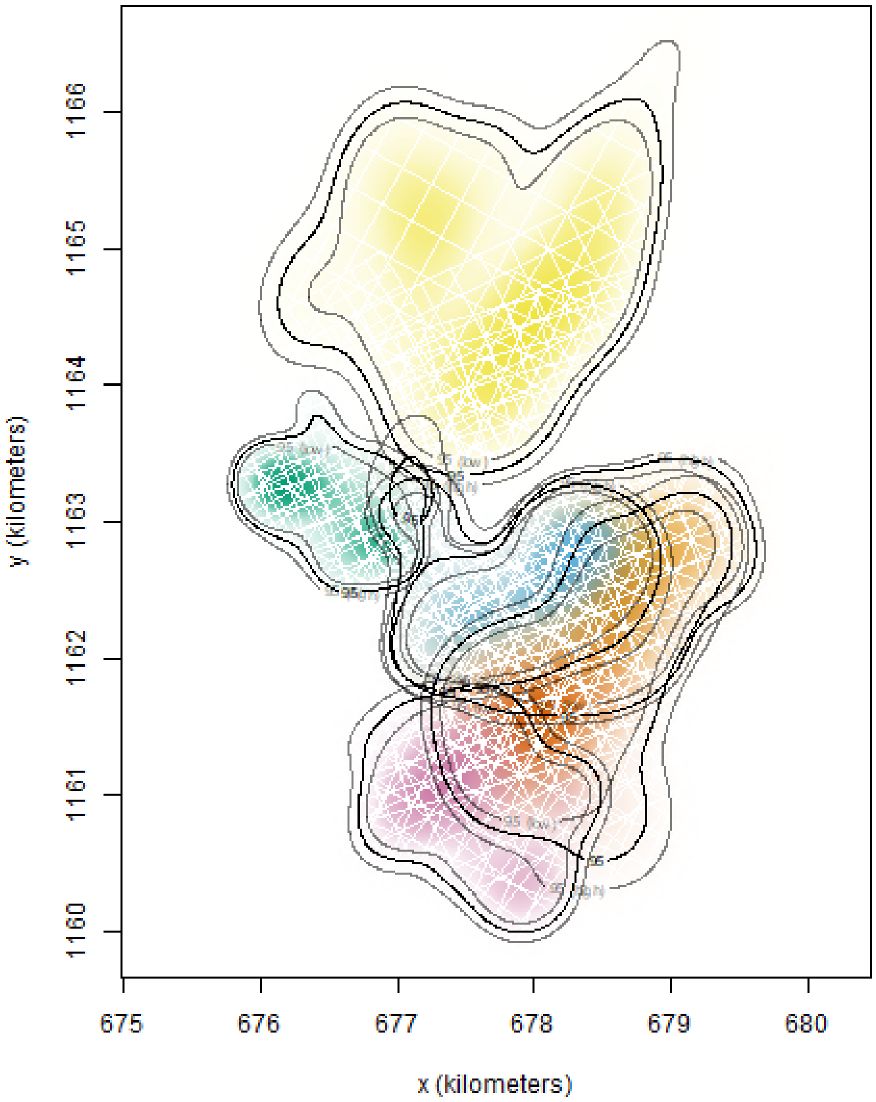

Figure 5: Home range estimate (95% utilization distribution) mean contours and 95% confidence intervals from the six complete segments

```
# plot seperate
par(mfrow = c(2,3))
for(i in 1:length(UDs)){
  plot(DATA_bulk[[i]], UDs[[i]],
       col = colorblind_pal[[i]],
       col.DF=colorblind_pal[[i]],
       main = names(UDs[i]))
}
```

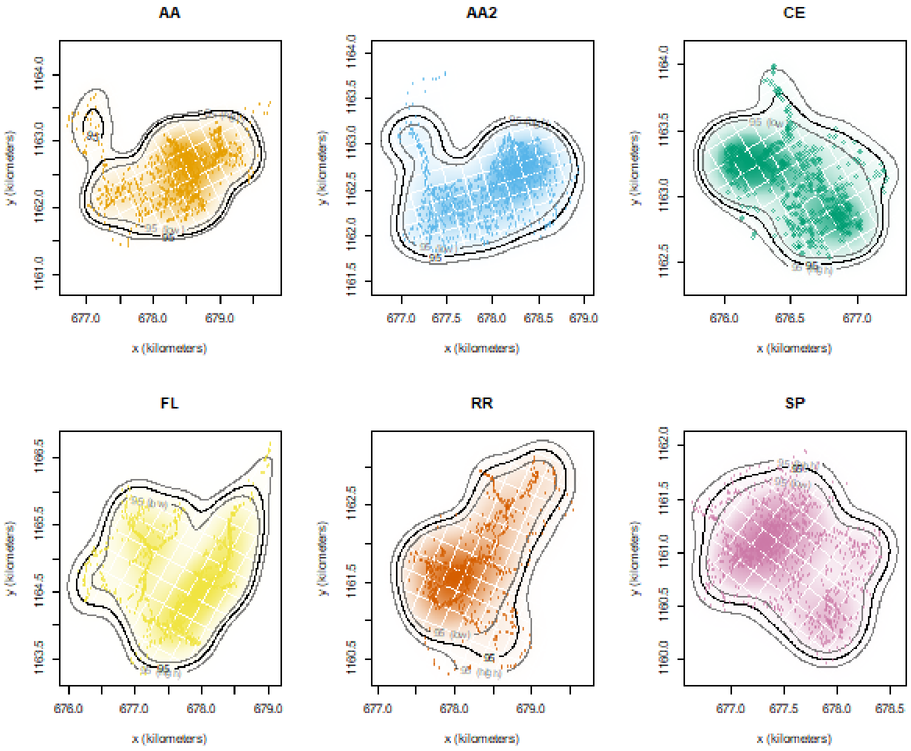

Figure 6: Home range estimate (95% utilization distribution) contours and 95% confidence intervals from the six complete segments plotted separately

You can compare home range areas using:

```
meta(UDs, variable = "area", main = "HR areas" col = colorblind_pal)
```

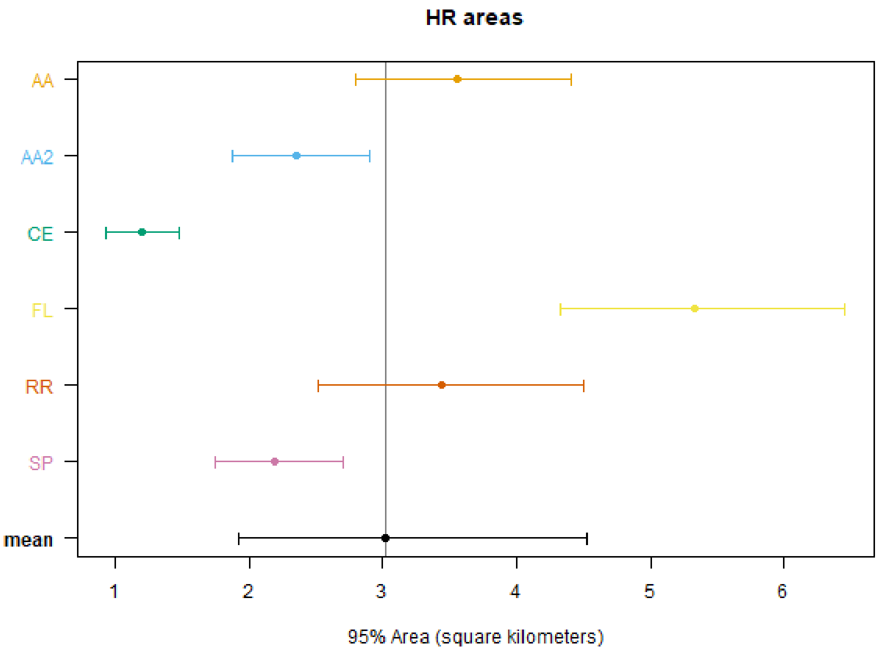

Figure 7: Plot showing the comparison of home range area and confidence intervals for all six complete segments. The colors correspond to the same colors in the home range plots. The mean area across the six complete segments is shown in black on the bottom

References

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Calabrese, Justin M., Chris H. Fleming, and Eliezer Gurarie. 2016. "Ctmm: An r Package for Analyzing Animal Relocation Data as a Continuous-Time Stochastic Process." *Methods in Ecology and Evolution* 7 (9): 1124–32. https://doi.org/https://doi.org/10.1111/2041-210X.12559.

Calabrese, Justin M., Christen H. Fleming, Michael J. Noonan, and Xianghui Dong. 2021. "Ctmmweb: A Graphical User Interface for Autocorrelation-Informed Home Range Estimation." *Wildlife Society Bulletin* 45 (1): 162–69. https://doi.org/10.1002/wsb.1154.

Diggle, Peter, and Paulo J. Ribeiro. 2007. *Model-Based Geostatistics*. Springer Series in Statistics. New York, NY: Springer.

Fleming, C. H., D. Sheldon, W. F. Fagan, P. Leimgruber, T. Mueller, D. Nandintsetseg, M. J. Noonan, et al. 2018. "Correcting for Missing and Irregular Data in Home-Range Estimation." *Ecological Applications* 28 (4): 1003–10. https://doi.org/10.1002/eap.1704.

Fleming, Christen H., and Justin M. Calabrese. 2017. "A New Kernel Density Estimator for Accurate Home-Range and Species-Range Area Estimation." *Methods in Ecology and Evolution* 8 (5): 571–79. https://doi.org/10.1111/2041-210X.12673.

Fleming, Christen H., Justin M. Calabrese, Thomas Mueller, Kirk A. Olson, Peter Leimgruber, and William F. Fagan. 2014. "Non-Markovian Maximum Likelihood Estimation of Autocorrelated Movement Processes." *Methods in Ecology and Evolution* 5 (5): 462–72. https://doi.org/10.1111/2041-210X.12176.

Fleming, Christen, Justin Calabrese, Thomas Mueller, Kirk Olson, Peter Leimgruber, and William Fagan. 2014. "From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes Across Spatiotemporal Scales." *The American Naturalist* 183 (May): E154–67. https://doi.org/10.1086/675504.

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Silva, Inês, Christen H. Fleming, Michael J. Noonan, Jesse Alston, Cody Folta, William Fagan, and Justin M. Calabrese. 2021. "Autocorrelation-Informed Home Range Estimation: A Review and Practical Guide." Preprint. EcoEvoRxiv. https://doi.org/10.32942/osf.io/23wq7.

Appendix 2: Home Range Analysis for the 60 Sampling Regimes

April 28, 2023

Background

The purpose of this document is to show the full results of the home range analysis from the 60 sampling regimes (i.e. the results of applying the analytical workflow presented in Appendix 1 to our study). This includes the: 1) variogram regressions with the fitted movement models, 2) the movement model summary information, and 3) home range estimates (See Appendix 1 for a detailed description of how home range analysis in *ctmm* works).

As a reminder, the 60 sampling regimes were generated from portions of our longitudinal movement dataset that were of the highest quality (two or more months of consistent data with very few temporal gaps), which we call “complete segments”. There are six complete segments from five groups because two of the complete segments came from the same group at different time periods (AA and AA2). How the sampling regimes were generated from the complete segments is described in the Methods section of the main text. We include the important information for every complete segment (i.e. labelled as “all”) and every sampling regime. The names of the sampling regimes are labelled with (C) for concentrated or (S) for spread, followed by the number of days in the data (e.g. C10).

Note on variograms: These plots are used as visualization tools to see if the data are sufficient to show range residency. Generally, what we are looking for is whether the empirical variograms plateau indicating range residency. If the variograms continue to increase, then this is an immediate sign that the data is not suitable for home range estimation. With irregular data, the variograms can look quite messy, which is generally not a problem. Also, they tend to be a bit more unpredictable toward larger time-lags which also is not normally an issue. In these plots, we also include the mean and confidence intervals for the top movement model (determined by AICc) fitted to the empirical variogram.

Note on model summaries: For the complete segments and sampling regimes from each group, we show a table showing the name of the selected movement model, the home range crossing time and the effective sample size. Overall, the *Ornstein–Uhlenbeck Foraging* (OUF) model was always selected, meaning that the data showed autocorrelated positions and velocities (See Appendix 1 for decriptions of the possible movement models). The effective sample sizes generally decrease with less days in the data. The effective sample sizes were generally above 10 for sampling regimes that had at least six days (e.g. C6, S6), but dropped to worrying low quantities with only 3 days (e.g. C3, S3).

Note on home range plots: These plots show the 95% UD estimates with 95% CIs of the AKDE home range estimates for the 60 sampling regimes. Each plot shows the total locations from the complete, but the closed green points are the locations that were selected in the regimes, and the open pink points are the locations that were thinned out.

The below figures and tables show the above information for each of the six groupings of sampling regimes (AA, AA2, RR, CE, SP, FL).

I. AA Group

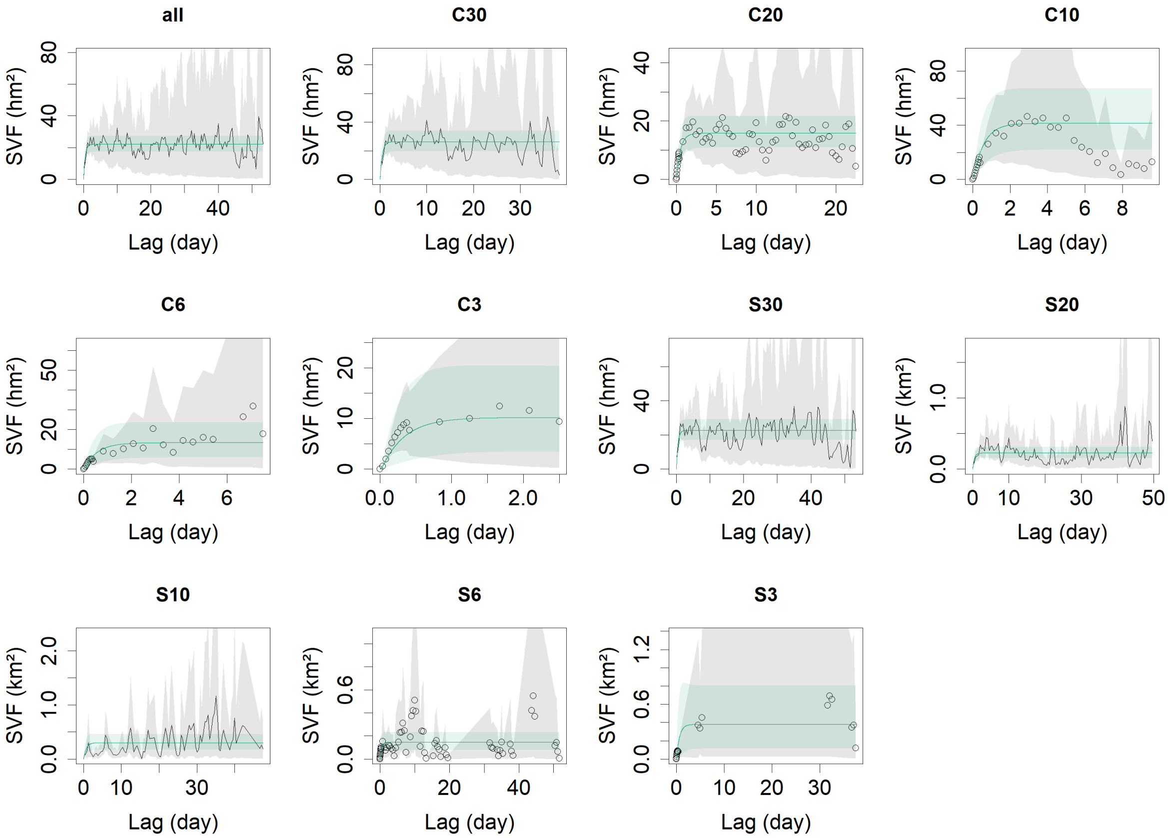

Figure 1: AA Variograms and Model Fits

Table 1: Model summary information for AA group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	11.371441	74.355955
C30	OUF anisotropic	11.411160	50.743983
C20	OUF	12.207090	33.361336
C10	OUF anisotropic	13.565069	12.821228
C6	OUF anisotropic	13.026774	8.754520
C3	OUF anisotropic	7.722914	5.405608
S30	OUF anisotropic	11.430881	55.372453
S20	OUF	10.920601	33.785164
S10	OUF	16.476402	17.054786
S6	OUF	10.689319	13.894728
S3	OUF	15.627924	4.502154

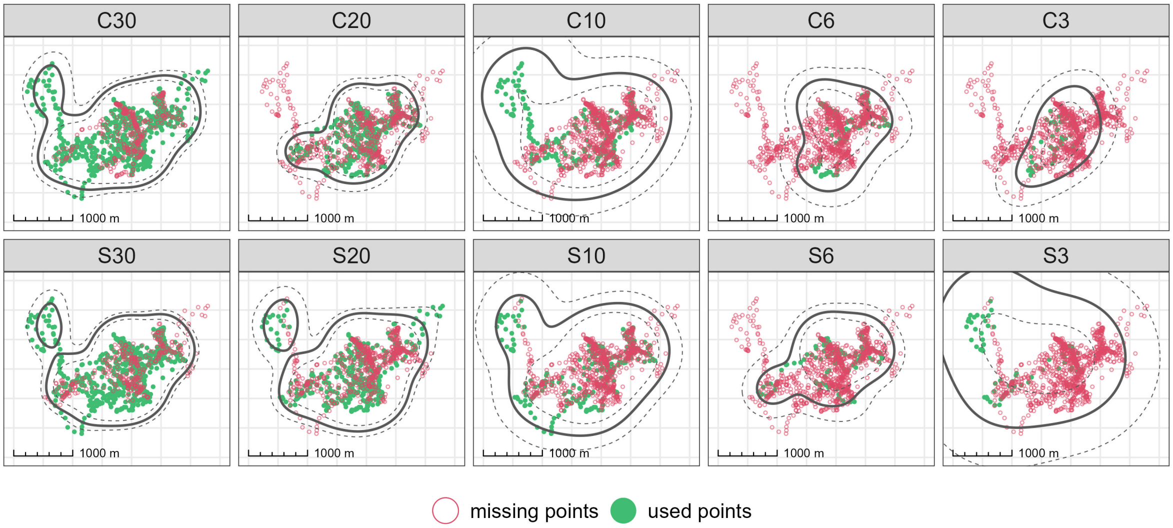

Figure 2: Home Range Estimates from AA sampling regimes plotted over data

II. RR Group

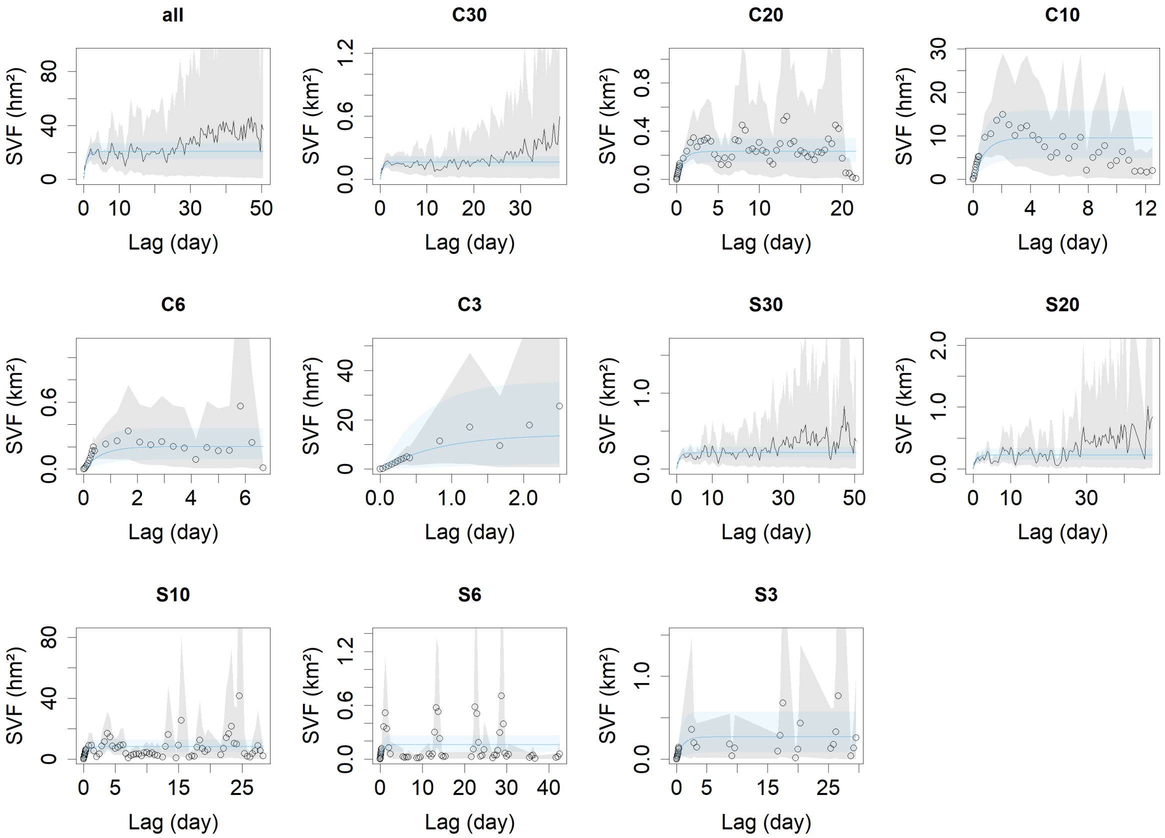

Figure 3: RR Variograms and Model Fits

Table 2: Model summary information for RR group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	18.978032	46.095745
C30	OUF anisotropic	14.940166	42.308345
C20	OUF anisotropic	18.378469	21.158712
C10	OUF anisotropic	18.983334	12.050660
C6	OUF anisotropic	15.490440	8.136280
C3	OUF anisotropic	19.279959	2.775899
S30	OUF anisotropic	19.606929	35.785444
S20	OUF anisotropic	21.798724	24.326656
S10	OUF anisotropic	9.871898	15.892846
S6	OUF anisotropic	15.080781	11.807712
S3	OUF anisotropic	24.882872	4.536988

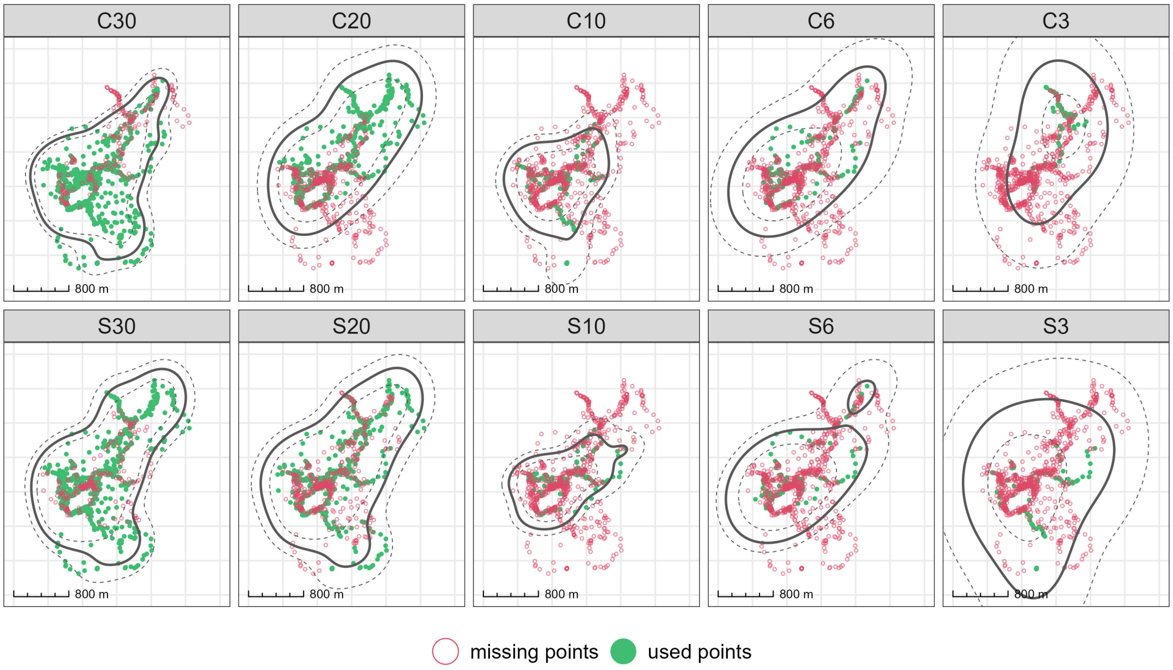

Figure 4: Home Range Estimates from RR sampling regimes plotted over data

III. CE Group

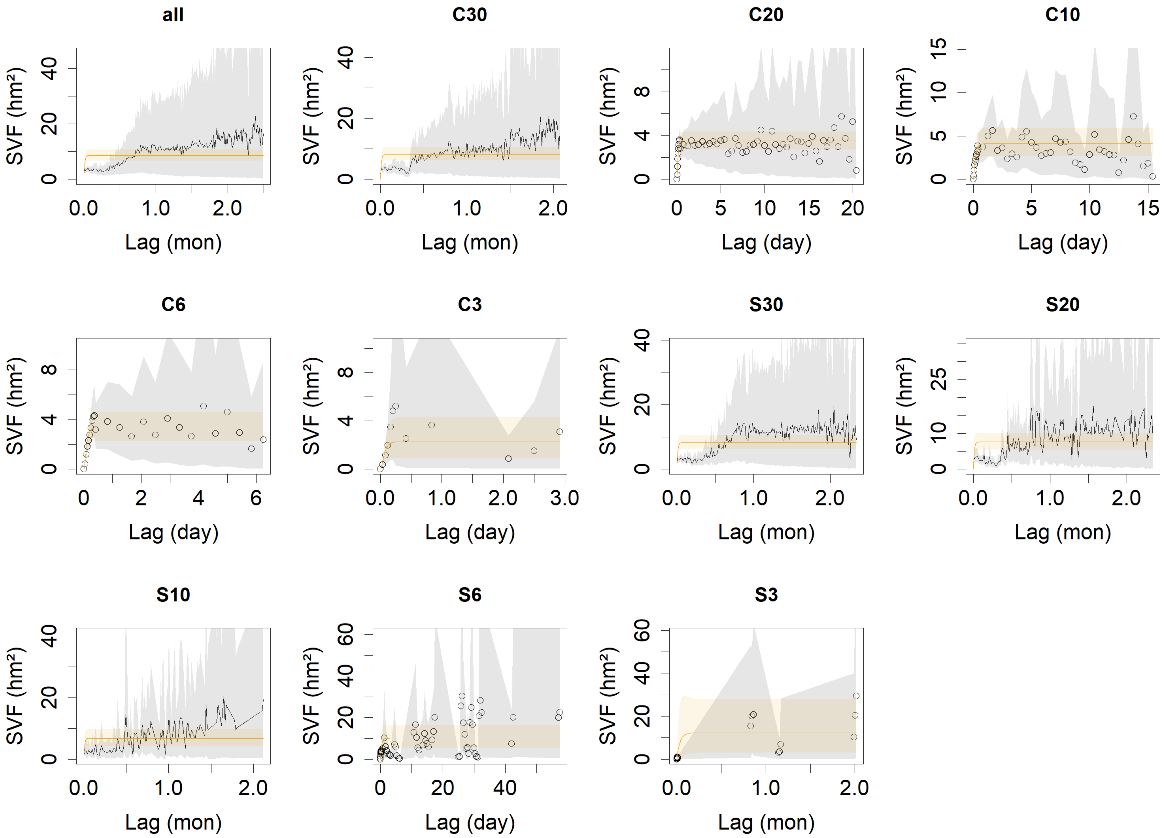

Figure 5: AA Variograms and Model Fits

Table 3: Model summary information for CE group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	8.7813209	73.193752
C30	OUF	7.8875677	57.588565
C20	OUF	3.1045567	71.052081
C10	OUF anisotropic	3.8892913	23.890902
C6	OUf	1.2448895	31.505435
C3	OUf	0.8695337	6.541128
S30	OUF anisotropic	8.3635957	57.523148
S20	OUF	8.1590701	40.592830
S10	OUF anisotropic	6.5044688	23.701797
S6	OUF anisotropic	8.7724103	12.174717
S3	OUF	24.8253527	3.605531

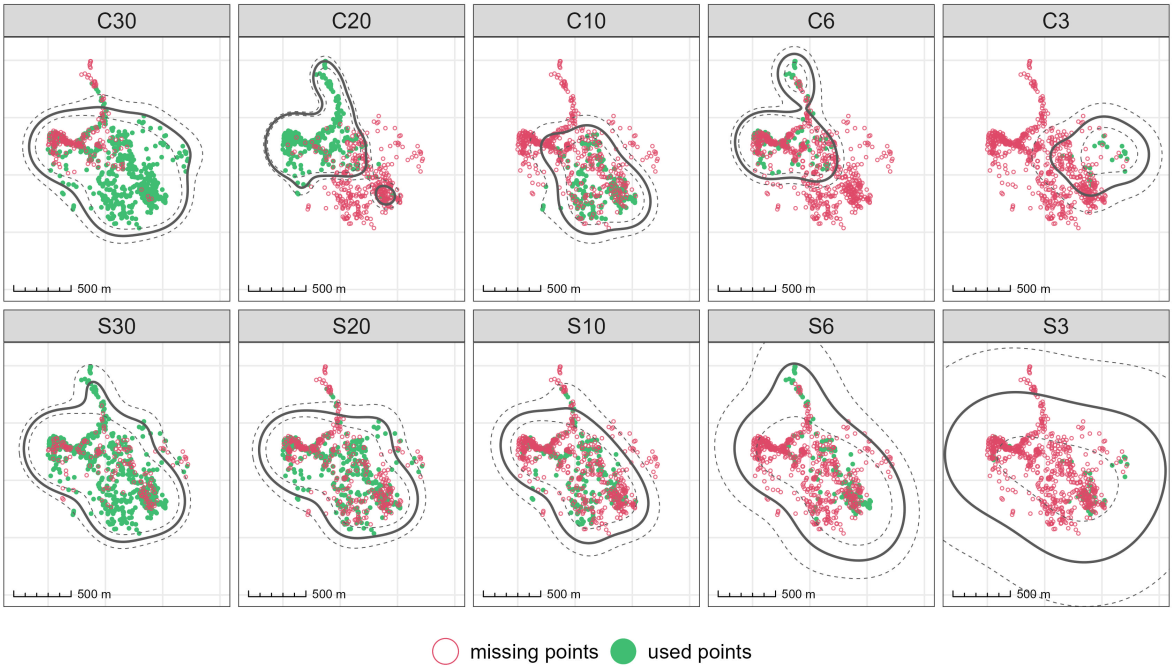

Figure 6: Home Range Estimates from AA sampling regimes plotted over data

IV. AA2 Group

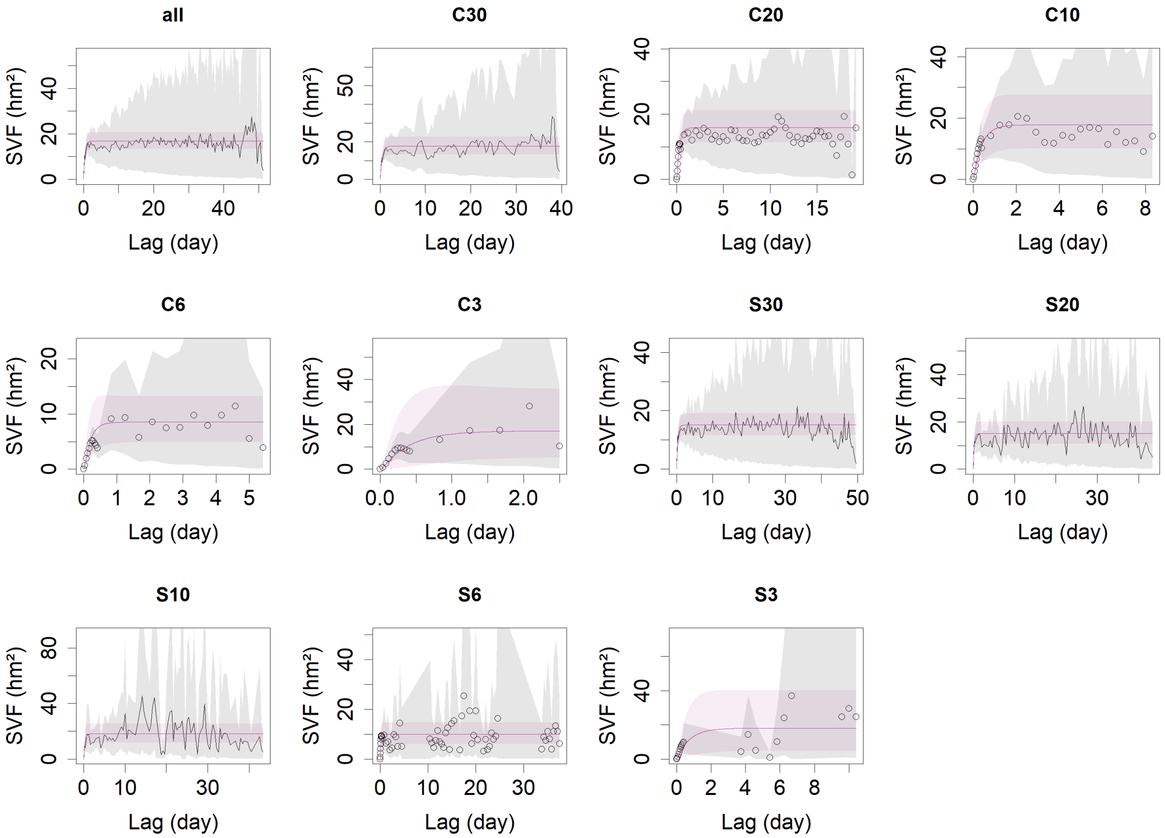

Figure 7: AA2 Variograms and Model Fits

Table 4: Model summary information for AA2 group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	9.273814	81.297831
C30	OUF anisotropic	10.385718	54.182818
C20	OUF anisotropic	6.939681	39.549168
C10	OUF anisotropic	9.232590	15.629816
C6	OUF	4.543344	15.999752
C3	OUF	9.248229	4.635231
S30	OUF anisotropic	7.992799	63.016910
S20	OUF anisotropic	5.932028	40.313983
S10	OUF	7.153679	27.176787
S6	OUF	4.132458	20.193451
S3	OUF anisotropic	17.471853	3.859595

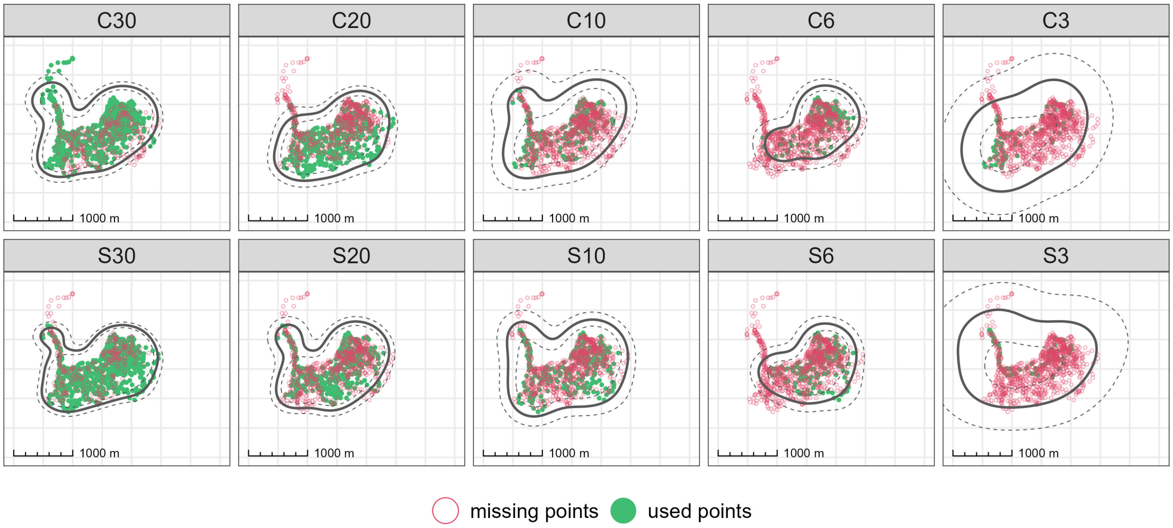

Figure 8: Home Range Estimates from AA2 sampling regimes plotted over data

V. SP Group

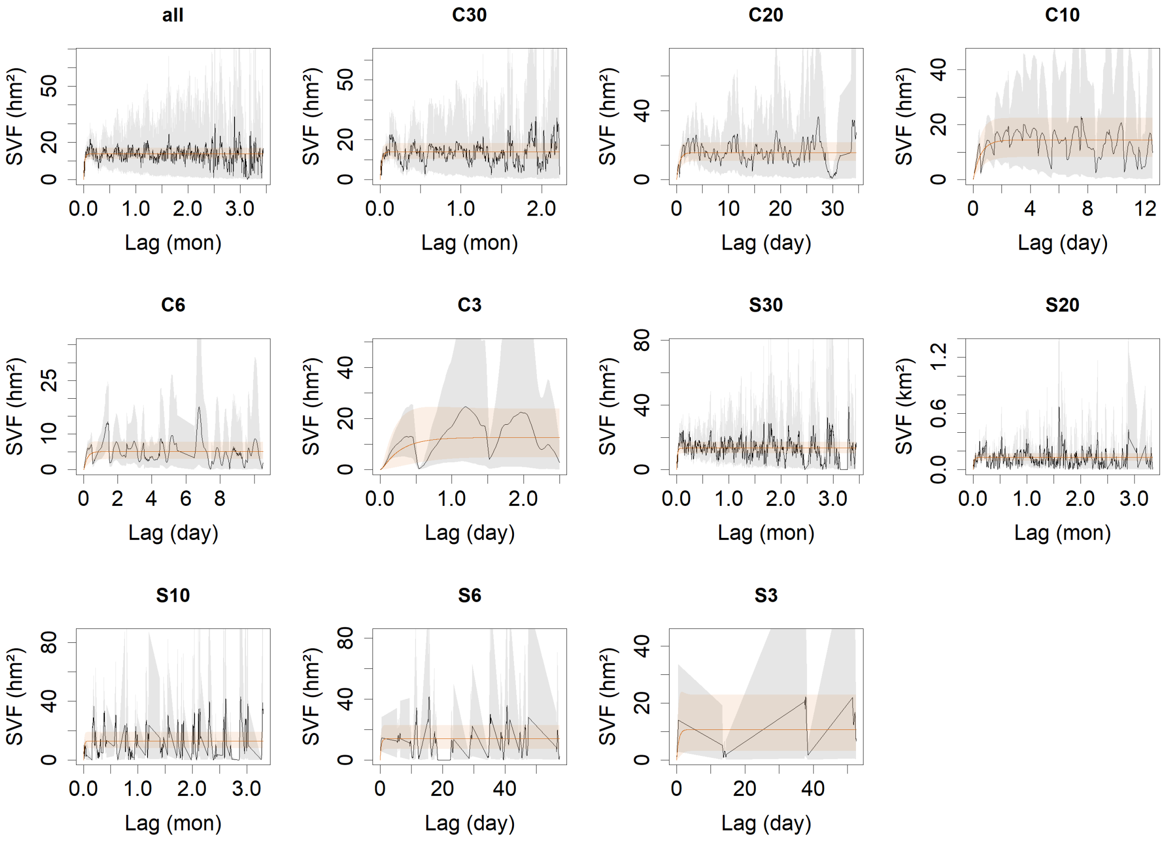

Figure 9: SP Variograms and Model Fits

Table 5: Model summary information for SP group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	13.624460	81.166993
C30	OUF anisotropic	14.526307	48.709825
C20	OUF	13.140053	31.818670
C10	OUF anisotropic	12.526639	15.743796
C6	OUF	4.702017	17.339935
C3	OUF	6.382257	6.674316
S30	OUF	11.509796	56.465935
S20	OUF anisotropic	11.075058	37.868752
S10	OUF anisotropic	9.578686	21.394681
S6	OUF anisotropic	8.567690	12.396154
S3	OUF	15.302549	4.384725

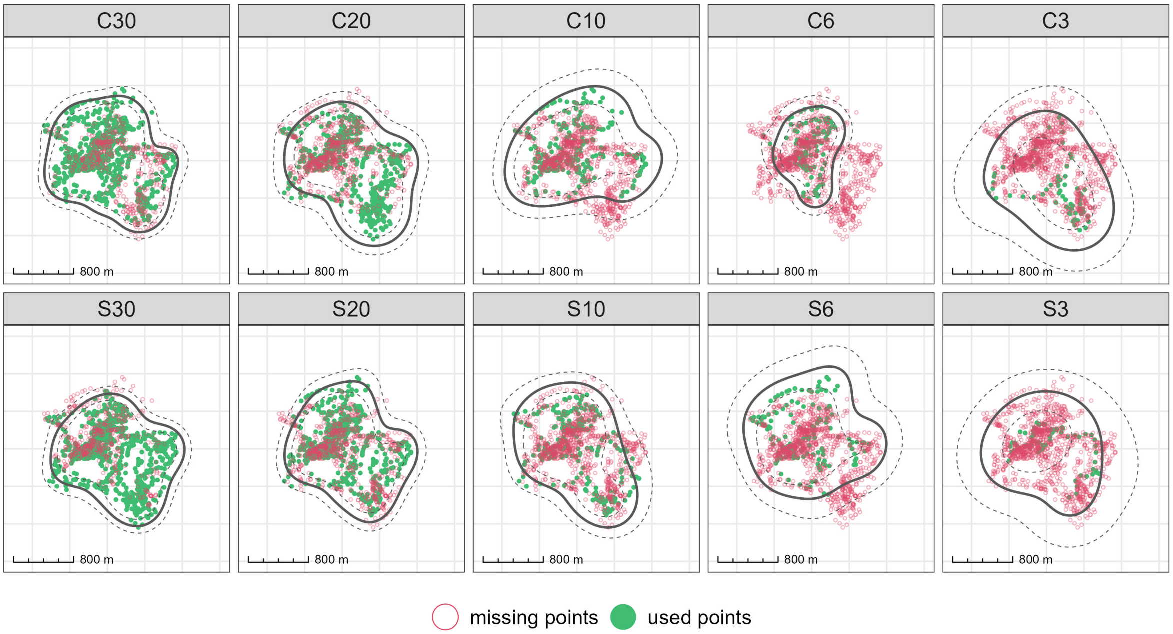

Figure 10: Home Range Estimates from SP sampling regimes plotted over data

VI. FL Group

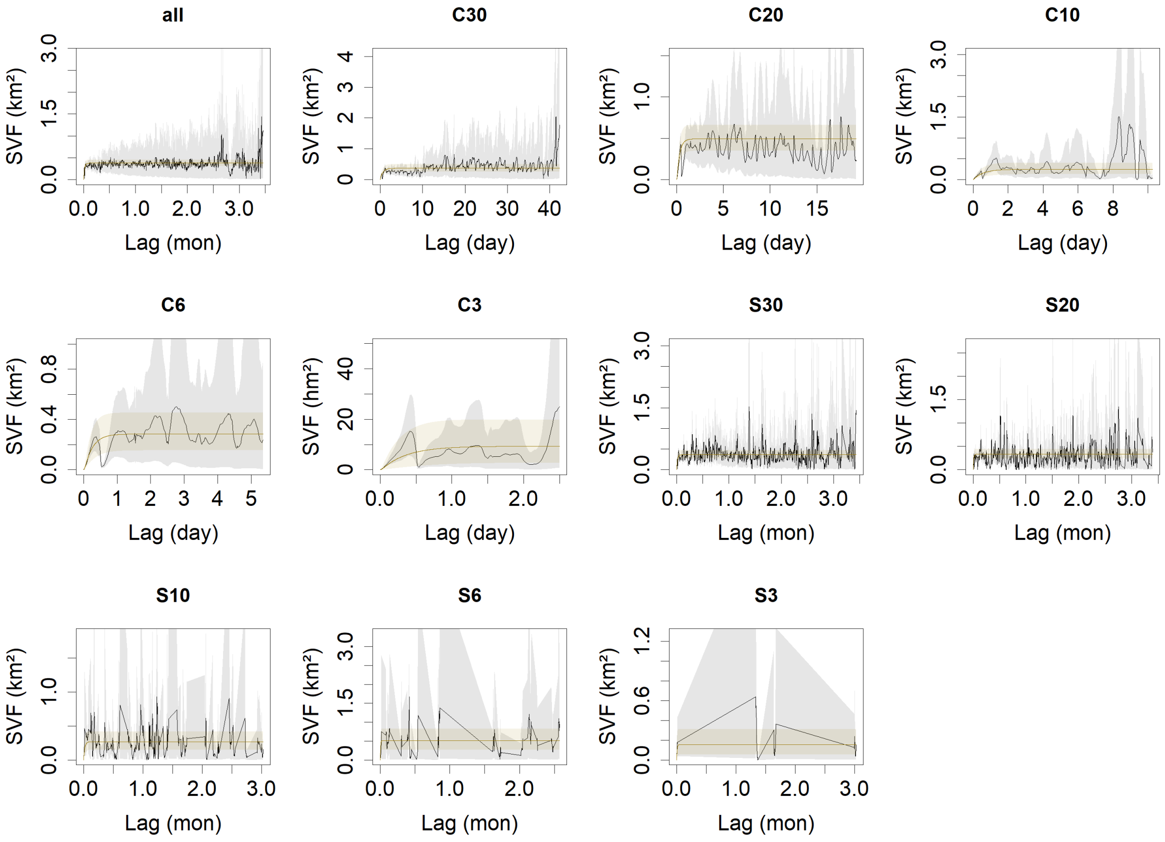

Figure 11: FL Variograms and Model Fits

Table 6: Model summary information for FL group

individual.local.identifier	Model Name	HR Crossing Time (hours)	Effective Sample Size
all	OUF anisotropic	12.992068	95.955636
C30	OUF anisotropic	15.395619	35.198133
C20	OUF anisotropic	7.218778	38.959380
C10	OUF anisotropic	13.643672	12.552170
C6	OUF anisotropic	5.710013	13.713607
C3	OUF anisotropic	8.373327	4.471325
S30	OUF anisotropic	12.263379	50.788178
S20	OUF anisotropic	7.592231	39.964504
S10	OUF anisotropic	14.236334	15.236985
S6	OUf anisotropic	2.445047	12.805342
S3	OUF anisotropic	6.705427	5.509169

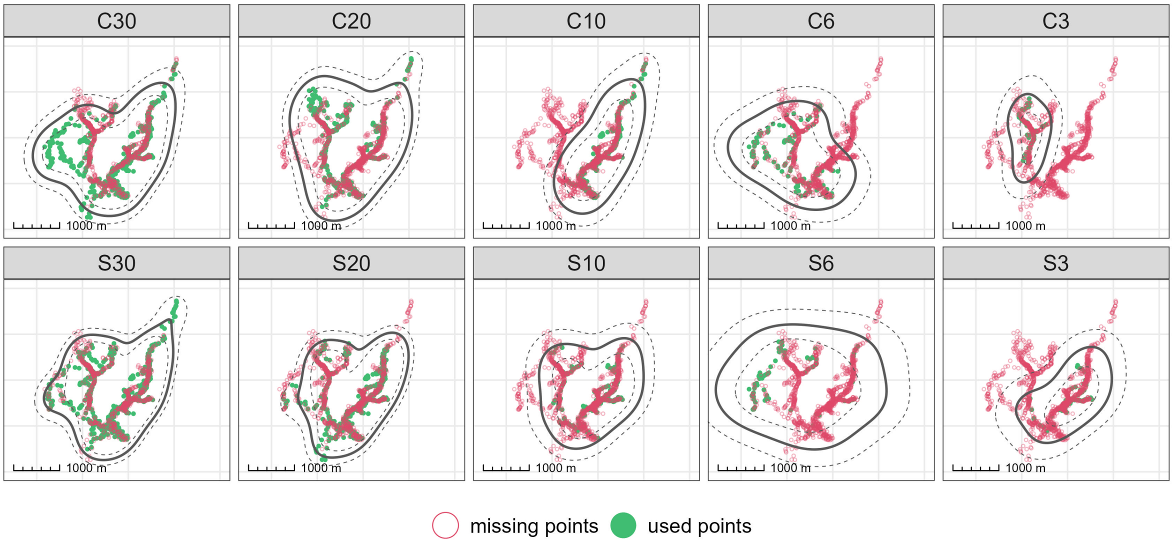

Figure 12: Home Range Estimates from FL sampling regimes plotted over data

Appendix 3: Varying Effects Plots and Model Posteriors

April 28, 2023

I. Background

This supplementary document presents additional information related to our statistical analysis. Our aim was to model the performance of home range estimation, as defined in the Methods section, based on different characteristics of the sampling regimes. To achieve this, we employed three binomial Bayesian generalized linear mixed models.

The first model utilized a binary predictor variable to indicate whether the data in the sampling regimes were concentrated or spread, to predict performance. The second model used the number of locations as the predictor, while the third model used the number of unique weeks. We included an interaction between the predictors and the binary variable indicating spread or concentrated data in the last two models, and all models have varying slopes and intercepts per group.

In this document, we provide varying effects plots as referred to in the main text (but not presented there), along with the posterior distributions for all three statistical models.

II. Model 1: HR Performance ~ Binary Predictor (spread vs. concentrated)

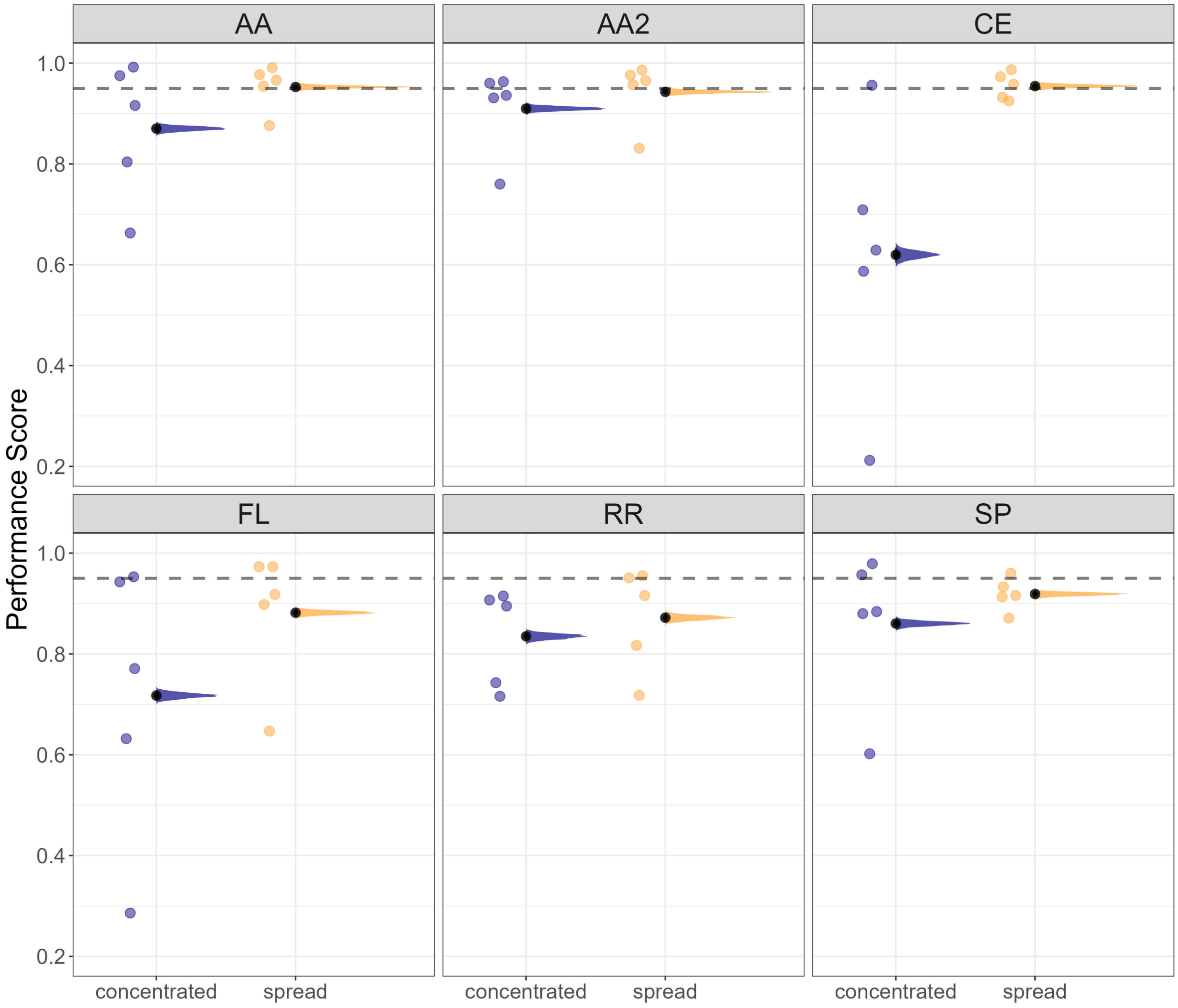

Figure 1: Group effects (varying slopes and intercepts) for binomial model predicting home range estimation performance by a binary variable indicating whether the data in the sampling regimes are concentrated or spread.

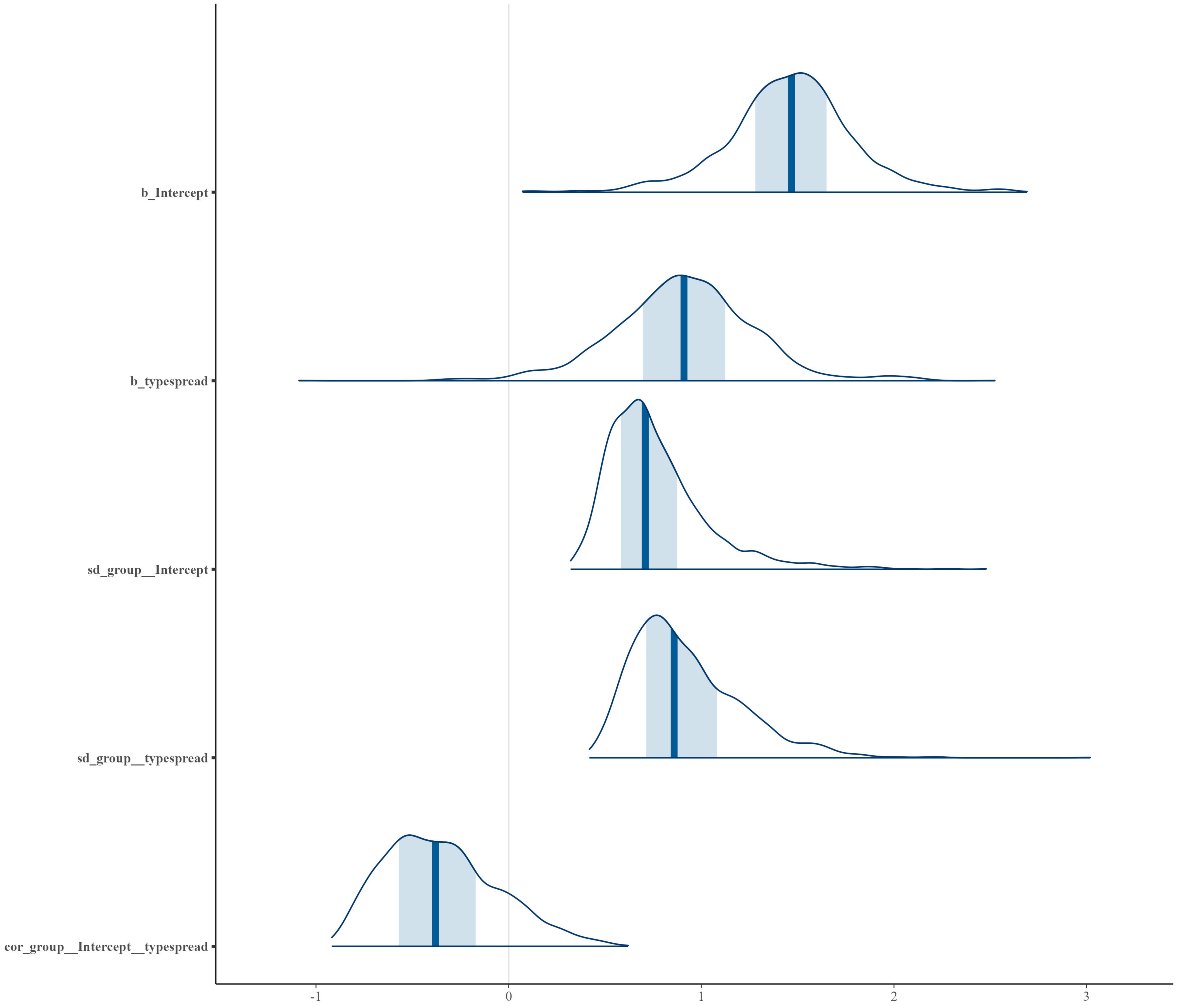

Figure 2: Posterior distributions for parameters in binomial model predicting home range estimation performance by a binary variable indicating whether the data in the sampling regimes are concentrated or spread. Group is included as a random effect (random slopes and intercepts). Posteriors include the median and 80% credible intervals.

III. Model 2: HR Performance ~ Number of Locations

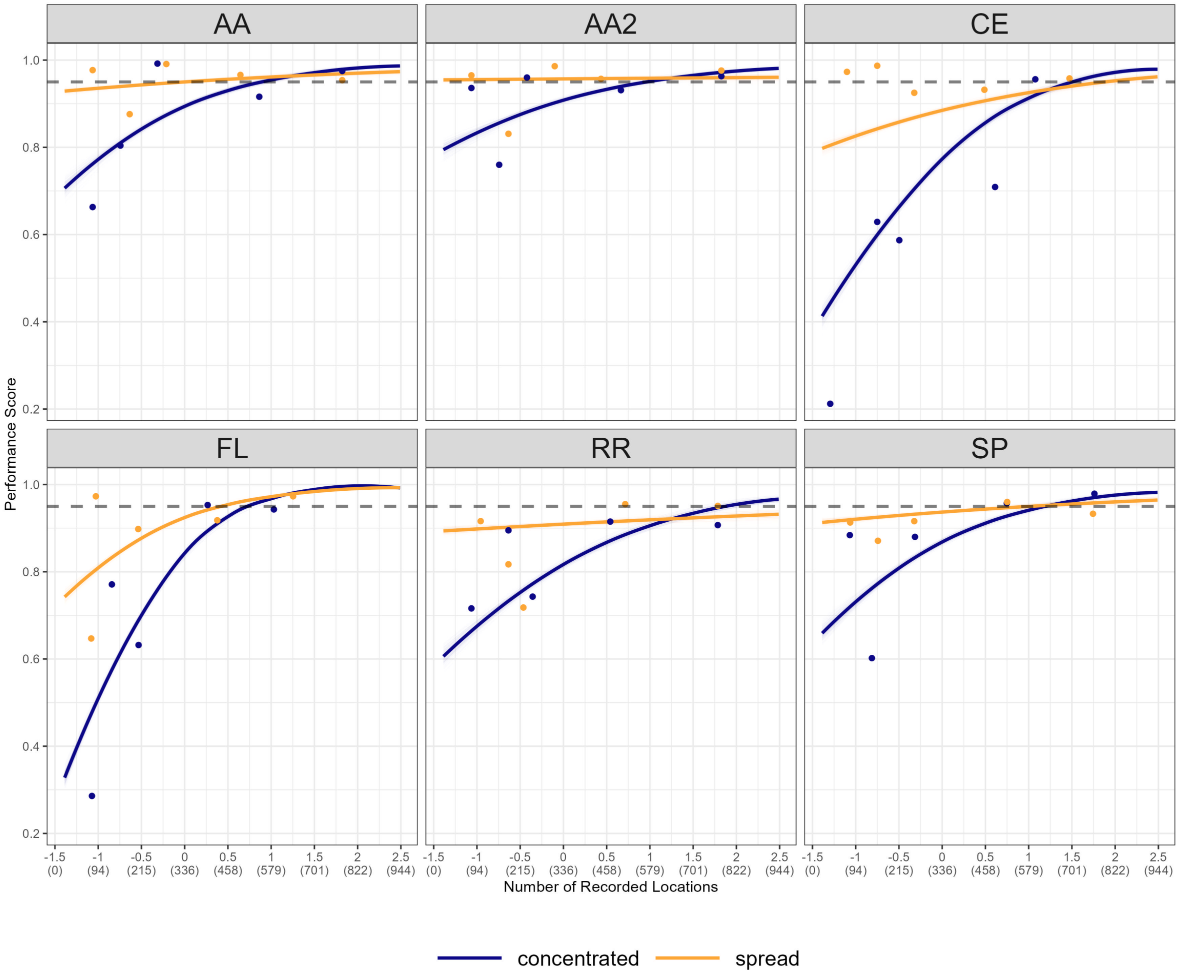

Figure 3: Group effects (varying slopes and intercepts) for binomial model predicting home range estimation performance by number of locations as predictor with an interaction with the concentrated vs spread variable. Notice that FL and CE require the most locations to achive optimal performance, and are the least robust to low quantities of locations. These groups also have the most fragmented habitats (see Discussion section in the main text).

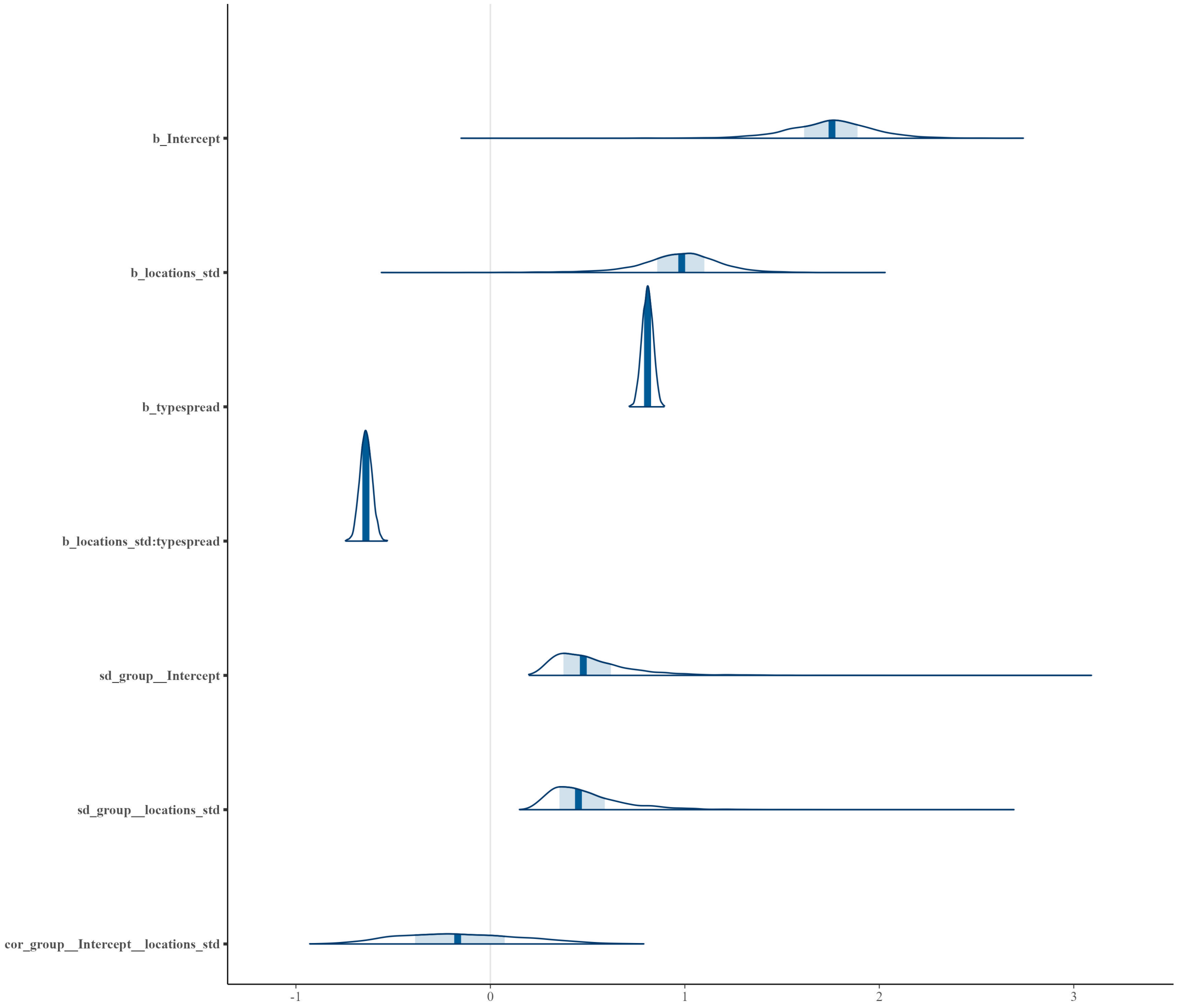

Figure 4: Posterior distributions for parameters in binomial model predicting home range estimation performance by number of locations as predictor with an interaction with the concentrated vs spread variable. Group is included as a random effect (random slopes and intercepts). Posteriors include the median and 80% credible intervals.

IV. Model 3: HR Performance ~ Number of Unique Weeks

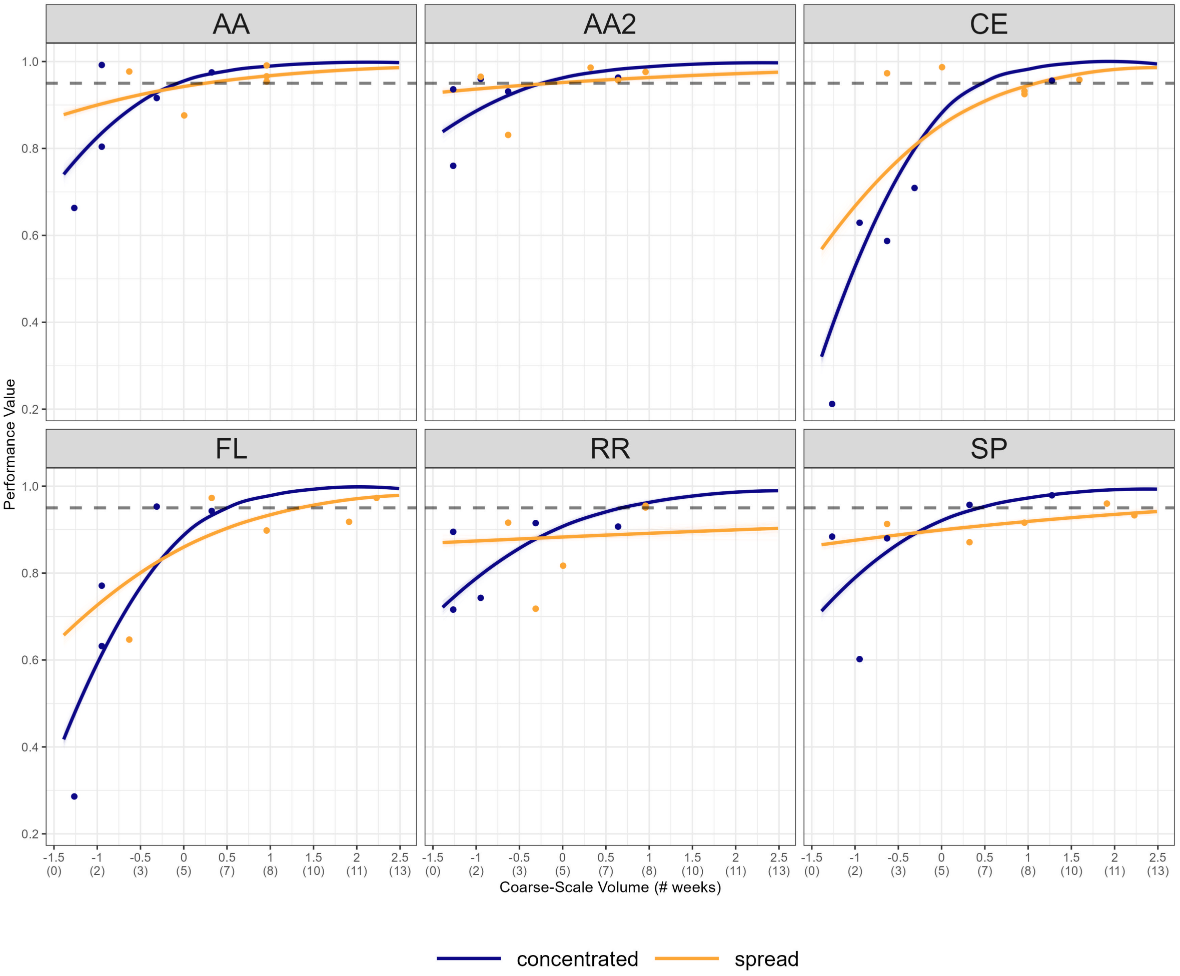

Figure 5: Group effects (varying slopes and intercepts) for binomial model predicting home range estimation performance by number of unique weeks as predictor with an interaction with the concentrated vs spread variable. Notice that FL and CE require the most weeks to achive optimal performance, and are the least robust to low quantities of weeks. These groups also have the most fragmented habitats (see Discussion section in the main text).

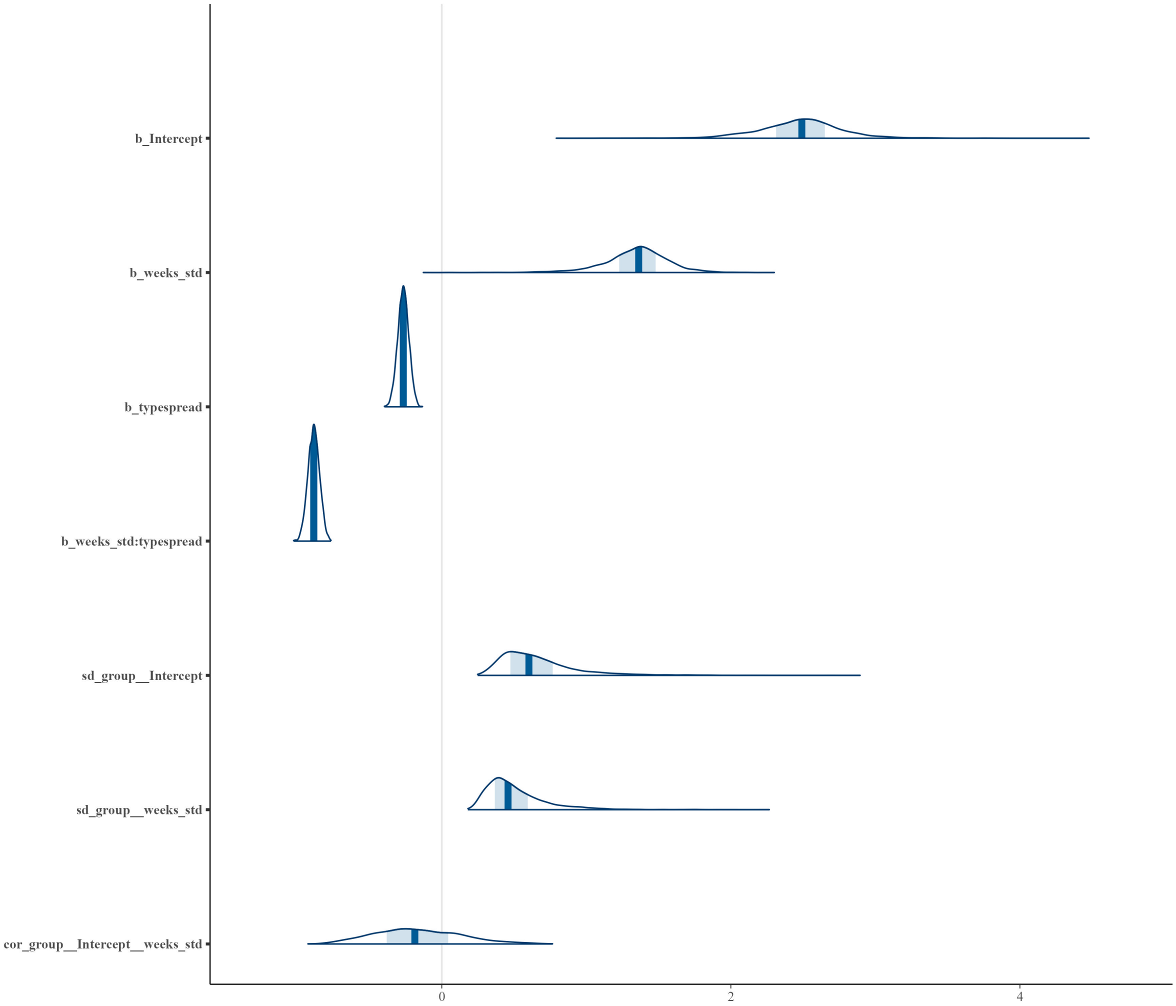

Figure 6: Posterior distributions for parameters in binomial model predicting home range estimation performance by number of unique weeks as predictor with an interaction with the concentrated vs spread variable. Group is included as a random effect (random slopes and intercepts). Posteriors include the median and 80% credible intervals.