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. The space-use patterns of habituated primates often are studied by using handheld GPS devices, which provide detailed movement information that can link patterns of ranging and space-use to the behavioral decisions that generate these patterns. However, these 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 problem, we used a 13-year dataset from 11 groups of white-faced capuchins (*Cebus capucinus imitator*) to examine the impact of sampling elements, such as sample size, regularity, and temporal coverage, on home range estimation accuracy. We found that accurate home range estimation is feasible with relatively small absolute sample sizes and irregular sampling, as long as the data are collected over extended time periods. Also, concentrated sampling can lead to bias and overconfidence due to uncaptured variations in space use and underlying movement behaviors. Sampling protocols relying on handheld GPS for home range estimation are improved by maximizing independent location data distributed across time periods much longer than the target species' home range crossing timescale.

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Resumen

Comprender la cantidad de espacio que necesitan los animales para satisfacer sus necesidades biológicas es esencial para entender su comportamiento, su papel ecológico dentro de su comunidad y para una planificación eficaz de la conservación y la gestión de los recursos. Con frecuencia, los primates habituados están estudiados utilizando datos de GPS portátil, que proporcionan información detallada sobre sus movimientos y permiten relacionar los patrones de desplazamiento y uso del espacio con las decisiones conductuales que los generan. Sin embargo, es posible que estos datos no representen con exactitud la totalidad de los movimientos de un animal, lo que plantea problemas cuando la inferencia deseada es a escala del área de campeo. Para abordar este problema, utilizamos un extenso conjunto de datos de 13 años de 11 grupos de capuchinos de cara blanca (*Cebus capucinus imitator*) para examinar el impacto de los elementos de muestreo, como el tamaño de la muestra, la regularidad y la cobertura temporal, en la precisión de la estimación del área de distribución. Encontramos que la estimación fiable del área de distribución es factible con tamaños de muestra absolutos relativamente pequeños y muestreos irregulares, siempre que los datos se recojan durante periodos de tiempo prolongados. También ilustramos cómo el muestreo concentrado puede conducir a sesgos y a un exceso de confianza debido a variaciones no capturadas en el uso del espacio y en los comportamientos de movimiento subyacentes. Los protocolos de muestreo basados en GPS portátiles para la estimación del área de distribución se mejoran maximizando los datos de localización independientes distribuidos a lo largo de periodos de tiempo mucho más largos que la escala temporal de cruce del área de distribución de la especie objetivo.***The translated abstract was not copy-edited by Springer Nature.**

Introduction

Animal space use often is described by 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" (p. 351). 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 various 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 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.

Although home-range estimation is a simple concept, in practice, it is logistically and statistically challenging (Fleming *et al*., 2015b). 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 (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 (Fleming *et al*., 2015b). Furthermore, 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 (Fleming & Calabrese, 2017).

Burt's definition (1943) provides a conceptual framework for the home range, but it lacks the statistical basis needed to quantify it (Silva *et al*., 2021). Early efforts quantify the home range by using the Minimum Convex Polygon (MCP), an approach that involves drawing the smallest convex polygon which encompasses all the recorded locations (Börger *et al*., 2020; Mohr, 1947). However, joining the outermost points in this manner yields biased estimates that are 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 or group 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, p. 1346; 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, p. 351).

Constructing UDs generally involves kernel density estimation (hereafter KDE). KDEs place kernels, or small probability density functions, over each location data point and averages them to acquire a total probability density function across all points (Börger *et al*., 2020; Worton, 1989). The resulting probability density function has the highest density where 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 by using VHF radiotelemetry (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 previous and subsequent observed locations. This is a false assumption with recent 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 (Fleming *et al*., 2015b). When the data are sampled at intervals short enough that recorded locations are correlated in space and time, which can be as coarse as one fix per day (Calabrese *et al*., 2016), the assumptions of the conventional KDE are violated (Fleming *et al*., 2015b).

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 (Fleming *et al.*, 2015b). 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 (Alston *et al.*, 2022) (Fig. 1).

Calculating the occurrence distribution is valuable for analytical purposes unrelated to home range estimation, such as path reconstruction (Fleming *et al.*, 2015a), and determining the times and locations of animal interactions or crossings over landscape features (Alston *et al.*, 2022). Several methods 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 (Fleming *et al.*, 2015a). Nevertheless, KDE is widely used to estimate the home range (hereafter referred to as the range distribution), instead of the occurrence distribution (Fleming *et al.*, 2015b), which is only suitable on the occasions where the recorded location data are independent and not autocorrelated (Börger *et al.*, 2020).

The autocorrelation found in most movement datasets generates UDs that more closely resemble the occurrence distribution, particularly when using KDE. As the occurrence distribution does not accommodate out-of-sample space use, the resulting area estimates are prone to negative bias and can lead to misinterpretation when the intended goal is home range estimation (Fleming *et al.*, 2014b). However, if the
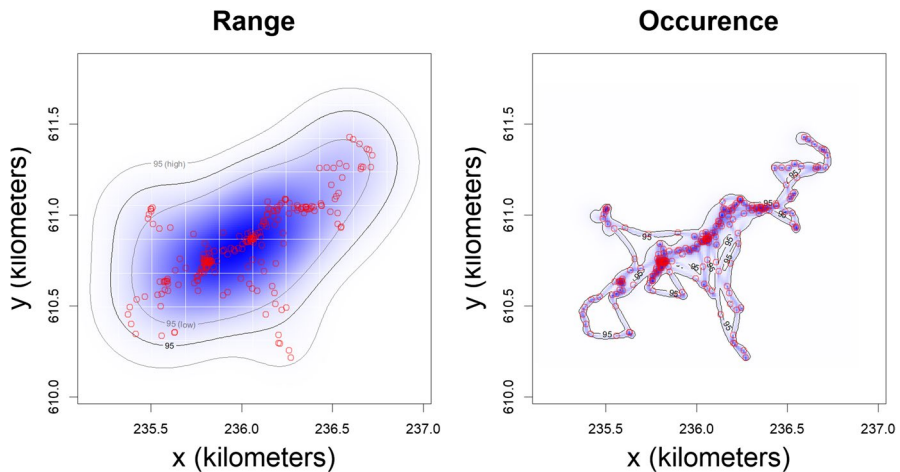

Fig. 1 Comparison of a range distribution estimate versus an occurrence distribution estimate calculated and depicted using the same location data collected from a single group of white-faced capuchins at the Lomas Barbudal Monkey Project in Costa Rica, September 12, 2010 to December 31, 2010. The range distribution is calculated using auto-correlated kernel density estimation and the occurrence distribution is calculated using time-series Kriging. 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.

desired outcome is occurrence estimation, KDE may be a viable option (Börger *et al*., 2020); thus, it is crucial for researchers to clearly identify their target of inference and select an appropriate estimator accordingly (Alston *et al*., 2022)

Recently developed home range estimation methods explicitly estimate the range distribution and account for the fact that animals' paths result from movement processes that are, by definition, spatiotemporally autocorrelated. These methods explicitly treat movement data as a sample of location estimates taken along an animal's mostly unobserved continuous movement path (Fleming *et al*., 2015b). One of these methods, auto-correlated kernel density estimation (hereafter AKDE), improves upon the KDE by modelling the underlying continuous-time movement process of the animal (Calabrese *et al*., 2016). AKDEs generate home-range estimates that are informed by autocorrelated data, rather than hindered by it. They also provide the analytical toolkit to handle several other obstacles, such as location error, irregular sampling, bandwidth optimization, and estimation uncertainty (Fleming & Calabrese, 2017; Fleming *et al*., 2018, 2020).

A thorough evaluation of the AKDE compared against commonly used approaches, such as the MCP, KDE, and Local Convex Hull (LocoH), shows that the AKDE is superior in capturing space use out of sample and is the only estimator capable of producing unbiased estimates with low effective sample sizes (Noonan *et al*., 2019). While AKDE is increasingly 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 studies still use methods, such as the MCP and KDE (Börger *et al*., 2020; Fleming & Calabrese, 2017; Hemson *et al*., 2005; Laver & Kelly, 2010; Powell, 2000). The potential presence of significant, systematic biases from applying these methods to estimate home-range area is concerning, because it can lead to erroneous conservation decision-making (Gaston *et al*., 2008) or inaccurate meta-analyses that influence public opinion and theoretical frameworks (Noonan *et al*., 2020). Also, particularly worrying is that the methods that are primarily used to record primate movement (e.g., handheld GPS) are different than those used on studies of most other species (e.g., GPS tags), introducing additional bias into any comparative work (McCann *et al*., 2021; Sennhenn-Reulen *et al*., 2017).

To estimate the home ranges of habituated groups or individuals, primatologists often gather location data via handheld GPS devices (e.g., ring-tailed lemurs (*Lemur catta*), Axel & Maurer, 2011; white-faced capuchins (*Cebus capucinus imitator*), Campos *et al*., 2014; Bornean southern gibbons (*Hylobates albibarbis*), Cheyne *et al*., 2019; Phayre's leaf monkeys (*Trachypithecus phayrei*), Gibson & Koenig, 2012; brown capuchins (*Cebus apella*), Hirsch *et al*., 2013; bonobos (*Pan paniscus*), McLester & Fruth, 2023; capuchins (*Cebus sp.*) and bearded sakis (*Chiropotes satanas*), Phillips *et al*., 1998; chimpanzees (*Pan troglodytes*), Potts *et al*., 2011; blue monkeys (*Cercopithecus mitis*), Roberts & Cords, 2015; mountain gorillas (*Gorilla beringei beringei*), Seiler & Robbins, 2020). These devices can be integrated easily into established data collection protocols (Brown & Crofoot, 2013) and provide a noninvasive means of tracking habituated animals in contrast to animal-borne tracking devices that require capture (e.g., VHF and GPS collars; Dore *et al*., 2020). The longitudinal datasets generated by using handheld GPS devices hold

significant potential, as they may span multiple 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 datasets can give rise to novel and important investigations that are not feasible for most tracking studies. Yet, the accumulated handheld GPS data from longitudinal studies often is underused (Brown & Crofoot, 2013), with inquiries on social behavior and life history generally being of higher priority. Consequently, there is a lack of understanding of what drives long-term movement and space-use patterns of primates and how these patterns link with fitness and population demography.

Another key issue is that most modern approaches for estimating the home range, including the AKDE, are 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 may be 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 pauses in data collection. Bias also is introduced when some areas are less accessible to observers, for example over cliffs or flooded rivers. Sampling disruptions can be nonrandom in time and across behaviors, as researchers can more easily lose groups in rainy seasons where visibility and audibility are limited, or when groups are moving rapidly.

While handheld GPS data continues to be a valuable tool for primatologists in assessing space use and addressing ecological questions, the extent to which conventional sampling protocols in field primatology yield home range estimates that represent the biological home range (i.e. "true" home range) remains uncertain. To address this problem, we present an extensive 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 capucinus imitator*) in Guanacaste, Costa Rica. This dataset exemplifies characteristic long-term datasets acquired in primate field studies, highlighting the significant challenges encountered by longitudinal studies in the context of handheld GPS sampling.

White-faced capuchins are well-suited for this study due to their residence within a specific range, making their movement data appropriate for estimating home ranges (Silva *et al*., 2021). Additionally, their tendency to move together as a group (Campos *et al*., 2014) enables the possibility of tracking groups using just one device operated by a human observer. They are platyrrhines that are primarily arboreal and live in multi-male, multi-female groups of approximately 5–40 individuals (mean = 18.8) (Perry, 2012). Females exhibit lifelong group fidelity, whereas males disperse during adolescence (mean age 7.6 years) (Perry *et al*., 2012). Their diet primarily consists of fruit and arthropods (McCabe & Fedigan, 2007; Perry & Jimenez, 2006), although they are dietary generalists and also consume flowers, eggs, pith, and small vertebrates. While home ranges frequently overlap with neighboring groups, they do not defend strict territorial boundaries; however, interactions

between groups can be aggressive and occasionally fatal (Crofoot, 2007; Gros-Louis *et al*., 2003; Perry, 1996).

Our goal was to understand how to maximize the potential of long-term, handheld GPS data for accurate home-range estimation while providing practical suggestions for reliable sampling design. We thinned continuous segments of capuchin movement 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. While the true biological home range remains unknown, employing this approach permits increased understanding of how essential aspects of movement datasets, such as limited sample sizes and irregular sampling, can impact the performance of home range estimates derived from observations collected via handheld GPS. We address the following questions with respect to our dataset:

1. What sample size from handheld GPS is necessary to maximize estimation performance?
2. At what temporal scales should we measure home ranges?
3. What are the most important considerations for obtaining representative samples?

Methods

Study Site

We conducted our field work at the Lomas Barbudal Monkey Project (referred to as "Lomas"), centered around the tropical dry forests of Reserva Biologica Lomas Barbudal (10°29–32′N, 85°21–24′W) in Guanacaste, Costa Rica. The field site also extends beyond the reserve to land owned by Finca El Pelón de la Bajura and other nearby private and public land. Initiating in 1990, the project has persisted until the present day, with its primary objective centered around the continuous monitoring of the social behavior and life history of white-faced capuchins (Perry *et al*., 2012).

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; virtually all annual rainfall (1,000–2,200 mm) occurs from May to 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 common in the dry season and increasingly so with stronger and more frequent El Niño events due to climate change (Campos-Vargas & Vargas-Sanabria, 2021; Perry *et al*., 2012). Additionally, human disturbance persists year-round at Lomas through agriculture, mining, poaching, and logging (Quesada & Stoner, 2004; Stoner & Timm, 2004; Jacobson, personal communication).

Data Collection

We collected data on the movement trajectories of capuchin groups from September 2009 to March 2020 by using handheld Garmin GPSmap Series units (62 s, 64, 64 s, 66sr) clipped on or placed in researcher backpacks. Researchers followed capuchin groups from dawn until dusk recording the groups' trajectory over the period when capuchins are expected to be active. During search days, researchers initiated GPS recording upon encountering groups and continued until the groups reached their sleeping site. When researchers were not collecting behavioral data on specific individuals, they positioned themselves as close to the geometric center of the group as feasible. Researchers maintained GPS recording as long as at least some individuals remained within visual contact, typically with 1–20 m between the researcher and the animal. However, in situations where researchers lost contact due to difficult conditions or when transitioning to study different groups, researchers would conclude GPS recording prematurely. Inefficiency of early GPS models and satellite disconnection due to cloud cover, cliff topography, or dense canopy also disrupted GPS data collection.

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 using reproducible scripts in the software environment R (R Core Team, 2022). We also wrote automated functions which flagged tracks outside of the typical study area or data collection period. We visualized tracks with the mapview package (Appelhans *et al*., 2022) to manually identity, flag, and remove erroneous points. Errors could result from satellite issues or researchers forgetting to turn off their GPS units once they left a focal group.

In our full dataset, there are a total of 3,086 tracks, including 1,937,900 recorded locations. 1,902 (62%) of the daily tracks are at least 10 h in duration, and 2,555 (83%) are at least 5 h. We programmed GPS units to collect locations at one fix per 5 min between 2009–2012. When GPSs were upgraded in 2013, they began collecting at one fix per 30 s, which remains the same today. While we maintained the original sampling rates to measure fine-scale movement patterns, such as daily path length, for the purposes of this study, we adjusted the sampling rate to one fix per 30 min to manage computational costs during home range estimation. After changing the sampling rate, our dataset includes 65,645 recorded locations, encompassing roughly 25,000 observation hours across 11 groups from 2009 to 2020 (Fig. 2).

There were six cases where specific groups were followed almost continuously for long periods of 2 to 4 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 create sampling regimes that varied in total duration, regularity of sampling effort, and volume of data.
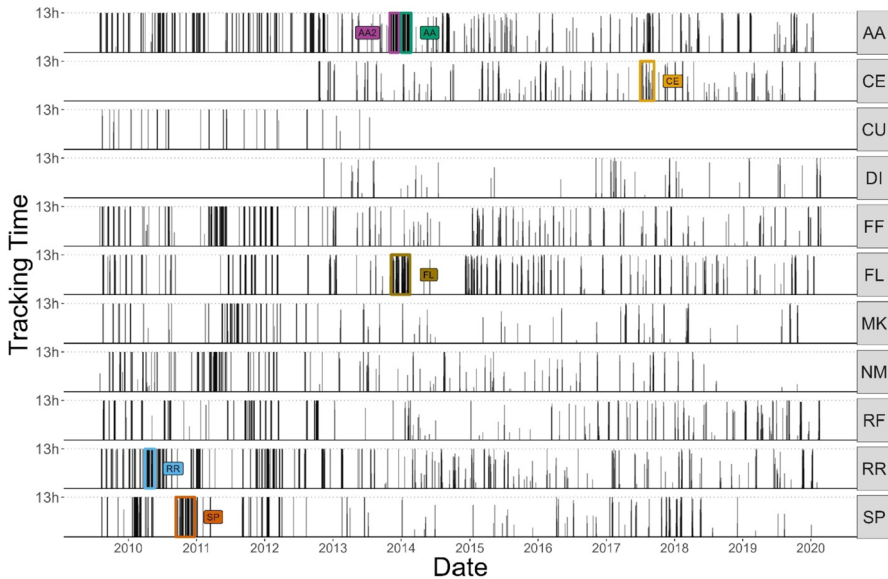
Fig. 2 Temporal representation of handheld GPS tracking data collected from 11 groups of white-faced capuchins at the Lomas Barbudal Monkey Project in Costa Rica, September 2009 to March 2020. Colored boxes show six near-continuous segments of data (i.e., "complete segments") selected from the total dataset to be thinned to create varying sampling regimes. Each vertical line shows the time sampled in a single day, with a maximum of 13 possible tracking hours (or 26 locations collected at a 30-min sampling rate). Group name is provided on the right side of the figure. Figure created using code from (Campos *et al.*, 2014).

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 data from these segments were collected over a period of no less than 50 days (with a maximum of 102 days), during which the data were recorded nearly continuously. We thinned each complete segment to generate ten alternative sampling regimes per complete segment, totaling 60 different regimes (Fig. 3). We thinned five of the ten sampling regimes created from each complete segment by removing days from either the beginning, the end, or both, thereby ensuring that these regimes maintained nearly continuous monitoring effort. We refer to these thinned regimes as "concentrated sampling regimes." We thinned the other five regimes by randomly removing days to create irregular sampling gaps. We refer to these regimes as "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).
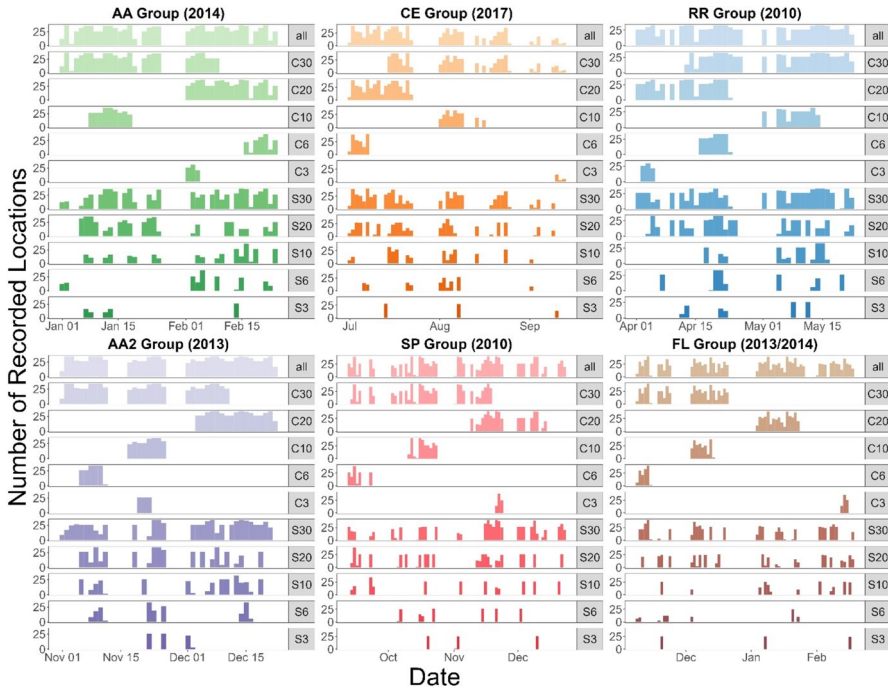
Fig. 3 Temporal representation of sampling regimes created by thinning near-continuous segments of data (i.e., "complete segments") collected from white-faced capuchins at the Lomas Barbudal Monkey Project in Costa Rica, September 2009 to March 2020. The top row of each plot (labelled "all") shows the total data from the complete segment. The following 10 rows of each plot depict different sampling regimes thinned from their respective complete segment, which are labelled with a sampling regime ID. "C" labels indicate concentrated data. "S" indicates spread data. Numbers indicate days in the sampling regime.

Home Range Estimation

We computed home range estimates using the AKDE method implemented in the ctmm package (Calabrese *et al.*, 2016) in R (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 employ the "weights = TRUE" option in the akde function to incorporate irregular data. This option assigns higher weights to under-sampled time periods and lower weights to over-sampled time periods (Fleming *et al.*, 2018). Furthermore, we address location error by incorporating an informative prior with a mean of 20 m and 2 degrees-of-freedom. This prior distribution provides a credible interval of approximately 7 to 33 m, which informs our movement models about the potential error associated with the location estimates (Fleming *et al.*, 2020). The inclusion of this prior accounts for satellite error, error caused by variation in group spread, and handheld GPS position relative to the capuchin group center. 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 show how we applied this method to the 60 sampling regimes for this study in Appendix 2.

Performance of Sampling Regimes for Home Range Estimation

To evaluate the performance of the 60 sampling 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). While the biological home range cannot be known with certainty, we assume that estimates that accurately represent the data from the complete segments are more likely to be closer to the biological 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 sampling regimes. This measure is hereafter referred to as "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. Also, because data from the sampling regimes 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.

To examine the relationship between key sampling characteristics (e.g., number of locations, number of weeks, and data irregularity or continuity) and home-range performance, we employ binomial generalized linear mixed models (GLMMs) implemented using the brms package (Bürkner *et al*., 2023). Our number of successes was the number of locations from the complete segment that fell within the 95% AKDE of each sampling regime, whereas the number of trials was the number of locations overall in the complete segment. 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 min per location). Finally, our third model predicts performance based on the number of 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. 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. We assessed the fit of our statistical models by employing posterior predictive checks by using the bayesplot package (Gabry *et al*., 2022). Posterior predictive checks evaluate model fit by comparing the observed data to simulated data from the posterior predictive distribution of the outcome variable inferred from the model (Rubin, 1984).

Finally, we compared the effects of increasing weeks versus increasing locations on the performance score. We did this by first z-score standardizing the number of weeks and locations in each regime. 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 size 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 (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 (Fleming *et al.*, 2019) or the mean number of times the animal crossed the linear extent of its home range (Fleming & Calabrese, 2017). It is estimated by dividing the sampling time (T) by the time-lag between locations required for independence (τ), which also corresponds to the approximate average home range crossing timescale (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 therefore is a better indicator of the reliability of home range estimates (Fleming *et al.*, 2019; Noonan *et al.*, 2019). See Appendix 4 for a comparison of absolute sample size and effective sample size.

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. Conversely, overestimating τ will result in negatively biased effective sample sizes, leading to exceedingly large uncertainties.

We consider the values of τ taken from the movement models fit to the complete segments as more reliable compared to estimates derived from the sampling regimes. This is because they are based on continuous data collected over extended periods, which effectively capture the timescale necessary for capuchin groups to fully use their entire range (determined by field-based approximations). We used these values to estimate reliable effective sample sizes for each sampling regime by dividing the sampling times (T) of the regimes by the τ values taken from the movement models fit to the complete segments. Subsequently, we contrasted these estimates to the effective sample size estimates derived from the movement models fit to the sampling regimes. Evaluating the discrepancy between these estimates offers

insights into potential sources of biases in τ (and consequently the effective sample size), stemming from variations in the sampling regimes.

Stationarity and Temporal Scale of Sampling Regime

To examine the long-term stability of home ranges and identify suitable time scales for estimating them in our longitudinal dataset we conducted a case study focusing on two groups: AA and RR. We calculated a single annual home range for each group (2014 for AA and 2012 for RR) in which the data met our criteria for adequate home range estimation performance, as determined from our evaluation of the effects of sampling elements. Subsequently, we investigated changes in space use over four years by examining whether location data from different time periods, not included in the data used for home range estimation, fell within the boundaries of the home range. Specifically, we analyzed the proportion of locations from the previous year, the subsequent year, and the subsequent next year that fell within the mean 95% UD boundary of the home range estimate. This analysis allowed us to assess the consistency of the home ranges over time. Additionally, we visually assessed whether data from different seasons represented distinct portions of the annual home range. This approach enabled us to evaluate the temporal consistency of home ranges and determine the feasibility of segmenting the data based on specific time periods, such as years or seasons.

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 2016–2022), 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 during 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 (ASAB Ethical Committee/ABS Animal Care Committee, 2023).

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

Results

Spread Sampling Outperforms Concentrated Sampling

Spread sampling regimes performed better on average, estimating home ranges that more closely approximated the target performance score of 0.95 (posterior median = 0.93, 95% credible interval: 0.87–0.96). Concentrated sampling regimes estimated home ranges that were more consistently negatively biased (posterior median = 0.85, 95% credible interval: 0.61–0.91) (Fig. 4a). Additionally, spread sampling regimes were more robust than concentrated sampling regimes to low quantities of recorded locations and weeks (Fig. 4b and c). Generally, home range
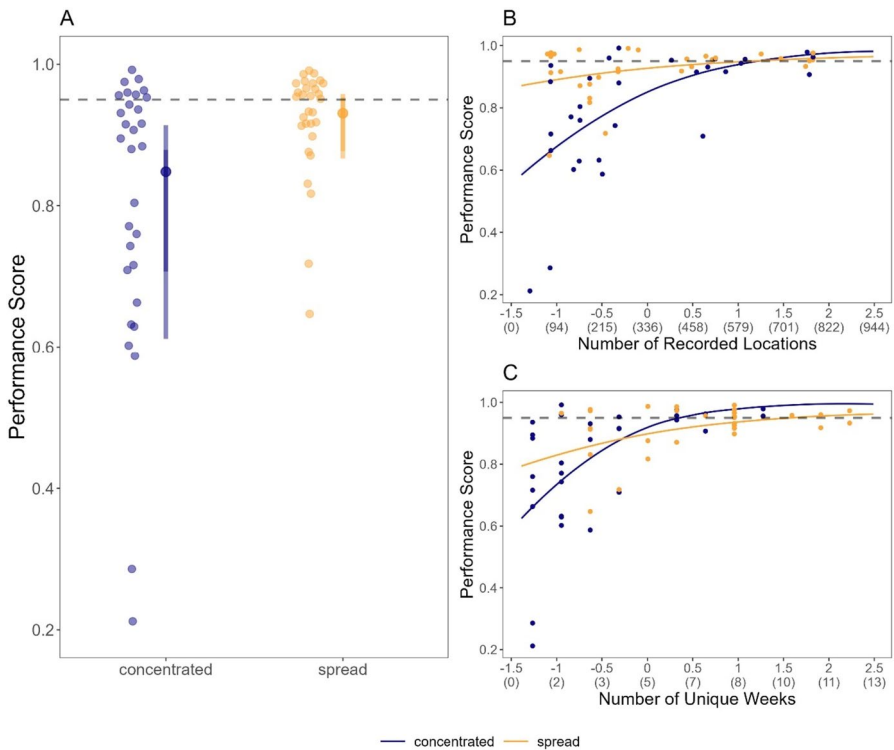
Fig. 4 Model predictions of home range estimation performance predicted by characteristics of sampling regimes for white-faced capuchin movement data collected at the Lomas Barbudal Monkey Project in Costa Rica, September 2009 to March 2020. (**A**) Plot showing the home range estimation performance score predicted by whether the data was concentrated (blue) or spread (orange). Within these two categories, raw data are shown on the left, and posterior point intervals are shown on the right. Posterior point intervals describe the median and 66% and 95% credible intervals of the posterior distribution. Model predictions for the effect of number of locations (**B**) and number of weeks (**C**) within the sampling regimes on performance score. Horizontal dashed line indicates optimal performance score of 0.95. Dark solid lines are the mean posterior predictions; lighter lines (although hard to see as they are very close to the mean) are 200 randomly sampled posterior predictions. Plots visualizing varying effects per group are shown in Figs. 1, 3, and 5 in Appendix 3.

estimates for concentrated sampling regimes performed worse with fewer locations and weeks, but their confidence intervals remained consistently narrow. In contrast, 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 (Fig. 5). Based on our findings, we established that for spread data, sampling regimes should encompass a minimum of 100 locations and span at least 5 weeks. For concentrated data, sampling regimes necessitate a minimum of 500 locations and 5 weeks.

More Data is Not Always Better

Increasing the temporal coverage (measured by the number of weeks) in sampling regimes had a greater positive effect on home range estimation performance compared to 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 approximately 23% (Fig. 6a). Meanwhile, a + 1 SD increase in weeks (3 weeks) boosted estimation performance by approximately 30% (Fig. 6c). This
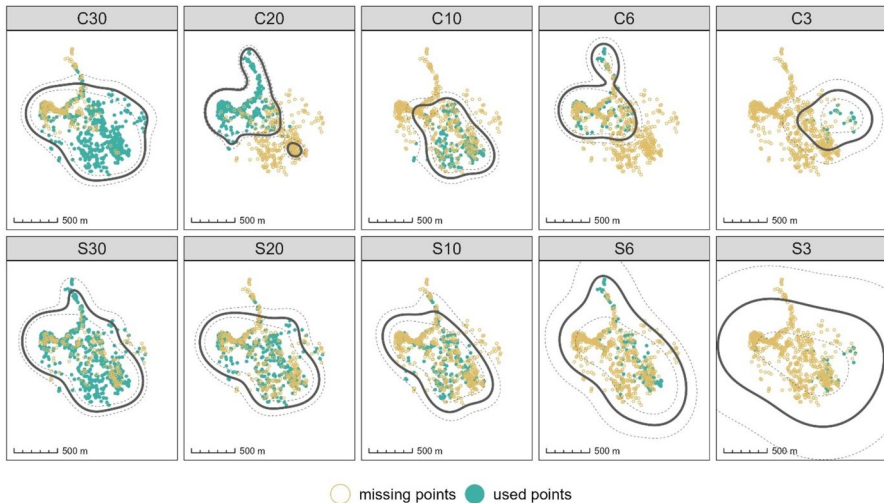
Fig. 5 Home-range estimates derived from ten varying sampling regimes created by thinning a near-continuous portion of the handheld GPS dataset from a single group (CE) of white-faced capuchins at the Lomas Barbudal Monkey Project in Costa Rica, July to October 2017 (Appendix 2 for all groups). The dark lines indicate the mean 95% utilization distribution contour and the dotted lines indicate the 95% confidence intervals. The open yellow points indicate the locations that were thinned from the complete segments and the filled green points indicate the locations that remained in the sampling regimes. The top row shows the concentrated sampling regimes and the bottom row shows the spread sampling regimes. Despite poor performance, home range estimates generated from sampling regime IDs C20, C10, C6, and C3 show narrow confidence intervals, suggesting biased and misleading effective sample sizes.
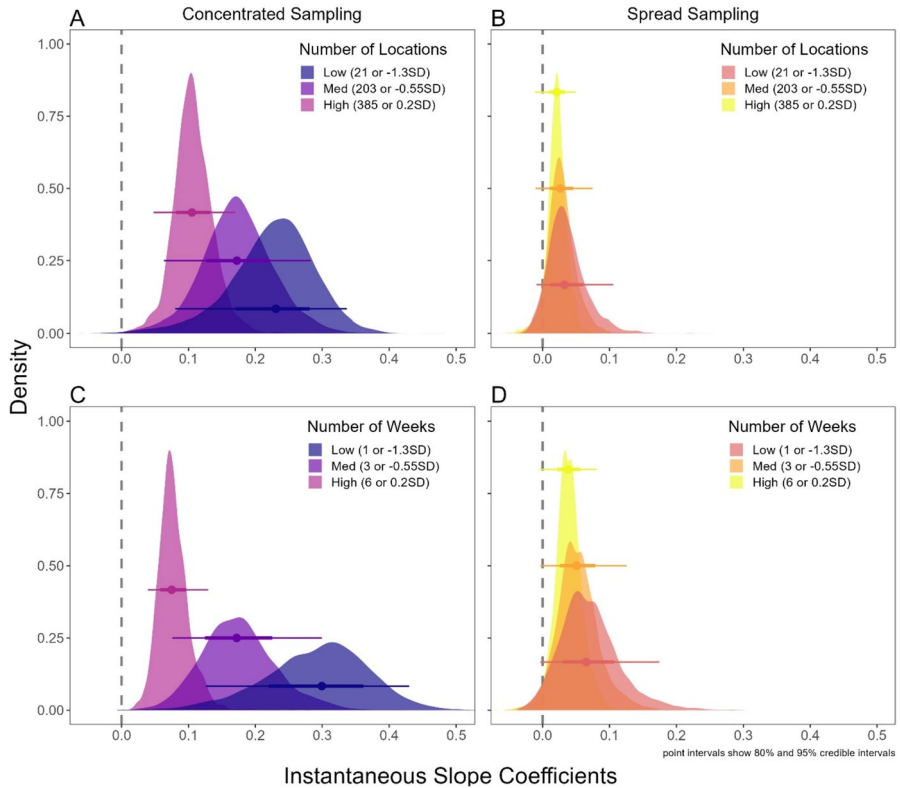
Fig. 6 Model estimates of the instantaneous slope coefficients (i.e., first derivatives) for increasing locations and weeks in sampling regimes on performance of home range estimates of white-faced capuchin groups at the Lomas Barbudal Monkey Project in Costa Rica, September 2009 to March 2020. Plots depict a combination of posterior densities, mean point estimates, and credible intervals (80 and 95%) for the instantaneous slope coefficients at varying quantities of weeks and recorded locations. Instantaneous slope coefficients represent the effect size of increasing 1 standard deviation in weeks or locations on the home range estimation performance score. Plots A and C (Blue-purple colors) represent concentrated sampling regimes. Plots B and D (orange-yellow) represent spread sampling regimes. Darker colors represent smaller quantities. Lighter colors represent greater quantities of weeks or locations.

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-min 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 the optimal performance value of 0.95. For instance, when concentrated sampling regimes had *medium* quantities of locations and weeks (*medium* = −0.55 SD corresponding to 3 weeks or 203 locations), a + 1 SD in weeks and + 1 SD in locations both improved performance by approximately 17%. At *high* quantities (*high* = 0.2 SD corresponding to 6 weeks or 385 locations), a + 1 SD increase in weeks improved performance by approximately

8% and a + 1 SD increase in locations improved performance by approximately 10%.

We found a similar trend for spread sampling regimes: increasing the number of weeks improved performance more than increasing the number of locations (Fig. 6b and d). However, the effects of increasing both weeks and locations were much smaller compared with concentrated sampling regimes, because spread sampling regimes already had performance scores relatively close to optimal even with *low* quantities of locations and weeks.

Concentrated Sampling is Prone to Bias in the Effective Sample Size

The absence of crucial data can result in skewed estimations of the effective sample size, especially for concentrated sampling regimes. Of the 60 sampling regimes, 12 concentrated sampling regimes and six spread sampling regimes showed significantly biased estimates (Fig. 7). The most substantial biases occurring in groups CE and FL, where several sampling regimes with seemingly adequate absolute sample sizes (~300–500 locations) and total time sampled (~10–20 full tracking days) had very large biases (e.g., off by effective sample sizes of approximately 50–150).
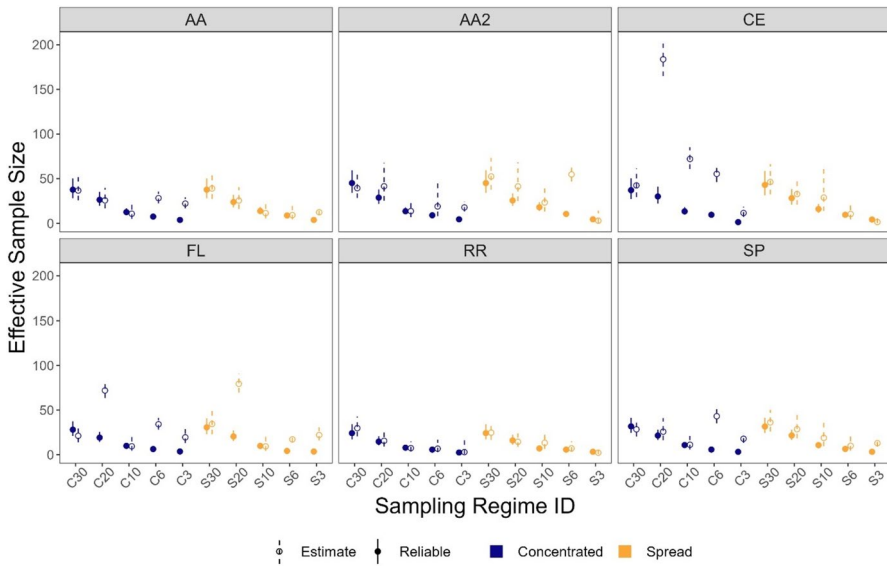
Fig. 7 Effective sample sizes of various sampling regimes collected from white-faced capuchin groups at the Lomas Barbudal Monkey Project in Costa Rica, September 2009 to March 2020. Each panel shows the effective sample size estimates of each sampling regime within a group (*Estimate* effective sample size: open circles indicate the means and dashed lines indicates 95% confidence intervals), and a comparison with what the effective sample size should be if the home range crossing time was informed by the complete segments (*Reliable* effective sample size: closed circles indicate the means and solid lines indicates 95% confidence intervals). Colors indicate whether the sampling regime had concentrated (blue) or spread (yellow) data.

These biases resulted in home range estimates with high levels of certainty but very low performance scores (Fig. 5).

Capuchin Space use Varies Across Years and Seasons

In our case study, assessing the stability of home ranges and identifying suitable temporal scales for home range estimation, we observed distinct trends in the space-use patterns of groups RR and AA. Locations of group AA were relatively stationary across the 4-year period, although there were some excursions into areas outside the 2014 home range contour in 2015. Group RR displayed stability for two consecutive years, as evident from a substantial proportion of observations the previous year in 2011 falling within the home range contour from 2012. However, over the subsequent 2 years (2013 and 2014), there was noticeable drift in the observed locations (Fig. 8).

For group AA, we estimated the home range for 2014 and found that 99% (95% CI: 0.985–0.996) of the locations from 2013 fell within the mean 95% UD boundary. Meanwhile, 88.7% (95% CI: 0.824–0.949) of the locations from 2015 and 96% (95% CI: 0.887–0.988) of the locations from 2016 were within the UD boundary. For group RR, we estimated the home range for 2012 and found that 98.4% (95% CI: 0.949–0.997) of the locations from 2011, 89.1% (95% CI: 0.830–0.932) of the locations from 2013, and 86.2% (95% CI: 0.842–0.900) of the locations from 2014 fell within the UD boundary. Furthermore, group RR showed consistent space-use
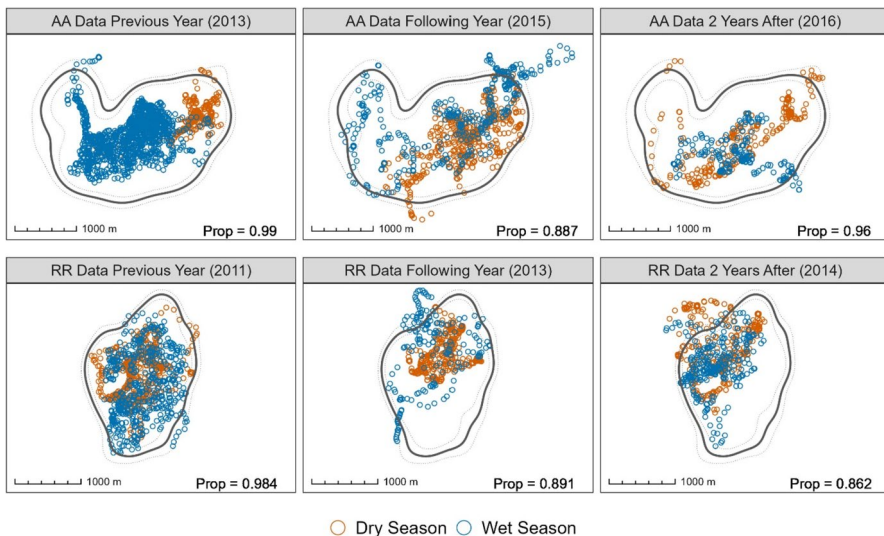

Fig. 8 Annual home-range estimates for two groups of white-faced capuchins at the Lomas Barbudal Monkey Project in Costa Rica (2011–2016) plotted alongside data from the preceding, subsequent, and next subsequent year. Dark lines indicate the mean 95% utilization distribution contour for 2014 (group AA) and 2012 (group RR). Dotted lines indicate the corresponding 95% confidence intervals.

patterns between the wet and dry seasons, whereas group AA showed potential seasonal variations in certain years.

Discussion

Our study shows that temporal coverage is a more important factor than the raw quantity of data for home range estimation. Sampling protocols that capture greater space-use variability by distributing location data over prolonged durations yield the most dependable home range estimates. Technological advancements in handheld GPS devices have facilitated the collection of location data with remarkable frequency, allowing measurements to be obtained at intervals as short as every second (Garmin Customer Support, n.d.). The enhanced capabilities of these devices, characterized by faster sampling rates and small error (~ 3 m), have paved the way for new opportunities to study the movement patterns of habituated animals in unprecedented detail. However, our findings indicate that, when examining home range estimates, faster sampling rates may not necessarily yield improved results, as locations collected quickly in succession tend to contribute redundant information at the home range scale.

We employed a relatively coarse sampling rate of one location every 30 min. The estimated time between locations necessary to ensure independence, known as range crossing time, averaged around 12 h. This duration, although short compared with other animals, such as big cats (Karelus *et al*., 2021; Morato *et al*., 2016), ungulates (Calabrese *et al*., 2016; Fleming *et al*., 2015b), and other large mammals (Noonan *et al*., 2020), meant that we obtained new and independent information about the home range approximately once every 24 consecutive locations. However, we found that further information about the range was provided when locations were separated by week-long intervals. These findings highlight the importance of prioritizing the collection of location data with larger time intervals between measurements.

Encouragingly for researchers employing handheld GPS data to estimate home ranges, our study revealed that sporadic gaps in data collection do not inherently compromise home range estimation performance. In fact, sampling regimes that sacrificed continuous observation for greater temporal coverage consistently outperformed sampling regimes that were continuous but concentrated into short time periods, even when effective sample sizes were equal. The enhanced performance of spread-out sampling strategies stems from longer total sampling durations providing capuchin groups more time to fully use their home range. Despite potential sampling gaps leading to missed range crossings, irregular data distributed over longer periods captured more variation in space use. Consequently, sampling regimes with extended durations should provide a more comprehensive representation of an animal's overall space use, provided that crucial changes in ranging behavior are not missed due to sampling gaps.

Concentrated sampling strategies occasionally yielded positively biased effective sample sizes, leading to overconfident home-range estimates. These sampling regimes failed to capture variations in underlying movement processes, specifically the sudden shifts occurring within the home range. We observed that

when capuchin groups temporarily confined their movements to specific subareas within their home range, the movement models fitted solely to the data from these specific periods yielded an overestimation of the effective sample size. This is because the capuchin groups repeatedly traversed this smaller area, which led to underestimated, home-range crossing times and overestimated effective sample sizes. As a result, the overestimated effective sample sizes constrained the confidence intervals, creating the illusion of high-quality home-range estimates, when in reality they were too small (Fig. 5, C20, C10, C6, and C3). This highlights the importance of examining home range estimate outputs in the context of the species' biology, and not solely relying on statistical criteria.

The influence of the movement and foraging behavior of the study species is likely a key determinant in the susceptibility of handheld GPS data to bias in the effective sample size. Species, such as frugivorous primates that forage on ephemeral and patchily distributed resources, must differentially allocate time across their home range so that search efforts align with when and where resources are most productive (Altmann, 1974; Janson, 2019). Frugivores may do this by foraging for extended periods in small areas (Oppenheimer, 1968) and then shifting within their home range in response to changing resource availability (Campos *et al*., 2014). Due to frugivores' sudden changes in space use, estimating their home-range crossing timescale poses challenges. It often requires more time to accurately summarize compared with folivorous primates, which usually move in more constant and predictable patterns, as their food resources are more evenly distributed (Reyna-Hurtado *et al*., 2018). However, even folivorous species, such as red colobus monkeys (*Piliocolobus tephrosceles*), have been observed to deplete food patches in an irregular manner as well (Snaith & Chapman, 2005).

Our examination of home range stability over extended periods through the case studies involving group AA and RR revealed considerable variation in space-use patterns over years and potentially across seasons. As a result, we determined that the most suitable temporal scales for estimating home ranges across our full longitudinal dataset are annual and seasonal scales. These scales strike a balance; they are long enough to capture the entire home range used by groups, while still allowing important changes to be discerned. Applying criteria based on our analysis of sampling elements, specifically requiring spread data to encompass at least 5 weeks across each segment and consist of at least 100 locations, we estimated annual and seasonal home ranges across the entire dataset from 2009 to 2020. Among a total of 117 annual and 212 seasonal segments encompassing 11 groups, we identified 97 annual and 127 seasonal segments that satisfied our criteria for reliable home range estimation.

Temporal Scale of Sampling Regimes

A crucial challenge in home range estimation revolves around determining the appropriate temporal scale. This involves ensuring that the chosen scale is sufficiently long to encompass the entire home range used by the animal. By doing so, we can ensure that variations in home range estimates carry biological significance

rather than being artifacts of sampling. Additionally, when investigating temporal changes, it is important to strike a balance where the temporal scale is not excessively long, thereby obscuring biologically meaningful changes in space-use patterns. As static representations of animal space use, home range estimates possess inherent limitations in detecting dynamic movement changes (Benhamou & Riotte-Lambert, 2012). Therefore, the decision of temporal scale and where to segment the data becomes critically important.

Several longitudinal studies have shown remarkable stability in primate home ranges over years, decades, and even across generations (Janmaat *et al*., 2009; Jolly & Pride, 1998; Poirier, 1968; Singleton and van Schaik, 2001). In group AA, we also observed a relatively long period of home-range stability of at least 4 years (Fig. 8). When home ranges remain stationary for prolonged periods, expanding the sampling window beyond the point of achieving a sufficient effective sample size is expected to have minimal impact on the estimation of the home range (Fleming *et al*., 2014b). Consequently, diffusion rates and/or the estimated home range area should have reached a plateau, indicating an adequate effective sample size has been reached and that further sampling does not result in more diffusion and/or size augmentation.

One key consideration for sampling design is determining the duration required to reach an adequate effective sample size, which depends on the specific timescale for the animal to fully use its entire home range. To achieve this, ten independent locations (i.e., observed home range crossings) are generally considered adequate for autocorrelated kernel density estimation (Fleming *et al*., 2019; Silva *et al*., 2021). Consequently, it is essential to ensure that the temporal scale chosen for home range analysis is at least as long as the timeframe necessary to meet this requirement (refer to Appendix 1 for a detailed walkthrough of this analysis). By adhering to this practice, researchers can establish a solid foundation for making meaningful comparisons across various species and sampling designs (Fleming & Calabrese, 2017).

A key challenge is that home ranges are not always stationary. For instance, group RR gradually shifted their range over a 4-year period. Other notable examples include seasonal shifts observed in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) (Li *et al*., 2001), shifts in response to habitat loss observed in vervet monkeys (*Cercopithecus aethiops*) (Isbell *et al*., 1990), and home range shifts following demographic changes observed in grey-cheeked mangabeys (*Lophocebus albigena*) (Janmaat *et al*., 2009). Because one of the critical assumptions underlying the range distribution is the stationary nature of the home range (Silva *et al*., 2021), it is important to segment the data before a change in stationarity occurs (Dettki & Ericsson, 2008), thereby estimating separate home ranges during these distinct periods.

An alternative and more conventional strategy involves reporting home-range estimates across various standardized temporal scales, such as monthly, quarter-annually, half-annually, and annually, because the outcomes can differ depending on the duration of these time periods (Börger *et al*., 2008; Campos *et al*., 2014; White & Garrott, 1990). While these scales are somewhat arbitrary, this approach ensures that important spatiotemporal variations in home range patterns are captured (Campos *et al*., 2014). Nonetheless, when an animal's home-range crossing time is relatively long, using shorter time scales, such as monthly or quarter-annually,

may yield estimates that align more closely with the occurrence distribution. Thus, area estimates will be underestimated if the intended target was the range distribution. If an adequate effective sample size is not attained, using arbitrary scales can introduce bias, particularly in cross-species comparisons when species differ in their home range crossing times (Fleming & Calabrese, 2017). Incorrect reporting of such results can mislead meta-analyses (Noonan *et al.*, 2020) or conservation plans (Brashares *et al.*, 2001; Gaston *et al.*, 2008). A justified approach, therefore, is to exclusively report estimates as the *home range* when temporal scales are long enough to ensure an adequate effective sample size and thus represent the range distribution. Additionally, in many cases, it may be appropriate to report home range estimates across temporal scales that hold biological significance, such as across seasons.

Species-level Differences in Home-Range Crossing Time

The estimated time intervals between recorded locations, ensuring their independence, bear biological significance, as they are directly proportional to the timescale of home range crossings. Hence, these intervals dictate the duration needed for sampling strategies to adequately capture the biological home range. When devising sampling protocols, it is crucial to acknowledge the considerable variation in the time taken by individuals or groups to traverse their respective home ranges, as this varies across different species and ecological contexts. Home ranges tend to be larger for frugivores than folivores (Milton & May, 1976) and large-bodied species compared to small-bodied species (Terborgh & Janson, 1986). While larger home ranges generally translates into longer home-range crossing times (Noonan *et al.*, 2020), this may not always be the case, particularly when movement speeds are variable between species. For instance, across mammals, carnivores typically have larger home ranges than herbivores, but herbivores tend to have longer home range crossing times (Noonan *et al.*, 2020), presumably due to their slower and more diffusive search patterns for food (Reyna-Hurtado *et al.*, 2018).

Among primates, 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). 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 nonterritorial species also may 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). For reference of how home-range crossing time translates to appropriate sampling design, the capuchin groups in our study had a mean home range crossing timescale of 12.5 (95% CI: 9.4–16.7) hours, which scales to about 1 day considering that they very

rarely move at night. To reliably estimate the home range, we found that sampling regimes should include approximately 100–600 locations distributed over at least 5–7 distinct weeks. A similar sampling duration (45–136 days) was required in a study on giant anteaters (*Myrmecophaga tridactyla*), where the average home range crossing time was approximately 2 days (Giroux *et al*., 2021). In contrast, a study on elongated tortoises (*Indotestudo elongata*) estimated a home range crossing time of 17 days on average (although sometimes much longer for particular individuals), and even with 1 year of consistent sampling, researchers were not able to achieve adequate effective sample sizes for several individuals (Montano *et al*., 2021). Studies on Mongolian gazelles have shown estimated range crossing times of around 5–6 months (Fleming *et al*., 2014a). Given they live an average of 4–8 years (Olson *et al*., 2014), attaining adequate effective sample sizes is challenging within an individual's lifespan (Fleming *et al*., 2019).

Relevance of Sampling Regime for Conservation

In our study, effective sample size bias was most problematic for groups that had the most fragmented habitats from roads and pastures (CE and FL group). Compared with other groups, CE and FL required more locations and weeks to reach the adequate home-range estimation performance. These greater sampling requirements 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. 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 (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 do not provide enough time for animals to cross between fragments will underestimate their home range crossing time and have highly biased effective sample sizes.

It is worrying that species of conservation concern often are prone to biased home-range estimates. High-risk species, such as large-bodied species with long home-range crossing times (Cardillo *et al*., 2005), are especially susceptible to underestimated home range areas due to challenges in obtaining sufficient effective sample sizes (Noonan *et al*., 2020). Similarly, our findings suggest that animals that live in fragmented habitats are prone to effective sample size bias. This bias can lead to both overconfident and underestimated home range estimates, which raises significant conservation concerns. Underestimated home range estimates may result in protected areas that are insufficient for population survival and reproduction (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 these results inform conservation initiatives.

Recommendations for Sampling Design

Based on our findings, we advise biologists to design appropriate sampling regimes (balancing effort with temporal coverage) by considering (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 given a consistent underlying movement process (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 are therefore when the sampling rate is as high as 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 independent location data points, is maximized (Fleming & Calabrese, 2017). As we have shown, 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. Maximize independent locations by spreading data across an adequate time period to cover the complete home range of study animals (Fleming *et al*., 2015b).
2. To correct effective sample size bias, account for species' home range crossing time. Use a pilot study or the Movedesign app (Silva *et al*., 2023) if a rough estimate is unknown.
3. When labelling results as *home ranges*, avoid temporal scales, such as "weekly" or "monthly." Choose time scales aligned with species' biology, such as seasonal sampling, or sufficiently long and comparable intervals, such as annual sampling, to ensure meaningful comparisons across studies (Fleming & Calabrese, 2017).
4. Integrate GPS data collection with other priorities like behavioral and phenology data collection. Periodically rotate among multiple groups or individuals if necessary, allowing for adequate temporal coverage of all study animals.
5. Acknowledge the limitations of handheld GPS data, especially if missing data are a result of researchers being unable to track primates in specific areas or during certain periods. In such cases, home range analysis may not be suitable.
6. Check data sufficiency using variogram regression (Appendix 1; Fleming *et al*., 2014b) or by plotting home range area over time/sampling effort to see if it has plateaued (Odum & Kuenzler, 1955).
7. If the data meet the requirements for home range estimation, use AKDE (Appendix 1 for a detailed walkthrough) as it considers autocorrelation and the range

distribution (Fleming & Calabrese, 2017). Newer versions integrate barriers and habitat components (Alston *et al*., 2023) to refine estimates.

Conclusions

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. Nonetheless, the reliability of home range estimates may be compromised when the sampling effort fails to capture the full extent of the biological home range or through inappropriate application of statistical approaches. This is concerning given that home range estimates play a crucial role in ecological inference and conservation decision-making. 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 an exceptional position to address these inquiries and connect them to fitness. Nonetheless, our study has revealed that the usefulness of handheld GPS data in estimating home ranges depends on whether the sampling regimes have adequate temporal coverage for the focal animals to use their entire home range. Adhering to sound scientific principles involves linking the data collection procedure to the specific process of interest. It is therefore necessary to take care when designing sampling protocols for home range estimation to ensure that they represent the biological home range of the species under investigation.

Declarations

Inclusion and Diversity Statement While citing references scientifically relevant for this work, we actively worked to promote gender balance in our reference list. Additionally, the acknowledgements section includes contributors from the location where the research was conducted, who participated in data collection and field-work management.

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