

# Foraging Profile, Activity Budget and Spatial Ecology of Exclusively Natural-Foraging Chacma Baboons (*Papio ursinus*) on the Cape Peninsula, South Africa

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**Abstract** Exploitation of anthropogenic foods has profound effects on various aspects of the behavior and ecology of nonhuman primates. On the Cape Peninsula, South Africa, incentives to exploit novel resources are high and most local chacma baboons (*Papio ursinus*) feed on anthropogenic foods. Here we investigate the foraging profile, activity budget, and ranging behavior of a Peninsula group that feeds exclusively on natural foods. We predicted that the group would exploit the marine foods available to them and feed more extensively on subterranean foods, spend more time feeding and traveling, and occupy a larger area and travel further than groups that feed on anthropogenic foods, and groups elsewhere that occupy highly productive habitats. We tracked the group using handheld GPS units, and recorded behavioral data using instantaneous scan sampling in four seasons through 13 months. Our predictions were supported with the study group feeding on marine foods during all for seasons, but allocating a small percentage (<5%) of their total feeding time to exploiting these foods. Also, the group used a greater area (45.3 km<sup>2</sup>) and traveled further (5.9 km/day), and allocated more time to feeding and traveling, than previously studied groups on the Peninsula that exploit anthropogenic foods. These findings highlight behavioral variation in baboons associated with anthropogenic food use. Comparison of our results with those reported elsewhere should allow management authorities to more accurately predict changes in behavior of cercopithecoid monkeys as their access to anthropogenic foods is gradually restricted.

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## Introduction

Many nonhuman primates (primates hereafter) display remarkable dietary breadth and flexibility (Chaves *et al.* 2011; DeVore and Hall 1965; Fan *et al.* 2008; Grueter *et al.* 2009, 2013; Masi *et al.* 2009; Mekonnen *et al.* 2010; Poulsen *et al.* 2001), adjusting their foraging efforts as food availability fluctuates (Gursky 2000; Hanya 2004a; Heiduck 1997; Stone 2007; Yiming 2006). Such fluctuations also often elicit changes in primates' activity budgets and ranging patterns. As food declines in terms of abundance or quality, many primates allocate more time to feeding or traveling (Doran 1997; Guo *et al.* 2007; Gursky 2000; Hanya 2004b; Li and Rogers 2004; Masi *et al.* 2009; Norscia *et al.* 2006; Overdorff *et al.* 1997), and, if the latter, exhibit concomitant home range expansion (Barton *et al.* 1992; Di Bitetti 2001; Grueter *et al.* 2008; Hanya *et al.* 2005; Riley 2008; Zhou *et al.* 2007). Fluctuations in food availability are typically related to seasonal processes that affect plant phenology (Furuichi *et al.* 2001; Tutin *et al.* 1997; Wrangham *et al.* 1998), but can also be driven by stochastic factors (Berenstain 1986).

Some primates supplement the natural-food component of their diets with anthropogenic foods, often in the form of crops (Hill 2005, 2017; Lee and Priston 2005). These foods may be more abundant, richer in energy or nutrients, or available through more of the year than natural foods (Forthman Quick and Demment 1988; Hill 2000; Hockings *et al.* 2009; Naughton-Treves *et al.* 1998). Exploitation of such foods commonly elicits marked changes in behavioral patterns (Altmann and Muruthi 1988; Chaves and Bicca-Marques 2017; Saj *et al.* 1999; Sha and Hanya 2013) and may confer considerable benefits on the primates in question (Strum 1994, 2010; Warren *et al.* 2011). There are, however, also costs associated with exploitation of anthropogenic foods, as the individuals involved may come into conflict with local humans, which can result in serious injury or even death (Beamish and O'Riain 2014; Eudey 1994; Katsvanga *et al.* 2006; Knight 1999; Marchal and Hill 2009; Srivastava 2006). These factors, and the potential social and economic benefits to local people, motivate conservation practitioners and researchers to investigate humane measures that reduce primates' use of anthropogenic foods (Hill and Wallace 2012; Kaplan *et al.* 2011). Given the broader effects of anthropogenic food use on primates, it is important to consider how loss of these foods from their diets might affect other aspects of their behavior.

Baboons (*Papio* spp.) are particularly adept at acquiring anthropogenic foods and have become involved in intense conflict with humans in diverse contexts (Fehlmann *et al.* 2017; Hill 2000; Kaplan *et al.* 2011; Naughton-Treves *et al.* 1998; Tweheyo *et al.* 2005; Van Doorn *et al.* 2010; Wallace and Hill 2012; Warren 2008). They are adaptable, generalist feeders that inhabit much of sub-Saharan Africa (Cowlshaw 1997a; Hamilton *et al.* 1976; Okecha and Newton-Fisher 2006; Rowell 1966) and exhibit marked inter- and intrapopulation variation in dietary composition (Alberts *et al.* 2005; DeVore and Hall 1965; Hamilton *et al.* 1978; Whiten *et al.* 1991). Plant-derived foods typically comprise the bulk of baboons' diets (Altmann and Altmann 1970; Codron *et al.* 2006; Harding 1976; Okecha and Newton-Fisher 2006; Post 1982; Whiten *et al.* 1987, 1991), but there are records of baboons feeding extensively on

animal-derived foods when these are extraordinarily abundant (Hamilton *et al.* 1978). Differences in diet composition between groups, or through time, are typically linked to variations in food availability. Chacma baboons (*Papio ursinus*) in the harsh montane environments of the Drakensberg, South Africa, for example, exploit subterranean foods such as corms and bulbs to a greater extent than most baboons elsewhere (Alberts *et al.* 2005; Davidge 1978; Hamilton *et al.* 1978; Okecha and Newton-Fisher 2006; Post 1982; Whiten *et al.* 1987, 1991). Savannah baboons increase their consumption of subterranean foods (grass corms) during the dry season when preferred foods are scarce (Alberts *et al.* 2005; Post 1982). Subterranean foods are not preferred over other foods, when these are available, because the gains associated with exploitation of the former are offset by the costs of excavating and cleaning them before ingestion (Alberts *et al.* 2005; Hamilton 1986). A high proportion of subterranean foods in a baboon group's diet is therefore broadly indicative of lower abundance of other foods that offer high net profit in that group's home range.

There is also marked variation in activity budgets and ranging behavior across baboon groups and populations, and through time (Alberts *et al.* 2005; Altmann and Muruthi 1988; Dunbar 1992; Hoffman and O'Riain 2012a; Post 1981). Feeding and traveling are typically the dominant activities in baboons' activity budgets (Alberts *et al.* 2005; Hill *et al.* 2003; Whiten *et al.* 1987), but time allocated to these activities varies. In Amboseli, Kenya female yellow baboons (*Papio cynocephalus*) increased foraging time at the expense of resting time during the harsh dry season, and sacrificed resting and social time in the face of severe habitat degradation (Alberts *et al.* 2005). In the Drakensberg, a chacma baboon group living in more adverse conditions at higher altitudes traveled further on a daily basis, and occupied a larger home range, than the other local group (Whiten *et al.* 1987). Groups that exploit anthropogenic foods typically spend less time foraging, occupy smaller home ranges, and travel shorter distances on a daily basis than natural-foraging groups (Altmann and Muruthi 1988; Hoffman and O'Riain 2012a; Strum 2010). Daily path length and home range size are, however, also linked to group size in baboons and other primates (Barton *et al.* 1992; Ganas and Robbins 2005; Gillespie and Chapman 2001; Hoffman and O'Riain 2012a; Iwamoto and Dunbar 1983; Li *et al.* 2000), which is why per capita area has been suggested as a more appropriate measure of range size for comparative purposes (Riley 2008). Per capita area, obtained by dividing home range size by the number of individuals in the group, indicates the extent of home range area per individual (Terborgh 1983).

Abundance and distribution of key resources affect not only home range size, but also area use within a group's home range. Like other primates (Grueter *et al.* 2008; Wallace 2006; Willems *et al.* 2009), baboons do not typically use all parts of their home range evenly (Cowlshaw 1997b; Henzi *et al.* 1992; Hoffman and O'Riain 2011; Pebsworth *et al.* 2012; Whiten *et al.* 1987). Factors that affect area use include distribution of food and sleeping sites, availability of water, and predator activity (Barton *et al.* 1992; Cowlshaw 1997a, 1997b; Hamilton 1986; Hamilton *et al.* 1976; Whiten *et al.* 1987). The effects of these factors may be profound and far reaching, as illustrated by that of sleeping site location. Trees and physiographic features suitable for use as sleeping sites are usually not homogeneously spread through baboon home ranges (Pebsworth *et al.* 2012; Rasmussen 1979), so baboons must adjust their ranging patterns in order to start and end each day's journey at a sleeping site. Baboons are

therefore restricted to spending a considerable amount of time (the early part of the morning and latter part of each afternoon) in close proximity to sleeping sites (Altmann and Altmann 1970; Schreier and Swedell 2008).

The baboons of the Cape Peninsula, South Africa occupy diverse habitat types, including natural, agricultural, and suburban land where they consume natural and anthropogenic foods (Hoffman and O'Riain 2011, 2012a, 2012b; Johnson *et al.* 2013; Kaplan *et al.* 2011; Van Doorn *et al.* 2010). The dominant natural vegetation type on the Peninsula, known as “fynbos”, is based on nutrient-poor sandstone-derived soils and is known for low productivity and a high prevalence of sclerophylly (Coetsee *et al.* 1997; Kruger 1977; Rebelo *et al.* 2006; Stock and Allsopp 1992). In light of this, it is perhaps unsurprising that local baboons favor human-modified habitats (where available) over natural habitats, and low-lying land, which is more productive than high-lying slopes and plateaus (Hoffman and O'Riain 2012b). Hoffman and O'Riain (2012b) posited that these patterns are indicative of a broader preference for areas that offer relatively abundant or easily acquired foods, and showed that this and a preference for land near sleeping sites (manifested as selection for steeply sloped land), were the main drivers of area use by Peninsula baboons.

Historically, baboons in the southerly part of the Peninsula fed on marine foods obtained from the intertidal zone (Davidge 1978; Hall 1962, 1963). This behavior is unusual, but has also been observed in yellow baboons in coastal southern Somalia (Messeri 1978). Peninsula baboons have been observed feeding on mussels (*Mytilus* sp.), limpets (*Patella* sp.), and the eggs of small shark species (likely either *Poroderma* sp. or *Haploblepharus pictus*), and the remains of crabs (*Cyclograpsus punctatus* and *Plagusia chabrui*) and sea lice (Isopoda) have been found in their feces (Davidge 1978; Hall 1962, 1963; Peschak 2005). Marine crustaceans and molluscs are attractive prey items because their soft tissues are rich in protein and, in some cases, energy (Erlandson 1988; Smith and Partridge 2004; Lewis *unpubl. Data*). Also, the baboons' principal prey species are largely sessile and abundant in intertidal zones along the Peninsula (Branch 1976; Bustamante *et al.* 1995; Xavier *et al.* 2007). Terrestrial consumers' access to intertidal organisms is, however, limited through periodic submersion (Branch *et al.* 1998). Thus, “maritime mammals” (*sensu* Carlton and Hodder 2003) typically time their forays into the intertidal zone to coincide with low tide (Conradt 2000; Gumert and Malaivijitmond 2012; Nielsen 1991). Despite the novelty of the behavior, no study to date has quantified the amount of marine foods consumed by Peninsula baboons that do not have access to anthropogenic foods or nutrient-rich seeds of alien trees.

At the time of this study only one of the remaining groups on the Peninsula (Kanonkop group) did not consume anthropogenic foods (including agricultural produce) or foods derived from alien-invasive plants (Hoffman and O'Riain 2012a; Johnson *et al.* 2013; Kaplan *et al.* 2011). Kanonkop group (KK) was included in a population-level assessment of habitat use and ranging behavior by Hoffman and O'Riain (2012a) but this was based on only 89 full days' worth of data collected across three seasons, and heavily biased toward winter and spring. This study suggested that KK could be used as a baseline group for predicting changes to the ranging patterns and behavior of Peninsula groups that are subject to active management, the goal of which is to prevent all access to anthropogenic foods.

The main objective of this study was therefore to expand on the work of Hoffman and O'Riain (2012a) by quantifying KK group's broad-scale foraging

profile, activity budgets, and ranging patterns across all four seasons. Our hypothesis was that the baboons of the study troop, being limited to foraging on natural foods in a landscape dominated by oligotrophic habitats, would exhibit behavioral responses to shortages of terrestrial foods. We predicted that unlike most Peninsula groups, which access anthropogenic foods, the group would feed extensively on marine foods in the intertidal zone. We also predicted that the group would feed more on subterranean foods, spend more time feeding and traveling, occupy a larger area, and travel further than groups that feed on anthropogenic foods, both on the Peninsula and elsewhere, and groups elsewhere that occupy highly productive habitats. Finally, we predicted that KK group would make preferential use of areas within their home range that offer relatively easy access to key resources, namely food and sleeping sites.

## Methods

### Study Site and Subjects

The Cape Peninsula is a ca. 50 km-long strip of land that juts out from the coast in South Africa's extreme south-west. The topography of the southern-most reaches of the Peninsula is dominated by a sandstone plateau roughly 150 m above sea level (Cowling *et al.* 1996). The region's temperate, Mediterranean-type climate is characterized by cool, wet winters and warm, dry summers (Kruger 1979), and rainfall on the southern Peninsula may be as low as 400 mm/y (Cowling *et al.* 1996).

The dominant vegetation on the south Peninsula is Peninsula Sandstone Fynbos, though patches of Hangklip Sand Fynbos are also present. Both of these types of Fynbos are based on acidic, nutrient-poor soils and are dominated by small-leaved evergreen shrubs (Rebello *et al.* 2006). Sclerophylly is a common trait in fynbos plants (Rebello *et al.* 2006), which results in their nutritive value to generalist herbivores being extremely low: leaves are low in protein and rich in fiber (leaves consumed by livestock in the region comprise <4% crude protein and >30% crude fiber) and most assayed to date contain secondary compounds, which may act as herbivore deterrents (Campbell 1986; Coetzee *et al.* 1997; Glyphis and Puttick 1988; Hattas *et al.* 2005). Several other vegetation types cover small areas and enhance the structural and functional diversity of the Peninsula's plant life (Mucina *et al.* 2006; Mucina and Geldenhuys 2006; Rebello *et al.* 2006). One of these is Cape Flats Dune Strandveld, in which tall, evergreen shrubs are interspersed with grasses and annual herbs, and more plants possess succulent, orthophyllous or drought-deciduous leaves (Rebello *et al.* 2006). Following the local extirpation of large mammalian carnivores (Skead 1980), the Peninsula is no longer home to any wild animals that might prey upon adult baboons.

The study group, Kanonkop (KK), is one of five groups within the Cape of Good Hope Section of the Table Mountain National Park (formerly known as the Cape of Good Hope Nature Reserve), located at the southern end of the Peninsula. With approximately 56 individuals and an adult sex ratio (male:female) of 1:3.4, it is the largest group in the reserve and the only one without a history of conflict with tourists and residents in the area.

## Permit Conditions

In light of KK group's status as the last remaining nonraiding group on the Cape Peninsula, South African National Parks (SANParks) staff expressed concern regarding the potential effects of research on the baboons' behavior. Our permit was granted on condition that human contact with the group should be kept to a minimum. Thus, it was stipulated that we could spend only 4 mo following the group over the course of a year (1 mo in each season) to collect data, and that we were not allowed to habituate the group to close (<20 m) human presence. We were later granted permission to collect data over a fifth shorter period in the winter of a second year.

## Data Collection

With the help of volunteer field assistants, we collected behavioral and ranging data on 136 days during five discrete fieldwork sessions across all four austral seasons (Kruger 1979). During each of the first four fieldwork sessions (June 2009, September 2009, January 2010, and March 2010) we attempted to collect data on 30 consecutive days within a calendar month to account for fluctuations in tide height through lunar cycles (Palmer 1995). A rotational roster was set up during each fieldwork session such that M. C. Lewis worked one shift with each assistant every 4 days. During each of these shifts M. C. Lewis cross-checked the assistant's categorization of habitat types and behavior as scans were conducted, thus ensuring consistency across observation periods and reducing the possible effects of observer bias.

We collected data while following the group on foot at a distance of 20 m. We could not conduct follows from sleeping site to sleeping site because of the Park's rules regarding use of roads; road use was restricted to the hours between sunrise and sunset. In winter, the earliest sunrise occurred at 07:52 h and the latest sunset at 17:45 h. In summer, the earliest sunrise occurred at 05:37 h and the latest sunset at 20:01 h. We attempted to find the baboons before they left their sleeping site, and to follow them until they had arrived at their evening sleeping site, each day. This was often not possible, but we were able to infer which sleeping site the group slept at on most days (90%,  $N = 136$ ). Durations of full-day follows (see later for definition) varied across seasons; mean full-day follows ranged from 8 h 16 min ( $\pm 41$  min,  $N = 38$ ) in winter, to 12 h 12 min ( $\pm 22$  min,  $N = 24$ ) in summer. On full days in winter we recorded the first point of the day at or prior to 09:00 h on 84% of days, and the last point of the day at or following 16:30 h on 92% of days ( $N = 38$ ). On full days in summer we recorded the first point of the day at or before 07:00 h on 71% of days, and the last point of the day at or following 18:45 h on 96% of days ( $N = 24$ ). If the group split up into foraging groups during follows we tracked the larger group (based on numbers of visible individuals) until the groups remerged.

**Behavioral Data** We collected general behavioral data by means of instantaneous scans (Altmann 1974), recorded every 10 min, using a CyberTracker® Screen sequence uploaded to a Fujitsu Siemens® Pocket LOOX N500 pocket-PC. We conducted scans from the estimated center of the group (or from a position as close to the estimated center as could be occupied without disturbing the baboons), and included all individuals that were visible within 3 min of commencement of the scan. We identified each



baboon to sex and age class where possible, and recorded its behavior. If a baboon that had already been included in a given scan moved out of sight, individuals of the same sex and age class as that animal that later became visible were not included in the scan. The mean ( $\pm$  SD) number of individuals included in scans throughout the study was 10.8 ( $\pm$  5.2).

We recorded four behavioral categories: feeding, traveling, social behavior, and resting, as these activities are known to constitute >95% of baboons' time budgets (Dunbar 1992). When baboons were feeding while stationary, as opposed to "snacking" (sensu Rothman *et al.* 2008), we classified the food item being consumed as far as possible. We classified foods as terrestrial or marine, then plant or animal, then (if terrestrial) subterranean or above ground. We inferred the percentage composition of the group's foraging profile from the percentages of scan observations during which baboons fed on foods belonging to different categories (above-ground plant, subterranean plant, terrestrial unknown, or marine foods).

To control for the effects of seasonal fluctuations in day length on time allocated to different activities (Hill *et al.* 2003, 2004), we converted behavioral scan data to time spent engaged in different activities each day, as follows. First, we calculated the percentage of scan observations comprised of different activities within discrete time periods (starting at the turn of each hour) each day. We then multiplied these percentages by the duration (in minutes) of each period to calculate the number of minutes allocated to different activities during that period. We summed these values through each day to obtain daily values for the activity in question. We did this because we were not able to collect equal numbers of scan samples during each hour through the day (numbers of scans were lower shortly after sunrise and before sunset). Activity budgets based on scans throughout the day would therefore likely have been biased against resting and grooming, as baboons tend to allocate more time to these behaviors at the beginning and end of each day (Altmann and Altmann 1970; Davidge 1978; Hall 1962). We calculated percentage time activity budgets (PTAB), which may also be informative in studies of seasonal variation in behavior (Van Doorn *et al.* 2010), by dividing the values calculated as described earlier by the number of hours in the day in question.

**Spatial Data** For analysis of ranging behavior, we recorded the geographic coordinates of the estimated center of the group in degrees and minutes every 10 min. When we could not move to the estimated center of the group at the appointed time without disturbing the baboons, we waited until they had moved away before doing so, and recording coordinates. We determined coordinates using a Garmin® e-Trex hand-held GPS unit. On days when we could not follow the group from sleeping site to sleeping site, we added coordinates retrospectively. Thus, we added points when we encountered the group near a sleeping site and could infer which sleeping site had been used, or when we left the group prior to sunset but identified which sleeping site would be used. When this was the case, we assumed that the group had taken the most direct route to or from the sleeping site in question and added points at equal intervals along this line. In each case, the number of points was equal to the number of 10-min intervals between sunrise and our arrival (in the morning), or between our departure and sunset (in the evening). Inferred points comprised 5.4% ( $N = 9459$ ) of the total number of GPS points. For the purposes of analysing ranging patterns, we defined "full days" as days on which we recorded, or were able to infer, points that constituted the path from

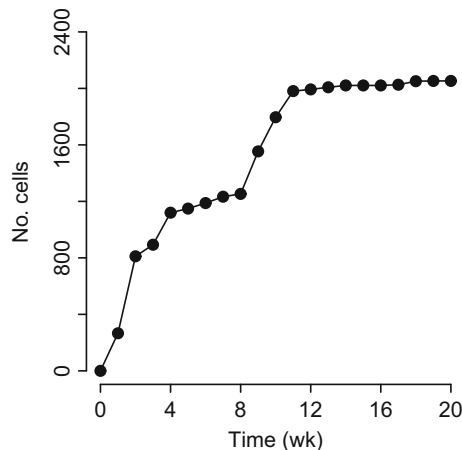
morning sleeping site to evening sleeping site. If we lost the group during the course of the day, but reestablished visual contact within 60 min, we still considered that day to be a full day.

**Ranging Patterns** We converted geographic coordinates to decimal degrees using the formula:

$$Dd = D + \frac{M}{60}$$

where  $Dd$  is latitude or longitude in decimal degrees,  $D$  is the degree value, and  $M$  is the minute value, at that point. We rounded off  $Dd$  values to nine decimal places, and imported the points into ArcView 3.3 (ESRI 2002) and projected them in Transverse Mercator, spheroid WGS 84, central meridian 19. We used the Repeating\_shapes (repeat\_shapes.avx) extension to ArcView 3.x (Jenness 2005) to superimpose a grid of  $150 \times 150$  m cells (clipped at the coast) on these points (Hoffman and O’Riain 2011). We defined “entered cells” as those within the grid that contained at least one GPS point, or through which the baboons had traveled. When estimating home ranges, we included entered cells; cells that were bounded on any three sides, or on two opposite sides, by entered cells, or by entered cells and the coast; and cells in areas that were completely enclosed by these cells. These criteria were based on those used for a previous study of Peninsula baboon spatial ecology (Hoffman and O’Riain 2011), but with minor modification owing to proximity to the coast. The cell accumulation curve for the home range estimated thus reached a plateau after 11 weeks of data collection (Fig. 1).

To calculate daily path length and rates of travel, we determined the distances between consecutive points on all full days (according to ranging criteria,  $N = 121$ ) using the Nearest\_features (nearfeat.avx) extension, in ArcView 3.3 (Jenness 2004), and then manipulated these as required. To determine daily path lengths, we summed all distances traveled between consecutive points on each day. We multiplied distances traveled during interscan intervals by 6 to calculate hourly rates of travel.



**Fig. 1** The cumulative number of cells included in a baboon group’s estimated home range per week. GPS data for KK group on the Cape Peninsula, South Africa, May 29, 2009–June 27, 2010.



## Statistical Analysis

**Foraging Profile, Behavior, and Path Length** We conducted 7075 scans through 1330 h of observation. For analysis of the group's foraging profile, we included data from days on which we were with the group through at least half of daylight hours, using scans as the defining characteristic of time spent with the group. We did this to avoid underestimating the importance of marine foods to the group; we collected data for a companion study on aspects of marine foraging and were therefore more likely to miss scans on days when the baboons fed on marine foods. In the case of activity budgets, we analyzed data collected on full days only. We arcsine transformed percentage foraging profile composition values and PTAB values before further analysis, because these values were percentages (Quinn and Keough 2003). When analyzing differences in time spent engaged in different behaviors across seasons we used untransformed values for analyses. To investigate seasonal differences in daily path length and rates of travel, we included all full-day daily path length values in analyses, but took random subsamples of rate of travel values (from full days only) such that sample sizes were equal across all seasons ( $N = 1798$  for each season).

To analyze seasonal variation in percentage foraging profile composition, time activity budgets and PTAB (inferred from instantaneous scan data), daily path length, and rates of travel, we used appropriate statistical tests, depending on whether or not the assumptions of normality and homogeneity of variances were met. Thus, we used Kruskal–Wallis rank sum tests to determine whether or not there were seasonal variations in percentage foraging profile composition, time activity budgets, PTAB, and rates of travel. Where there were significant differences, we used Wilcoxon's rank sum tests (with a Holm correction applied to  $P$ -values; Holm 1979), to determine which seasons differed in terms of that variable. We used a parametric analysis of variance (ANOVA) to test for differences in daily path length. The ANOVA indicated that there were significant differences, so we performed Tukey's Honestly Significant Difference (HSD) test to elucidate these differences. Hereafter, we use "seasonal variation" to refer to observed differences across sampling periods, each of which was in a different season within the 1-year data collection period.

**Home Range Use** We used the grid cells within the group's home range as sampling units for investigation of factors affecting intensity of use of different parts of the home range. To control for differences in cell size (clipped cells along the coast were smaller than inland cells), we adjusted the number of GPS points in each cell using the formula:

$$Adj_i = Obs_i / Area_i \times 0.0225$$

where  $Adj_i$  is the adjusted value for cell  $i$  (rounded to the nearest unit),  $Obs_i$  is the recorded number of GPS points in cell  $i$ , and  $Area_i$  is the area (in  $\text{km}^2$ ) of cell  $i$ .

We quantified geographical and biological properties of each cell within the group's home range ( $N = 2058$ ) (Hoffman and O'Riain 2011, 2012b). We calculated average altitude (m) and average slope ( $^\circ$ ) in each cell in ArcView 3.3 (ESRI 2002) using a 10-m digital elevation model (DEM; City of Cape Town, 2008. CMA 10 m DEM, City Maps, City of Cape Town). We calculated the straight-line distances from each cell to the nearest sleeping site (distance-to-sleeping site), the nearest perennial source of fresh surface water (distance-

to-water), and the nearer coast (distance-to-coast), in ArcView 3.3 (ESRI 2000) using the Nearest\_features (nearfeat.avx) extension to ArcView (Jenness 2004). Finally, we determined the dominant habitat type in each cell (by percentage area), using a shapefile provided by Mucina and Rutherford (2006). The habitat types thus included were beach-type habitats (both sandy and rocky shore), Peninsula Sandstone Fynbos, Hangklip Sand fynbos, and Cape Flats Dune Strandveld. We tested for collinearity between numerical predictor variables by performing Pearson correlations between all pairs of variables, and set the threshold value of the Pearson correlation coefficient ( $|r|$ ) at 0.7 (Dormann *et al.* 2013). We standardized all predictor variables before running the models (Zuur *et al.* 2009). We used the number of GPS points in each cell as the response variable in the models described in the text that follows.

**Model Building** We used a sparse spatial generalized linear mixed model (SGLMM; Hughes and Haran 2013) to examine the relationships between frequency of use of home range cells and environmental and topographic factors. The sparse SGLMM, an extension of the generalized linear model (GLM; Nelder and Wedderburn 1972), alleviates spatial confounding (a common phenomenon in data of this type; Aarts *et al.* 2008) by incorporating the spatial structure in the data into the model. In a sparse SGLMM, the random effects take the form of eigenvectors (of the Moran operator; Moran 1950), which represent potential patterns of spatial dependence in the data (Hughes and Haran 2013).

The variance-to-mean ratio of the response variable (31.6) indicates that the data are overdispersed (Potts and Elith 2006). The *ngspatial* package does not yet, however, allow for assumption of a negative binomial distribution (Hughes 2014), which might have provided a better fit for the data (Ver Hoef and Boveng 2007), so we ran the model assuming a Poisson distribution. We included predictor variables that have previously been shown to affect baboon ranging patterns in the full model (Altmann and Altmann 1970; Hoffman and O'Riain 2011, 2012b; Rasmussen 1979). Thus, the first stage of the model is described by the equation (in vectorized form):

$$g(\mu) = X\beta + M\gamma$$

where  $X$  is the design matrix, i.e., fixed effects of altitude, slope, distance-to-sleeping site, distance-to-coast, distance-to-water, and vegetation type. The second stage, that is the prior for  $\gamma$ , is described by the equation:

$$p(\gamma | \tau_s) \text{ proportional to } \tau_s^{q/2} \exp\left(-\frac{\tau_s}{2} \gamma' M' Q M \gamma\right)$$

where  $\tau_s$  is a smoothing parameter and  $Q$  is the graph Laplacian. As the response variable follows a Poisson distribution,  $\beta$  and  $\gamma$  are updated using Metropolis–Hastings random walks with normal proposals.

We included data from all home range cells in the model and used the default priors and default value for the number of Moran eigenvectors ( $q$ ) in the initial run (Hughes 2014). We assessed spatial autocorrelation (SAC) in the residuals of the models with Moran's  $I$  tests for SAC (Dormann *et al.* 2007; Moran 1950). In light of significant

SAC in the residuals of the model (Moran's  $I = 0.211$ ,  $P < 0.001$ ), we increased the number of eigenvectors by 25 and ran the model again. We repeated this step until the resultant model yielded residuals that did not exhibit significant SAC (model with  $q = 200$ : Moran's  $I = 0.042$ ,  $P = 0.077$ ). Values of all estimate-to-Monte Carlo standard error ratios for different predictors were indicative of convergence of the Markov chain (Jones *et al.* 2006). We did not investigate the effects of removing predictor variables from the model because none of the highest posterior density (HPD) intervals generated included 0. We evaluated the model by determining the Pearson's correlation coefficient ( $r$ ) and Spearman's rank correlation coefficient ( $\rho$ ) of observed and fitted values, as suggested by Potts and Elith (2006). We fitted the sparse SGLMM using the *ngspatial* package (Hughes and Cui 2013), in the statistical platform R (R Core Team 2014).

## Ethical Note

The research complied with all national laws and was approved by the UCT Animal Ethics Committee.

## Data Availability

The datasets generated and analyzed during this study are available from M. C. Lewis on reasonable request.

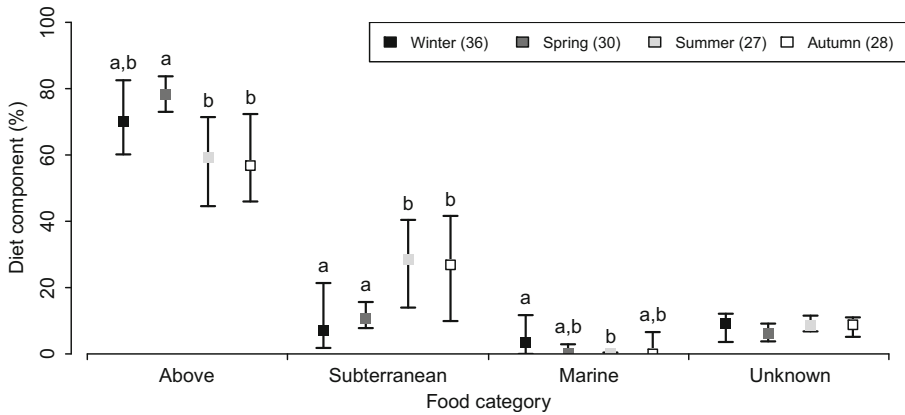
## Results

### Foraging Profile

KK group's foraging profile was dominated by above-ground terrestrial plants throughout the study (Fig. 2). There was, however, significant seasonal variation in the dietary contributions of above-ground terrestrial foods, subterranean foods, and marine foods (Table I; Fig. 2). The percentage of daily feeding time spent feeding on marine foods was higher during winter than summer (Table II; Fig. 2), but was low during all four seasons through the study period (mean  $\pm$  SD = 4.4%  $\pm$  7.9%,  $N = 121$ ). The group spent more time feeding on above-ground foods in spring than in summer or autumn, and less time feeding on subterranean foods in winter and spring than in summer or autumn (Table II; Fig. 2). Throughout the study period, the baboons of KK group did not acquire anthropogenic foods from humans or the human-constructed infrastructure within their home range.

### Activity Budgets

During all four seasons through the study period, KK baboons allocated more time (measured in minutes) to feeding and traveling than resting and social activity (Fig. 3).



**Fig. 2** Foraging profile of a natural-foraging troop of chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa during different seasons, inferred from instantaneous scan data collected from June 1, 2009 to June 27, 2010. Points indicate median values, and error bars denote interquartile ranges. Letters above error bars indicate significant differences among seasons. Unknown = terrestrial food that could not be classified further.

There were no significant seasonal differences in time allocated to feeding within the sampling period, but time spent traveling, resting, and engaged in social behavior varied significantly across seasons (Table III). The group spent more time traveling in summer and autumn than in winter or spring; more time resting in summer than in winter, spring, or autumn and less time resting in winter than in spring; and more time engaged in social behavior in spring than in winter (Table IV; Fig. 3a).

The percentage time activity budgets displayed a similar pattern to time spent engaged in activities, in that the larger percentages of the group's time in each of the seasons were spent feeding and traveling (Fig. 3b). Significant differences across seasons, for given behaviors, were not the same, however. The percentages of time allocated to feeding, resting, and travel differed significantly across seasons, while time allocated to social activity did not (Table III). The group allocated a larger percentage of time to feeding in winter than in summer or autumn; a larger percentage of time to resting in summer than in winter, spring, or autumn; and

**Table I** Results of Kruskal–Wallis rank sum tests for seasonal differences in time spent feeding on foods of different categories by a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, between June 1, 2009 and June 27, 2010

Food category	$\chi^2$	Df	<i>P</i>
Above-ground	<b>17.89</b>	3	< 0.001
Subterranean	<b>19.43</b>	3	< 0.001
Marine	<b>11.59</b>	3	0.009
Unknown	3.95	3	0.268

$N_{winter} = 36$ ,  $N_{spring} = 30$ ,  $N_{summer} = 27$ ,  $N_{autumn} = 28$ ; bold font denotes significance at the 5% significance level.

**Table II** Results of Wilcoxon's rank sum tests for differences in time spent feeding on foods of different categories across seasons by a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, between June 1, 2009 and June 27, 2010

Food category	Seasons	W	$P_{\text{Holm}}$
Above-ground	Winter–spring	680	0.290
	Winter–summer	358	0.290
	Winter–autumn	375	0.290
	Spring–summer	<b>637</b>	0.001
	Spring–autumn	<b>188</b>	0.002
	Summer–autumn	365	0.835
Subterranean	Winter–spring	639	0.414
	Winter–summer	<b>714</b>	0.008
	Winter–autumn	<b>709</b>	0.018
	Spring–summer	<b>184</b>	0.002
	Spring–autumn	<b>604</b>	0.018
	Summer–autumn	367	0.861
Marine	Winter–spring	358	0.059
	Winter–summer	<b>288</b>	0.017
	Winter–autumn	417	0.657
	Spring–summer	443	0.657
	Spring–autumn	485	0.657
	summer–autumn	468	0.321

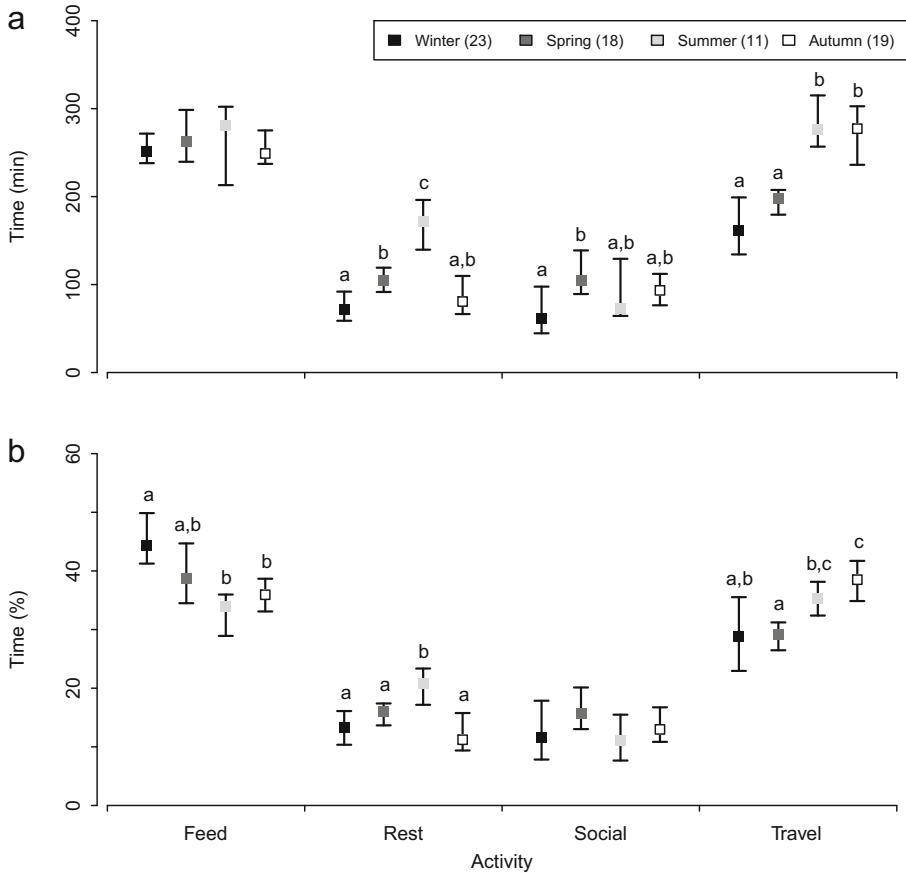
$N_{\text{winter}} = 36$ ,  $N_{\text{spring}} = 30$ ,  $N_{\text{summer}} = 27$ ,  $N_{\text{autumn}} = 28$ ; bold font denotes significance at the 5% significance level based on  $P$ -values with a Holm correction applied.

larger percentages of time to traveling in autumn than in winter or spring, and in summer than in spring (Fig. 3b; Table IV).

## Ranging

**Home Range Use** The home range used by the group over the entire study period covered 45.3 km<sup>2</sup>, extended to the coast on both the east and west sides of the Peninsula (Fig. 4a), and did not include any thickets of alien invasive trees. Thus, the per capita area of KK group was 0.81 km<sup>2</sup> per baboon. There was considerable variation in frequency of use of cells (0–140 GPS points) across the group's home range, but the majority of cells (89.1%,  $N = 2058$ ) contained fewer than 10 GPS points. The areas within the group's home range used during different seasons differed in size. The largest area was used during summer (41.5 km<sup>2</sup>) and the smallest during winter (32.1 km<sup>2</sup>; Fig. 4). Considering only areas used during each season, the group's per capita area values were 0.74 km<sup>2</sup> per baboon in summer and 0.57 km<sup>2</sup> per baboon in winter.

Strong correlations between observed and fitted cell use values (Pearson's  $R = 0.72$ ,  $N = 2058$ ,  $P < 0.001$ ) and their ranks (Spearman's  $\rho = 0.61$ ,  $N = 2058$ ,  $P < 0.001$ ) indicated that the model of home range use had good



**Fig. 3** Activity budgets of a troop of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, divided into times (in minutes) allocated to different activities (a), and percentages of daylight hours allocated to different activities (b). Values were derived from data collected through instantaneous scan sampling between June 1, 2009 and June 27, 2010. Values in parentheses in the legend indicate numbers of full days per season; error bars indicate standard errors; lowercase letters in plots indicate significant differences (values that share letters are not significantly different).

**Table III** Results of Kruskal–Wallis rank sum tests for seasonal differences in time allocated to different activities by a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, between June 1, 2009 and 27 June 27, 2010

Activity	Time (min)			Time (% daylight hours)		
	$\chi^2$	df	<i>P</i>	$\chi^2$	df	<i>P</i>
Feeding	2.33	3	0.507	<b>21.39</b>	3	< 0.001
Resting	<b>27.62</b>	3	< 0.001	<b>17.00</b>	3	< 0.001
Social activity	<b>8.65</b>	3	0.034	5.23	3	0.156
Travel	<b>37.49</b>	3	< 0.001	<b>18.46</b>	3	< 0.001

$N_{\text{winter}} = 23$ ,  $N_{\text{spring}} = 18$ ,  $N_{\text{summer}} = 11$ ,  $N_{\text{autumn}} = 19$ ; bold font denotes significance at 5% significance level.

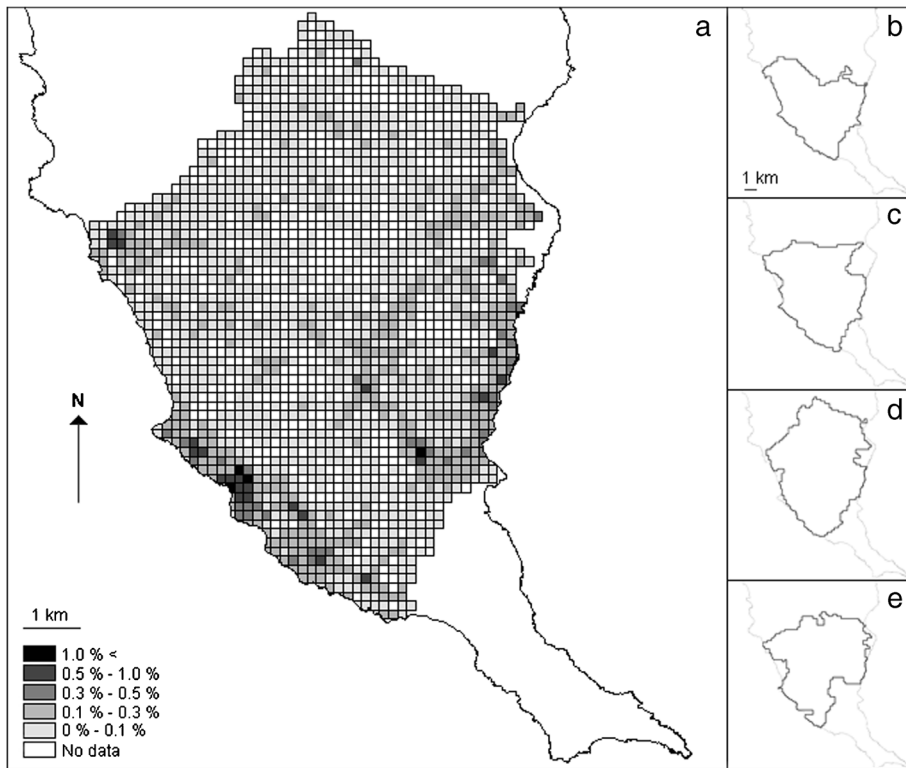


**Table IV** Results of Wilcoxon's rank sum tests for differences in time spent feeding on foods of different categories across seasons by a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, between June 1, 2009 and June 27, 2010

Food category	Seasons	Time (min)		Time (% daylight hours)	
		<i>W</i>	<i>P</i> <sub>Holm</sub>	<i>W</i>	<i>P</i> <sub>Holm</sub>
Feeding	Winter–spring	—	—	135	0.179
	Winter–summer	—	—	<b>28</b>	< 0.001
	Winter–autumn	—	—	<b>63</b>	< 0.001
	Spring–summer	—	—	147	0.124
	Spring–autumn	—	—	120	0.252
	Summer–autumn	—	—	133	0.252
Resting	Winter–spring	<b>317</b>	0.010	256	0.410
	Winter–summer	<b>247</b>	< 0.001	<b>220</b>	0.001
	Winter–autumn	262	0.306	193	0.532
	Spring–summer	<b>16</b>	< 0.001	<b>35</b>	0.013
	Spring–autumn	124	0.306	114	0.258
	Summer–autumn	<b>17</b>	< 0.001	<b>24</b>	0.001
Social activity	Winter–spring	<b>309</b>	0.040	—	—
	Winter–summer	161	0.860	—	—
	Winter–autumn	299	0.220	—	—
	Spring–summer	123	0.880	—	—
	Spring–autumn	136	0.880	—	—
	Summer–autumn	120	0.880	—	—
Travel	Winter–spring	286	0.081	217	0.805
	Winter–summer	<b>242</b>	< 0.001	181	0.137
	Winter–autumn	<b>400</b>	< 0.001	<b>345</b>	0.005
	Spring–summer	<b>13</b>	< 0.001	<b>42</b>	0.038
	Spring–autumn	<b>298</b>	< 0.001	<b>291</b>	< 0.001
	Summer–autumn	85	0.420	141	0.245

$N_{\text{winter}} = 23$ ,  $N_{\text{spring}} = 18$ ,  $N_{\text{summer}} = 11$ ,  $N_{\text{autumn}} = 19$ ; bold font denotes significance at the 5% significance level based on *P*-values with a Holm correction applied.

predictive value. All predictor variables included in the model had significant effects on frequency of cell use within KK group's home range (evidenced by highest posterior density intervals that did not include 0; Table V). The model output indicated that frequency of cell use decreased with increasing altitude, distance-to-sleeping site, distance-to-coast, and distance-to-fresh water. The magnitudes of the effects of these predictors varied, however: the effect of distance-to-sleeping site on frequency of cell use was greater in magnitude than those of other numerical predictor variables. Slope showed a positive effect on frequency of cell use. Frequency of use was highest in cells dominated by beach-type habitats and the group used Peninsula Sandstone Fynbos-dominated cells least frequently relative to these cells.

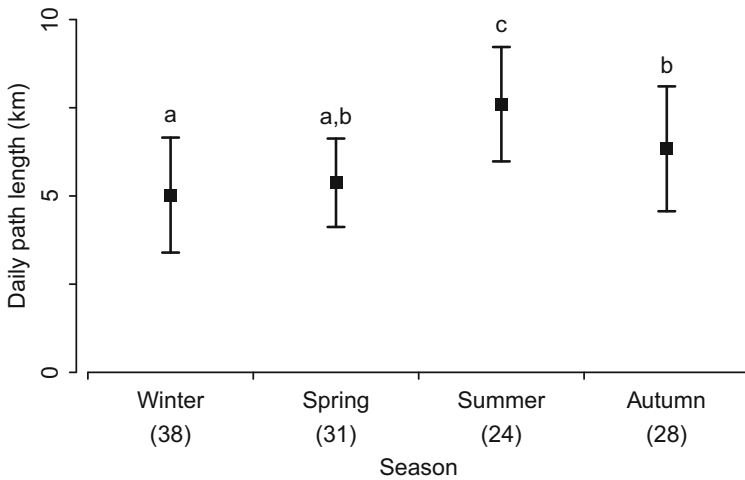


**Fig. 4** The home range of a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, from May 29, 2009 to June 27, 2010 (**a**; shade of cells indicates frequency of use as denoted in the legend), in winter (**b**), spring (**c**), summer (**d**), and autumn (**e**).

**Ranging Behavior** The group's mean ( $\pm$  SD) daily path length throughout the study was 5.93 ( $\pm$  1.83) km ( $N = 121$ ). The group's daily path length varied significantly across seasons (ANOVA:  $F_{3, 117} = 15.078$ ,  $P < 0.001$ ; Fig. 5). Daily path length was longer in summer than

**Table V** Results of a sparse SGLMM fitted to frequency of use of cells within the home range of a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa

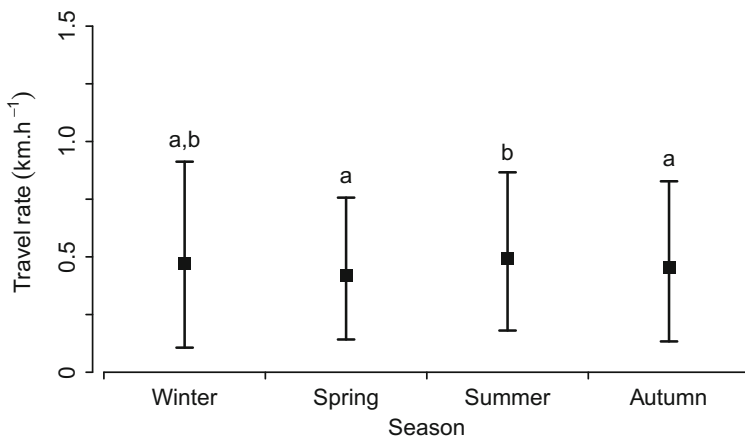
Predictor	Estimate	Highest posterior density interval limits		Monte Carlo SE
		Lower	Upper	
Intercept (Beach)	1.479	1.371	1.588	0.0012
Altitude	-0.166	-0.206	-0.122	0.0006
Slope	0.156	0.129	0.184	0.0003
Distance to sleeping site	-0.392	-0.445	-0.332	0.0010
Distance to coast	-0.293	-0.358	-0.228	0.0008
Distance to water	-0.075	-0.132	-0.021	0.0008
Cape Flats Dune Strandveld	-0.617	-0.729	-0.510	0.0014
Hangklip Sand Fynbos	-0.453	-0.628	-0.289	0.0025
Peninsula Sandstone Fynbos	-0.727	-0.848	-0.606	0.0017



**Fig. 5** Daily path lengths traveled by a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, between May 29, 2009 and June 27, 2010. Points indicate means and error bars denote standard deviations. Lowercase letters indicate significant differences (values that share letters are not significantly different); numbers in parentheses indicate sample sizes.

in winter (Tukey's HSD test 95% CI:  $-3.6; -1.5$ ), spring (95% CI:  $1.1; 3.3$ ), or autumn (95% CI:  $0.1; 2.4$ ), and longer in autumn than in winter (95% CI:  $-2.3; -0.3$ ).

The group's mean ( $\pm$  SD) rate of travel throughout the study was  $0.56 (\pm 0.50)$  km/h. There were significant differences in the group's travel rates across seasons (Kruskal–Wallis rank sum test:  $\chi^2 = 20.267$ ,  $df = 3$ ,  $P < 0.001$ ; Fig. 6), with travel rates being significantly higher during summer (median =  $0.49$  km/h, interquartile range:  $0.19\text{--}0.87$  km/h) than during spring ( $W = 1,472,900$ ,  $N_{\text{summer}} = 1798$ ,  $N_{\text{spring}} = 1798$ ,  $P_{\text{Holm}} < 0.001$ ) or autumn ( $W = 1,531,900$ ,  $N_{\text{summer}} = 1798$ ,  $N_{\text{autumn}} = 1798$ ,  $P_{\text{Holm}} = 0.033$ ).



**Fig. 6** Travel rates of a group of natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa, recorded between May 29, 2009 and June 27, 2010. Points indicate medians and error bars denote interquartile ranges. Lowercase letters indicate significant differences;  $N = 1798$  in all seasons.

## Discussion

### Foraging Profile and Activity Budgets

KK group’s foraging profile was dominated by plant material acquired in terrestrial habitats during all four seasons within the data collection period. Within this component of the foraging profile, above-ground plants consistently accounted for a larger proportion than subterranean foods. As we predicted, KK group fed on marine foods, and did so more than other Peninsula groups for which similar data are available (Davidge 1978; Lewis *unpubl. data*), but the amount of feeding time allocated to exploiting marine foods through the study period was low (<5%). This is somewhat surprising given that primates are capable of exploiting marine foods to a greater extent; ca. 20% of the diet of crab-eating macaques (*Macaca fascicularis*) in southern Vietnam comprises marine invertebrates (Son 2003). The ecological contexts in question differ, however, as the macaques’ principal marine prey are different from those of the baboons (Son 2003), and they acquire marine foods in intertidal habitats under mangrove trees where wave action is reduced (Mazda *et al.* 1997).

There may be an element of choice in KK baboons not feeding on marine foods to a greater extent, but our companion study suggests that abiotic factors play a role in limiting the behavior. Models indicated that probability of marine foraging during a given hour decreased with increasing tide and wave height, as did intensity of marine foraging with increasing tide height (Lewis and O’Riain *in press*). These findings corroborate Hall’s statements that marine foraging occurred “almost daily when wind and tide allow ... easy access to intertidal rock pools and to the sea verge” (Hall 1963, p. 17) but that baboons on rocks at the sea’s edge “would rush away on the approach of a large wave” (Hall 1962, p. 210). This does not, however, preclude the potential limiting effects of other factors, which require further investigation.

KK group allocated markedly more feeding time to acquiring and ingesting subterranean foods (average of ca. 20%) than groups in Mpumalanga Province, South Africa (Henzi *et al.* 2011), the eastern highlands of Zimbabwe (Katsvanga *et al.* 2009), and the Okavango Delta (Hamilton *et al.* 1978), but less time than groups living in untransformed, subalpine habitats in the Drakensberg, South Africa (Whiten *et al.* 1987). The KK group spent significantly more time feeding on subterranean food in summer and autumn, which is similar to findings for yellow baboons in Amboseli, Kenya that allocated more than 50% of feeding time to less preferred subterranean foods during the dry months (Alberts *et al.* 2005). The relatively high proportion of subterranean foods in KK group’s diet may therefore be interpreted as broadly indicative of a lower abundance of other foods that offer high net profit in this group’s home range, particularly during the warm, dry summer and autumn months. Comparisons of feeding time across time and space are interesting and informative, but this quantity does not equate to food mass intake or nutrient intake (Muruthi *et al.* 1991; Zinner 1999). Also, as is the case for all seasonal patterns reported here, changes in subterranean food consumption were observed across seasons through 13 mo. Stochastic variation therefore cannot be ruled out, but given the documented importance of seasonality in this population (Van Doorn *et al.* 2010), it seems likely that it was the primary driver of this and other differences between sampling periods.

As a percentage of KK group’s total time, foraging time (*sensu* Bronikowski and Altmann 1996) was higher than that of congeneric groups that regularly feed on

anthropogenic foods elsewhere (Altmann and Muruthi 1988; Bronikowski and Altmann 1996; Forthman Quick 1986) and on the Peninsula (Hoffman 2011; Van Doorn *et al.* 2010); was comparable to that of natural-foraging groups in Amboseli, Kenya (Bronikowski and Altmann 1996; Post 1981); and was lower than that of natural-foraging groups in the Drakensberg (Whiten *et al.* 1987). Seasonal variation in the percentages of time the group allocated to feeding and traveling is similar to that observed in a group in the Drakensberg (Whiten *et al.* 1987). Percentage time activity budget comparisons across seasons at nonequatorial sites should be treated with caution, however, as these data fail to account for seasonal changes in time available for allocation to different activities caused by variation in day length (Hill *et al.* 2003, 2004).

Foraging time (*sensu* Bronikowski and Altmann 1996) varied with season, but this was entirely due to variation in time spent traveling, as time spent feeding varied little across seasons. KK group spent significantly more time traveling during the warm, dry summer and autumn months than during winter or spring. A similar seasonal pattern was observed in the time allocation of baboons at De Hoop Nature Reserve (a fynbos habitat at a similar latitude to the east of the Cape Peninsula; Hill *et al.* 2003) and even a semiprovisioned Peninsula group (Van Doorn *et al.* 2010). The amount of time that KK group allocated to foraging was similar to that allocated by the study group of Hill *et al.* (2003) in De Hoop (similar habitat to the Peninsula), and much greater than that allocated by the study groups of Van Doorn *et al.* (2010) on the Peninsula. Thus, it seems that KK group is typical of fynbos-dwelling groups with no access to anthropogenic foods in this regard.

There was seasonal variation in resting time; KK group spent more time resting in summer than in winter and spring. This may seem counterintuitive in light of the differences in ranging behavior through seasons, and the tendency of baboons elsewhere to sacrifice resting time in favor of foraging time (Alberts *et al.* 2005). There is, however, a plausible explanation for this pattern that does not contradict the inferences drawn from foraging profile and other activity budget data: KK baboons might spend more time resting in summer to reduce energy expenditure. This has been invoked as the explanation for other primates increasing resting time in response to shortages of preferred foods (Chaves *et al.* 2011; Di Fiore and Rodman 2001; Norscia *et al.* 2006; Vasey 2005). As has been reported in geladas (Dunbar and Dunbar 1988), time allocated to social activity did not change through the seasons. The percentage of time that KK group allocated to social activity was similar to that reported for other groups in several regions, including the Cape Peninsula (Alberts *et al.* 2005; Altmann and Muruthi 1988; Hoffman 2011), and the amounts of time spent grooming in different seasons were similar to, but more constrained than, those observed in De Hoop baboons (Hill *et al.* 2003).

## Ranging Patterns

Comparisons with groups elsewhere indicate that for a group occupying low-altitude habitats in a temperate region, KK group ranged over a surprisingly large area (Table VI). Controlling for group size, *i.e.*, considering per capita area, the area occupied by KK group was larger than those occupied by chacma baboon groups in the Namib desert, Namibia (Hamilton *et al.* 1976); in the Okavango, Botswana (Hamilton *et al.* 1976); elsewhere on the Cape Peninsula (DeVore and Hall 1965; Hoffman and O'Riain 2012a); in Suikerbosrand Nature Reserve (Anderson 1981) and at Tshipise (Stoltz and Saayman 1970), both of which are in South Africa; and all but

**Table VI** Group sizes, home range sizes, per-capita areas, densities, and daily path lengths of baboon (*Papio* spp.) groups with similar social structures to KK

Species	Group size	Home range (km <sup>2</sup> )	Per capita area (km <sup>2</sup> /individ.)	Density (indiv./km <sup>2</sup> )	Daily path length (km)	Locality	Reference
<i>Papio ursinus</i>	20	9.1	0.45	2.2		Cape Peninsula, R.S.A.	DeVore and Hall 1965
	35	14.8	0.42	2.4		Cape Peninsula, R.S.A.	DeVore and Hall 1965
	80	33.7	0.42	2.4		Cape Peninsula, R.S.A.	DeVore and Hall 1965
	115	9.5	0.08	12.1	3.0	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	49	37.7	0.77	1.3	5.6	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	36	9.1	0.25	4.0	4.9	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	35	10.6	0.30	3.3	4.1	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	26	9.3	0.36	2.8	3.2	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	24	8.3	0.35	2.9	2.9	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	22	7.5	0.34	2.9	6.6	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	16	1.5	0.10	10.4	1.8	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	16	5.6	0.35	2.8	3.9	Cape Peninsula, R.S.A.	Hoffman and O'Riain 2012a
	9	18.9	2.10	0.5	4.3	Drakensberg, R.S.A.	Whiten <i>et al.</i> 1987
	14	10.0	0.71	1.4	3.8	Drakensberg, R.S.A.	Whiten <i>et al.</i> 1987
	60	23.3	0.39	2.6		N. Limpopo Province, R.S.A.	Stoltz and Saayman 1970
	77	13.0	0.17	5.9		N. Limpopo Province, R.S.A.	Stoltz and Saayman 1970
	40	15.5	0.39	2.6		N. Limpopo Province, R.S.A.	Stoltz and Saayman 1970
	88	28.3	0.32	3.1	4.5	Suikerbosrand, R.S.A.	Anderson 1981
74	24.9	0.34	3.0	3.1	Suikerbosrand, R.S.A.	Anderson 1981	
82	24.8	0.30	3.3	4.8	Suikerbosrand, R.S.A.	Anderson 1981	
68	20.5	0.30	3.3	5.4	Suikerbosrand, R.S.A.	Anderson 1981	
108	4.7	0.04	23.0		Okavango, Botswana	Hamilton <i>et al.</i> 1976	



Table VI (continued)

Species	Group size	Home range (km <sup>2</sup> )	Per capita area (km <sup>2</sup> /indiv.)	Density (indiv./km <sup>2</sup> )	Daily path length (km)	Locality	Reference
<i>P. anubis</i>	109	6.5	0.06	16.8		Okavango, Botswana	Hamilton <i>et al.</i> 1976
	39	2.1	0.05	18.6		Okavango, Botswana	Hamilton <i>et al.</i> 1976
	71	4.8	0.07	14.8		Okavango, Botswana	Hamilton <i>et al.</i> 1976
	35	9.4	0.27	3.5		Namib Desert, Namibia	Hamilton <i>et al.</i> 1976
	33	4.0	0.12	7.0		Namib Desert, Namibia	Hamilton <i>et al.</i> 1976
	50	19.7	0.38	2.5		Gilgil, Kenya	Harding 1976
	100	43.8	0.44	2.3	5.6	Laikipia Plateau, Kenya	Barton <i>et al.</i> 1992
	12	5.2	0.43	2.3		Nairobi, Kenya	DeVore and Hall 1965
	17	23.8	1.40	0.7		Nairobi, Kenya	DeVore and Hall 1965
	24	18.1	0.76	1.3		Nairobi, Kenya	DeVore and Hall 1965
	28	7.8	0.28	3.6		Nairobi, Kenya	DeVore and Hall 1965
	28	40.1	1.43	0.7		Nairobi, Kenya	DeVore and Hall 1965
	40	24.9	0.62	1.6		Nairobi, Kenya	DeVore and Hall 1965
	77	30.3	0.39	2.5		Nairobi, Kenya	DeVore and Hall 1965
87	35.8	0.41	2.4		Nairobi, Kenya	DeVore and Hall 1965	
58	3.9	0.07	14.9		Queen Elizabeth N.P., Uganda	Rowell 1966	
32	5.4	0.17	5.9		Queen Elizabeth N.P., Uganda	Rowell 1966	
<i>P. cynocephalus</i>	42	24.1	0.57	1.7	5.5	Amboseli, Kenya	Altmann and Altmann 1970
	106	16.7	0.16	6.3		Amboseli, Kenya	Altmann and Altmann 1970

Indiv. = individual(s); N.P. = National Park; R.S.A. = Republic of South Africa; where group size varied through a study, we based calculations on maximum recorded group size.

two groups of olive baboons (*Papio anubis*) near Nairobi, Kenya (DeVore and Hall 1965); as well as groups of olive baboons on the Laikipia Plateau (Barton *et al.* 1992) and at Gilgil (Harding 1976), both of which are in Kenya; in Queen Elizabeth National Park, Uganda (Rowell 1966); and groups of yellow baboons in Amboseli (Altmann and Altmann 1970). Elsewhere, the group that was most similar to KK group in terms of home range size was a group in the Drakensberg Mountains, South Africa, where baboons must endure persistent food shortages and considerable thermal stress (Henzi *et al.* 1992; Whiten *et al.* 1987).

KK group also traveled surprisingly far, given the size of the group, the altitude and latitude at which its home range is situated, and local climatic conditions. The group's daily path lengths were greater than those of all but one of the recently studied groups on the Peninsula with access to anthropogenic foods or tissues of alien-invasive trees (Hoffman and O'Riain 2012a), the exception being a group that was aggressively herded across its home range by sanctioned baboon monitors (Hoffman *pers. comm.*). KK group's daily paths were also longer than those of groups in the Drakensberg mountains (Whiten *et al.* 1987) and at Suikerbosrand Nature Reserve (Anderson 1981), both of which are in South Africa; and groups of olive baboons on the Laikipia Plateau (Barton *et al.* 1992) and yellow baboons in Amboseli (Altmann and Altmann 1970), both of which are in Kenya (Table VI). These comparisons should be treated with caution, however, as group size and daily path length are correlated in chacma baboons (Dunbar 1992; Hoffman and O'Riain 2012a) and none of the groups in question were similar in size to KK group.

Variation in per capita area and daily path lengths across seasons suggests that the drivers of KK group's ranging behavior change through time. The large areas used in summer and autumn, and the long daily paths traveled (and concomitant higher rates of travel), by KK group in summer, suggest that food might be less abundant, or of lower quality, during the warm, dry season. This is likely related to seasonal changes in plant phenology (Pierce 1984; Stock *et al.* 1987) and perhaps changes in the nutritional reward offered by marine intertidal foods per unit foraging effort. That is, the same amount of foraging effort might yield soft tissue of greater mass, or with higher concentrations of macronutrients such as protein or lipids, immediately prior to the spawning season of baboons' marine invertebrate prey (Hodgson 2010; Van Erkom Schurink and Griffiths 1991).

As we predicted, KK group made preferential use of areas that provided relatively easy access to food and sleeping sites. The latter is manifested as selection for parts of the home range close to sleeping sites and steeply sloped land (Hoffman and O'Riain 2012b). Food-related area preferences were manifested as selection for more productive habitat types among those available (Zhao and Running 2010), land at lower altitudes (which is more productive; Hoffman and O'Riain 2012b), and, we hypothesize, land near the coast. Given that the intertidal zone is devoid of other ecologically important resources, KK baboons likely spent time near the coast in order to maximize foraging opportunities at the marine-terrestrial interface. This may seem counterintuitive in light of KK group's foraging profile, but is lent credence by the fact that marine foraging bouts occurred during more than 22% of daylight hours in winter and >13% of daylight hours in spring and autumn (Lewis and O'Riain *in press*). That said, much terrestrial land near the coast is low-lying and so might, by virtue of being more productive (Hoffman and O'Riain 2012b), offer more abundant food resources. It is therefore probable that these factors act in concert to attract baboons to land near the coast.

## Conclusion

Unlike baboons in all other recently studied groups on the Cape Peninsula, KK baboons do not feed on anthropogenic foods but do feed on marine foods in the intertidal zone, albeit to a limited extent. Time spent feeding on subterranean foods comprises a much smaller percentage of the group's feeding time than above-ground terrestrial foods, and falls within the range of values observed in other groups across the genus's distribution. The group allocated more time to feeding and traveling than groups that exploit anthropogenic foods, but not markedly more than natural-foraging groups elsewhere. For a group of this size, KK group occupied a relatively large area and traveled long distances on a daily basis. The group's use of areas within its home range was not uniform, and model output suggests that food availability and sleeping site location were the primary drivers of area use.

Together, these results provide an important baseline for the long-term management of the Peninsula baboon population. Currently 15 of the 16 groups access anthropogenic foods but the goal of the Baboon Technical Team responsible for their management is to ensure a diet comprising solely of natural foods. Our data presented here suggest that this goal will result in significant increases in groups' per capita areas, daily path lengths, and time spent feeding and traveling. In addition, we predict that baboons managed thus will, where possible, return to the intertidal areas of their home ranges to supplement their diet with marine foods. Further research is required to elucidate how chemical, physical, and nutritional properties of both marine and terrestrial foods might affect exploitation by these baboons.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest and no competing financial interests.

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