

RESEARCH ARTICLE

Troop Size and Human-Modified Habitat Affect the Ranging Patterns of a Chacma Baboon Population in the Cape Peninsula, South Africa

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Differences in group size and habitat use are frequently used to explain the extensive variability in ranging patterns found across the primate order. However, with few exceptions, our understanding of primate ranging patterns stems from studies of single groups and both intra- and inter-specific meta-analyses. Studies with many groups and those that incorporate whole populations are rare but important for testing socioecological theory in primates. We quantify the ranging patterns of nine chacma baboon troops in a single population and use Spearman rank correlations and generalized linear mixed models to analyze the effects of troop size and human-modified habitat (a proxy for good quality habitat) on home range size, density (individuals/km²), and daily path length. Intrapopulation variation in home range sizes (1.5–37.7 km²), densities (1.3–12.1 baboons/km²), and daily path lengths (1.80–6.61 km) was so vast that values were comparable to those of baboons inhabiting the climatic extremes of their current distribution. Both troop size and human-modified habitat had an effect on ranging patterns. Larger troops had larger home ranges and longer daily path lengths, while troops that spent more time in human-modified habitat had shorter daily path lengths. We found no effect of human-modified habitat on home range size or density. These results held when we controlled for the effects of both a single large outlier troop living exclusively in human-modified habitat and baboon monitors on our spatial variables. Our findings confirm the ability of baboons, as behaviorally adaptable dietary generalists, to not only survive but also to thrive in human-modified habitats with adjustments to their ranging patterns in accordance with current theory. Our findings also caution that studies focused on only a small sample of groups within a population of adaptable and generalist primate species may underestimate the variability in their respective localities. *Am. J. Primatol.* 74:853–863, 2012. © 2012 Wiley Periodicals, Inc.

Key words: chacma baboon; troop size; human-modified habitat; intrapopulation variation; primate ranging patterns

INTRODUCTION

Differences in group size [e.g. Barton et al., 1992; Ganas & Robbins, 2005] and habitat use [e.g. Izumiya et al., 2003; Riley, 2008; Takasaki, 1981] are associated with extensive variation in ranging patterns across the primate order [Chapman & Chapman, 2000; Clutton-Brock & Harvey, 1977; De Luca et al., 2009; Mitani & Rodman, 1979]. As primate group sizes increase, so intragroup feeding competition increases [Isbell, 1991; Isbell & Young, 1993; Wrangham et al., 1993], forcing larger groups to cover larger areas as the individual group members strive to obtain enough food [Chapman et al., 1995; Janson & Goldsmith, 1995; Milton, 1984]. Therefore, if other variables are controlled (e.g. habitat), an increase in group size should result in a corresponding increase in daily path length [DPL] and home range size [Chapman & Chapman, 2000], as reported for several taxa [*Theropithecus gelada*: Iwamoto & Dun-

bar, 1983; *Procolobus badius*: Gillespie & Chapman, 2001; *Presbytis thomasi*: Steenbeck & van Schaik, 2001; *Brachyteles arachnoides hypoxanthus*: Dias & Strier, 2003, home range size only; *Gorilla gorilla beringei*: Ganas & Robbins, 2005; McNeilage, 1995; Watts, 1991, 1998].

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Primate ranging patterns also reflect habitat characteristics, including food availability and distribution [Barton et al., 1992; Clutton-Brock, 1975; Ganas & Robbins, 2005; Riley, 2008], water availability [Altmann & Altmann, 1970; Chapman, 1988], and sleeping-site location [Crook & Aldrich-Blake, 1968; Whiten et al., 1987; Zhou et al., 2007]. Where food resources are widely dispersed and unpredictably available, primates must travel far and cover large areas to meet their nutritional requirements [Ganas & Robbins, 2005; Li et al., 2005; Wieczkowski, 2005]. Conversely, when food resources are concentrated and predictably available, like those in some human-modified habitats (e.g. agricultural and urban habitat), primates may exhibit reductions in home range size and DPL [Saj et al., 1999; Hoffman & O’Riain, 2010] and disproportionate range use [Hill, 2005; Hoffman & O’Riain, 2010; Riley, 2008], even though group size [Fuentes et al., 2005; Hoffman & O’Riain, 2010] and density [Brennan et al., 1985; Hoffman & O’Riain, 2010] increase. Such changes to ranging patterns and demography are most prevalent in species (e.g. baboons, genus *Papio*) that are behaviorally adaptable and dietary generalists [Swedell, 2011].

Determining the relative effects of group size and habitat characteristics on primate ranging patterns can be difficult given that their influences, and the relationships among them, are complex [Robbins & McNeillage, 2003; Strier, 1987; Watts, 1998] and dynamic [Riley, 2008]. Ideally, studies aiming to discern such effects would be conducted on a large sample of groups within a single population and occupying comparable ecological conditions [Majolo et al., 2008]. However, with few exceptions [Butynski, 1990; Hamilton et al., 1976; Henzi et al., 1997; Takasaki, 1981] our understanding of primate ranging patterns stems from studies of single groups [Strier, 2007] and both intra- and inter-specific meta-analyses [e.g. Bettridge et al., 2010; Majolo et al., 2008]. Studies with large sample sizes of groups or those that incorporate whole populations remain rare [Bronikowski & Altmann, 1996] but important for testing socioecological theory in primates. Here, we provide such a study.

We investigated the effects of troop size and human-modified habitat on the ranging patterns of chacma baboon groups (*Papio ursinus*) in a single, geographically discrete population. Our study site in the Cape Peninsula, South Africa, offered a useful setting for assessing the effects of troop size on ranging patterns as it contained multiple troops ranging in size from 16 to 115 individuals [Beamish, 2010]. While troop sizes varied considerably, they fell within the species’ range from multiple sites [Swedell, 2011] and did not exceed the maximum ecologically tolerable size based on the mean annual rainfall and mean annual temperature of the study area [Dunbar, 1992]. Our study site also offered

an ideal setting for assessing how human-modified habitat influences ranging patterns as 37% of the Cape Peninsula landscape was transformed by human habitat modification [Richardson et al., 1996]. Along with natural habitat (fynbos vegetation), local troops had various levels of access to three types of human-modified habitats—agricultural habitat, urban habitat, and invasive alien vegetation—all of which are known to affect baboon ranging patterns locally [Hoffman & O’Riain, 2010] and elsewhere across their distribution [Hill, 2005; Strum, 2010]. Furthermore, because all troops lived within one degree of latitude and longitude they were exposed to similar climatic conditions [Cowling et al., 1996] and we could assume negligible effects of variation in day length, temperature, and rainfall. Finally, no natural baboon predators occurred in the Cape Peninsula. While nonnatural predators (humans and domestic dogs) did occur locally, hunting in the Cape Peninsula was illegal [Western Cape Province, 1999, Proclamation no. 50/1998 for the hunting seasons, daily bag limits and hunting by the use of prohibited hunting methods.] and therefore attacks on baboons were rare [Beamish, 2010]. Thus, we consider that all troops experienced similarly low levels of predation risk.

We determined home range sizes, densities, and DPLs of nine of the 12 troops present in the Cape Peninsula and quantified their use of natural and human-modified habitat. We investigated whether ranging patterns were influenced by troop size (H1) and predicted, given the extensive heterogeneity in local habitat conditions, that the effect of habitat on baboon ranging patterns would be so great that this population would not exhibit the usually expected relationships between troop size and home range size or troop size and DPL [Chapman & Chapman, 2000]. We also investigated whether ranging patterns were influenced by the human-induced habitat changes that have introduced high quality food into an otherwise nutrient-poor natural environment [H2; Bigalke, 1979; Simmons & Cowling, 1996]. We predicted that troops with greater access to human-modified habitats would have smaller home ranges [Saj et al., 1999], higher densities [Brennan et al., 1985], and shorter DPLs [Saj et al., 1999] than troops occupying natural habitat, irrespective of troop size.

METHODS

Study Site

The Cape Peninsula is the southwestern most point of the African continent, in the Western Cape Province of South Africa (Fig. 1). It covers 470 km² and comprises natural and human-modified habitats bounded by the Atlantic Ocean. With an altitudinal range from sea level to 1,100 m, the topography is characterized by the Peninsula Mountain chain

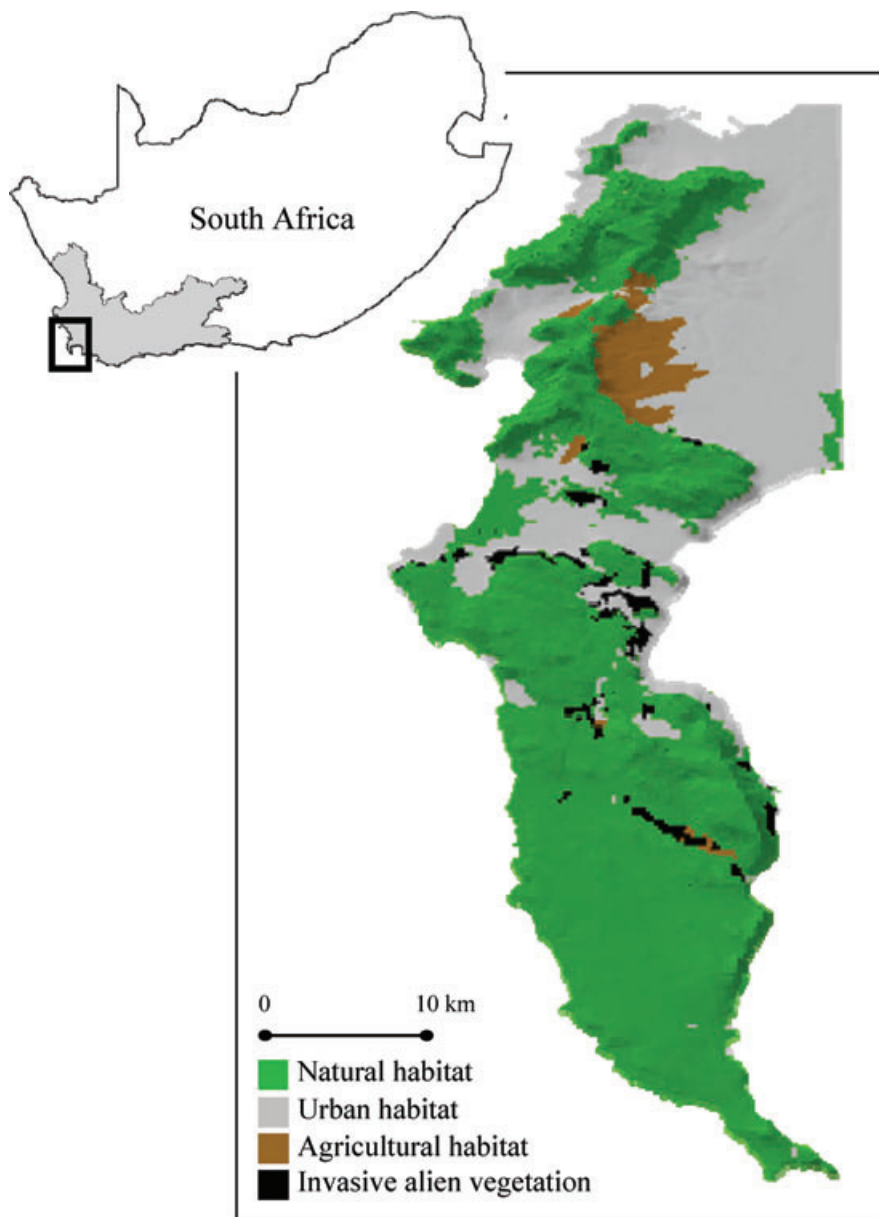


Fig. 1. A map of South Africa (inset) with the black block indicating the location of the Cape Peninsula in the Western Cape Province (shaded grey). The larger map shows the habitat types of the Cape Peninsula.

stretching from Table Mountain in the north to Cape Point in the south. The climate is Mediterranean, with winter characterized by cool, wet conditions, and short day lengths, and summer characterized by hot, dry conditions, and long day lengths. This climatic pattern results in higher primary production in winter relative to summer [Cowling et al., 1996]. The fauna is characterized by moderate species diversity but low endemism and numbers [Picker & Samways, 1996] and chacma baboons are the only nonhuman primates.

More than half of the Cape Peninsula is undeveloped and has conservation status under the protection of the Table Mountain National Park (TMNP).

The lower elevations are predominantly urbanized, some of the midelevations 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 [Bigalke, 1979; Simmons & Cowling, 1996], sclerophyllous shrubland that is a key component of the Cape Floristic Region [Cowling et al., 1996]. With such heterogeneity of habitat cover, the Cape Peninsula offers baboons diverse natural and anthropogenic food sources. Natural food sources include fynbos plant matter and marine organisms (e.g. mussels, limpets, and shark eggs) that occur along the coastline. Anthropogenic food

sources include items in invasive alien vegetation (e.g. seeds from *Pinus* and *Acacia spp.*), agricultural habitat (e.g. grapes in vineyards, pine nuts in *Pinus* plantations, ostrich feed in livestock farms), urban habitat (e.g. fruit trees in gardens, garbage in refuse bins, food items in houses), and food sources associated with visitors to the TMNP (e.g. items from backpacks, picnics, and motor vehicles).

Study Animals

At the onset of data collection the Cape Peninsula baboon population comprised 12 troops [Beamish, 2010] ranging in size from 16 to 115 baboons. The troops ranged freely in approximately 250 km² of natural habitat, with urban habitat and neighboring troops serving as the only major barriers to movement. All troops interacted with humans to some degree (Table I) and were therefore habituated to close (≤ 10 m from baboons) behavioral observations when the study began. All but one troop (KK) raided anthropogenic food sources, but because of financial constraints, only four of the eight raiding troops were managed by baboon monitors (Table I). Monitors are employed by the local management authorities to reduce the frequency with which baboons access residences and gardens within urban habitat [Kansky & Gaynor, 1998; van Doorn, 2009]. Monitor teams typically comprise two men who use whistling, shouting, and hand clapping to deter and discourage baboons raiding in urban habitat [van Doorn, 2009]. Monitors do not influence baboon ranging patterns in other habitat types.

Spatial Data Collection

To determine baboon ranging patterns, we recorded Global Positioning System (GPS) data points for each troop. Physical limitations imposed by landscape (e.g. impassable mountain terrain and impenetrable vegetation) and threats to personal

safety (e.g. muggings in TMNP) prevented us from following certain troops on foot and necessitated the use of GPS tracking collars (Table II). However, park management restricted the use of tracking collars to four groups only. We collected GPS points for five troops using handheld devices (Garmin eTrex; Table II), for three troops using tracking collars and for one troop (CP) using both methods. Of the four baboons collared, two were adult females and two were young subadult males [Altmann, 1980]. The two adult females were not visibly pregnant, lactating, or weaning an offspring when we collared them. However, both conceived, delivered, and weaned offspring while collared. We removed collars only after their infants were fully weaned. The other two collars remained in place for at least 1 year. We collected data for seven troops between March 2006 and August 2009, while data for DG and PR were collected during 2004 and 2005 by van Doorn [2009; Table II].

Directly observed groups were followed by a field team (T. Hoffman along with 27 medium-term [2 months to 1 year] assistants and 13 short-term [< 1 month] assistants), which recorded the GPS location of the visually estimated troop center point (geometric center) at 20-min intervals between sunrise and sunset for an average of 109 days (± 28 days SE, range: 71–170 days, $N = 6$ troops; Table II) per troop. All assistants had at least one full day of training in data collection protocols before they recorded GPS data points. Further, T. Hoffman supervised all assistants on a daily basis to ensure that they adhered strictly to the data collection protocols. The terrain within the home ranges of observed troops was easily traversable on foot and visibility of baboons within all habitat types was excellent.

For troops whose ranging was monitored with tracking collars, we recorded GPS points at 3 hourly intervals between sunrise and sunset for an average of 302 days (± 54 days SE, range: 247–334 days, $N = 3$ troops; Table II) per troop. For DPL estimates, which occurred on a subset of these days, we remotely

TABLE I. Human Interactions, Raiding Behavior, and Management of Each Study Troop by Baboon Monitors

Troop	Human interactions	Raiding behavior	Baboon monitors	Data collection days with baboon monitors present
TK	F, U	B, C	Winter	17%
KK	T, U	—	—	—
PR	F, T, U	B, C	—	—
DG	U	B, H, U	Annual	100%
SWB	T, U	B, H, U	—	—
SK	U	B, H, U	Annual	96%
CP	T	B, H, U	Annual	100%
RH	U	B, H, U	—	—
BB	T	B, H, U	—	—

Troops are listed in descending order of troop size.

Human interactions: F, Farmers; T, Tourists; U, Urban residents.

Raiding categories: B, Bins; C, Crops; H, Humans; U, Urban (includes residential properties and restaurants).

TABLE II. Details of the Data Collection Processes Carried Out for Each Study Troop

Troop	Study period	Data collection days ^a								Total days	GPS locations recorded	Data collection method
		Summer Dec–Feb		Autumn Mar–May		Winter Jun–Aug		Spring Sep–Nov				
		Full	Part	Full	Part	Full	Part	Full	Part			
TK	2006–2007	15	17	16	18	24	32	15	—	137	2990	Field researchers
KK	2007–2008	13	1	—	—	45	—	31	1	91	2543	Field researchers
PR	2004–2005	21	10	26	18	36	41	15	3	170	5018	Field researchers
DG	2004–2005	24	2	23	24	13	32	6	10	134	4307	Field researchers
SWB	2008–2009	12	77	—	91	14	38	—	92	324	1907	Collar
SK	2008–2009	15	70	—	91	15	53	—	90	334	2021	Collar
CP	2007–2008	18	58	—	91	13	60	—	90	330	2282	Field researchers and collar
RH	2008–2009	14	74	—	27	15	38	—	79	247	1668	Collar
BB	2007–2008	24	5	24	4	11	3	—	—	71	1882	Field researchers

Details include Study Period; Number of Data Collection Days; Number of GPS Locations Recorded, and Data Collection Methods. Troops are listed in descending order of troop size.

^aFull = days where troops were tracked from sunrise to sunset with GPS data points recorded every 20 min; Part = days where troops were not tracked from sunrise to sunset or when GPS data points were recorded at 3 hourly intervals.

altered the sampling frequency of the tracking collars to 20-min intervals, which matched the frequency of sampling by researchers using handheld GPS devices. The 20-min sampling interval was maintained for an average of 14 days (± 1 day SE, range: 12–15 days, $N = 3$ troops) during summer and 14 days during winter. In total we recorded 24,618 GPS points for the population, with an average \pm SE of $2,735 \pm 768$ GPS points per troop (range: 1,668–5,018, $N = 9$ troops; Table II). To compare the two data collection methods (observational data recorded by field researchers vs. data recorded by tracking collars), we compared how they estimated (1) home range size and habitat composition and (2) DPL. For (1) we compared 4 months of observational data with 12 months of collar data recorded for the CP troop, and found <5% difference in the home range sizes calculated from the observational vs. collar data, and <0.01% difference in the estimated habitat composition of the home range (see Spatial data analysis for methods). To compare the two methods' estimates of DPL (2), we took advantage of group-follow data from a separate short-term study of SK troop: we compared 14 days on which our collar and a researcher from the separate study [T. Quayle, unpublished data, under the protection of a security guard] recorded GPS readings simultaneously at hourly intervals. We used the data from the separate study for method comparisons only, and did not include them in any ranging pattern determinations. The two methods yielded indistinguishable measures of DPL (paired t -test: $t = 0.42$, $N = 14$ days, two-tailed $P = 0.679$). These analyses suggest that data collected using the two methods produced comparable ranging estimates.

To determine the size of each study troop, we analyzed demographic data (counts of all individuals including infants) collected twice annually as part of a separate and ongoing census project [Beamish, 2010; E. K. Beamish, unpublished data]. During each census, Beamish repeatedly counted the number of individuals in a given troop on consecutive days until she obtained maximal counts that were consistent for at least three consecutive days. We calculated mean troop size (Table III) by averaging the semiannual counts recorded for each troop during its respective data collection period (Table II).

The research complied with protocols approved by the ethics committees of the University of Cape Town, South African National Parks, and the Society for the Prevention of Cruelty to Animals, adhered to South African legal requirements and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

Spatial Data Analysis

We imported all GPS points of troop locations into ArcView 3.3 and projected them in Transverse Mercator, spheroid WGS84, central meridian 19. We analyzed 24,618 GPS points with an accuracy of ≤ 10 m. We generated troop home ranges using the quadrat method [e.g. Henzi et al., 1992; Riley, 2008; Whiten et al., 1987], analyzing GPS points within a grid of cells that spanned the full extent of the Cape Peninsula [details in Hoffman & O'Riain, 2012]. All inland cells covered a 0.02 km^2 area ($150 \text{ m} \times 150 \text{ m}$), while coastal cells, which were clipped to the coastline of the Cape Peninsula to prevent their boundaries from extending into the ocean, had areas less

TABLE III. Details of Troop Sizes, Home Ranges, and Mean Daily Path Lengths

Troop	Size	Home range					Mean daily path length (\pm SE)
		Area	Density	% cells not entered	% cover of human-modified habitat ^a	% use of human-modified habitat cells ^a	
TK*	115	9.50 km ²	12.1/km ²	12.60	98.82	99.93	2.96 \pm 0.28
KK	49	37.65 km ²	1.3/km ²	54.70	0.35	1.99	5.64 \pm 0.54
PR	36	9.05 km ²	4.0/km ²	20.90	18.91	48.32	4.85 \pm 0.28
DG*	35	10.58 km ²	3.3/km ²	20.00	28.51	46.57	4.13 \pm 0.33
SWB	26	9.26 km ²	2.8/km ²	20.50	36.53	34.60	3.17 \pm 0.55
SK*	24	8.28 km ²	2.9/km ²	25.80	28.80	43.33	2.89 \pm 0.53
CP*	22	7.46 km ²	2.9/km ²	19.90	1.01	1.99	6.61 \pm 0.74
RH	16	1.54 km ²	10.4/km ²	10.10	24.64	18.91	1.80 \pm 0.21
BB	16	5.63 km ²	2.8/km ²	32.80	3.40	29.50	3.92 \pm 0.28

Home ranges are calculated using the quadrat method. All inland home range cells covered a 0.02 km² area (150 m \times 150 m), while coastal cells, which were clipped to the coastline of the Cape Peninsula so as to prevent their boundaries from extending into the ocean, had areas <0.02 km². Home range areas were calculated as the sum of all the cell areas within it. *Indicates troops managed by baboon monitors. Troops are listed in descending order of troop size.

^aThe remaining % cover and % use is assigned to natural habitat.

than 0.02 km². We selected the quadrat method over other home range methods (e.g. minimum convex polygons, kernel density estimates) as it allowed us to analyze our data at a scale relevant to the habitat conditions of our study area, and to account for the effects of troop spread [Hoffman & O’Riain, 2010]. We continued to collect data for each troop until either the number of new cells entered per month reached an asymptote ($N = 8$ troops) or until we had collected a full year of data ($N = 1$ troop). We recognized an asymptote when the number of new cells entered per month increased by less than 5% for 2 months or more (Fig. S1). We calculated the total size of each home range by summing the areas of all home range cells. For each troop, we divided the mean troop size by its respective home range area to determine the number of individuals per km² of home range (density).

For each home range, we calculated the total cover (km²) of natural and human-modified habitat and converted those values to percentages based on the home range area. We also analyzed patterns of habitat use by each troop. To perform these analyses we used GIS maps [map details in Hoffman & O’Riain, 2010] containing landscape information specific to the Cape Peninsula to categorize the habitat of each grid cell. We verified these habitat categorizations using observer records of location-specific habitats, and information gleaned from Google Earth imagery. We used 2009 Google Earth imagery coinciding with our final data collection year. We categorized cell habitat as natural or human modified, where natural habitat included indigenous vegetation, rocky shores and beaches, and human-modified habitat included urban habitat, agricultural habitat, or invasive alien vegetation. We calculated the per-

centage cover of natural and human-modified habitat within every cell using the intersect function of the Geoprocessing Wizard in ArcView 3.3. We converted the percentage values to categorical variables, assigning habitat categories based on the dominant habitat (>50% of cover) within each cell. Where this rule was not met (<3% of all grid cells), we assigned the habitat category of the habitat type covering the largest area within the cell, irrespective of its overall percentage value. For each home range, we calculated the total number of GPS points recorded in cells categorized as natural habitat and cells categorized as human-modified habitat. To allow for meaningful inter-group comparisons we converted these numbers to percentages of GPS points for each troop.

We determined DPLs for all troops from full-day journeys only [Altmann & Altmann, 1970; $N = 498$ DPLs; Table II], using the Nearest_features extension to ArcView [Jenness, 2004]. For each GPS data point included in each DPL, we assigned a habitat category (natural or human modified) according to the cell in which it occurred. We used these categorizations to calculate a % use of human-modified habitat for each DPL. Finally, for each troop, we averaged the DPLs to determine a mean annual DPL for that troop.

Effects of Troop Size (H1) and Human-Modified Habitat (H2) on Baboon Ranging Patterns

With a sample size of nine troops our first tests of the predications of H1 (the effect of troop size on ranging patterns) and H2 (the effect of habitat on ranging patterns) were limited to univariate analyses. We used Spearman rank correlations to test for

significant relationships between home range size and troop size, home range size and % use of human-modified habitat, and density and % use of human-modified habitat. We repeated these correlation tests three times to investigate whether our results remained consistent when we included all troops in the analyses (Test 1; $N = 9$ troops), when we excluded a troop outlier (TK) from the analyses (Test 2; $N = 8$ troops), and when we excluded from the analyses three troops (SK, DG, CP) that were monitored by baboon monitors on more than 95% of data collection days (Test 3; $N = 6$ troops; Table I). For all correlations, we used the Hochberg–Benjamini false discovery rate (FDR) correction to adjust the P -values for multiple tests [Benjamini & Hochberg, 1995].

We used two generalized linear mixed models (GLMM), implemented in GenStat [13th edition; Payne et al., 2010], to analyze the effects of troop size and human-modified habitat on DPL. The first GLMM (Model 1) included all nine troops ($N = 498$ DPLs). In the second GLMM (Model 2), we excluded the three troops (SK, DG, CP) that were monitored on more than 95% of data collection days ($N = 371$ DPLs; Table I) to test whether baboon monitors were significantly influencing our model results. For both models we set troop size and % use of human-modified habitat as fixed effects and, because troop DPLs were collected in different years (Table II), included year as a random effect.

RESULTS

Home ranges of the nine troops varied dramatically in size from 1.5 to 37.7 km² with a mean size of 11.0 km² (± 6.8 km²; Table III; Fig. 2). Cells that were enclosed within the home ranges but were not entered accounted for 10.1–54.7% of home ranges with a mean of 24.2% ($\pm 8.7\%$). Densities varied from 1.3 to 12.1 baboons/km² with a mean density of 4.7 baboons/km² (± 2.5 baboons/km²). One troop (TK) was geographically isolated from all other troops by urban development, while the mean percentage overlap of all other troop home ranges was 7.3% ($\pm 4.9\%$, $N = 6$ pairs). During our research, we observed temporal overlap (i.e. troop interactions) between three pairs of troops (KK and BB; KK and CP; BB and CP), but on only one occasion per pair. Thus while neighboring troops almost certainly influence one another, direct interactions are rare.

Home ranges varied in their habitat compositions (Table III). Natural habitat was present in all home ranges covering 1.2–99.7% of the areas, with a mean cover of 73.3% ($\pm 19.7\%$). Human-modified habitat was also present in all home ranges covering 0.3–99.8% of the areas, with a mean cover of 26.8% ($\pm 19.7\%$). Troops differed in their use of natural and human-modified habitats, spending between 0.1% and 98.0% of their time in natural habitat (mean

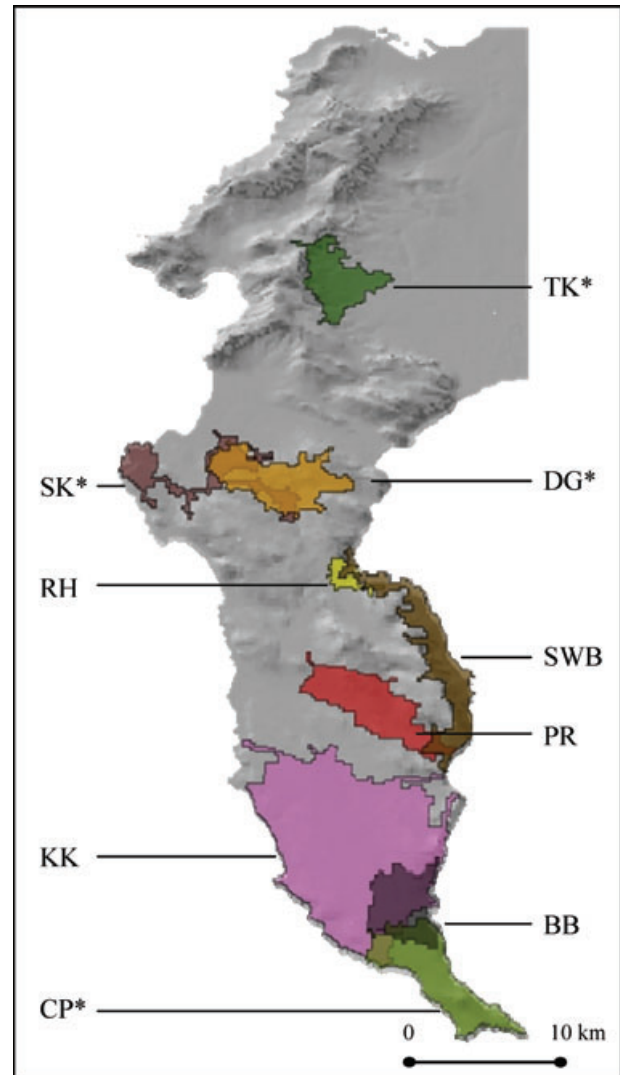


Fig. 2. A map of the Cape Peninsula showing the home ranges of the nine troops in this study. Monitored troop are marked with an asterisk.

use: $63.9 \pm 19.4\%$; Table III) and between 2.0% and 99.9% of their time in human-modified habitat (mean use: $36.1 \pm 19.4\%$). DPLs varied from 1.80 to 6.61 km (mean: 4.00 ± 0.98 km, $N = 9$ troops; Table III) and differed significantly among troops ($F = 1333.02$, $df = 497$, $P \leq 0.001$; Table S1).

Effects of Troop Size (H1) and Human-Modified Habitat (H2) on Baboon Ranging Patterns

Home range size correlated positively with troop size (Table IV). This relationship held when we excluded from the correlation analyses TK (a troop outlier; Test 2; Table IV), and the three troops that were monitored annually (Test 3). Troop size also had a significant positive effect on DPL (Model 1; Table V)

TABLE IV. Results of Spearman Rank Correlations Testing for Significant Relationships Between Home Range Size, Troop Size, and Human-Modified Habitat

Correlation tests	Test 1 (All troops)			Test 2 (TK excl.)			Test 3 (SK, DG, CP excl)		
	r_s	Adjusted P	N	r_s	Adjusted P	N	r_s	Adjusted P	N
Home range size vs. Troop size	0.88	0.008	Nine troops	0.92	0.017	Eight troops	0.87	0.024	6 troops
Home range size vs. % use of human-modified habitat	0.28	0.153	Nine troops	0.20	0.419	Eight troops	0.01	0.872	6 troops
Density vs. % use of human-modified habitat	0.49	0.122	Nine troops	0.27	0.526	Eight troops	0.75	0.028	6 troops

All troops are included in the first analysis (Test 1); TK is excluded from the second analysis (Test 2); SK, DG, and CP (troops monitored on >95% of data collection days) are excluded from the third analysis (Test 3). To correct for multiple testing P -Values have been adjusted using the HochbergBenjamini false discovery rate. Statistical tests are two-tailed; bold values indicate significant differences at $P \leq 0.05$.

TABLE V. Results of the GLMMs Used to Investigate the Effects of Troop Size and Human-Modified Habitat on Daily Path Length

Model	Fixed effect	Estimate	SE	Wald	P
1: all troops	Troop size	0.03	0.01	4.30	0.039
	% use of human-modified habitat	-0.01	0.004	13.98	<0.001
	Constant	3.74	8.30		
2: unmonitored troops only (SK, DG, CP excl.)	Troop size	0.04	0.01	26.00	<0.001
	% use of human-modified habitat	-0.01	0.01	14.51	<0.001
	Constant	3.78	1.96		

Model 1 includes DPL data from all troops (nine troops, 498 DPLs); Model 2 Includes DPL data from unmonitored troops only (six troops, 371 DPLs). Year has been included as a random term in both models. Statistical tests are two-tailed; bold values indicate significant differences at $P \leq 0.05$.

with DPL increasing by 0.03 km for every increase in individual. This relationship held when we excluded all monitored troops (Model 2; Table V). We found no correlation between home range size and % use of human-modified habitat, or between density and % use of human-modified habitat (Table IV). However, Model 1 revealed that human-modified habitat had a significant negative effect on DPL (Model 1; Table V) with DPL decreasing by 0.01 km for every % increase in human-modified habitat. This relationship held even once we had excluded troops monitored annually from the model (Model 2; Table V).

Qualitative comparisons of troops across the population provided further evidence for the influence of habitat on ranging patterns. The troop (KK: 49 baboons) with the largest home range (37.7 km²), lowest density (1.3 baboons/km²), and second-longest mean DPL (5.64 km), was the only troop to live almost exclusively (99.7%) within natural habitat and to forage exclusively on natural food sources. This troop’s home range was four times larger than the home range of the largest troop (TK: 9.5 km²), 3.5 times larger than the second-largest home range (DG: 10.4 km²) and three times

larger than the population average (11.0 km²). Conversely, the home range (9.5 km²) of the largest troop (TK: 115 baboons), which was dominated by human-modified habitat (93.6%), was smaller than the population average, the density (12.1 baboons/km²) was the highest locally and, despite its large size, the DPL of TK was not significantly different from those of the two smallest troops (RH and BB; Table S1).

DISCUSSION

The chacma baboon troops in the Cape Peninsula exhibit substantial intrapopulation variation in ranging patterns. This variation is expected [Chapman & Chapman, 2000; Bronikowski & Altmann, 1996] given the wide range of troop sizes and extensive habitat heterogeneity present in the Cape Peninsula. Variation in home range size was greater than the intrapopulation variation reported for chacma populations elsewhere [e.g. 1.9–3.5 km, Limpopo, South Africa: Stoltz & Keith, 1973; 2.1–6.5 km, Okavango Delta: Hamilton et al., 1976]. Further, the variation in home ranges sizes in the Cape Peninsula (1.5–37.7 km²) equaled those

previously reported across the entire chacma distribution, ranging from 1.9 km² [Limpopo (was Northern Transvaal), South Africa: Stoltz & Keith, 1973] to 37.0 km² [Cape Peninsula, South Africa (C troop): Davidge, 1978] and among other primates, was most comparable to the variation reported for a wild population of Japanese macaques [*Macaca fuscata*; 0.24–26.7 km²: Takasaki, 1981].

Similar to Takasaki [1981], but contrary to our first hypothesis (H1), we found that troop size exerted a significant influence on baboon ranging patterns. Despite the extensive heterogeneity of habitat cover in the Cape Peninsula, and a diverse range of anthropogenic influences [van Doorn, 2009], home range size increased with troop size. Thus the Cape Peninsula population conforms to the theoretical expectation that larger troops will occupy larger home ranges and travel farther on a daily basis [sensu Chapman & Chapman, 2000]. In partial accordance with our second hypothesis (H2) we found that human-modified habitat also significantly influenced baboon ranging patterns, with increased use of human-modified habitat corresponding to shorter DPLs.

Primate species with access to high quality and predictably available resources, such as those found in human-modified habitats typically show reductions in home range sizes and DPLs, and increases in group sizes and densities [Brennan et al., 1985; Fuentes et al., 2005; Saj et al., 1999]. Thus it is unsurprising that the two troops (TK and RH) with the smallest home ranges, the highest densities and two of the shortest DPLs enjoyed unrestricted access to human-modified habitats, namely urban (RH) and agricultural habitat (TK). In contrast, (KK) with the least access to human-modified habitats had the largest home range, lowest density, and one of the longest DPLs of all Cape Peninsula troops. The extent of the differences among these troops is highlighted by the fact that KK occurs at a density (1.3 baboons/km²) comparable to that of troops occupying seasonally harsh environments like the Drakensberg mountains [0.95 baboons/km² (High troop): Whiten et al., 1987], while TK and RH occur at densities (TK: 12.1 baboons/km²; RH: 10.4 baboons/km²) most similar to troops found in fertile environments like the Okavango Delta [16.8 baboons/km² (G1 and H troops): Hamilton et al., 1976].

Two factors, namely concentrated food sources [Forthman-Quick & Demment, 1998; Riley, 2007; Singh & Vinathe, 1990] and sleeping-site availability [Anderson, 1984], may explain the effects of human-modified habitat on the ranging patterns of baboons in the Cape Peninsula. Within its home range TK could access abundant and concentrated high-quality food sources [i.e. pine nuts in plantations and grapes and grains in vineyards; Hoffman & O'Riain, 2010] situated in close proximity to an extensive supply of tree sleeping sites (i.e. pine and eucalyptus

plantations). The RH home range contained urban food within a residential suburb that was overlooked by a cliff sleeping-site, and on a near daily basis the troop moved directly from this sleeping-site to raid readily accessible urban food [Kaplan et al., 2011]. Consequently, both TK and RH were able to satisfy their nutritional and resting requirements within very small areas. This resulted in short daily distances traveled, small home ranges, and ultimately higher densities. Similar effects on ranging patterns have been reported for baboons and other primates that have access to human-modified habitats [Brennan et al., 1985; Hill, 2005; Siemers, 2000] and anthropogenic food sources [Altmann & Muruthi, 1988; Saj et al., 1999; Strum, 2010]. In stark contrast, the KK home range was dominated by nutrient-poor natural vegetation [Cowling et al., 1996; Hoffman 2011; Hoffman & O'Riain, 2010]. Resource scarcity typically drives an increase in home range size [Barton et al., 1992] and of all Cape Peninsula troops KK occupied the largest home range, foraging almost continuously as it covered large distances between east and west coast sleeping-sites.

In summary, we found that ranging patterns of the chacma baboons in the Cape Peninsula were significantly affected by both troop size and human-modified habitat. Despite extensive heterogeneity in habitat use, and the presence of baboon monitors, the ranging patterns of nine troops from this single population supported the theoretical expectation that larger troops will have larger home ranges and longer DPLs. Furthermore, more time spent in human-modified habitat, with its availability and concentration of high-quality food sources, corresponded to shorter DPLs. Finally, the Cape Peninsula exhibited extensive intrapopulation variation in baboon ranging patterns. This is not only evidence of the exceptional adaptability and behavioral plasticity of baboons, but also cautions that studies focused on only a small sample of troops within a population of adaptable and generalist species may underestimate the variability in their respective localities [Bronikowski & Altmann, 1996].

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