

The Spatial Ecology of Chacma Baboons (*Papio ursinus*) in a Human-modified Environment

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Abstract Anthropogenic habitat alteration can have a dramatic effect on the spatial distribution and ranging patterns of primates. We characterized the spatial ecology of a free-living troop of chacma baboons (*Papio ursinus*) in a human-modified environment in the Cape Peninsula, South Africa. We used GPS and behavioral observations collected over 1 yr to quantify the troop’s home range size, habitat selection, choice of sleeping site, and foraging patterns. The troop comprised 115 individuals living in a home range of 9.50 km², giving a density of 12.1 baboons/km². Area use correlates positively with exotic vegetation and negatively with indigenous vegetation and altitude. The troop spent significantly more time in low-lying human-modified environments, i.e., plantations, vineyards, and urban habitat, than in indigenous vegetation that was largely restricted to steeper slopes at higher elevations. The troop slept exclusively in exotic trees, 94% of which were located in the plantation, 3% in urban habitat, and 3% in vineyards. The most consumed food items were exotic grasses, subterranean food items, and exotic pine nuts. The survival and persistence of the focal troop in close proximity to the urban edge while ≥3 neighboring troops were previously extirpated suggests that access to low-lying land in conjunction with a land-use practice that does not preclude baboon presence has been fundamental to both their survival and persistence at such a high density. The almost exclusive use of exotic vegetation both as a food source and as a safe refuge for sleeping highlights the ecological flexibility of baboons, but the systematic loss of low-lying productive land poses the single greatest threat to their continued persistence on the Cape Peninsula.

Keywords Anthropogenic habitat alteration · Chacma baboon · Habitat use · Home range · Seasonality

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Introduction

Anthropogenic habitat alteration can have a dramatic effect on the availability and distribution of primate food resources, affecting primate spatial distribution and ranging patterns. Where habitat alteration reduces habitat quality and food supply, primates travel farther to meet their nutritional requirements (Ganas and Robbins 2005; Lee 1997; Li *et al.* 2005; Li and Rogers 2005; Menard and Vallet 1997; O'Brien and Kinnaird 1997; Singh *et al.* 2001; Wieczkowski 2005). Conversely, when ecologically flexible primates are able to take advantage of highly concentrated and predictable food resources, such as those offered by agricultural and urban habitat, they may exhibit group size (Fuentes *et al.* 2005) and density (Brennan *et al.* 1985) increases, home range size, and daily path length reductions (Saj *et al.* 1999), disproportionate range use (Hill 2005; Riley 2008), and a reduction in time spent feeding (Forthman Quick 1986; Forthman Quick and Demment 1998; Lee *et al.* 1986).

The primates exhibiting the greatest degree of spatial overlap with humans are members of *Macaca*, *Papio*, and *Cercopithecus* (Hill 2005). Their success in human-modified environments is attributed to their intelligence, agility, dexterity, and high levels of sociality and cooperation, combined with dietary and behavioral flexibility (Else 1991; Swedell, *in press*). Within this group baboons (*Papio*) are reported as pests in Uganda (Hill 2000), Nigeria (Pepeh 1996), Cameroon (van Oosten 2000), Kenya (Strum 1994), Tanzania (Mascarenhas 1971), Malawi (Morris 2000), and South Africa (Brown *et al.* 2006; Kansky and Gaynor 2000), and in some agricultural areas cause more crop damage than any other primate (Hill 2000; Naughton-Treves 1996; Tweheyoa *et al.* 2005) as well as all other wildlife species (Biryahwaho 2002; Naughton-Treves *et al.* 1998).

The chacma baboon (*Papio ursinus*) population in the Cape Peninsula, South Africa, provides one of the best examples of baboon commensalism with humans. The 12 troops that comprise this population are geographically isolated from other populations as a result of urban sprawl. All troops have contact with humans, albeit to different degrees, in both residential and tourist-frequented areas. Despite the baboons' access to large expanses of indigenous vegetation within the Table Mountain National Park (TMNP), conflict between baboons and humans, both within and outside the park, is widespread (Kansky and Gaynor 2000). Historically, this conflict has led to the extirpation of whole troops (Skead 1980), and more recently it is manifest in high levels of human-induced injury and mortality (E. K. Beamish, University of Cape Town, *unpubl. data*).

Anthropogenic habitat alteration and management activities within and immediately adjacent to the TMNP have had an enormous effect on the landscape structure and composition of the Cape Peninsula (Richardson *et al.* 1996). In particular, the introduction and spread of exotic (non-native) plant species has increased above-ground biomass by 3- to 10-fold (van Wilgen and Richardson 1985). It is unknown to what extent these anthropogenic habitat alterations influence the spatial ecology of extant troops and hence human–baboon conflict.

We studied a baboon troop inhabiting the Tokai region of the Cape Peninsula to investigate the spatial and behavioral ecology of the resident baboons. The Tokai region includes commercial plantations of exotic pines and eucalyptus, vineyards

and various forms of urban land use, and large tracts of indigenous vegetation on the upper slopes of the TMNP, an urban park that runs the length of the Cape Peninsula. At the time of our study, the baboons in this area also had unrestricted access to the vacant home ranges of ≥ 3 extirpated troops (E. K. Beamish, *pers. comm.*) that included large areas of indigenous vegetation across a range of altitude and slopes. Our study objectives were to quantify the ranging and resource selection patterns of baboons (the Tokai troop of the Cape Peninsula) living in a human-modified environment, and to quantify their home range, habitat selection, sleeping site preference, daily distance traveled, and foraging patterns. We compare these data with those reported for baboons living in natural habitats, to examine whether access to highly concentrated and predictable food resources, such as those offered by agriculture, i.e., forestry and vineyards, and urban habitat result in an increase in group size, density, and home range size and a decrease in daily path length and time spent feeding as suggested by previous studies of various primates that have been exposed to a human-modified environment.

Methods

Study Site

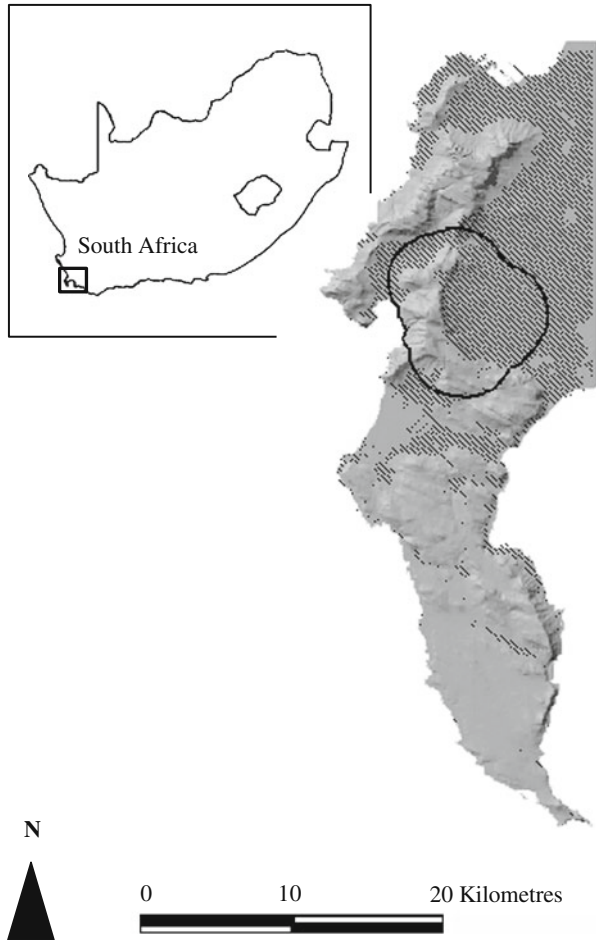
The Cape Peninsula, South Africa (Fig. 1) covers a 470-km² area. Its topography is characterized by the Peninsula Mountain chain, which stretches from Table Mountain in the north to Cape Point in the south. More than half of this area is undeveloped and has conservation status under the protection of the TMNP. The lower elevations are predominantly urbanized, some of the mid-elevations are used for agriculture, and the higher elevations are almost exclusively indigenous fynbos vegetation that is only minimally fragmented by urban roads. Fynbos is a species rich but nutrient poor sclerophyllous shrubland that is a key component of the Cape Floristic Region (Cowling *et al.* 1996).

The climate of the Cape Peninsula is Mediterranean, with hot, dry summers and cool, wet winters. This climatic pattern results in higher primary production in winter relative to summer (Cowling *et al.* 1996). The Cape Peninsula is devoid of baboon predators. Our study site, in the Tokai Region, was located in the northern reaches of the Cape Peninsula (34°03'33 S, 18°24'35 E) on the lower slopes of Constantiaberg Mountain. It consisted of a large tract of indigenous vegetation surrounded in part by the urban habitat, the Atlantic Ocean, and agricultural land, including commercial exotic plantations and vineyards. The altitudinal range in the study area spans from sea level to 700 m.

Focal Subjects and Habitat Characteristics

Our focal troop, the Tokai (TK) troop, was the most northerly and most geographically isolated (from other troops) of the 12 Cape Peninsula troops. During the study period, E. K. Beamish (University of Cape Town, *unpubl. data*) conducted a census of the TK troop as part of a long-term study on population dynamics of the Cape Peninsula baboon population and estimated the troop size at 115 baboons. The

Fig. 1 Topographic profile of the Cape Peninsula indicating the distribution of developed land (shaded area) and the area available to the TK troop (black line inside Peninsula outline); inset shows the location of the study area in the Cape Peninsula, South Africa.



Tokai plantation is a popular recreational area for the local populace. Tokai baboons are thus accustomed to the presence of people and consequently they were habituated to close (≤ 10 m from baboons) behavioral observations when the study began. The terrain within the study area was easily traversable on foot, and visibility of baboons within all habitat types was excellent.

Data Collection

T. Hoffman and 5 medium-term (2 mo–1 yr) volunteers collected behavioral data while 17 short-term (< 1 mo) volunteers assisted in locating the troops in the morning, GPS data collection, and logistical support. Volunteers began data collection only when their records matched those of T. Hoffman with an accepted error level of $< 5\%$ for behavioral and dietary recordings made over a full day of data collection. T. Hoffman supervised all volunteers daily to ensure that they adhered strictly to data collection protocols.

We tracked and observed the TK troop for 137 d, including 74 full-day follows (morning to evening sleeping site) and 63 part-day follows from March 2006 to February 2007. On part-day follows we typically tracked baboons for half the day (sunrise to midday or midday to sunset) or on occasion for only a few hours during the day, e.g., when we had difficulty locating the troop. We collected data on 7–23 d for all months except November, with an average of 12 data collection days per month (± 3.4 d, $n=11$ months). Seasonally, we collected data on 34 d in autumn (March–May), 56 d in winter (June–August), 15 d in spring (September–November), and 32 d in summer (December–February). The data set consists of 1030 h of observations (mean \pm SEM=93.6 \pm 26.09 hours/month, $n=11$ mo). On the rare occasions ($n=15$ d) that the TK troop fragmented into subgroups, we followed the larger of the subgroups.

We recorded the GPS coordinates of the center point of the troop (visually estimated) at 20-min intervals and conducted instantaneous scans on the hour and half hour. To obtain a representative measure of troop behavior and habitat use during each scan, an observer walked in a straight line (transect) from the visually estimated troop center to the edge of the troop (the last baboon visible to the left or right of the transect line), recording en route the behavior and habitat of every baboon within a 90° arc centered on the transect trajectory. We made transects in the order of north, south, east, and west in each successive scan. Transects were not perfectly straight lines, as we took care not to walk directly toward baboons. When a baboon was on the transect line, we deviated around the individual and returned immediately to the original bearing, using a hand-held compass, to complete the scan. This method ensured that all troop members had an equal probability of being sampled, while controlling for potential spatial biases of troop members, e.g., flank vs. leading edge. We recorded data for male and female adults, subadults, and juveniles, with a mean of 11 \pm 1 SEM (range: 1–34) individuals per scan. We classified behavior as foraging, socializing, resting, or moving, as these activities constitute >95% of a baboon's time budget (Dunbar 1992). In the case of foraging, which included all behaviors related to food—searching, handling, feeding—we noted the food item being consumed when possible. Habitat categories included indigenous vegetation, standing exotic plantations, cleared exotic plantations, vineyards, and urban. We recorded each individual as a separate data point, with the number of sampled individuals varying across scans because of variability in the spatial distribution of troop members. We recorded the GPS positions of all sleeping sites and categorized them as exotic trees, indigenous trees, or cliffs.

Baboon monitors are employed by the local management authorities to minimize human–baboon conflict by herding baboons away from urban habitat (Kansky and Gaynor 2000; van Doorn 2009). Baboon monitors employed a holding the line strategy on 17% of study days between June 2006 and February 2007. This involves preventing the troop from entering the urban habitat but has a negligible effect on troop movement beyond the urban edge. In Tokai, the urban habitat is restricted to the lower elevations, and thus the presence of the monitors may have caused us to underestimate the troop's use of lower elevations. Further, unlike the baboon herding strategy (van Doorn 2009), the holding the line strategy is not prescriptive on baboon behavior and is thus unlikely to affect the behavioral data recordings. However, because of the discrepancy in the number of days with monitors (17%)

compared to the number of days without monitors (83%), we were unable to test this statistically.

We recorded site-specific ambient temperature measurements within and immediately adjacent to the Tokai plantation from June to August 2006 via ClimaStats i-buttons® (TIs). We positioned 4 TIs in plantation pine trees (*Pinus radiata*) at 200 m, 260 m, and 325 m elevations and on a rock in fynbos at an elevation of 430 m. We positioned the TIs 10 cm above the ground facing a southerly direction, and adhered them to the substrates with marine silicone. The TIs recorded shaded ambient temperature hourly for a period of 85 continuous days. We downloaded the recorded information via ClimaStats Lite 3.3 and exported it for analysis.

Data Analysis

We analyzed our data on annual and seasonal scales. We included all data collected during the year in our annual data analyses. We restricted seasonal analyses to the extremes of winter (June–August), characterized by cool, wet conditions and short day lengths, and summer (December–February), characterized by long days with hot and dry conditions. Data for spring and autumn showed intermediate patterns and are not included here.

We obtained daily regional temperature data and sunrise and sunset times from the South African Weather Service, Climate Information Office. Study days were shorter in winter (10.33 ± 0.03 h, $n=92$ d; $t=-77.09$, $df=180$, $p \leq 0.001$) than in summer (13.97 ± 0.08 h, $n=90$ d) and cooler in winter ($13.1 \pm 0.3^\circ\text{C}$, $n=92$ d; $t=-28.16$, $df=180$, $p \leq 0.001$) than in summer ($21 \pm 0.4^\circ\text{C}$, $n=90$ d). We obtained rainfall data specific to the Tokai plantation from the South African National Parks weather station. There were more rainy days in winter (32 d) than in summer (11 d), and the mean monthly rainfall was higher in winter (162.33 ± 36.66 mm, $n=3$ mo; $t=5.22$, $df=4$, $p \leq 0.001$) than in summer (32.33 ± 32.29 mm, $n=3$ mo).

Area Use We imported all GPS data points of troop locations ($n=2990$) into ArcView 3.3 and projected them in Transverse Mercator, spheroid WGS84, central meridian 19. To establish an appropriate area in which to evaluate home range selection and resource selection with the home range, we placed circular zones (buffers) with 3 km radii around the 2990 troop locations. We defined the area contained within the outermost borders of the outlying buffers as the study area. We based buffer radius lengths on the median daily distance traversed by the troop during the observational period, yielding a realistic measure of the area accessible to the troop within a day's journey. On its western side we clipped the study area to the Cape Peninsula coastline. We overlaid a grid of $150 \text{ m} \times 150 \text{ m}$ (0.023 km^2) cells onto the study area using the Repeating_shapes extension to ArcView (Jenness 2005). We made our grid size smaller than those of Whiten *et al.* (1987; 1 km^2) and Henzi *et al.* (1992; 4 km^2) to reduce the likelihood of the troop being spread through >1 cell simultaneously (Henzi *et al.* 1992). We ensured that the total area of each cell was sufficient to encompass the average troop spread ($0.021 \pm 0.01 \text{ km}^2$, $n=5$ spreads) as well as the average area of plantation plots ($0.015 \pm 0.003 \text{ km}^2$, $n=591$ plots), thereby improving the efficiency of fine-scale habitat analyses.

We used the GPS positions of the troop center recorded at 20-min intervals to class cells that contained one or more GPS data point as entered cells. The home range of the troop included all entered cells, as well as those bounded on ≥ 3 sides by entered cells. We joined isolated cells to the nearest cluster of contiguous entered cells using the most direct route possible. We also classed cells that the troop was known to traverse, based on analyses of daily movement paths, as entered cells, even if the rate of movement meant that no GPS data points were recorded in them. We calculated the total home range size by multiplying the number of cells entered by the standard cell area, and determined an annual point frequency value for each entered cell by counting the number of GPS data points within it. We used the same techniques to calculate seasonal range sizes and cell use frequencies using the 700 GPS data points collected during each winter and summer.

We investigated patterns of resource selection using Pearson partial correlations to analyze cell use within the study area and the annual and seasonal ranges as a function of the following explanatory variables: altitude, gradient, habitat type, and the distance to permanent water sources. We calculated the Mean_Altitude for each cell using a 30-m digital elevation model. We used the coefficient of variation (CV) for the elevation of each cell as a measure of Gradient, with higher CV values indicating a steeper slope. We calculated distances to permanent water sources (Distance_to_Water) using an ArcView shapefile that details drainage systems in the region (Glcveg.shp; South African National Parks, *unpubl. data*). We used ArcView shapefiles describing the regional and local habitat (lease_2006_06_28.shp; South African National Parks, *unpubl. data*) to allocate a categorical habitat value to each cell (Habitat). We used observer records of location-specific habitats and information gleaned from digitisation of the Tokai area, based on aerial photography of the region, to validate and identify habitat types in areas where the extent and or the detail of the geographic information system (GIS) layers was insufficient or inaccurate in its descriptions. We categorised Habitat broadly as indigenous vegetation, exotic vegetation, or urban habitat. We subdivided exotic vegetation into standing plantation plots, harvested plantation plots, and vineyards. The plantation was dominated by *Pinus* species (67% of land area) and *Eucalyptus* species (11%). Sixty-five percent of the plantation plots were standing, with plantation trees dominating the vegetation ground cover. Thirty-five percent of the plantation plots were harvested, with indigenous and exotic pioneer plant species occurring between the stumps of harvested trees. The vineyards fruited during summer months (January–March), and in the wet winter months (July–August) farmers planted grains between vineyard rows to stabilize the soil. The urban habitat, which we defined as any area with human-made structures such as buildings, roads, sports fields, and gardens and grass patches adjacent to buildings, predominantly comprised residential houses with gardens and several recreational areas such as picnic sites. Woody plants in the form of fruit trees and patches of pine and eucalyptus stands were also present in the urban habitat. Two sections of urban habitat occurred in the study area: one surrounded by the plantation and vineyards, and the other peripheral to the plantation and vineyards.

We assigned an elevation value to each GPS point using ArcView, and used *t*-tests to compare the elevation records in winter and summer ($n=700$ GPS points/season). We used observational data to determine the percentage use of each habitat type annually ($n=1732$ scans) and seasonally ($n=372$ scans/season). We could not transform these habitat use data to normality, so we used Kruskal-Wallis tests with multiple comparisons of mean ranks (Zar 1999) to identify significant differences in the annual use of habitat types, and used Mann-Whitney *U* tests to compare the seasonal use of habitat types.

Movement Patterns We determined movement patterns from full-day journeys (Altmann and Altmann 1970) and calculated total daily distances via the Nearest features extension to ArcView (Jenness 2004). We calculated the distances traveled between scans and then summed distances from the 3 consecutive 20-min scans taken per hour to provide one measure of distance traveled per hour (Henzi *et al.* 1992). We used Pearson correlations to test for relationships between total daily distance traveled and mean temperature and day length (Bronikowski and Altmann 1996; Henzi *et al.* 1992). We collected ranging data on 32% of the days on which we recorded rainfall during the total study period, but we did not collect data on days when it was raining heavily because of poor GPS functioning. Thus the movement data are biased toward days with light or no rainfall and so we did not test for correlations between total daily distance traveled and rainfall. For all full-day follows in the winter and summer data sets ($n=17$ days/season) we used *t*-tests to investigate significant differences in the mean number of cells entered per day, the daily distance traveled, and the hourly travel rate. We log transformed the daily distance and hourly travel rate variables for both seasons.

Behavior and Diet For each scan we calculated the total number of records of each behavioral category and dietary item, and converted these totals to percentages. We used the mean of scan percentages from all months to calculate an annual activity budget for the troop, and used the mean of scan percentages from the full-day data sets from winter and summer to calculate seasonal activity budgets. We analyzed only behavioral data collected during full-day follows to avoid overrepresenting activities that occur only or more often at specific times of the day. Activity budget analyses included all troop individuals with the exception of infants.

To account for the effect of seasonal differences in day length on time allocated to each activity (Hill *et al.* 2003, 2004), we converted daily activity budgets from percentages to hours. We did this for each day per season by multiplying the daily percentage for each activity by the number of hours that we recorded data on that day (data hours). Data hours were shorter than actual day length for both seasons (difference in winter 3.24 ± 0.58 h; difference in summer 4.35 ± 1.25 h) but provided a more accurate indication of time engaged in each activity than day length. We investigated seasonal differences in activity using Mann-Whitney *U* tests.

We used the scan percentages to calculate the contribution of each food type to the troop's annual and seasonal diet. We could not transform these habitat use data to normality, so we used Kruskal-Wallis tests with multiple comparisons of mean ranks (Zar 1999) to identify significant differences in the annual consumption of the

various food types, and used Mann-Whitney U tests to compare the seasonal consumption of food types.

We considered results with $p \leq 0.05$ as significant. All statistical tests were 2-tailed. We express all values as means \pm SEM.

Results

Study Area Use

The 86-km² study area (home range plus buffer) comprised urban habitat (42%), fynbos vegetation (37%), exotic plantations (11%), and vineyards (11%; Fig. 2). Surface water sources were present throughout the area. During the study period, the baboons used only 11.1% of the total study area, including 65% of the plantation area, 19% of the vineyard area, 3% of the urban area, and only 1% of the fynbos vegetation area. With the effects of altitude, gradient, and distance to water controlled, we found a negative correlation between cell use and the percentage cover of indigenous vegetation of the cell (Pearson $r = -0.34$, $p \leq 0.001$, $n = 3829$) and a positive correlation between cell use and the percentage cover of exotic vegetation of the cell ($r = 0.58$, $p \leq 0.001$, $n = 3829$). With the effects of habitat type, gradient, and distance to water controlled, we found a negative correlation between cell use

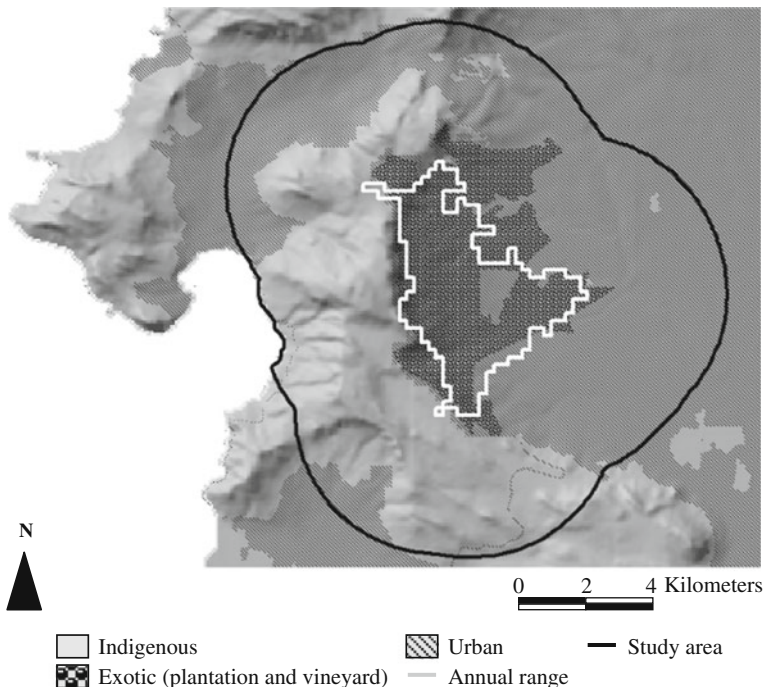


Fig. 2 Topography and broad-scale habitat composition of the study area, including the location of the TK troop's annual home range.

and the mean elevation of the cell ($r=-0.17$, $p\leq 0.001$, $n=3829$). With the effects of habitat type and altitude controlled, we found no correlation between cell use and the gradient of a cell ($r=-0.03$, $p=0.09$, $n=3829$) and cell use and the distance of a cell to water ($r=0.02$, $p=0.13$, $n=3829$).

Temperatures recorded at midday within the plantation (at 200 m, 260 m, and 325 m elevations) and within fynbos (430 m elevation) differed ($F_{3,336}=42.23$, $p\leq 0.001$); a *post hoc* Tukey comparison revealed that this effect is attributable mainly to temperature differences between the fynbos and the plantation ($MS_{336}=19.30$, $p\leq 0.001$). Mean midday temperatures in the fynbos ($20.45\pm 1.40^{\circ}\text{C}$, $n=85$; altitude=430 m) were higher ($U=4779.0$, $p\leq 0.001$) than in the plantation ($14.27\pm 0.70^{\circ}\text{C}$, $n=85$; altitude=200–325 m). Further, the daily range in temperature was greater ($U=3696.50$, $p\leq 0.001$) in the fynbos ($10.27\pm 0.38^{\circ}\text{C}$, $n=85$) than in the plantation ($3.60\pm 0.14^{\circ}\text{C}$, $n=85$).

Annual Range Use, Behavior, and Diet

The cumulative frequency of new cells entered by the troop per month reached an asymptote in the tenth month. The home range of the troop was 9.50 km^2 (Fig. 2), giving a baboon density in the home range of 12.1 baboons/ km^2 . The home range varied in altitude from 20 to 567 m, with a mean altitude of 176 ± 11 m. Habitat cover was dominated by exotic vegetation (91.2%) in the form of the plantation and the surrounding vineyards. The remainder of the home range included urban habitat (7.2%) and indigenous vegetation (1.7%). Enclosed cells that were not entered accounted for 12.2% of the home range (Fig. 3).

Spatial use of the home range was not uniform (Fig. 3), with standing plantation used significantly more than all other habitat types (Fig. 4), and indigenous vegetation used significantly less than all other habitat types (Kruskal-Wallis test: $H(4, n=6730)=1674.504$, $p\leq 0.001$). There were no other significant differences in habitat use (Table I). Of the GPS points recorded in the urban habitat, 68% were located within the urban habitat encompassed by the plantation, e.g., sports fields and school, while 32% were on the edge of the plantation within residential urban habitat. Baboon monitors actively discouraged baboons from entering the residential urban habitat and the vineyards. Both habitat types thus represent permeable barriers to baboon movement, and the proportion of use depends on the response of individual property owners to the presence of baboons. Not surprisingly, the urban periphery was the more secure boundary, with baboons intruding ≤ 334 m into this habitat type vs. 822 m into the vineyards. Clearly the extent of the vineyards made detection of the baboons more difficult, which accounts for a greater level of penetration into this habitat type.

The baboons used 66 of the home range cells as sleeping sites, a total area constituting 14% of the home range. Sleeping sites were widely spread throughout the home range instead of clustered in particular areas. They were all exotic trees (86% pine; 14% eucalyptus), of which 94% were located within the plantation, 3% within the urban habitat, and 3% within the vineyards.

The troop's mean daily travel distance was 2.93 km (± 0.27 km, $n=74$ d). Daily distance traveled correlates positively with day length (Pearson $r=0.41$, $p\leq 0.001$, $n=74$ d).

Fig. 3 Use of cells within the home range from March 2006 to February 2007. Percentage values are derived from the number of GPS points in each cell relative to the total number of GPS points collected. Cells with numbers in them are sleeping sites; the number indicates the number of nights the baboons slept there.

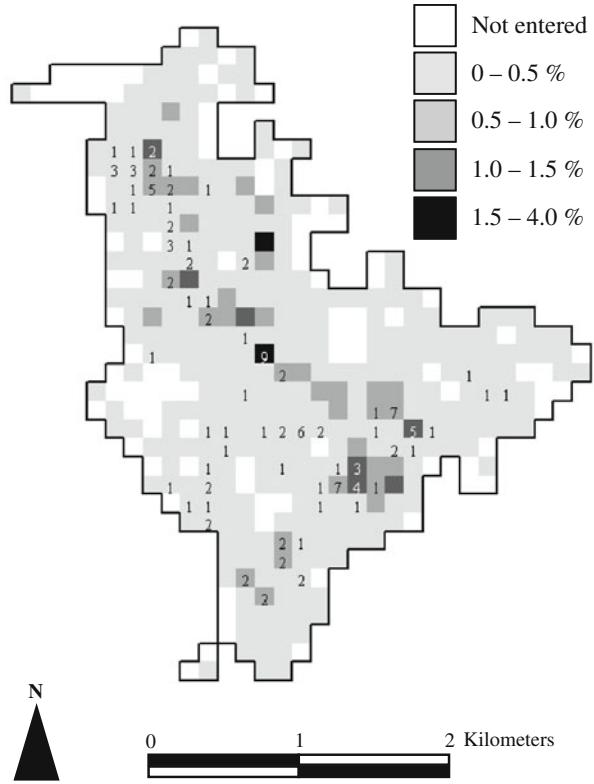


Fig. 4 Mean (\pm SEM) percentage of each habitat type used annually ($n=1732$ scans) and seasonally ($n=372$ scans/season). The dashed lines divide the habitats into groups that were used significantly differently on an annual basis. An asterisk indicates habitat types that were used significantly differently in winter and summer.

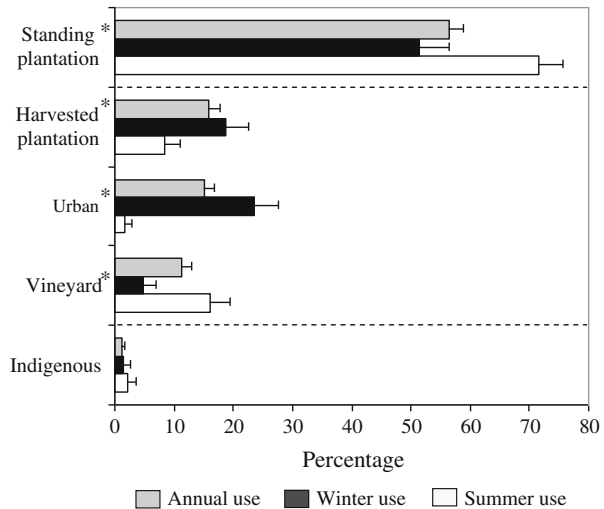


Table I z' and p values from a multiple comparison of mean ranks test after a Kruskal-Wallis ($H(4, n=6730)=1674.504, p=0.000$) indicating significant differences in the annual use of habitats

	SP		HP		UR		VI		IN	
	z'	p	z'	p	z'	p	z'	p	z'	p
SP	–	–	20.345	<0.001 ^a	21.170	<0.001 ^a	21.966	<0.001 ^a	27.985	<0.001 ^a
HP	20.345	<0.001 ^a	–	–	0.824	1.000	1.621	1.000	7.639	<0.001 ^a
UR	21.170	<0.001 ^a	0.824	1.000	–	–	0.796	1.000	6.815	<0.001 ^a
VI	21.966	<0.001 ^a	1.621	1.000	0.796	1.000	–	–	6.019	<0.001 ^a
IN	27.985	<0.001 ^a	7.639	<0.001 ^a	6.815	<0.001 ^a	6.019	<0.001 ^a	–	–

HP: harvested plantation; SP: standing plantation; IN: indigenous vegetation; UR: urban; VI: vineyard

^a Significant differences

Over the year, the troop spent 39.4% of its time foraging, 16.0% walking, 20.6% resting, and 24.2% socializing. The annual diet included roots and bulbs, unidentified items in soil, sand and leaf litter, grass, flowers, mushrooms, bark, leaves, fruits, pine nuts, and refuse. We found significant differences in the consumption of food items (Kruskal-Wallis test: $H(7, n=9056)=948.1369, p\leq 0.001$; Table II), with the most frequently consumed food items (>10% of items consumed; Fig. 5) being grasses (33.6%), unidentified items in soil (18.9%), and pine nuts (10.5%).

Seasonal Range Use, Behavior, and Diet

The baboons showed marked shifts in range use patterns across seasons (Fig. 2). They occupied a larger area in winter (4.19 km^2) than in summer (3.40 km^2), and the mean elevation in winter was significantly lower ($107\pm 6 \text{ m}$) than in summer ($227\pm 6 \text{ m}$; $t=-32.06, df=1398, p\leq 0.001$). On a daily basis, the troop used a smaller area in winter ($0.38\pm 0.01 \text{ km}^2$) than in summer ($0.68\pm 0.04 \text{ km}^2$; $t=15.33, df=32, p\leq 0.001$), but used a near equivalent number of sleeping sites during winter (15 cells) and summer (13 cells).

Summer area use correlates positively with the topographic variables of mean altitude ($r=0.18, p\leq 0.001, n=422$ cells) and slope ($r=0.11, p\leq 0.05, n=422$ cells) and negatively with distance to water ($r=-0.13, p\leq 0.001, n=422$ cells). Winter area use correlates negatively with mean altitude ($r=-0.17, p\leq 0.001, n=422$ cells) but does not correlate with either slope ($r=-0.08, p=0.08, n=422$ cells) or distance to water ($r=0.04, p=0.44, n=422$ cells). The baboons used standing plantations ($U=55043.0, p\leq 0.001$) and vineyards ($U=55555.0, p\leq 0.001$) significantly more in summer than in winter (Fig. 4), and used the urban habitat ($U=52503.0, p\leq 0.001$) and harvested plantations ($U=63085.5, p\leq 0.001$) significantly more in winter than in summer. They used indigenous vegetation similarly in both seasons ($U=68450.0, p=0.80$).

The troop traveled farther on summer days ($4.67\pm 0.65 \text{ km}$) than on winter days ($2.08\pm 0.53 \text{ km}$) ($t=7.7654, df=32, p\leq 0.001$), although hourly travel rate was similar ($t=1.9886, df=32, p=0.06$) for both seasons (summer: $0.46\pm 0.07 \text{ km/h}$; winter: $0.37\pm 0.10 \text{ km/h}$).

Table II z' and p values from a multiple comparison of mean ranks test after a Kruskal-Wallis ($H(7, n=9056)=948.1369, p=0.000$) indicating significant differences in the annual diet

	Grass		Items in soil		Pine nuts		Items in leaf litter		Leaves		Roots and bulbs		Fruits		Flowers	
	z'	p	z'	p	z'	p	z'	p	z'	p	z'	p	z'	p	z'	p
Grass	–	–	5.635	<0.001 ^a	10.860	<0.001 ^a	10.962	<0.001 ^a	12.961	<0.001 ^a	14.156	<0.001 ^a	16.614	<0.001 ^a	17.442	<0.001 ^a
Items in soil	5.635	<0.001 ^a	–	–	5.225	<0.001 ^a	5.327	<0.001 ^a	7.326	<0.001 ^a	8.521	<0.001 ^a	10.979	<0.001 ^a	11.807	<0.001 ^a
Pine nuts	10.860	<0.001 ^a	5.225	<0.001 ^a	–	–	0.102	1.000	2.101	0.999	3.296	0.028 ^a	5.754	<0.001 ^a	6.582	<0.001 ^a
Items in leaf litter	10.962	<0.001 ^a	5.327	<0.001 ^a	0.102	1.000	–	–	1.999	1.000	3.194	0.039 ^a	5.652	<0.001 ^a	6.480	<0.001 ^a
Leaves	12.961	<0.001 ^a	7.326	<0.001 ^a	2.101	0.999	1.999	1.000	–	–	1.195	1.000	3.653	0.007 ^a	4.481	<0.001 ^a
Roots and bulbs	14.156	<0.001 ^a	8.521	<0.001 ^a	3.296	0.028 ^a	3.194	0.039 ^a	1.195	1.000	–	–	2.458	0.391	3.286	0.028 ^a
Fruits	16.614	<0.001 ^a	10.979	<0.001 ^a	5.754	<0.001 ^a	5.652	<0.001 ^a	3.653	0.007 ^a	2.458	0.391	–	–	0.828	1.000
Flowers	17.442	<0.001 ^a	11.807	<0.001 ^a	6.582	<0.001 ^a	6.480	<0.001 ^a	4.481	<0.001 ^a	3.286	0.028 ^a	0.828	1.000	–	–

^a Significant differences

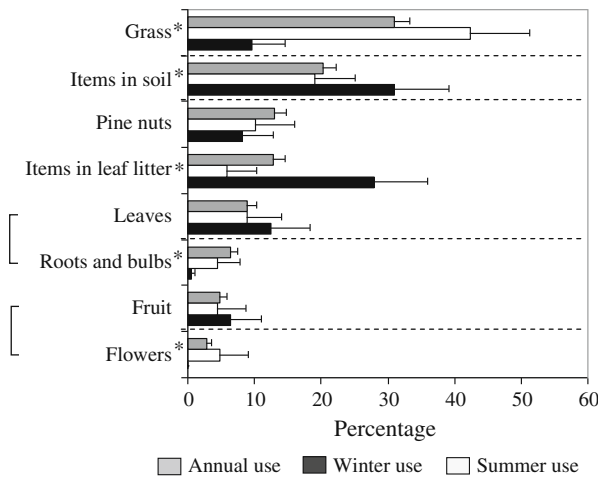


Fig. 5 Mean (\pm SEM) percentage of foraging records for each food type consumed annually ($n=1132$ scans) and seasonally ($n=372$ scans/season). We included only items that contributed $\geq 5\%$ to the diet. The dashed lines divide the food types into groups that were consumed differently on an annual basis. Connectors link food types that are not significantly different from each other despite their overall separation into different groups. An asterisk indicates food sources that were consumed significantly differently in winter and summer.

Time spent foraging was similar in winter (3.17 ± 0.65 h) and summer (3.15 ± 0.92 h). However, in the longer summer days, the troop walked (2.40 ± 0.62 h) and rested (2.33 ± 0.63 h) for more hours than they did in winter (walking: 0.78 ± 0.28 h, resting: 1.62 ± 0.36 h; $U=6.0$, $p \leq 0.001$ for walking, $U=41.0$, $p \leq 0.001$ for resting). The troop also socialized for more hours in summer (2.92 ± 0.72 h) than in winter (1.9 ± 0.37 h; $U=46.0$, $p \leq 0.001$).

Roots and bulbs made up $4.5 \pm 3.4\%$ of the troop’s diet in winter (Fig. 5), which is significantly higher ($U=2801.0$, $p \leq 0.05$) than the amount consumed in summer ($0.5 \pm 0.7\%$). Items in the leaf litter made up $6.0 \pm 4.5\%$ of the winter diet, which is significantly less than the $28.0 \pm 7.9\%$ that the food group contributed to the summer diet ($U=2006.0$, $p \leq 0.001$). Grasses made up nearly half of the troop’s winter diet ($42.4 \pm 9.0\%$), which is significantly higher than the consumption of this food group in summer ($10.9 \pm 4.9\%$; $U=1710.0$, $p \leq 0.001$). Flowers made up $4.8 \pm 4.4\%$ of the troop’s summer diet, which is significantly greater than in winter, when they were not consumed at all ($U=2923.0$, $p \leq 0.05$). There are no significant seasonal differences for pine nuts ($U=3009.0$, $p=0.55$), leaves ($U=2773.5$, $p=0.10$), or fruit ($U=2966.5$, $p=0.28$).

Discussion

The mean size of 61 troops in the eastern part of South Africa was 22 (Henzi and Lycett 1995), with troop sizes of 9–50 individuals reported for various locations in the western part of South Africa (Erasmus 1993; Hill *et al.* 2004). Troops in the Cape Peninsula follow a similar trend with a mean group size of 34 (± 16 , $n=12$ troops; E. K. Beamish, University of Cape Town, *unpubl. data*). The TK troop is

thus large ($n=115$), both locally and regionally, and more comparable in size to troops (109–128 individuals) in the fertile Okavango Delta in Botswana (Hamilton *et al.* 1976). The density of baboons in the home range, at 12.1 baboons/km², is also more comparable to the density of troops in the Okavango Delta (24 baboons/km²; Hamilton *et al.* 1976) than it is to various density estimates for troops in the Drakensberg, South Africa (0.9–2.7 baboons/km²; Henzi *et al.* 1992; Henzi and Lycett 1995; Whiten *et al.* 1987) and in the Kuiseb Canyon, Namibia (5.3 baboons/km²; Hamilton *et al.* 1976).

The TK troop used a very small portion (11.1%) of the total study area. Given that ≥ 3 neighboring troops were removed from this area in recent decades (E. K. Beamish, *pers. comm.*), the size and location of TK's home range does not appear to be influenced by either competition with other troops or a lack of access to indigenous vegetation. The TK troop does not use the steep slopes to the west, or cross the ridge top, or use the even steeper western slopes descending to the sea (Fig. 1). It exclusively uses most of the available lower slope, with a more gentle gradient, and plantation habitat and intrudes into peripheral vineyard cultivation and urban settlements in low-lying alluvial areas. The survival of the TK baboons relative to their neighbors is thus almost certainly a consequence of their having retained access to low-lying land that is spatially continuous, i.e., not bisected by major roads or urban habitat, with the traditional refugia and sleeping sites found on the steep slopes and high altitudes within the TMNP. It is possible that the mountainous spine that runs the length of the Cape Peninsula has never provided sufficient food resources to support a large continuous baboon population and thus baboons have always been reliant on access to low-lying land to obtain sufficient food. The lower slopes of the Tokai region have been transformed but fortunately the land-use practice of forestry does not preclude baboon presence. Further, on maturation the pine plantations offer both food (pine nuts) and sleeping sites and consequently the TK troop has not only persisted but appears to thrive in this human-modified environment.

The current home range attributes of the TK troop represent the baboons' selection of particular habitats within an already restricted range of key geophysical attributes. As resource scarcity limits primate group size (Altmann 1974; Anderson 1984; Barton *et al.* 1992; Hamilton and Tilson 1982) and increases home range size (Barton *et al.* 1992), the large size and high density of the TK troop suggests that the current home range is rich in the resources considered most important to baboons, i.e., sleeping sites (Altmann and Altmann 1970; Anderson 1984; DeVore and Hall 1965), food (Altmann 1998; Altmann and Altmann 1970; Barton *et al.* 1992; DeVore and Hall 1965), and water (Altmann 1998).

Resource location explained much of the variation in the intensity of home range use. The distribution and abundance of food sources—grasses, unidentified items in the soil and pine nuts—in the immediate vicinity of the Tokai plantation made it unnecessary for the baboons to venture far beyond its boundaries in search of food. On no occasion did the baboons use any habitat other than plantation trees as sleeping sites despite having access to a variety of traditional baboon sleeping sites such as caves and cliff-faces (Hamilton 1982). Previously, baboon troops in the Cape Peninsula were reported to sleep exclusively on cliff faces (Hall 1963); however, recent data indicate that, similar to the TK troop, troops that have access to both

cliffs and large exotic trees show a distinct preference for the latter as sleeping sites (van Doorn *et al.* 2010; T. S. Hoffman, University of Cape Town, *unpubl. data*). This trend provides support for the suggestion that the establishment of large trees within the home range of baboons may alter their preference for sleeping sites and thereby influence the shape and size of a troop's home range (Anderson 1984).

On average, the TK troop traveled 2.93 km/d. This distance is shorter than that recorded for other baboon troops in the Cape Peninsula (4.7 km; Hall 1962), as well as for other groups of chacma, yellow (*Papio cynocephalus*), olive (*Papio anubis*), and hamadryas (*Papio hamadryas*) baboons (8.0 km, 4.2 km, 6.4 km, 13.2 km, respectively; Altmann and Altmann 1970). The established link between day-journey length and the distribution of resources (Barton *et al.* 1992) suggests that the relatively short daily distances traveled by baboons in Tokai are indicative of a high concentration of critical resources within the home range. The spatial concentration of high-quality food resources in agricultural areas has a similar effect on the ranging patterns of baboons in Uganda (Hill 2005) and other primate species elsewhere (Brennan *et al.* 1985; Saj *et al.* 1999; Siemers 2000). In Sulawesi Tonkean macaques (*Macaca tonkeana*) living in human-modified environments, food availability predicts daily movement better than group size (Riley 2008). Because we studied a single troop, we could not determine the effects of group size on daily movement, but the short daily travel distances of the large TK troop relative to troops elsewhere support this notion.

The annual activity budget of the TK troop was similar to the activity budgets typical of baboon populations in the Western Cape, South Africa and populations elsewhere (Dunbar 1992; Hill *et al.* 2003; Swedell, *in press*). However, the TK troop does not exhibit the same reduction in time spent feeding as observed for provisioned baboon troops (Altmann and Muruthi 1988; Eley *et al.* 1989) and other provisioned primate species (Riley 2008; Singh and Vinathe 1990). The proportion of time that primates spend feeding is dependent on a number of factors including, but not limited to, the richness, spatial proximity, and processing time of food sources (Altmann 1974). Thus despite the spatial concentration of food sources that allow for a relatively small home range, the food sources in Tokai may not be associated with a handling time or ingestion time low enough to reduce the amount of time that the baboons allocate to foraging. Further research is required to test this hypothesis.

During the dry and warm summer months, the troop frequented the higher elevations of its home range more relative to the cool, wet winter months, both for daytime activity and sleeping sites. Seasonal changes in ranging patterns for chacma baboons in the Drakensberg Mountains in South Africa (Whiten *et al.* 1987) are believed to occur in response to nutritional bottlenecks and the thermoregulatory stresses of higher altitudes (Whiten *et al.* 1987). Seasonal shifts in range extent and location have also been observed in response to changes in the distribution of water sources (Altmann and Altmann 1970). Altitudinal similarities in temperature within the plantation make it unlikely that the seasonal shift of the TK troop is associated with the same degree of thermoregulatory stress experienced by chacmas in the Drakensberg Mountains (Whiten *et al.* 1987) and De Hoop Nature Reserve (Hill *et al.* 2003). Further, the year-round availability of drinking water in the study area suggests that water sources are an improbable cause of vertical movement. Only

0.3% of behavioral observations indicated that drinking was taking place, and none of these records involved drinking sessions (*sensu* Altmann and Altmann 1970) wherein many baboons converge at a waterhole and drink simultaneously. Rather, individual baboons drank infrequently on an opportunistic basis at streams, rain puddles, and even swimming pools in urban habitat.

What did appear to drive the seasonal altitudinal shift was the onset of winter rainfall in May 2006, resulting in the emergence of annual grasses (Milton 2004) predominantly in exposed, i.e., not under the plantation canopy, and transformed, e.g., urban edge and sports fields, areas at lower altitudes. The appearance of these annuals coincided with the movement of the troop to lower altitudes and a significant dietary shift toward grasses and roots and bulbs. In contrast, during summer, the baboons used standing plantation plots and vineyards significantly more than in winter, and focused their foraging efforts on the extraction of items in the leaf litter and in soil. The lack of significant seasonal difference in time spent foraging suggests that regardless of items consumed, the baboons require similar amounts of time to satisfy their nutritional requirements within both seasons. The significant increase in socializing, resting, and walking in summer vs. winter may simply reflect the significantly longer day length compared to winter (Hill *et al.* 2003).

The total area used by the troop during winter was greater than during summer. As primate home ranges may increase in size in response to food scarcity (Clutton-Brock 1977), the seasonal size discrepancy suggests that food resources are scarcer during winter than summer. Further, in winter the increased reliance on fallback foods such as grasses that are readily available in the environment but are nutritionally poor (Wrangham *et al.* 1998), in addition to subterranean food items that have increased exploitation costs but yield highly nutritious returns (Byrne *et al.* 1993, Hill and Dunbar 2002; Whiten *et al.* 1987), suggests that winter may be the season of relative food scarcity in the Tokai region.

In summary, human-induced habitat change, within and immediately adjacent to the TMNP, has had a significant impact on the group size, density, home range size, travel distances, range use, and foraging patterns of the TK troop. The small home range of the TK troop in addition to the almost complete avoidance of the steep slopes and cliffs at higher elevations suggests that the combination of abundant sleeping sites at lower elevations and in close proximity to preferred food items may explain the short daily path length, low overall travel time, and hence the unusually small home range for such a large troop.

A generalization that appears true for most mammals on the Cape Peninsula is that the low abundance of individuals in the indigenous fynbos vegetation (Cowling *et al.* 1996; Wright 1988) is attributed to the low forage quality. The greatly reduced home range and large troop size of the TK troop serves to highlight how anthropogenic habitat alteration can have a positive feedback on the density of native fauna, presumably as a consequence of higher above-ground plant biomass. Further, the almost complete avoidance of indigenous vegetation suggests that the ecological role of baboons within the TMNP may be greatly diminished and will remain minimal as long as baboons have access to exotic vegetation with higher productivity at low elevations.

The Tokai Plantation is to be commercially harvested over the next 15 yr, and felled areas are to be restored to indigenous vegetation (Table Mountain National

Park 2009). This change in land cover will have a direct bearing on the abundance and concentration of food and sleeping site resources within the TK troop's home range. Given the baboons' selection of exotic vegetation, it is likely that large-scale tree harvesting will affect the spatial ecology of the troop as they actively track remaining pockets of plantation. Of primary concern is a shift of home range into the urban habitat that contains large numbers of desirable woody exotics, including fruit trees. It is highly plausible that the troop will preferentially target this resource over the high-lying indigenous vegetation and thus set the stage for large-scale human–baboon conflict. Such conflict, in conjunction with a reduced carrying capacity of the land during the restoration process, may result in a decrease in growth rate of the troop or a division of the troop into smaller units.

Our results suggest that ecologically flexible primates such as chacma baboons are not only capable of adapting to broad scale human habitat transformation but may also benefit from an increase in the availability of sleeping sites and above-ground plant biomass that are associated with the planting of exotic vegetation. Adapting to novel resources may have a marked effect on the spatial ecology of primates, but their ultimate survival and persistence within a human-modified environment appears to be largely contingent upon the type of land use, e.g., urban vs. plantation, and whether they retain access to adequate tracts of low-lying land to provide a sufficient resource base of either indigenous or exotic vegetation.

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