

The Relationship Between GPS Sampling Interval and Estimated Daily Travel Distances in Chacma Baboons (*Papio ursinus*)

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Abstract

Modern studies of animal movement use the Global Positioning System (GPS) to estimate animals' distance traveled. The temporal resolution of GPS fixes recorded should match those of the behavior of interest; otherwise estimates are likely to be inappropriate. Here, we investigate how different GPS sampling intervals affect estimated daily travel distances for wild chacma baboons (Papio ursinus). By subsampling GPS data collected at one fix per second for 143 daily travel distances (12 baboons over 11–12 days), we found that less frequent GPS fixes result in smaller estimated travel distances. Moving from a GPS frequency of one fix every second to one fix every 30 s resulted in a 33% reduction in estimated daily travel distance, while using hourly GPS fixes resulted in a 66% reduction. We then use the relationship we find between estimated travel distance and GPS sampling interval to recalculate published baboon daily travel distances and find that accounting for the predicted effect of sampling interval does not affect conclusions of previous comparative analyses. However, if short-interval or continuous GPS data-which are becoming more common in studies of primate movement ecology-are compared with historical (longer interval) GPS data in future work, controlling for sampling interval is necessary.

Keywords Daily travel distance \cdot Day path length \cdot GPS \cdot Movement ecology \cdot *Papio ursinus*

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Introduction

Understanding how animals interact with and move through their environment enables researchers to better understand animal behavior, physiology, and ecology (Getz and Saltz 2008; Nathan *et al.* 2008). Modern studies of animal movement use the Global Positioning System (GPS) to estimate animals' travel distance over a given time period. Researchers record GPS fixes at intervals along the journey of a focal animal or group— either using a handheld GPS (Santhosh *et al.* 2015; Schreier and Grove 2010), or by attaching a GPS logger to a focal animal (Hampson *et al.* 2010a,b; Ren *et al.* 2008)—and sum the distances traveled between GPS fixes. More refined estimates of distance traveled are also possible; for example, modeling movement as a continuous-time stochastic process minimizes the effects of position and velocity autocorrelation that are inherent in such data (Calabrese *et al.* 2016).

Recording of GPS at intervals in time (rather than continuously) is common because it saves battery life and allows researchers to increase the time over which data are collected (Mitchell *et al.* 2019; Ryan *et al.* 2004; Sahraei *et al.* 2017). However, this practice underestimates travel distance (McGavin *et al.* 2018; Sennhenn-Reulen *et al.* 2017). For example, a study of Guinea baboons (*Papio papio*) (Sennhenn-Reulen *et al.* 2017) examined differences in travel distance estimates from 2-h periods by subsampling GPS data collected at one fix per second, finding that travel distances were significantly shorter if less frequent GPS fixes were used in calculations. Indeed, extensive theoretical and empirical work has shown that the temporal resolution of GPS fixes needs to match those of the behavior of interest; otherwise estimates are likely to be inappropriate (Borger *et al.* 2006; de Weerd *et al.* 2015; Ganskopp and Johnson 2007; Johnson and Ganskopp 2008; McGavin *et al.* 2018; Mills *et al.* 2006; Mitchell *et al.* 2019; Noonan *et al.* 2019; Postlethwaite and Dennis 2013; Rowcliffe *et al.* 2012; Sennhenn-Reulen *et al.* 2017; Swain *et al.* 2008; Tanferna *et al.* 2012).

Here, we estimate daily travel distances for chacma baboons (*Papio ursinus*) using GPS data collected at one fix per second synchronously for 12 adult individuals over 11–12 days. By sampling different temporal resolutions from this high-frequency GPS data set, we investigate the relationship between estimated travel distances and GPS sampling frequency (Sennhenn-Reulen *et al.* 2017). Then, we use the quantified relationship between estimated travel distance and GPS sampling interval to recalculate published baboon daily travel distances (e.g., Dunbar 1992; Johnson *et al.* 2015) and see how estimates alter when accounting for the relationship between estimated distance and GPS sampling interval found in our own data set.

Methods

Study System

We studied wild adult chacma baboons in the Da Gama group in Cape Town, South Africa (34.1617° S, 18.4054° E). The group's home range includes urban areas comprising residential suburbs and natural areas that fall mostly within Table Mountain National Park which are dominated by indigenous fynbos vegetation with smaller patches of exotic vegetation (Hoffmann and O'Riain 2012). The Mediterranean climate of the Cape Peninsula is characterized by hot dry summers and mild winters with moderate-high rainfall (Hoffman and O'Riain 2012), and in this study we use GPS data collected during winter (August) of a field season lasting from July to November 2018. The Da Gama group comprised 2 adult males, 19 adult females, and *ca.* 30 subadults, juveniles, and infants.

Movement Data

During the field season, we recorded GPS data for 13 individuals (2 males, 11 females) for a mean \pm SD of 42.77 \pm 9.92 days, range = 21–54 days (Bracken *et al.* in press) using in-house assembled SHOALgroup collars (F2HKv3) containing GiPSy 5 GPS loggers (TechnoSmArt, Italy) recording GPS fixes at 1-s sampling intervals between 06:00:00 and 18:00:00 UTC (Bracken *et al.* in press). Here we use a subset of these GPS data that provide continuous data for 12 baboons (2 males, 10 females) for 11–12 days in August 2018, representing 143 daily travel distances.

Before calculating daily travel distances (below), we removed erroneous GPS fixes outside the study area, or successive GPS fixes between which it would have been impossible for the baboons to travel (Bracken *et al.* in press). These fixes represented a median 0.01% of GPS fixes per collar (range 0.00%–0.01%) and the remaining missing or removed fixes that lasted a time period of less than or equal to 10 s, were interpolated using the fixLocNA function in the swaRm package (Garnier 2016) following O'Bryan *et al.* (2019) and Bracken *et al.* (in press). This resulted in a median 0.01% of each baboon's tracks being interpolated (range 0.00%–0.01%). Remaining missing fixes lasting >10 s represented a median 0.56% per collar (range 0.00%–1.61%).

Daily Travel Distances

To investigate the effect of GPS sampling interval on estimated daily travel distance, we subsampled the high-frequency GPS data and calculated travel distances for each baboon, for each day, using GPS fixes set at 1 s, 30 s, 60 s, 300 s, 1200 s, 3600 s, and 7200 s. We estimated daily distance by summing distances between GPS fixes and used fixed time intervals from the 1 s data set, since we wanted to simulate different programmed sampling intervals used by on-animal GPS loggers.

Because travel distance estimates made using short GPS sampling intervals will be more sensitive to measurement error than estimates made using longer GPS sampling intervals, we also calculated daily travel distances using 1 s smoothed data in an attempt to reduce high-frequency noise (Noonan *et al.* 2019). To smooth data, we used the function TrajSmoothSG from the trajr package in Rstudio (version 1.3.0), which uses a Savitzky–Golay ethod (McLean and Skowron Volponi 2018). We applied a filter order of 2 and a filter length of 7, which approximately corresponds to our maximum level of GPS error and was thus expected to reduce potential noise while retaining track characteristics (McLean and Skowron Volponi 2018). We performed *ad hoc* checks of the GPS data using known landmarks at the field site in South Africa, and in Swansea, UK and these indicated positional accuracy always to be within 5 m.

GPS Sampling Interval and Daily Travel Distances

We investigated how GPS sampling interval affected daily travel distance estimates by fitting a linear mixed-effect model in RStudio using the lme4 package (Bates *et al.* 2015). We fitted daily travel distances (N = 1144) as our response variable and sampling interval (1 s, 1 s [smoothed], 30 s, 60 s, 300 s, 1200 s, 3600 s, and 7200 s) as a fixed categorical effect. We fitted baboon identity as a random effect to control for potential interindividual differences in travel distance, checked model residuals, and used the emmeans package (version 1.4.8; Lenth 2020) for *post hoc* (Tukey method) tests for each combination of sampling interval.

Quantifying the Reduction in Daily Travel Distance

We compared estimated daily travel distance using one fix per second GPS data to different GPS sampling intervals to quantify the reduction in estimated distance when using less frequent sampling intervals and expressed this value as a proportion. We found the reduction in estimated distance traveled was proportional to GPS sampling interval and was best modeled by a logarithmic function. Using this model, we recalculated travel distances for 38 baboon groups (provided by Johnson *et al.* 2015) that provide information on GPS sampling intervals.

Ethical Note

To fit collars, a veterinarian anesthetized baboons using Ketamine (dose adjusted for body mass) after cage trapping conducted by service providers in accordance with local protocols (described by Fehlmann *et al.* 2017a). Collars were approved by Swansea University's Ethics Committee (IP-1314-5), weighed mean 2.2% baboon body mass (range 1.2%-2.6%), and were fitted with a drop-off mechanism (version CR-7, Telonics, Inc.) to avoid the need for recapture (ESM Fig. S1). The authors declare that there are no conflicts of interests.

Data Availability The dataset generated and analyzed during is available in the Electronic Supplementary Material (ESM 3).

Results

The mean estimated daily travel distance across all days and baboons was 10.86 km when calculated using a 1 fix per second sampling interval and 2.71 km when using a 7200 s sampling interval. The estimated daily travel distance becomes progressively shorter with less frequent GPS sampling because fewer GPS fixes do not properly capture the animal's movement path (Fig. 1; ESM Video S1). As a result, less frequent GPS fixes result in a significant reduction in calculated daily travel distances (Fig. 2a; ESM Table S1; Video S1), and this reduction changes with GPS sampling interval according to a logarithmic function (proportion distance captured = $0.081\ln(\text{sampling interval}) + 0.9682$; $r^2 = 0.99$; Fig. 2b and c).

y coordinate



Fig. 1 Path traveled (black line) by one adult female chacma baboon between 06:18 and 18:00 UTC on August 4th, 2018 in Cape Town, South Africa, estimated using a GPS sampling interval of (a) 1 s, (b) 1 s smoothed, (c) 30 s, (d) 60 s, (e) 300 s, (f) 1200 s, (g) 3600 s, and (h) 7200 s. In (b)–(h) an additional green line representing the path estimated using 1-s sampling interval is shown for comparison.

Applying our model to published baboon daily travel distances (Fig. 3a), we found travel distances were \geq 50% farther when using one fix per second sampling interval



Fig. 2 (a) Kernel probability density of daily travel distances by 12 chacma baboons over 11-12 days, in Cape Town, South Africa, measured using GPS sampling intervals ranging one fix per second to one fix per 7200 s; smoothed 1-s data (1S) are also shown. **(b)** Comparison of the estimated distance calculated with one fix per second GPS compared to less frequent GPS sampling intervals, expressed as a proportion. **(c)** Comparison of the estimated distance calculated with one fix per second GPS compared to less frequent GPS sampling intervals, expressed as a proportion. **(c)** Comparison of the estimated distance calculated with one fix per second GPS compared to less frequent GPS sampling intervals (log scale). For **(b)** and **(c)** individual baboon data (N = 12) are modeled by colored lines, and the fitted logarithmic function across all data is given by the black line. The vertical axis in **(b)** and **(c)** is reversed to aid interpretation.

(Fig. 3b). We found that the range of GPS sampling intervals used in the published work is small (300–3600 s; Fig. 3a), and the proportion of distance captured did not get larger or smaller for groups that travel farther (Fig. 3b and c).

Discussion

Using less frequent GPS sampling intervals to estimate chacma baboon daily travel distances reduces the opportunity to measure an animal's deviation from a linear path, resulting in smaller estimated daily travel distances. The reduction in estimated travel



Fig. 3 (a) Comparison of the estimated distance calculated with one fix per second GPS (filled circle) compared to less frequent GPS sampling intervals, expressed as a proportion. The dashed box indicates the range of GPS sampling interval (300–3600 s) used in 38 published groups' daily travel distances (Johnson *et al.* 2015). **(b)** Estimation of the proportion of distance captured for 38 published group daily travel distances (data points given by open circles inside the dashed box) based on their reported GPS sampling intervals, using the relationship modeled in **(a)**. One fix per second GPS data used in the current study is shown by the filled circle data point. **(c)** Predicted daily distance traveled for 38 published groups (Johnson *et al.* 2015), based on the reported groups' daily travel distances and their GPS sampling interval, using the model shown in **(a)**. One fix per second GPS data (current study) is shown by the filled circle that falls on a 1:1 line.

distance seen with increasing GPS sampling interval (here, the difference between estimates at one fix per second and other intervals) can be modeled by a logarithmic function. Our findings therefore support empirical and theoretical work showing that the interval at which GPS fixes are taken can systematically change movement distances calculated (Borger *et al.* 2006; de Weerd *et al.* 2015; Ganskopp and Johnson 2007; Johnson and Ganskopp 2008; McGavin *et al.* 2018; Mills *et al.* 2006; Mitchell *et al.* 2019; Noonan *et al.* 2019; Postlethwaite and Dennis 2013; Rowcliffe *et al.* 2012; Sennhenn-Reulen *et al.* 2017; Swain *et al.* 2008; Tanferna *et al.* 2012) and affirm research with Guinea baboons reporting similar findings when estimating travel distances over a shorter time frame (2-h blocks) and with fewer baboons (N = 4) (Sennhenn-Reulen *et al.* 2017).

Miscalculation of travel distances can have important implications for studies of movement ecology (Hebblewhite and Haydon 2010; Patterson *et al.* 2008; Schick *et al.* 2008), disease dynamics (Dougherty *et al.* 2018; White *et al.* 2018) and designation of conservation spaces (Cristescu *et al.* 2013; Darnell *et al.* 2014; Douglas-Hamilton *et al.* 2005). For example, distances traveled calculated from GPS data have been used to estimate the energy cost coefficients of locomotion (e.g., Brosh *et al.* 2010) and these will alter substantially if the relationship between estimated distances and sampling interval that we report is typical across species and contexts. Indeed, our baboon case study suggests that moving from a GPS frequency of one fix every second to one fix every 30 s results in a 33% reduction in estimated daily travel distance, while using hourly GPS fixes results in a 66% reduction in estimated daily travel distance.

Future studies should consider the impact of GPS sampling intervals on distance estimates. Assuming that estimated distances change with GPS sampling interval according to a logarithmic function may be informative, but other factors will also need to be considered. In the context of baboon behavior, for example, 1) the tortuosity of the travel path and 2) the speed of travel will affect how much a path is underestimated (Sennhenn-Reulen *et al.* 2017), because while slower movement decreases travel distance, more tortuous movement increases travel distance (Johnson *et al.* 2015). Therefore, while the logarithmic relationship we describe could be a general phenomenon, the effect size (exponent) will change with a myriad of social and ecological factors (Dunbar 1992; Johnson *et al.* 2015). Where high-accuracy estimates of travel distance are needed, researchers should therefore consider continuous-time stochastic process models (Calabrese *et al.* 2016) to minimize confounding effects of position and velocity autocorrelation.

Comparative investigations of daily travel distances between species and populations rely on estimates of travel distances, typically from GPS data (Carbone *et al.* 2005; Dunbar 1992; Johnson *et al.* 2015). Given the significant differences in estimated distances according to GPS sampling interval, this could result in flawed comparisons. Using the relationship described for our data, we calculated daily travel distance for 38 baboon groups (Johnson *et al.* 2015) as if they had used a GPS sampling interval of one fix per second. Published travel distances captured a minimum 50% of the distance predicted if a 1-s sampling interval was used, but because the range of GPS sampling intervals used by baboon researchers to date is small (300–3600 s) the model predicted distances did not systematically vary across groups/sampling intervals. Previous comparisons of daily travel distances in baboons are therefore sound. However, if highresolution GPS data (as used in the present study) were to be included in such comparisons in future, this would introduce pronounced differences in travel distance estimates. Estimated travel distances using high-frequency GPS data therefore cannot be compared to published distance estimates (that use less frequent sampling intervals) without properly controlling for differences in sampling regimes.

Our case study also highlights an understudied aspect of high-resolution GPS data in animal movement studies: positional accuracy. Because GPS positional error is Gaussian in nature, this error will not tend to systematically alter estimates of interindividual distances (Haddadi et al. 2011; King et al. 2012) or interaction with features of the environment (Fehlmann et al. 2017a; Strandburg-Peshkin et al. 2017), or conspecifics (Farine et al. 2016, 2017; Strandburg-Peshkin et al. 2015), and therefore does not normally need to be accounted for in such contexts. However, calculated distance traveled estimates are sensitive to positional measurement error (McGavin et al. 2018; Noonan *et al.* 2019), and these errors are pronounced at short GPS sampling intervals which will affect the estimated travel path. We therefore smoothed our 1-s GPS data in an attempt to reduce the impact of such high-frequency noise, and this resulted in significantly shorter distance estimates (ESM Table SI). Further work is now needed to explore if such smoothing is required because GPS loggers have on-board smoothing algorithms (which typically cannot be accessed by the end-user). These algorithms minimize "jitter" or "drift" when the logger is slow-moving or stationary (see ESM Fig. S2 for an example from our data) making it challenging to determine if post hoc smoothing removes "real movement," "noise," or both. Combining aerial video footage and GPS data of moving animals in the wild (e.g., on a beach where tracks are left) would be one way to investigate the relationship between true movement and GPS measured movement. Another would be to match GPS data to acceleration data to distinguish between active and nonactive time periods (Fehlmann et al. 2017b).

Finally, our findings highlight the need to choose an appropriate GPS sampling interval. The smaller the sampling interval, the higher the number of GPS fixes taken within a given time frame and the higher the accuracy of any subsequent distance estimate. But this comes at the cost of shorter battery life, and hence a shorter data collection period. This makes high-resolution GPS sampling less practical for longer-term studies in primate spatial ecology because collars need to increase in size and weight to accommodate larger batteries. However, this issue can be overcome if collars use solar cells with rechargeable batteries and dynamically switch between different sampling rates depending on the animal's activity (e.g., Wilson *et al.* 2018). Given these tradeoffs, studies will likely continue to use different GPS sampling regimes, and so our case study provides useful rule-of-thumb for the magnitude of change expected when estimated travel distances with different GPS sampling intervals.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-021-00220-8.

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Author Contributions AJK and IF conceived the study. AB and CC constructed the tracking collars and collected data in the field. AB processed the data. RMcC analyzed the data and conducted statistical analyses with input from AJK, IF, and AB. RMcC wrote the first draft of the manuscript, which was revised by AJK with input from all authors, who read and approved the final manuscript.

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