



Intrinsic and extrinsic factors combine to affect baboon movements across natural and urban environments

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Wildlife movement in urban environments can differ significantly from that in natural environments due to intrinsic factors (individual phenotype) as well as extrinsic factors (such as changes to the landscape and increased interactions with people). Here, we used tracking collars equipped with 1 Hz GPS to investigate the variation in fine-scale movement (individual step lengths, path tortuosity and residence times) of chacma baboons, *Papio ursinus*, across natural and urban environments in Cape Town, South Africa. We showed that the baboons exhibited limited interindividual differences in average movement (intrinsic factor: behavioural type), but large differences across environment (extrinsic factor: behavioural plasticity), where all baboons travelled faster and straighter, and spent less time in one location, when in urban space compared to natural space. We showed large intraindividual differences in baboon movement (behavioural predictability), indicating that some individuals exhibit greater consistency in movement than others. Finally, we showed an interaction between individual (ID) and environment (urban) for all metrics, where individuals differed in how much their movement in urban space changed compared to their movement in natural space. The individuals that changed their movement the most tended to be higher-ranking, socially connected baboons, which are the focus of the city's baboon management programme, seeking to keep baboons out of urban areas. We therefore suspect these changes in movement between natural and urban space to be partly a result of human–baboon interactions. Taken together, our results show how individual animal movement can be impacted by changing environments, affecting certain baboon phenotypes more than others.

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An animal's own intrinsic characteristics, as well as its extrinsic environment, determines how it moves (Nathan et al., 2008). Individuals within the same population can differ in their movement patterns as a result of various intrinsic factors, such as their sex (Bar-Ziv et al., 2022; Conde et al., 2010; McCorquodale, 2003), size (Hillaert et al., 2018; Sánchez-González & Nicleza, 2021), social dominance (Wittemyer et al., 2007) and personality (Dingemanse et al., 2010; Nilsson et al., 2014). Common extrinsic factors affecting movement patterns include resource availability (Abrahms et al., 2021; Doherty et al., 2019), weather and climate (Neumann et al., 2023; Wittemyer et al., 2007), habitat type (Fahrig, 2007; McCabe et al., 2021) and inter- and intraspecies interactions (Giuggioli & Kenkre, 2014). With an expanding human population encroaching on natural landscapes, the use of urban spaces by

wildlife is increasing (Lowry et al., 2013; Rodewald & Gehrt, 2014), presenting numerous additional extrinsic factors that can affect individuals' movement patterns (Anadón et al., 2012; Dowding et al., 2010; Fahrig, 2007; Wat et al., 2020). Moreover, while extrinsic factors may interact with intrinsic factors to shape individual behaviour (e.g. predation risk, Dingemanse et al., 2007; Fürtbauer et al., 2015; Quinn et al., 2012; or ambient temperature, Spiegel et al., 2015), how they combine to affect individual animal movement in urban space is not well studied because of the difficulties in acquiring appropriate data.

The use of novel technologies has enabled the simultaneous tracking of animal movements at high spatial and temporal resolution (Fehlmann & King, 2016) across a range of habitat types (Hertel et al., 2019, 2020; Spiegel et al., 2015). Repeated measures of individual movement metrics allow researchers to adopt a 'behavioural type' approach and study individual consistency and flexibility in movement, and responses to change (Bailey et al.,

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2021; Hertel et al., 2019, 2020; Spiegel et al., 2017). In statistical terms, this involves examining interindividual variation in movement ('behavioural type', where individuals show a higher or lower average behavioural expression), individual variation in response to environmental gradients ('behavioural plasticity', where some individuals can more flexibly adapt their behaviour with environment) intraindividual variation in residual movement ('behavioural predictability', where greater variability around an individual's average behavioural expression may help to buffer risky situations, Hertel et al., 2021) and correlations between these (Hertel et al., 2020). Understanding movement variation at an individual level has numerous applications for animal conservation and wildlife management (Hertel et al., 2019; Honda et al., 2018; Merrick & Koprowski, 2017). For example, differences in individual movement can predict individual risk for hunting or poaching (Leclerc et al., 2019), locate 'problem' individuals in a population (Honda et al., 2018; Merrick & Koprowski, 2017) and highlight individual differences in stress responses to anthropogenic change (Carere et al., 2010; Merrick & Koprowski, 2017).

Here, we studied how intrinsic and extrinsic factors combine to affect chacma baboon, *Papio ursinus*, movements across natural and urban environments. Baboons are generalists in habitat and diet (Barton & Whiten, 1994; Hill & Dunbar, 2002; Johnson et al., 2015), highly social (Alberts, 2019; Silk et al., 2009) and show extreme behavioural flexibility (Alberts & Altmann, 2006), allowing them to adapt to novel environments and situations (Fehlmann et al., 2017b; van Doorn et al., 2010). In Cape Town, South Africa, baboons routinely enter urban environments for food (Fehlmann et al., 2017a; Hoffman & O'Riain, 2012b) and move in and out of natural and urban space. Previous research on the group studied here has shown that socially peripheral, low-ranking female baboons show greater use of urban space (Bracken et al., 2021) because they have weaker social affiliations to higher-ranking, socially connected baboons (i.e. the alpha male and high-ranking females) that are the focus of efforts by field rangers to keep most of the troop out of urban areas. Using high-frequency GPS data (recording at 1 Hz) for 13 adult baboons in a troop that ranges at the edge of the City of Cape Town, we examined fine-scale differences in three commonly studied movement metrics (Barraquand & Benhamou, 2008; Hertel et al., 2020): step length, path tortuosity and residence time.

First, we tested for the effect of intrinsic factors on movement metrics, and examined whether baboon identity (individual, I) explains variation in movement metrics (Spiegel et al., 2015) and/or whether variation is related to other intrinsic traits: body size (Doherty et al., 2019), social dominance (Murray et al., 2007; Wittemyer et al., 2007) and sociality (Balasubramaniam et al., 2020; Morrow et al., 2019). Second, we investigated the effect of extrinsic factors (environment, E) on baboon movement, by comparing movement metrics of individuals in natural versus urban space. We predicted that when baboons are in urban space seeking high-calorie food resources they would display quicker, more directed movements, with less time spent at one location (Troup et al., 2020) as they navigate human-made structures and avoid people. As mentioned above, it has previously been shown that some individuals in this troop use the urban space much more than others (Bracken et al., 2021). Individuals that use the urban space more are those with lower dominance rank and social cohesion, as the city's baboon management programme targets its herding efforts towards adult males and therefore high-ranking females and offspring, in an effort to deter most of the troop from the urban space (Bracken et al., 2021). We therefore used an individual's urban space use as a proxy for management influence and examined its effect on baboon movement. We predicted that individuals who use the urban space less will exhibit a greater change in movement (greater step lengths, lower sinuosity and lower residence times)

when using the urban space, as they are subject to higher herding effort, in comparison to individuals subject to lower herding effort. Third, we investigated whether there is an interaction between intrinsic and extrinsic factors (individual*environment interaction, I*E) using a reaction norm approach (Dingemans et al., 2010), as certain intrinsic factors may constrain or promote an individual's response to different environments (Merrick & Koprowski, 2017; Sih et al., 2004). Additionally, we examined intraindividual predictability in residual movement, which can further elucidate how individuals respond to extrinsic factors (Hertel et al., 2021; Merrick & Koprowski, 2017; Sih et al., 2004), as urban environments may promote a wider behavioural expression due to heightened risks and rewards (Hertel et al., 2021).

METHODS

Study Site and Subjects

We studied the Da Gama baboon troop on the Cape Peninsula, South Africa. The troop comprised two adult males, 19 adult females and approximately 30 subadults, juveniles and infants of both sexes. The troop's home range includes urban and natural space (Hoffman & O'Riain, 2012b; van Doorn & O'Riain, 2020). The urban space mainly consists of housing, surfaced roads and local amenities, interspersed with small patches of exotic vegetation in urban greenbelts. The natural space is dominated by indigenous fynbos vegetation with smaller patches of exotic vegetation (Hoffman & O'Riain, 2011; van Doorn & O'Riain, 2020). The troop was managed daily from dawn to dusk by a team of eight field rangers, from the company Human Wildlife Solutions (<https://hwsolutions.co.za>). We studied the troop between July and November 2018 and here used data collected mainly during the austral winter (July, August) when our GPS collars were active and when the Peninsula baboons show greater use of urban space (Hoffman & O'Riain, 2012b; van Doorn et al., 2010). During the 54 days when the GPS collars were recording baboon movement (between last collar deployed and last collar failed, 2 August 2018 to 24 September 2018; Table A1), we conducted 38 full observation days, 9 partial days and 6 nonobservation days, and on any given fieldwork day baboons were followed by two to four researchers.

GPS Data

To examine individual patterns of movement, 16 adults were fitted with SHOAL group (Sociality, Heterogeneity, Organisation And Leadership group, based at Swansea University, U.K.) in-house constructed collars (F2HKv3), after cage trapping and anaesthetization by a local veterinarian (Bracken et al., 2021). Each baboon was weighed at the time of capture while under anaesthetic (Table A1). Tracking collars recorded GPS positional data at 1 fix/s between 0800 hours and 2000 hours local time (GiPSy 5 tags, TechnoSmArt, Rome, Italy). We used daytime hours for the troop in our analyses (0800–1800 hours local time), as the troop tended to be at their sleep site after sunset (1800 hours; Bracken et al., 2021). Time of morning departure was recorded before 0800 hours for 35 days during the time collars were recording. Data from 15 collars were retrieved (one collar was not found after release) and two collars failed to record GPS, resulting in GPS data for $N = 13$ baboons (two males and 11 females, representing 61% of all adults in the troop) over a mean \pm SD of 42.77 ± 9.92 days, range 21–54 days (Table A1). Ad hoc checks of the GPS data compared to known landmarks in Cape Town, South Africa, and in Swansea, U.K., indicated positional accuracy was always within 5 m (and often much less than this; Bracken et al., 2021). However, some GPS error was observed, and we processed data to remove erroneous fixes

(median 0.01% of the data set, range 0.00–0.03%) and to linearly interpolate missing fixes under 10 s in duration (median 0.02% of the data set, range 0.00–0.07%), as described in Bracken et al. (2021). The small sample size of individuals ($N = 13$) limited the number of covariates we could include in models, and we therefore selected those most relevant to our research questions and study system (detailed below).

Natural and Urban Environments

To examine individual movement trajectories in both natural and urban space, the group's 95% home range was calculated using fixed kernel densities and an ad hoc method for choosing the smoothing parameter using the function `getVolumeUD` in the `adehabitat` package in R (see Bracken et al., 2021; Calenge, 2006). Areas of the home range were designated as 'urban' by drawing a polygon around land dominated by residential buildings and surfaced roads, using Google satellite imagery and OSM standard maps, in QGIS (QGIS, 2020). We then used the function `getRecurSIONInPolygon` from the `recurse` package in R (Bracis et al., 2018), to obtain the total time (s) each baboon spent in the urban and natural environments from their GPS data. A visual example of a daily trajectory for a single baboon is depicted in Fig. 1.

Movement Metrics

Movement parameters can be calculated using GPS fixes summarized across different time intervals. Here, we subsampled high-frequency GPS data and calculated parameters using GPS data at 1 min intervals. This resolution is expected to retain information about the movement path, while minimizing any false movement that can occur at higher GPS resolutions due to positional error (McCann et al., 2021; McGavin et al., 2018; Noonan et al., 2019; Ranacher et al., 2016). Using different subsampling (10 s, 30 s, 60 s, 120 s) of the GPS data did not qualitatively affect the findings (Figs A1–A3). We analysed daily median values of each movement parameter in urban and natural space, as these data were left-skewed (Fig. A4). Metrics were calculated separately for each baboon, for each day where data were available. Since separate values were calculated for urban and natural space (and baboons did not always enter urban space each day), this resulted in a mean of 60 values per baboon, range 33–74, over a mean of 40 days per baboon (range 21–47 days).

We calculated movement metrics commonly used to analyse individual movement trajectories (Pasquaretta et al., 2021) that

have been used for understanding responses of wildlife to anthropogenic landscapes (Troup et al., 2020) and in the identification of behavioural types (Hertel et al., 2020): step length, path sinuosity and residence time (Barraquand & Benhamou, 2008; Benhamou, 2004; Fig. 2).

Analyses were conducted in R Studio, version 4.2.3 (R Core Team, 2020). Step length and sinuosity were calculated using the package `trajr` (McLean & Skowron Volponi, 2018) and residence time was adapted from online code (Seidel, 2018). Because step length is a stepwise path characteristic (Edelhoff et al., 2016), a daily median average was calculated across each minute of data (i.e. distance between steps, Calenge et al., 2009). Sinuosity is a measure of the tortuosity of a path and is calculated as a function of the mean cosine of turning angles (Fig. 1; Benhamou, 2004), where high values indicate a more tortuous path. Sinuosity is a path metric, requiring multiple relocations (a path segment, Edelhoff et al., 2016), and was therefore calculated for periods of time in natural or urban space of at least 5 min, and up to the entire day, in duration. If there were multiple path segments in urban or natural space in a day, a median average was taken to give a daily measure of sinuosity. Residence time is commonly calculated as the length of time an individual spends inside a circle with a radius equal to its mean step length centred on its GPS fix location, without leaving the radius for more than a specified cutoff time (Fig. 1; Calenge, 2006). Residence time is also a stepwise path metric (Edelhoff et al., 2016); however, since it requires a cutoff time, we calculated residence time for trajectories with a minimum of five consecutive GPS fixes (i.e. a path segment of ≥ 5 min, as with sinuosity), while setting the cutoff time at 5 min. This increased the likelihood that residence time was calculated only for times individuals were in either urban or natural space. As with sinuosity, if there were multiple path segments in urban and natural space, these were median averaged for residence time.

Variation in Individuals' Urban Space Use

We determined urban space use by overlaying the urban polygon with $150\text{ m} \times 150\text{ m}$ grid cells (larger than the average spread of a group on the Cape Peninsula, Hoffman & O'Riain, 2012a) in QGIS, and then calculated the intensity of cell use using fixed kernel densities and an ad hoc method for choosing the smoothing parameter, with the function `getVolumeUD` from the package `adehabitat` in R (Calenge, 2006), using all available GPS data for each baboon across the study period. This resulted in $N = 55$ intensity of cell-use values for each individual (as there were 55 urban grid cells), varying from



Figure 1. GPS trajectory for a single baboon moving in both natural (green line) and urban (yellow line) space. (a) A whole day's trajectory (26 August 2018) and (b) a zoomed in view of the urban area. The white polygon denotes the urban cadastral boundary.

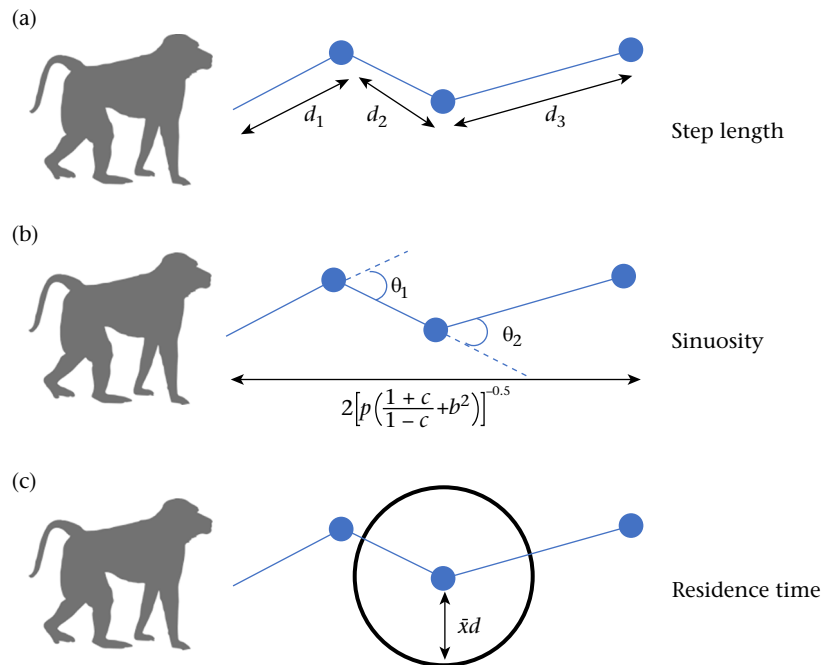


Figure 2. Movement metrics calculated from GPS data. (a) Step length (m): distance d travelled between steps; (b) sinuosity (unitless): path tortuosity across path segments, where the equation is a function of the mean cosine of turn angles: c is the mean cosine of turn angles, θ , and p and b are the mean and coefficient of variation of the step length; (c) residence time (min): time spent in an area, which is calculated in a radius of an individual's mean step length ($\bar{x}d$) centred on its GPS fix location. Step length was calculated over every minute. Sinuosity was calculated for path segments of a minimum of five steps (5 min) and up to a day in duration. Similarly, residence time was calculated for path segments of ≥ 5 min. Metrics were median averaged across urban and natural space per day.

0 to 100; with 0 indicating no use, and 100 indicating complete use (as a function of the utilization distribution). We examined variation in individual baboons' urban space use by subtracting an individual's urban grid cell use from the group average; the result indicated whether an individual used a given cell more or less than the group average (see Bracken et al., 2021, for full details). While we recognize intraindividual variation in urban grid cell use is lost using this method, this process shifts the distribution of the urban space use variable so that its mean becomes zero, making it easier to interpret relationships in our models (below).

Dominance Rank

Dominance rank was determined from direct ad libitum observations over 78 days of aggressive interactions (displacements, chases and aggressive displays) between pairs of baboons, in which there was clear submission of one individual (Bracken et al., 2021; Fürtbauer et al., 2020). Baboons were habituated to close human observation; however, a minimum distance of 10 m was maintained to reduce intrusion by observers. Female dominance rank was calculated from 634 interactions (median = 96, range 11–129) using the IS&I method and the packages aniDom and compete in R (Sánchez-Tójar et al., 2018). Male dominance rank was calculated from 75 interactions: M1 won 28 interactions (37%) and M2 won 16 interactions (21%), with 31 interactions undecided (41%), and therefore M1 was ranked first. Adult males outranked adult females in baboon groups (Engl et al., 2009; Kitchen et al., 2009). Ranks were standardized between 0 and 1 (with 0 being the lowest and 1 being the highest ranking individuals), using the rescale function from the scales package in R (Wickham, 2014).

Social Cohesion

Eigenvector centrality from proximity-based social networks were used as a measure of each baboon's social cohesion (Bracken

et al., 2021). Proximity networks were constructed based on occasions that 10 or more individuals were outside the urban space (following a sensitivity analysis, see Bracken et al., 2021). Association networks were constructed using the spatSoc package in R (Robitaille et al., 2019). Baboon GPS fixes were grouped spatio-temporally, where individuals within 5 m and 1 min of one another were assumed to be in association, using the 'chain rule' (Castles et al., 2014) and a 'gambit-of-the-group' approach (Franks et al., 2010). Network edges (the strength of associations between baboon dyads) were weighted using the simple ratio index (Farine & Whitehead, 2015).

Statistical Analyses

Throughout our analyses we follow the Bayesian approach in the R tutorial published in Hertel et al. (2020). Accordingly, we fitted models using the brms package (Bürkner, 2017), based on the Bayesian software Stan (Stan Development Team, 2024). We used the default prior for random and fixed effects. We ran models with four chains over 10 000 iterations, with a warmup of 500 iterations and a thinning interval of 10. We verified model convergence with sufficient mixing of trace plots and all \hat{R} values = 1. We log transformed all response variables to approximate normality, which we assessed using graphical procedures (histograms and Q-Q plots). We scaled continuous covariates (i.e. body mass and mean urban space use; mean = 0, SD = 1) to aid model fitting.

We ran models to examine intrinsic and extrinsic effects on baboon movement, and to test for their correlations. We first fitted a univariate mixed model including date and ID as random factors (m1). We included the following fixed effects: body mass (kg), social dominance and eigenvector centrality in the association network (intrinsic factors), as well as environment (urban/natural, E) and mean urban space use (extrinsic factors). We calculated repeatability (an individual's 'behavioural type', I) by dividing the posterior distribution for the variance explained by ID by the total variance.

To test if intrinsic and extrinsic factors combine to determine movement patterns, we then ran the model again (m2), testing for an individual ID*environment effect (I*E), using a reaction norm approach (Dingemans et al., 2010). Specifically, we fitted a random intercept, random slope model with respect to ID and environment, and determined a meaningful effect by a lower WAIC (widely applicable information criterion) value for the model allowing individual ID to vary across environment (random intercept, random slope) compared to a model only allowing individuals to vary (random intercept). A difference in WAIC larger than 7 indicates a better model fit (Hertel et al., 2020).

Finally, we ran a double hierarchical mixed-effects model (m3) which allowed us to fit fixed and random effects to both the mean and residual parts of the model (Cleasby et al., 2015), where the mean model estimates behavioural types and the residual model estimates residual intraindividual variation, rIIV ('behavioural predictability'). To the mean part of the model, we fitted the same fixed effects (as in m1 and m2), as well as the random effect of environment over ID. We also fitted an interaction term between environment and mean urban space use to see if change in movement was linked to individual differences in use of the urban space. To the residual part of the model we fitted mean urban space use (to see whether residual variance in movement was also linked to use of the urban space) and the random effect of ID. We calculated behavioural predictability (differences between individuals in intraindividual variance) using the standard deviation across baboons in residual variance (ω ID). We also calculated the coefficient of variation (CVp) to estimate the degree of variation in predictability among the baboons. We calculated the mean and 95% credible interval of all pairwise behavioural correlations (Hertel et al., 2019; Housley & Wilson, 2017). Where 95% credible intervals spanned zero, we concluded there was no evidence of statistically significant correlations between our response variables (note this cannot be used to assess significance for repeatability estimates, which by definition are always positive, Hertel et al., 2020).

Ethical Note

Our work was undertaken by research agreement with South African National Parks (SANParks), permit number CRC/2018-2019/008-2018/V1. Cage trapping to fit tracking collars on baboons was organized by Human Wildlife Solutions and conducted according to the Baboon Technical Team's protocols (Hoffman, 2011) as described in the supplementary information of Fehlmann et al. (2017c), and approved by Swansea University's Ethics Committee (IP-1314-5). Collars were fitted to individual baboons after sedation by a certified local veterinarian using Ketamine (dose adjusted to body mass). To facilitate capture, fruit and vegetables were provided in and around cages for 10 days prior at the trapping location. Cages were covered to minimize stress during capture, and baboons were monitored postsedation before and after release. One trapped female had an infant. The infant was temporarily removed and held under a cotton sheet by a management professional from Human Wildlife Solutions during collaring. Baboons touched the collar directly after release, but then ignored the presence of the collar. Full descriptions of the collars and components are provided in the supplementary information of Fehlmann et al. (2017c) and McCann et al. (2021). Collars weighed 460 g, which was a mean of 2.2% of baboon body mass (range 1.2–2.6%, see Table A1 for baboon weights) and contained an inner lining of soft leather to improve comfort and fit. Collars had a drop-off mechanism (version CR-7, Telonics, Mesa AZ, U.S.A.) to avoid the need for recapture, which was programmed to release on 16 October 2018 (78–83 days after deployment). Drop-off mechanisms failed for two collars and these

individuals were retrapped for collar retrieval. There were no signs of injury or irritation from the collars.

RESULTS

Intrinsic Factors

Baboon movement was not predicted by intrinsic factors (body mass, dominance rank or social cohesion; Table 1) and baboons showed limited differences attributable to behavioural type (Table 2, Fig. 3a–c). However, baboons did show consistent differences in residual intraindividual variation (rIIV) for all three metrics (Table 2, Fig. 3g–i), which was weakly related to mean urban space use for residence time, where individuals with higher residual variation in residence time showed greater use of urban spaces (Table 1, Fig. 3f).

Extrinsic Factors

All baboons travelled faster and straighter, and spent less time in one location, in urban space when compared to natural space (greater step lengths, lower path sinuosity and lower residence times respectively; Table 1).

Intrinsic–Extrinsic Interaction

The magnitude of change in movement metrics across natural and urban environments differed between individuals for all metrics (models accounting for random intercept and slope performed better than models accounting for random intercept only: lower WAIC; Table 2, Fig. 3d–f). Mean urban space use showed an interaction with environment for step length and residence time, where individuals that used the urban space less took longer steps and spent less time in the urban space than individuals that used the urban space more often (Table 1).

DISCUSSION

We found that variation in individual movement was largely determined by extrinsic factors, rather than intrinsic factors, for chacma baboons moving in natural and urban spaces at the edge of the City of Cape Town. Together these results suggest that baboons (1) exhibit limited interindividual differences in average movement, but (2) exhibit large intraindividual differences in residual movement, and (3) vary from one another in the extent to which they alter movement across the environment. These results indicate behavioural flexibility in response to environment, which is linked (for step length and residence time at least) to baboon use of the urban environment (driven by their dominance rank and social connectedness).

Intrinsic Factors

Baboons showed limited evidence for intrinsic effects on movement. Individual differences in step lengths, path sinuosity and residence times were not predicted by body mass, dominance rank or social network position. There was little evidence for movement variation attributable to behavioural type. Individuals did differ significantly from one another in their residual movement, however, where some baboons showed low residual variation (high predictability) and others high residual variation (low predictability) in movement for all metrics. We found a positive relationship between greater use of the urban space and intraindividual variance for residence time, indicating that baboons that use urban spaces the most (low-ranking, socially peripheral

Table 1
Importance of intrinsic and extrinsic factors on baboon movement ($N = 13$) across natural and urban space in Cape Town, South Africa

	Fixed effects	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Step length (log)					
Mean model	Body mass (kg)	0.03	0.05	-0.07	0.12
	Dominance rank	-0.33	0.22	-0.79	0.11
	Eigenvector centrality	-0.38	0.34	-1.06	0.28
	Environment (urban)	1.08	0.08	0.91	1.24
	Mean urban space use	-0.05	0.09	-0.22	0.12
	Environment*Mean urban space use	-0.29	0.08	-0.46	-0.13
Residual model	Sigma (Mean urban space use)	0.04	0.06	-0.08	0.15
Sinuosity (log)					
Mean model	Body mass (kg)	-0.01	0.02	-0.06	0.03
	Dominance rank	-0.00	0.11	-0.22	0.21
	Eigenvector centrality	0.03	0.14	-0.23	0.31
	Environment (urban)	-0.27	0.04	-0.35	-0.19
	Mean urban space use	0.01	0.04	-0.06	0.09
	Environment*Mean urban space use	0.00	0.04	-0.08	0.09
Residual model	Sigma (Mean urban space use)	0.13	0.09	-0.04	0.31
Residence time (log)					
Mean model	Body mass (kg)	0.03	0.04	-0.06	0.13
	Dominance rank	0.14	0.20	-0.27	0.54
	Eigenvector centrality	0.01	0.31	-0.65	0.59
	Environment (urban)	-0.68	0.06	-0.80	-0.55
	Mean urban space use	0.03	0.07	-0.12	0.17
	Environment*Mean urban space use	0.26	0.06	0.14	0.39
Residual model	Sigma (Mean urban space use)	0.14	0.04	0.07	0.21

Results taken from the double hierarchical mixed-effects model: m3. Body mass and mean urban space use are scaled (mean = 0, SD = 1) in all models. Significant effects are shown in bold. Residual model is presented on the log scale. CI: confidence interval.

Table 2
Estimation of behavioural type (intercept: I), individual*environment interaction (I*E) and residual intraindividual variation (rIIV) in baboon movement ($N = 13$) across natural and urban space in Cape Town, South Africa

Metrics (median log)	Behavioural type (I)	Individual*Environment interaction (I*E)	Residual intraindividual variation (rIIV)	
	Repeatability	WAIC	Residual variance (ω ID)	Coefficient of variation (CVp)
Step length	$R=0.04$	m1: 1567.715	1.46	CVp=0.18
	CI=[0.00, 0.12]	m2: 1528.560 (Δ WAIC: 39.155)	CI=[1.18, 1.80]	CI=[0.09, 0.30]
Sinuosity	$R=0.06$	m1: 374.371	1.79	CVp=0.29
	CI=[0.00, 0.16]	m2: 364.844 (Δ WAIC: 9.527)	CI=[1.30, 2.44]	CI=[0.13, 0.47]
Residence time	$R=0.03$	m1: 1455.894	1.14	CVp=0.06
	CI=[0.00, 0.08]	m2: 1429.124 (Δ WAIC: 26.77)	CI=[1.00, 1.33]	CI=[0.00, 0.14]

Repeatability in movement taken from m1. We compared m1 and m2 using WAIC (widely applicable information criterion) to estimate plasticity (I*E). Predictability in movement is taken from m3, and as sigma components are calculated on the log scale, we exponentiated the estimate, and then squared it to calculate the residual variance. Significant effects are shown in bold. CI: confidence interval.

females, which we assume to be less affected by management, Bracken et al., 2021) show higher variability in residence times. However, when plotting these data, we see the three baboons with highest intraindividual variability in residence time were those baboons that used the urban space the least (Fig. 3f), and so this relationship is not straightforward.

Other research has indicated that behaving unpredictably is an adaptive response to predation threat (Briffa, 2013), and that some animals vary their behaviour in risky situations/environments (Brand et al., 2023; Horváth et al., 2019). It could be the case here that some baboons show greater unpredictability in movement expression as a response to changing environmental risks and rewards that they encounter. From these results, it seems that some baboons are acting in more flexible ways than others, which could be due to intrinsic variation, or a factor we have not accounted for; for example, energetic traits (Biro et al., 2018; Brand et al., 2023; Velasque & Briffa, 2016). This intraindividual variation may be masking any interindividual differences in average movement, which might not be picked up with our small sample size of individuals. In any case, our results corroborate other work on baboons in Cape Town showing that individuals exhibit great

behavioural flexibility in response to urban environments (Fehlmann et al., 2017b).

Elsewhere, baboons have been shown to exhibit certain behavioural types (Seyfarth et al., 2012), with 'bolder' individuals performing better on problem-solving tasks (Carter et al., 2014) and discovering new food patches when information is unreliable (Carter et al., 2013). Since space use for our study troop is largely dictated by management (Bracken et al., 2021, 2022), it was a poor assay for exploring individual behavioural differences. However, it would be interesting to study unmanaged troops exploiting urban areas to understand how certain traits (e.g. 'boldness' or 'risk taking') might relate to other phenotypic characteristics and influence how individuals exploit high-calorific food but risky food resources.

Extrinsic Factors

All baboons increased their step lengths and decreased path sinuosity and residence time in urban space (Fig. 3g–i). Greater travel distances and faster travel speeds, as well as more directed paths and less time in one location in urban space, are probably due to the heterogeneous distribution of food resources, along with

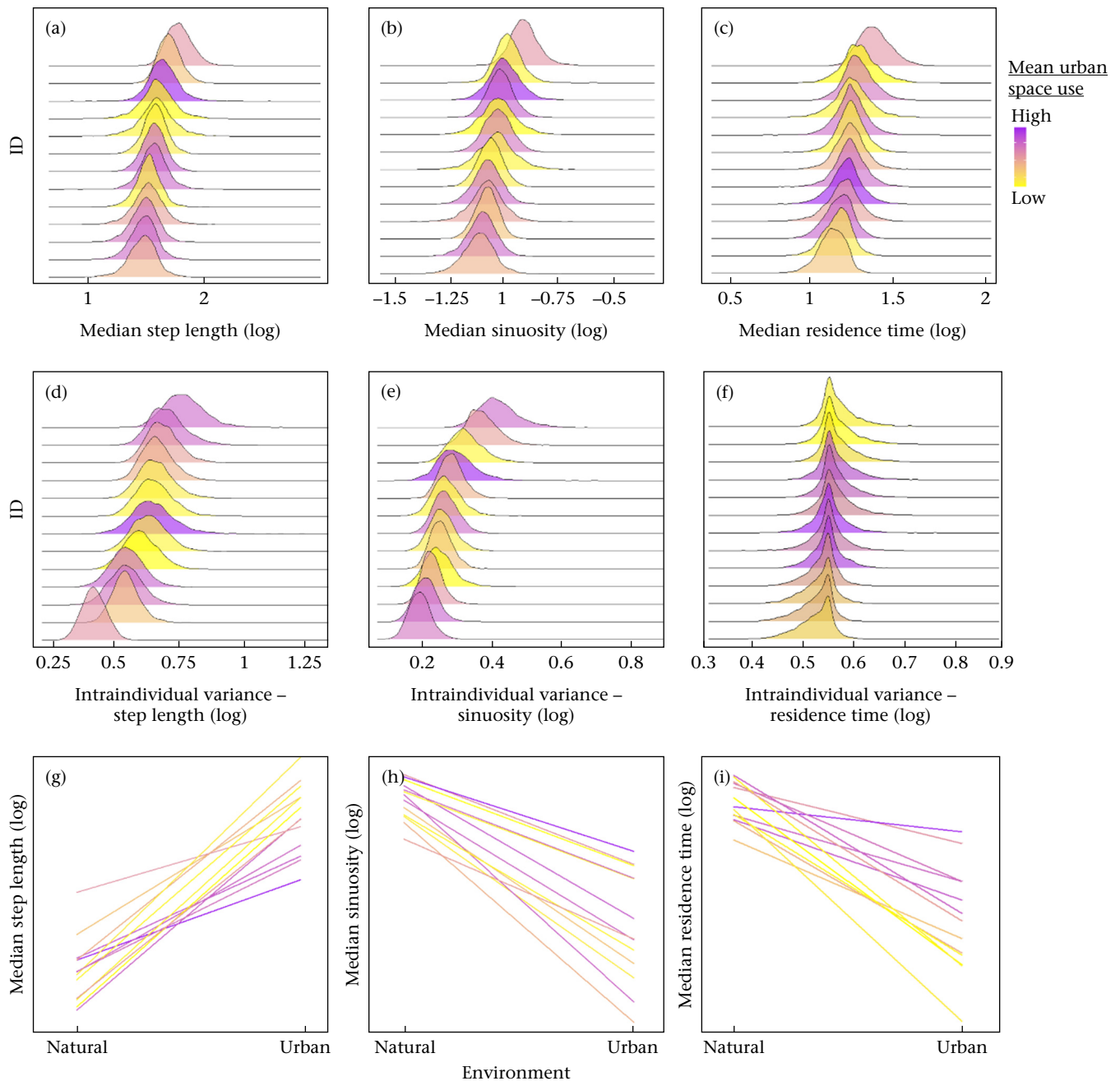


Figure 3. Baboon movement metrics. Interindividual differences in baboon (a) step length, (b) sinuosity and (c) residence time, and intraindividual differences in baboon (d) step length, (e) sinuosity and (f) residence time, shown as density histograms for each of $N = 13$ baboons. Intraindividual variance (d–f) is back-transformed to original log scale for comparability with intercept (a–c). The relationship between individual intercepts (movement metric) and the effect of the environment (slope) for (g) step length, (h) sinuosity and (i) residence time, where each line represents data for an individual. Individuals are coloured by mean urban space use in all plots (yellow–purple = low–high urban space use).

higher environmental risks and rewards (Fehlmann et al., 2021). Indeed, adult male Cape baboons have previously been shown to adopt a ‘sit-and-wait’ strategy, spending much time on the urban edge and then making high-activity forays into urban space (Fehlmann et al., 2017a). This drastic change in movement in response to anthropogenic environments and/or human presence is seen across animal groups and species (Doherty et al., 2021; Fahrig, 2007). For example, grizzly bears, *Ursus arctos*, and grey wolves, *Canis lupus*, living within and adjacent to Banff National Park, Canada, increase travel speeds when near to towns and other

areas of high human activity (Whittington et al., 2022). Additionally, in a population of crop-foraging baboons in South Africa, activity of baboons was significantly reduced within 100 m of field edges, but significantly increased when in crop fields (Walton et al., 2021). Disentangling environmental effects on baboon movement (i.e. management pressure from other landscape and habitat factors) might be possible by examining movement metrics over a wider range of habitat categories. Indeed, though the urban space is distinguished from the rest of the baboons’ home range by a higher level of human habitation, there is human infrastructure and

smaller settlements in the 'natural space' (i.e. a main tarmacked road, dams, a water treatment plant, etc.), which could influence individual movement.

Intrinsic–Extrinsic Interaction

The magnitude of change in movement across environment varied between individuals for all metrics (random slope, random intercept model performed better than random intercept model only). This was related to use of the urban space for step length and residence time, with individuals that use urban spaces less (which tend to be high-ranking and socially connected) increasing their step lengths and decreasing their residence times even more when in urban space compared to individuals with higher use of urban spaces (their low-ranked, socially peripheral counterparts). We expect management directly influences step lengths and residence times in urban space (herding the baboons towards natural space) and because management often focuses efforts on adult males and (therefore indirectly high-ranking, socially connected females, Bracken et al., 2021) we see a disproportionate influence on fine-scale baboon movement for these individuals. Interestingly, the same pattern with urban space use was not seen for sinuosity, which decreased for all baboons regardless of their urban space use (and therefore their exposure to targeted management effort). Increased directedness of paths is often employed by wildlife in high-risk situations (e.g. African elephants turn less frequently when at risk of poaching, Ihwagi et al., 2019). We therefore propose the decreased sinuosity (straighter paths) of baboons in urban space could result from risk factors not associated with management (e.g. dogs, traffic, residents), or due to more goal-oriented movements between food resources (Benhamou, 2004) that tend to be more predictable in urban spaces (e.g. waste bins, fruiting trees, compost heaps). It is also likely that human infrastructure itself constrains or promotes straighter movement paths since olive baboons, *Papio anubis*, in Laikipia, Kenya, are seen to move in a faster, directed manner when on roads (Strandburg-Peshkin et al., 2017). While all baboons travelled straighter in urban space, the random slope, random intercept model still performed better than random intercept model only. This is because the individuals that exhibited the highest path sinuosity on average tended to change their sinuosity the least in urban space, a finding which we discuss below.

Further work can now test whether the individual differences we found here are driven by other intrinsic factors we have not measured, such as cognitive differences or physiology (Jolles et al., 2019). For example, individuals that take more tortuous paths may do so because they are more reliant on gathering personal information (i.e. 'producers') over public or social information (i.e. 'scroungers', Harel et al., 2021; Ward et al., 2011), and individuals that travel faster/take larger steps may have greater aerobic capacity and be more efficient in their travel (Stuedel, 2000). Furthermore, investigation of these potential relationships may help explain why those baboons that travelled the straightest on average travelled even straighter in urban space (Fig. 3h). For instance there may be potential links between extrinsic factors (linked to resources, risk and infrastructure; see above paragraph) and individual differences (here, in sinuosity), where specific cognitive or physiological traits reduce the need for behavioural adjustments, similar to work showing that animal personality predicts plasticity (Dingemans et al., 2007; Fürtbauer et al., 2015; Occhiuto et al., 2023; Quinn et al., 2012; Spiegel et al., 2015). Future work would need to test these ideas.

Additionally, though we have demonstrated that management probably exerts a large driving force on baboon movement, it would be interesting to examine the influence of other types of human

groups. During field observations we saw that some residents showed greater tolerance of baboon presence within or near their property than others (A. M. Bracken, C. Christensen, personal observations), and studies elsewhere have shown that baboons vary in their responses to approaches by researchers (Allan et al., 2020, 2021). Finally, other intrinsic factors, such as consistent interindividual differences in spatial positioning in the group (Farine et al., 2017), may combine with human factors to influence movement. For example, individual animals on the periphery of groups often interact more with people (Balasubramaniam et al., 2020; Bracken et al., 2021), potentially causing greater changes to their movement than individuals occupying more central positions.

Conclusion

Overall, we provide direct evidence of how individual movement changes in response to human-altered landscapes for chacma baboons, and how the degree of this change can differ between individual baboons ranging across natural and urban environments. We reinforce the evidence that baboons exhibit flexibility in movement, which we believe is largely because of different management pressures faced by individuals in the urban environment. Our findings therefore highlight the importance of considering the dynamic human component in studies relating to anthropogenic environments and how these may drive variation in plasticity (Bailey et al., 2021; Hertel et al., 2020). Uncovering these drivers (i.e. intrinsic or extrinsic factors) can help predict how animals will cope under future scenarios of climate and land-use change.

Author Contributions

Anna M. Bracken: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Charlotte Christensen:** Data curation, Investigation, Writing – review & editing. **M. Justin O'Riain:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Ines Fürtbauer:** Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Andrew J. King:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Visualization, Writing – review & editing.

Data Availability

All data used in the study are provided in the Supplementary Material. Original code is not reported.

Declaration of Interest

The authors declare no competing interests.

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Supplementary Material

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Appendix

Table A1

Details of the GPS recording period for each collared adult baboon

Collar	Individual	Body mass (kg)	GPS Start	GPS End	Total duration (days)
1	M1	38.45	30 July 2018	11 September 2018	44
2	M2	33.85	30 July 2018	10 September 2018	43
3	F1	22.95	No data		
4	F2	No data	25 July 2018	13 September 2018	50
5	F4	19.14	No data		
6	F5	19.72	26 July 2018	09 September 2018	46
7	F6	21.4	26 July 2018	07 September 2018	44
8	F7	17.72	26 July 2018	09 September 2018	46
9	F9	17.84	26 July 2018	15 August 2018	21
10	F10	17.84	30 July 2018	12 September 2018	45
11	F13	23.69	02 August 2018	24 September 2018	54
12	F14	17.84	02 August 2018	25 August 2018	24
13	F15	18.29	26 July 2018	07 September 2018	44
14	F17	19.45	02 August 2018	19 September 2018	49
15	F18	19.11	26 July 2018	09 September 2018	46
16	F19	19.70	No data		

F = female, M = male. One collar was not retrieved after drop-off (F1). Two collars failed to record GPS data (F4 and F19).

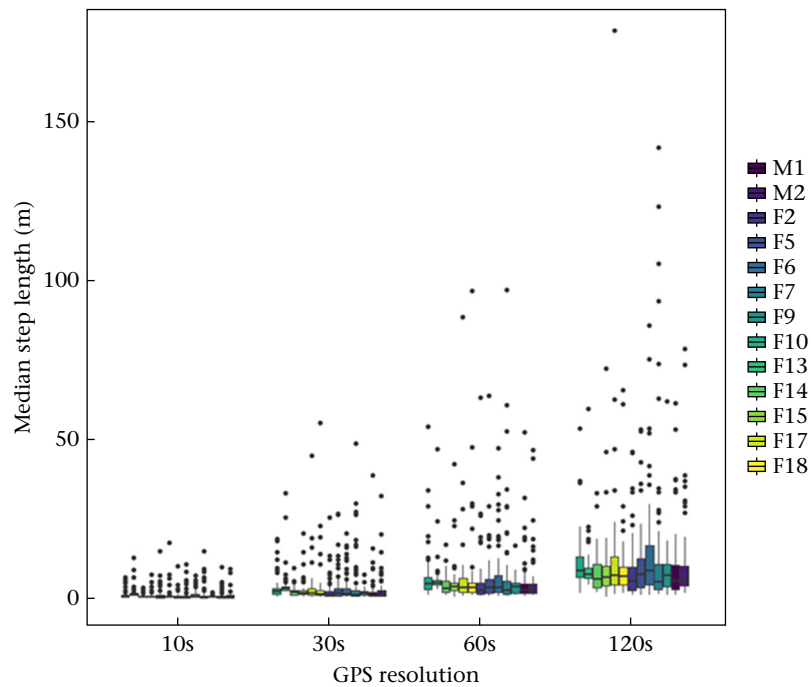


Figure A1. Median step length (m) for different GPS resolutions. The box plots show the median and 25th and 75th percentiles, for each individual; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

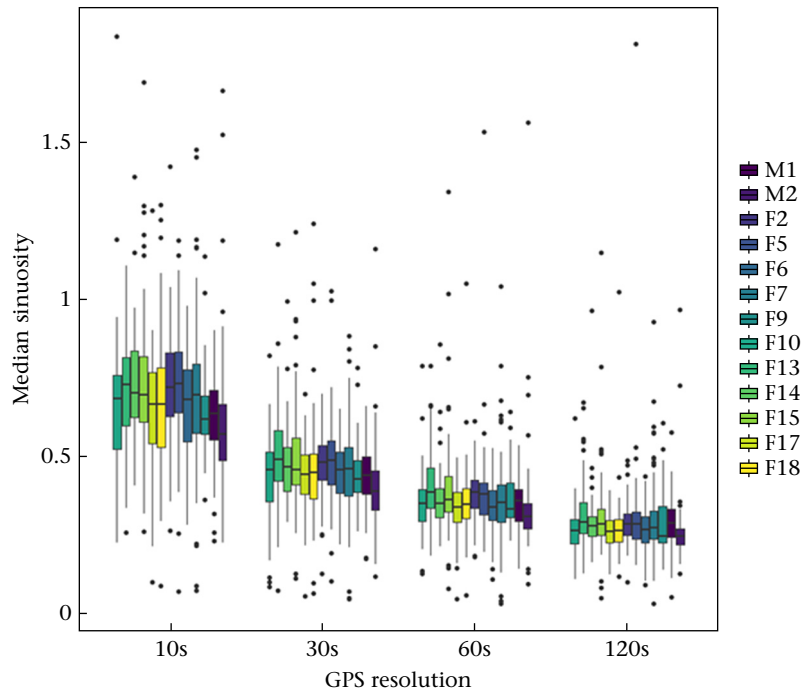


Figure A2. Median sinuosity (unitless) for different GPS. The box plots show the median and 25th and 75th percentiles, for each individual; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

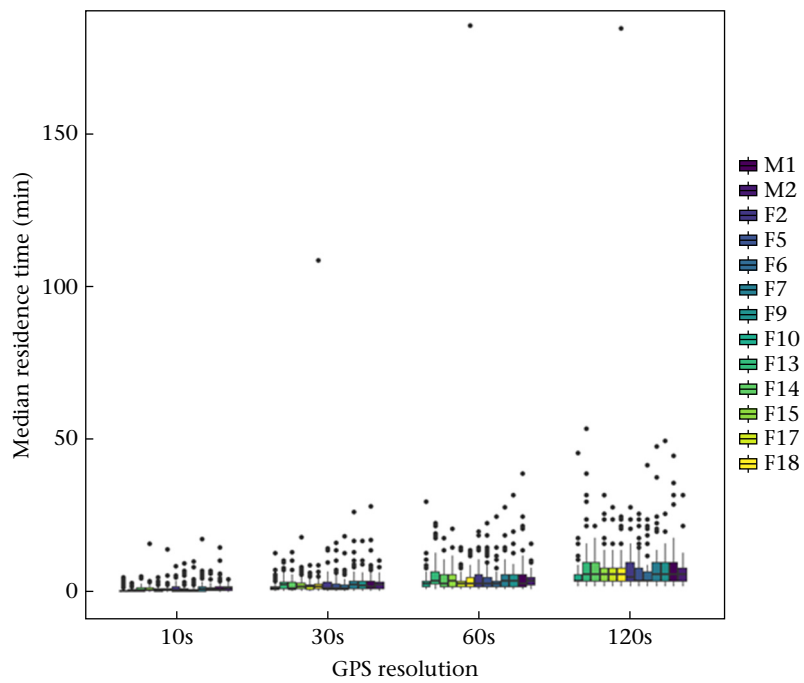


Figure A3. Median residence time (min) for different GPS resolutions. The box plots show the median and 25th and 75th percentiles, for each individual; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

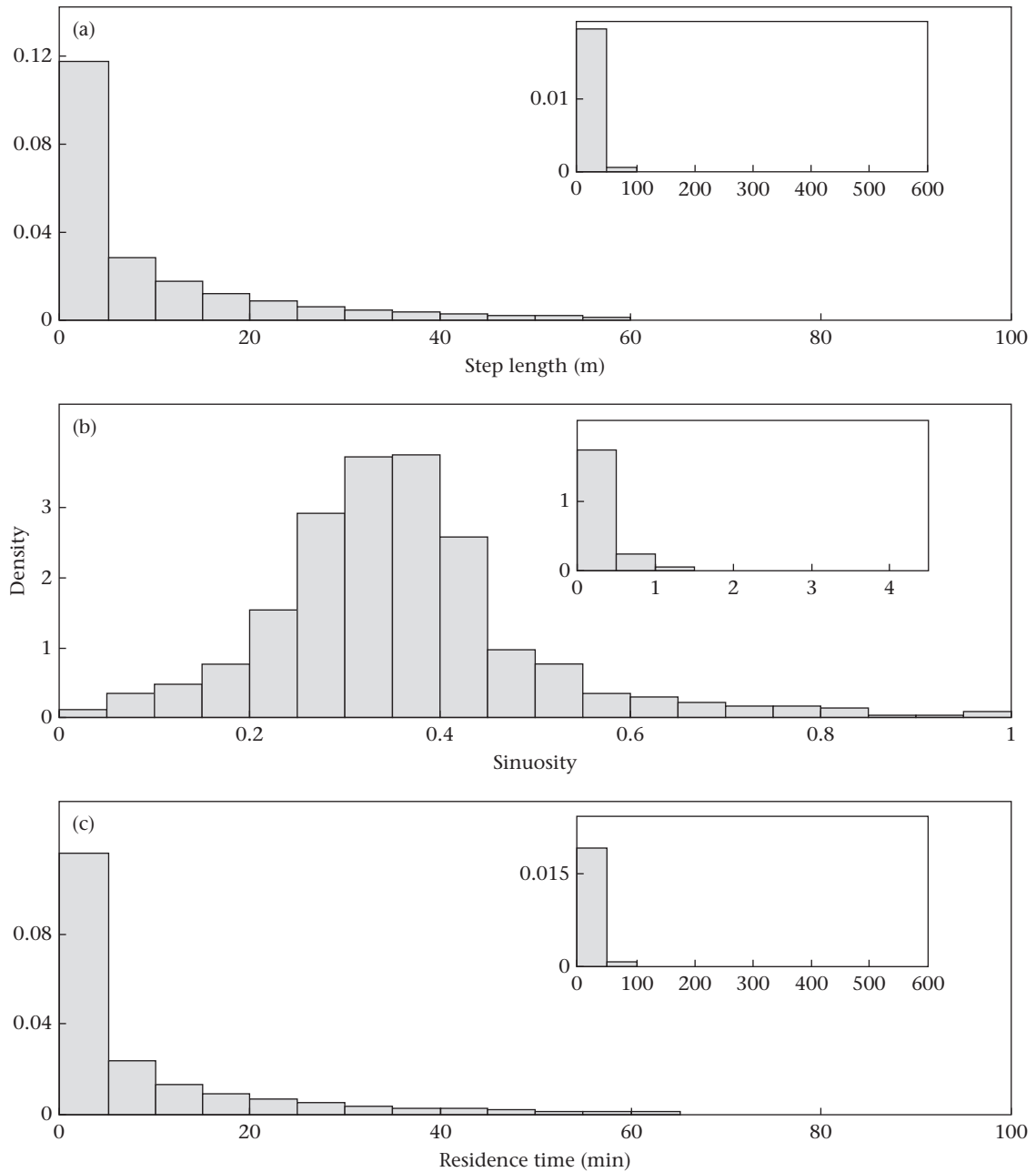


Figure A4. Histograms showing the distribution of (a) step length (m), (b) sinuosity (unitless) and (c) residence time (min). Main plot X axes are restricted to show the distribution of most values; insets show distribution of all values. Values are taken from every minute of data, for all baboons ($N = 13$).