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Monkey Management: Using Spatial Ecology to Understand the Extent and Severity of Human–Baboon Conflict in the Cape Peninsula, South Africa

*Tali S. Hoffman*¹ and *M. Justin O'Riain*¹

ABSTRACT. Conflict with humans poses one of the greatest threats to the persistence and survival of all wildlife. In the Cape Peninsula, South Africa, human–baboon conflict levels remain high despite substantial investment by conservation authorities in a variety of mitigation measures. Here we explore how spatial ecology can inform wildlife managers on the extent and severity of both current and projected human–baboon conflict. We apply conservative and generous densities—2.3 and 5.9 baboons/km²—to hypothetical landscape management scenarios to estimate whether the chacma baboon (*Papio ursinus*) population in the Cape Peninsula is currently overabundant. We correlate conflict indices with spatial variables to explain intertroop differences in conflict levels. We investigate how an understanding of key elements of baboon ecology, including sleeping-site characteristics and intertroop territoriality, can direct management efforts and mitigate conflict. Our findings suggest that the current population of 475 baboons is below even the most conservative density estimate and that the area could potentially sustain up to 799 baboons. Conflict levels correlated positively with the loss of access to low-lying land through habitat transformation (Pearson $r = 0.77$, $p = 0.015$, $n = 9$ troops), and negatively with the distance of sleeping sites from the urban edge (Pearson $r = 0.81$, $p = 0.001$, $n = 9$ troops). Despite the availability of suitable sleeping sites elsewhere, more than half of all troops slept <500 m from the urban edge, resulting in increased spatial overlap and conflict with residents. Evidence for intertroop territoriality suggested that troop removal to mitigate human–baboon conflict would only be a short-term solution because neighboring troops are predicted to usurp the vacated home range and thus perpetuate the cycle of conflict. Together these findings suggest that an understanding of wildlife spatial ecology in a semi-urban context can be used to identify current and predicted landscape-level causes of human–baboon conflict. This information can be used to formulate sustainable long-term landscape management and conservation plans so that less costly and controversial direct wildlife management is required, and so ultimately fewer animals and humans suffer the costs of conflict.

Key Words: *Cape Peninsula, South Africa; chacma baboon; human–baboon conflict; human–wildlife conflict; monkey management; spatial ecology; wildlife management*

INTRODUCTION

Conflict has characterized the relationship between humans and wildlife throughout history (Heydon et al. 2010). However, the transformation of global landscapes from predominantly wild to predominantly anthropogenic over the last three centuries (Ellis et al. 2010) has seen competition between humans and wildlife for space and resources reach unprecedented levels (Siex and Struhsaker 1999, Bulte and Rondeau 2005, Woodroffe et al. 2005). Associated increases in human–wildlife conflict now pose one of the greatest threats to the persistence and survival of many animal species (Dickman 2010) and finding ways to manage and resolve these conflicts is vital for their long-term conservation (Heydon et al. 2010). A multitude of methods are employed to reduce human–wildlife conflict including the management of animal numbers (e.g., culling, translocation) and the separation of wildlife from humans using a host of deterrents (e.g., electric fences, herders (Dickman 2010)). However, there is rarely a single panacea to the problem; instead a variety of strategies typically need to be implemented for successful conflict mitigation (Distefano 2005).

With their adaptability, intelligence, agility, dexterity, and high levels of sociality and cooperation (Else 1991, Swedell 2011), nonhuman primates present one of the greatest and most complex challenges to human–wildlife conflict mitigation. In particular, baboons (*Papio*) exhibit unrivalled levels of contact with humans (Strum 2010, Swedell 2011), are considered the most troublesome nonhuman primate genus (Hill 2005), and are reported as pests in Uganda (Hill 2000), Nigeria (K. Pepeh *unpublished manuscript*), Cameroon (van Oosten 2000), Kenya (Strum 1994), Tanzania (Mascarenhas 1971), Malawi (Morris 2000), and South Africa (Kansky and Gaynor 2000; L. R. Brown et al. *unpublished manuscript*). Although most baboons, including the chacma baboon (*Papio ursinus*), are not currently listed as threatened or endangered (IUCN 2010), the high levels of human–baboon co-existence and the associated conflict seen throughout Africa (Strum 1994, Hill 2005, Strum 2010) are likely to increase as human populations continue to expand and land development proliferates.

In the Cape Peninsula, South Africa, as the size of the human population and the extent of landscape transformation and

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fragmentation have increased, so too have levels of human–baboon conflict (HBC) between the local human and chacma baboon (*Papio ursinus*) populations (Beamish 2010). For humans this conflict has meant property damage, economic losses related to crop raiding, and harassment by baboons for food (van Doorn et al. 2009; Hoffman and O’Riain 2010, Kaplan et al. 2011). For baboons the conflict has resulted in high levels of human-induced injury and mortality (Beamish 2010). A suite of management methods have been employed in an attempt to reduce local levels of human–baboon conflict, including: troop extirpation (Skead 1980), legislation to protect baboons from hunting (South Africa 2001), waste management (Kaplan et al. 2011), public education, the euthanasia of specific “problem” individuals, the localized installation of electric fencing, the herding of select troops away from urban habitat by dedicated baboon monitors (Kansky and Gaynor 2000, van Doorn 2009), and provisioning (Kaplan et al. 2011). However, despite these efforts, levels of human–baboon conflict remain high. In 2008 alone, there were 29 human-induced deaths of baboons (Beamish 2010), equating to a loss of 7% of the total population, with troop-specific losses ranging from 5 to 27% (Beamish 2010). Of further concern is that both the human population and the spatial extent of the city of Cape Town outside of the Table Mountain National Park have doubled over the last 30 years, thus putting more people in close contact with baboons, and thereby increasing the potential for further human–baboon conflict. It is thus evident that alternative and novel management techniques are required to reduce the frequency and severity of human–baboon conflict, in addition to having a better understanding of the fundamental drivers of this conflict.

Our primary aims were to explain: (1) why human–baboon conflict levels remain high despite current mitigation measures, and (2) why some baboon troops experience higher levels of human–baboon conflict than others. To do this we first investigated whether human–baboon conflict levels could be attributable to an overabundance of baboons given that the densities of troops with access to anthropogenic (urban and agricultural) food sources in human-modified habitats are markedly higher than those of troops with access to natural habitat only (Hoffman 2011). Second, we provide four spatial ecology variables that may prove heuristic in understanding why levels of human–baboon conflict vary so dramatically between troops, namely: (1) the percentage of land adjacent (within a mean day journey length) to each troop’s home range that is urbanized, (2) the percentage of land <100 m in elevation within the troop’s home range that is urbanized, (3) the extent of home range perimeter that abuts the urban edge, and (4) the mean proximity of sleeping sites to urban habitat. Based on the preference shown by baboons for low elevations (Hoffman and O’Riain 2012) we predict that these analyses will reveal that troops with the least access to nonurbanized, low-lying land within and adjacent to their current home ranges will experience the highest levels of human–baboon conflict.

Furthermore, based on the preference shown by baboons for human-modified habitat (Hoffman and O’Riain 2012) we predict that human–baboon conflict levels will correlate with the extent of home range perimeter that abuts the urban edge and the proximity of sleeping sites to the urban edge.

Our secondary objective was to establish how ecological data can inform current baboon management practices and lead to the development of novel management techniques. To this end we analyzed key elements of baboon ecology including the proximity of troop sleeping sites to urban areas and how intertroop territoriality may influence the implementation of troop removal as a potential, long-term, conflict-mitigation strategy.

METHODS

Study site

The Cape Peninsula is located at the southwestern-most point of the African continent, in the Western Cape Province of South Africa (Fig. 1). It spans 470 km² and comprises a combination of natural and human-modified habitats bounded by the Atlantic Ocean. Renowned for its floral diversity (Cowling et al. 1996) the Cape Peninsula is one of eight areas of the Cape Floristic Region, which a recognized world heritage site (United Nations 2010) and is currently predominantly conserved within Table Mountain National Park. Humans have transformed a minimum of 37% of natural habitat in the Cape Peninsula through urbanization and agriculture (Richardson et al. 1996). Low-lying land has been the most severely affected by these transformations, while the biodiversity of high-lying land is most threatened by self-sown invasive alien vegetation (Richardson et al. 1996). The human population of the City of Cape Town was estimated to be 3.4 million in 2007 (City of Cape Town 2008a) and is projected to show an increase of 17% by the year 2020 (City of Cape Town 2008b). The Cape Peninsula also serves as a major attraction to tourists and, with 1.8 million international tourists visiting in 2007 (City of Cape Town 2008a), is considered the second most popular tourist attraction in South Africa after the Kruger National Park (Macdonald and Cowling 1996).

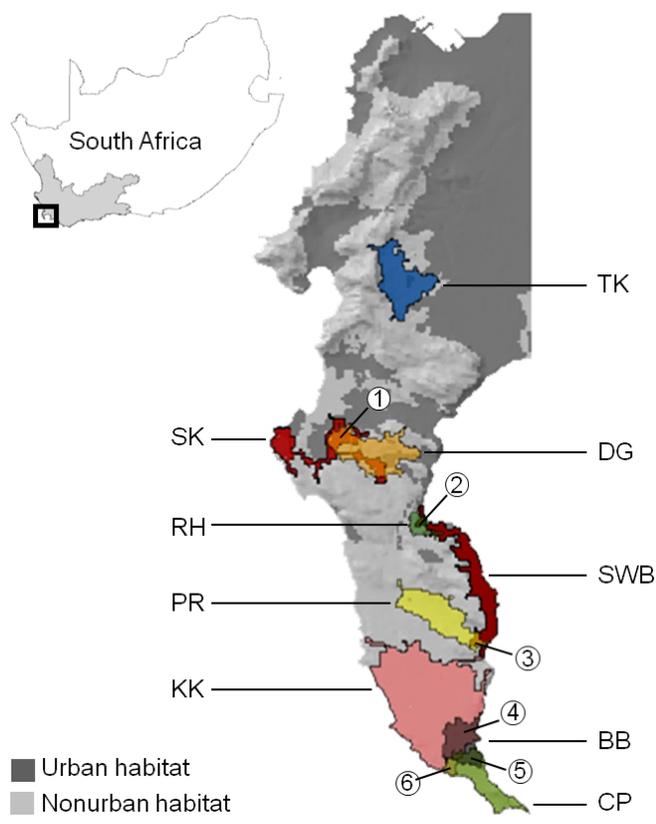
For analytical purposes we used the Repeating_shapes extension (Jenness 2005) in ArcView (Environmental Systems Research Institute 2002) to generate a grid system (150×150 m) which we superimposed on detailed maps of the Cape Peninsula. We then used relevant shapefiles to classify each cell in this grid system according to its dominant (>50%) habitat type, mean elevation, and mean slope (for details see Hoffman and O’Riain 2012).

Study animals

At the start of our study period, in March 2006, the Cape Peninsula population numbered 354 baboons (Beamish 2010) living in 12 troops extending from Tokai in the north to Cape Point in the south. Urban sprawl in the Cape flats has effectively cut these baboons off from all other extant troops

in South Africa and thus they are currently managed as a geographically discrete population. Our study animals included a subsample of nine troops that varied in size from 16 to 115 baboons (Fig. 1) with significant variation in their home range sizes, home range densities, day range lengths, travel rates, behavior, and diet (Hoffman 2011). The details of how we collected spatial and behavioral data for each troop are summarized in Appendix 1.

Fig. 1. The location of the Cape Peninsula in South Africa (inset) and the home ranges of the nine chacma baboon troops included in this study. Encircled numbers indicate areas of spatial home range overlap, and correspond to the pair number column in Table 4.



Conflict despite mitigation efforts

Because the baboons are an isolated population, with no natural predators and in chronic conflict with humans, there is considerable public pressure for wildlife managers to estimate an upper limit of the number of baboons that can be sustained on the Cape Peninsula. We applied two different baboon density estimates to hypothetical scenarios of available land and available habitat, to explore the total number of baboons that the Cape Peninsula could potentially support. We based the first density estimate of 2.3 baboons/km² on the mean density of three local troops that forage almost exclusively in natural habitat (Hoffman 2011). Two of these

troops access anthropogenic food sources only opportunistically at tourist nodes, with non-natural food items constituting only a small component (<1.5%) of their respective diets (Hoffman 2011). We based the second estimate of 5.9 baboons/km² on the mean density of six troops that have regular access to both natural and anthropogenic food sources (Hoffman 2011).

We applied these two density estimates to eight hypothetical scenarios of land availability, each with a particular spatial extent and set of habitat conditions. The only restriction for all scenarios was that we assumed troops were denied access to urban habitat and to the small patches of natural habitat fully subsumed within urban habitat. To account for differences in the forage potential of different habitats, across all scenarios we applied the conservative density estimate to natural habitat, and the generous density estimate to agricultural habitat and invasive alien vegetation.

We divided the eight hypothetical scenarios of available land into two categories, each comprising four scenarios (Fig. 2). In Category A we included land found across the full extent of the Cape Peninsula landscape, from Table Mountain in the north to Cape Point in the south (Fig. 2). In Category B we included less land based on the fact that baboons do not currently range across the full extent of the Cape Peninsula (e.g., Table Mountain, Lion's Head, Devil's Peak), and that the relocation of entire troops to such areas is not part of the current baboon management strategy. Thus, in this category we limited the available land to that contained within, or directly adjacent to, the combined "accessible areas" of each extant troop. For each troop we defined the "accessible area" as the land which could be traversed within a mean day range length from the troop's existing home range.

For both Category A and B, the details of Scenarios 1 to 4 are as follows: Scenario 1 represents existing habitat in the Cape Peninsula and assumes baboons have unlimited access to natural habitat, agricultural habitat, and invasive alien vegetation. We derived Scenario 2 from Scenario 1, but here we included the planned landscape changes for the Cape Peninsula, with all invasive alien vegetation removed and the commercial plantations restored to natural habitat. We derived Scenario 3 from Scenario 2, but here we worked on the assumption that as a result of the success of intervention measures (e.g., electric fencing, baboon monitors) baboons were unable to access all remaining agricultural habitat (i.e., vineyards, ostrich farm). We derived Scenario 4 from Scenario 3 but, based on our understanding of the foraging behavior of this population, here we included only natural habitat ≤600 m elevation. We selected this value because this contour line was nearest to the highest elevation at which we recorded foraging behavior for any troop (567.2 m (Hoffman and O'Riain 2011)).

Spatial variables and human–baboon conflict indices

We calculated two indices of human–baboon conflict for each troop for the population from 2005 to 2007 (Beamish 2010). For the first conflict index (Index 1) we calculated the total

number of baboons per troop that suffered either human-induced death or human-induced injury over the 3-year period. We refined these totals to control for differences in troop size by generating a second conflict index (Index 2) that represented the mean annual percentage of troop members to suffer either human-induced death or human-induced injury over the 3-year period.

To determine if select spatial ecology variables provided explanations for the varying levels of human–baboon conflict we used Pearson correlations to correlate Index 1 and Index 2 with the following spatial variables for each troop: (1) the percentage of “accessible area” that was urbanized, (2) the percentage of home range area <100 m elevation that was urbanized, (3) the percentage of home range perimeter abutting the urban edge, and (4) the mean proximity of sleeping sites to urban habitat. We used the Cape Peninsula grid system to calculate the first two variables, and the Clip function in the GeoProcessing wizard in ArcView (Environmental Systems Research Institute 2002) to measure the third variable. To calculate the fourth variable we conducted the following for each troop: (a) we used the Nearest_features extension (Jenness 2004) to ArcView to calculate the mean distance of every sleeping site to its five nearest urban habitat grid cells, and (b) we averaged these values to calculate the overall mean sleeping-site distance from the urban edge, weighted by the proportion of use of each sleeping site.

Sleeping sites

During data collection (see Appendix 1) we identified the sleeping sites used by each troop and categorized them as buildings, trees, or cliffs. For each troop we then calculated the percentage of sites included in each sleeping-site category. We analyzed all troop sleeping sites collectively to calculate the mean elevation and slope (\pm SEM) of the populations’ cliff sleeping sites. To determine whether the use of buildings or trees was a function of choice or of limited availability of cliff sleeping sites we used ArcView (Environmental Systems Research Institute 2002) to identify grid cells across the Cape Peninsula that were ≥ 500 m from the urban edge, comprised of natural habitat, and were within the same range of elevation and slope values (mean \pm SEM) as known cliff sleeping sites. We based the urban edge proximity on the mean hourly travel rate of Cape Peninsula baboon troops (0.42 ± 0.11 km/h (Hoffman 2011)) to ensure that we only identified suitable sleeping sites that were >1 h mean travel time from the urban edge.

Territoriality

To determine whether community-level influences on troop-level ranging patterns may impact baboon management we investigated patterns of overlap and territoriality for neighboring troops. We quantified the spatial association of neighboring troops by calculating the percentage overlap of home ranges and core ranges ($n = 6$ troops) using the Clip function in the Geoprocessing wizard in ArcView (Environmental Systems Research Institute 2002). We defined

the core range as the area of the home range that included the minimum number of grid cells accounting for 75% of total usage frequencies (Chapman and Wrangham 1993; Lehmann and Boesch 2003). To quantify the temporal overlap of troops we analyzed data collected over the same time periods and at synchronous time intervals for three neighboring troops. We used the Nearest_features extension (Jenness 2004) in ArcView to calculate the mean distance between these troops at any given time ($n = 719$ points over 17 days for three troops).

We used two measures to assess primate territoriality: Mitani and Rodman's (1979) defensibility index (D), and Lowen and Dunbar's (1994) fractional monitoring rate (M). Mitani and Rodman's (1979) defensibility index (D) relates day range length to home range size, working on the assumption that home ranges are circular. We used the following formula to calculate D for all study troops:

$$D = d/(4A/\pi)^{0.5}$$

where,

d = mean day range length (km),

A = home range area (km²),

$D > 1$ indicates that animals are territorial or that territoriality is economically feasible but not necessarily in operation, and

$D < 1$ indicates that animals are not territorial.

More recently, Lowen and Dunbar (1994) developed a more thorough method for assessing primate territoriality. Their fractional monitoring rate (M) takes into account territorial boundary length, the distance at which neighboring troops can be detected, and the number of foraging groups. M is calculated by

$$M = N(sv/d^2)$$

where,

N is the number of foraging parties,

s is the mean distance at which intruders can be detected,

v is the mean day range length (km), and

d is the diameter of the circle equivalent in area to the home range.

Where $M \geq 0.08$ primates can be considered territorial, and where $M < 0.08$ primates can be considered nonterritorial. We calculated M for all study troops, working on the assumption that $N = 1$, and with a mean detection distance set at 0.5 km (Lowen and Dunbar 1994). Finally, we recorded all intertroop interactions ad libitum.

RESULTS

Conflict despite mitigation efforts

The conservative and generous baboon density estimates applied to the hypothetical scenarios of available land in Category A yielded population sizes ranging from 586 to 799 baboons (Fig. 2, Table 1). The same two density estimates applied to the hypothetical scenarios of available land in

Fig. 2. Three-dimensional maps of the Cape Peninsula showing eight hypothetical scenarios of available land for baboons. We combined these scenarios with two baboon density estimates to explore the total number of baboons that the Cape Peninsula could support. In both A and B, the total areas of available land decrease progressively from 1 to 4 in accordance with increasing access restrictions. A includes all land in the Cape Peninsula, while B includes only land immediately adjacent to troop home ranges and accessible within a one-day journey. In all scenarios baboons are denied access to urban habitat. In both A and B the details of Scenarios 1 to 4 are as follows: In Scenario 1 baboons are allowed unlimited access to natural habitat, invasive alien vegetation, and agricultural habitat. Scenario 2 is based on Scenario 1 but considers that all invasive alien vegetation and the Tokai plantation have been restored to natural habitat. Scenario 3 is based on Scenario 2 but denies baboons access to remaining agricultural habitat (vineyard, ostrich farm). Scenario 4 is based on Scenario 3 but includes only natural habitat ≤ 600 m (see methods for rationale).

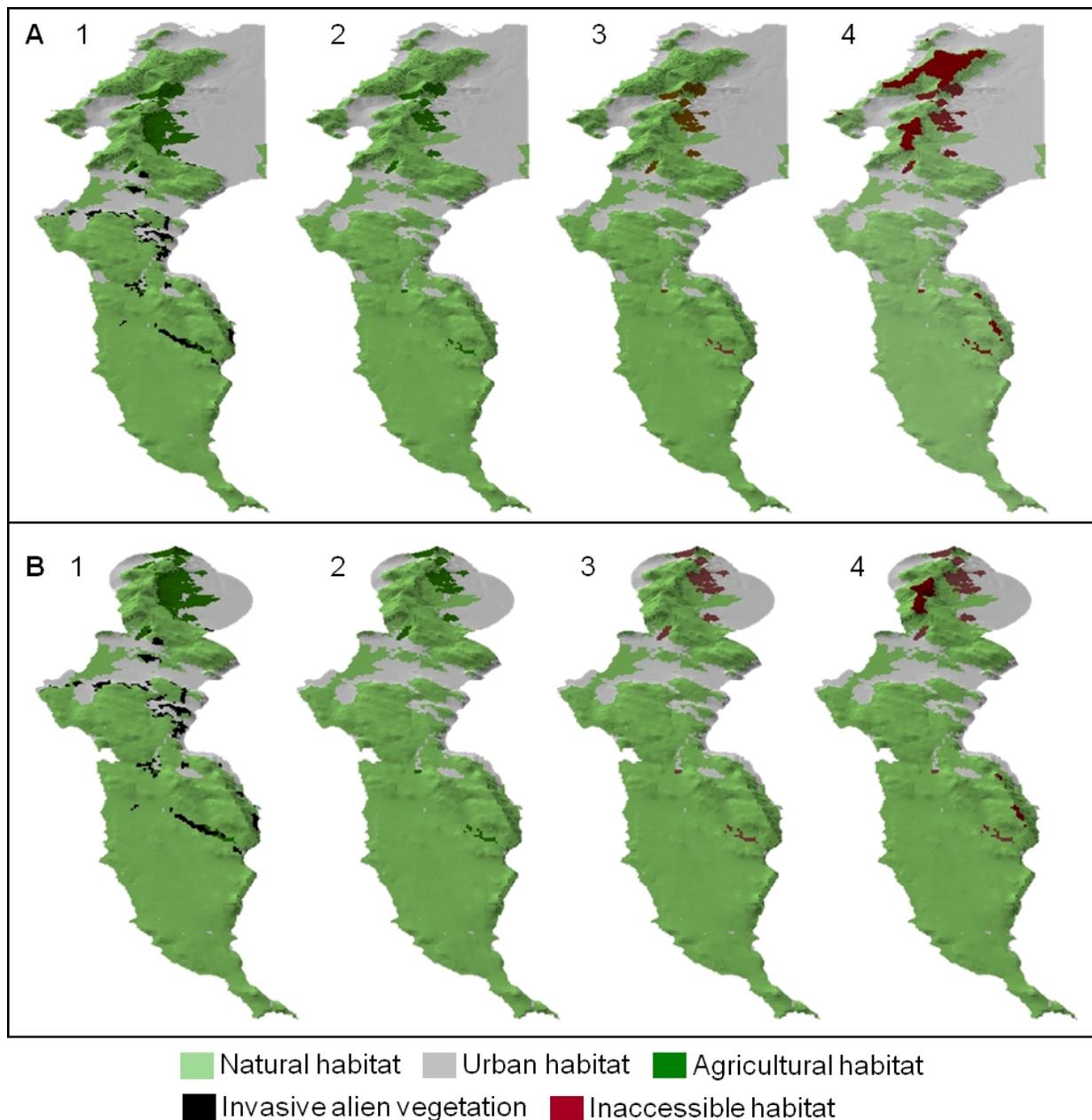


Table 1. Estimated size of the Cape Peninsula baboon population, by land-availability scenario and habitat composition.

Category	Scenario	Natural (2.3 baboons/km ²)		Invasive alien vegetation (5.9 baboons/km ²)		Agriculture (5.9 baboons/km ²)		Estimated population size (no.)
		Area (km ²)	Baboons (no.)	Area (km ²)	Baboons (no.)	Area (km ²)	Baboons (no.)	
A	1	265.95	612	8.83	52.08	22.96	135	799
	2	285.44	657	-	-	12.30	73	729
	3	285.44	657	-	-	-	-	657
	4	254.91	586	-	-	-	-	586
B	1	197.35	454	8.80	51.94	21.00	124	630
	2	216.82	499	-	-	10.34	61	560
	3	216.82	499	-	-	-	-	499
	4	212.26	488	-	-	-	-	488

Category B yielded population sizes ranging from 488 to 630 baboons. The scenario offering baboons the greatest area of land with the fewest habitat restrictions (Category A, Scenario 1 (Fig. 2))—which also most accurately reflects current conditions locally—indicated that the Cape Peninsula could support 799 baboons. The scenario offering the smallest area of land with the most habitat restrictions (Category B, Scenario 4 (Fig. 2)), indicated that the Cape Peninsula could support 488 baboons.

Spatial variables and human–baboon conflict indices

The total number of baboons per troop experiencing human–baboon conflict (Table 2) correlated positively with the percentage of each troop’s accessible area that was urbanized (Table 3). With troop size controlled for, the mean annual percentage of each troop experiencing human–baboon conflict correlated positively with the percentage of home range area ≤100 m elevation that was urbanized, and negatively with the mean distance of troop sleeping sites to urban habitat. We found no significant correlations between the conflict indices and the percentage of home range perimeter abutting the urban edge (Table 3).

Sleeping sites

Baboon sleeping sites (black cells (Fig. 3)), were located in close proximity to both urban areas—where preferential food sources occur—and along the coastline, where suitably steep and high sleeping-site cliffs occur. Troops slept in trees, on cliffs, and on the rooftops of buildings (Table 2). Four out of the six troops that had access to all forms of sleeping sites slept in trees more often than on cliffs. The mean elevation of cliff sleeping sites used was 167.07 m (±53.47 m SEM) and the mean slope was 21.91° (±5.86° SEM). The Cape Peninsula also included an area of 11.6 km² (504 grid cells) of suitable but unused sleeping-site area (pink cells (Fig. 3)). These grid cells were all situated ≥500 m from the urban edge, comprised natural habitat, and matched the elevation and slope characteristics of cliff sleeping sites used currently.

Fig. 3. A three-dimensional habitat map showing the distribution of grid cells currently used as sleeping sites (black) and grid cells not used as sleeping sites (pink) that are ≥500 m from the urban edge and which match the characteristics of used cliff sleeping sites.

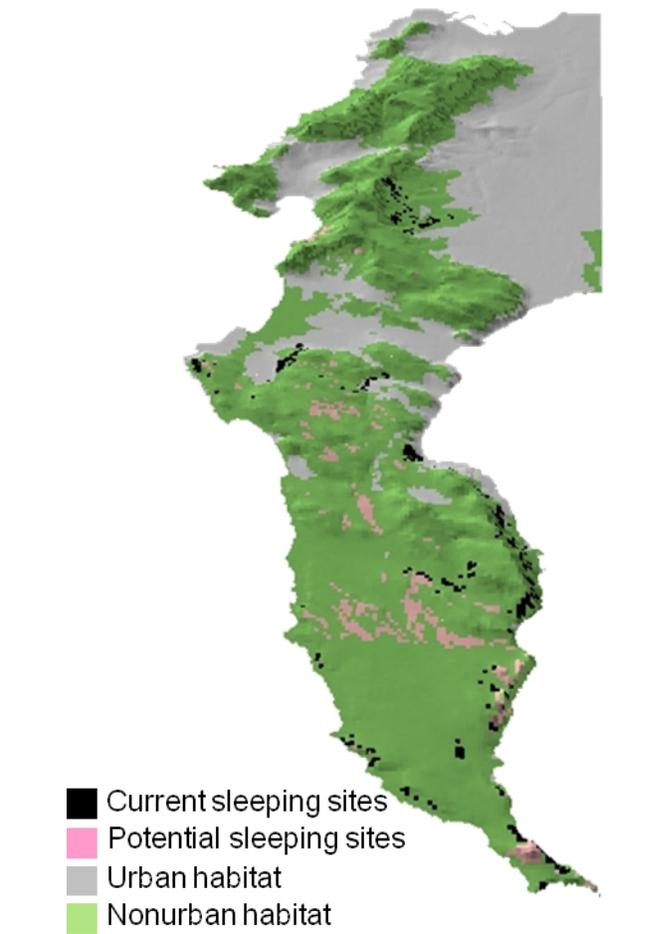


Table 2. Measurements used to determine why some troops experience higher levels of human–baboon conflict than others, and the characteristics of the sleeping sites used by each troop.

Troop	Conflict indices [†]		Spatial variables				Use of sleeping site types [‡]		
	Index 1: total HID and HII, 2005–2007 (no.)	Index 2: mean annual HID and HII (%)	Accessible area that is urbanized (%)	Area of home range area <100 m that is urbanized (%)	Home range perimeter abutting urban edge (%)	Mean distance of sleeping sites to urban habitat (km)	Trees (%)	Cliffs (%)	Buildings (%)
DG	11	10.1	32.2	48.1	15.9	0.10	63	14	23
TK	9	2.5	38.7	14.6	21.6	1.14	100	0	+
SK	8	11.0	29.9	52.8	20.4	0.20	29	54	16
PR	7	6.0	5.3	1.4	0.0	0.25	84	16	+
RH	5	11.9	26.7	78.6	25.1	0.12	+	100	+
SWB	5	6.0	13.8	60.1	27.8	0.45		100	+
CP	4	5.2	0.1	0.7	0.0	1.99		100	+
BB	2	5.6	0.6	5.0	0.0	0.61	67	33	+
KK	0	0.0	1.3	0.6	0.0	2.17	16	84	+

[†] HID = human-induced deaths. HII = human-induced injuries.

[‡] A blank cell means that the sleeping site type was not available in the troops home range while + indicates that the sleeping site type was available but not used.

Territoriality

Only one troop, i.e., the TK troop, was geographically isolated from all other troops by urban development (Fig. 1). For all other troops the percentage of home range spatial overlap varied from 0.7 to 17.2% with a mean overlap of 7.3% ($\pm 4.9\%$, $n = 6$ pairs) (Table 4). Core range overlap was restricted to five troops, with a mean overlap of 5.2% ($\pm 4.8\%$, $n = 4$ pairs). Three troops for which we had collected fine-scale spatial data simultaneously ranged at a mean distance of 4.19 ± 1.79 km from one another.

According to Mitani and Rodman's (1979) defensibility index (D), five troops occupied ranges where territorial defense was economically feasible (although not inherently necessary; $D \geq 1$; Table 5). Once these values had been adjusted to include the fractional monitoring rate (M) put forward by Lowen and Dunbar (1994), all troops bar one could be considered territorial, or spatially capable of territoriality ($M \geq 0.08$).

Despite having only one adult male (vs. the KK troop with $n = 6$ adult males, and the CP troop with $n = 3$ subadult males) and being numerically the smallest (the BB troop with $n = 16$ vs. the CP troop with $n = 22$, and the KK troop with $n = 49$), the BB troop displaced both the CP and KK troops on separate occasions as they approached the picnic site portion of their home range. The only animal from the BB troop involved in the displacement was the single adult male whose aggression resulted in different responses from the KK troop and the CP troop. During the aggressive encounter KK troop members grouped tightly together and the BB male herded the cohesive unit away from the picnic site. In contrast, CP troop members scattered and ran in different directions, with the BB male intermittently chasing individuals until the whole troop had vacated the picnic site.

DISCUSSION

Conflict despite mitigation efforts

An overabundance of baboons cannot be the explanation for the high levels of human–baboon conflict in the Cape Peninsula because none of the predicted baboon population sizes—which were calculated by applying both conservative and generous baboon densities to various hypothetical scenarios of available land and habitat cover—indicated that baboon numbers presently exceed the available space. Instead, the scenario that was best matched to prevailing landscape conditions (Scenario A-1 (Fig. 2)) showed that the current estimated population size (475 baboons, (E. K. Beamish unpublished data)) could increase by 324 baboons. At the opposite extreme, the scenario that set the greatest restrictions on available land and which denied baboons access to any human-modified habitats (Scenario B-4), still allowed for an increase of 11 animals.

Despite being empirically grounded in quantified patterns of baboon spatial ecology, these estimated population sizes should not be viewed as an authoritative “carrying capacity” for the Cape Peninsula because they fail to take into account the full ecological complexity of the local landscape. In so doing, they neglect to factor in the long-term effects of habitat on baboon reproductive output and survival rates. The inclusion of this level of complexity, however, would require detailed research on the nutritional composition of all baboon dietary items, including investigations into the nutritional variation found across natural habitats, plant ages, elevations, and seasons. Furthermore, these density estimates cannot be used to predict any oscillatory patterns of population size that could result from changes to foraging conditions, nor how these changes may impact upon the levels at which the population size self-regulates. Despite these shortcomings,

Table 3. Results of Pearson correlations testing for significant relationships between spatial variables and total number of human-induced deaths (HID) and human-induced injuries (HII) per troop, and between spatial variables and mean annual percentage of HID and HII per troop. Bold values indicate significant differences at $p \leq 0.05$.

	No. of HID and HII			% HID and HII		
	r	p	n	r	p	n
Accessible area that is urbanized (%)	0.80	0.010	9	0.47	0.207	9
Area of home range area <100 m that is urbanized (%)	0.37	0.326	9	0.77	0.015	9
Home range perimeter abutting urban edge (%)	0.50	0.166	9	0.49	0.179	9
Mean distance of sleeping sites to urban habitat (km)	-0.17	0.655	9	-0.80	0.001	9

these population estimates offer two important insights to management. Firstly, they serve as a precautionary forecast of the size towards which this baboon population will tend under different landscape management regimes. Secondly, they emphasize that, except under the most conservative of land-availability scenarios (B-4), management efforts will not need to engage in any immediate regulation of baboon numbers.

The loss of access to low-lying land as a result of urbanization, and the mean proximity of sleeping sites to urban habitat, provided the best explanations for why levels of human-baboon conflict remain high despite current management efforts. Troops with the least access to low-lying land and/or who slept closest to the urban edge were the same troops to experience the highest levels of human-induced death and human-induced injury. This relationship, which is perhaps unsurprising given the preference of baboons for low elevations (Hoffman and O’Riain 2012), provides important support for the suggestion by Hoffman and O’Riain (2010) that further development of both the low elevation areas of home ranges and the land immediately accessible to baboons from their home ranges will exacerbate levels of human-baboon conflict for all troops. The results also indicate the importance of managing baboon sleeping-site use, which is discussed in more detail below.

Although the percentage of each troop’s accessible area that was urbanized provided the best predictor of recent human-baboon conflict levels, it was not the only determinant. Two troops, i.e., TK and PR, whose home ranges comprised predominantly agricultural and natural habitat suffered the second and fourth highest numbers of human-induced deaths and injuries respectively. Even two of the three troops—i.e., BB and CP, ranging entirely within the protected natural habitat of Table Mountain National Park, and who had only minimal (<1% of home range) access to urban habitat—suffered human-baboon conflict. Importantly the only troop with no recorded human-baboon conflict was the KK troop. The single factor distinguishing this troop from all others was not the habitat composition of its home range, but the fact that it foraged entirely on natural food sources. This suggests that, while the type and coverage of human-modified habitats may dictate the frequency and severity of human-baboon conflict,

ostensibly any troop that consumes anthropogenic food sources is at risk of suffering from human-baboon conflict.

That two of the troops most affected by human-baboon conflict—i.e., the DG troop and the SK troop—are also the two that have been actively managed for the longest time suggests that loss of critical baboon land may result in chronically elevated levels of human-baboon conflict that current management practices cannot reduce. Together these results raise a pertinent question for baboon management: how can human-baboon conflict levels be reduced for troops that have already lost large amounts of low-lying land?

Spatial variables and human-baboon conflict indices

There is no single solution to reducing human-wildlife conflict (Distefano 2005). However, a thorough understanding of wildlife ecology is vital for the development of effective management and conservation plans (Sinclair et al. 2006). Analyses of patterns of baboon sleeping-site use and territoriality yielded interesting insight into how human-baboon conflict can be mitigated in the Cape Peninsula.

Baboons are known to utilize a variety of above-ground sleeping sites that offer safety from predators (DeVore and Hall 1965) and suitable vantage points for area surveillance (Anderson 1984). These include trees (e.g., DeVore and Hall 1965, Altmann and Altmann 1970), cliffs (e.g., Kummer and Kurt 1963, Crook and Aldrich-Blake 1968, Whiten et al. 1987), rocky outcrops (e.g., Altmann and Altmann 1970), and caves (e.g., Marais 1939, Hall 1963). Despite inhabiting a predator-free environment, the Cape Peninsula troops do not deviate from this pattern, sleeping predominantly in elevated tree and cliff sleeping sites.

What is concerning from a management perspective is that four troops preferentially selected sleeping sites in human-modified habitats over the widely available cliff sleeping sites in natural habitat. Furthermore, more than half of the troops slept <500 m from the urban edge. Two troops even habitually slept on building rooftops within urban habitat—the DG troop slept atop and inside sections of a residential apartment block, and the SK troop slept on the rooftop of a confectionary factory alongside hot-air vents. These patterns of sleeping-site use are not a consequence of limited sleeping-site availability,

Table 4. Details of the spatial overlap of troop home ranges and the mean (\pm SEM) temporal proximity of neighboring troops over a period of 17 days. Pair numbers correspond to the encircled numbers presented in Fig. 3. Troops are listed according to their geographical position from north to south.

Pair number	Troops	Spatial overlap		Temporal overlap	
		Home ranges (%)	Core ranges (%)	Mean proximity (km)	<i>n</i> (GPS points; no. days)
1	SK and DG	17.2	10.4	-	-
2	RH and SWB	3.9	-	-	-
3	PR and SWB	3.1	-	-	-
4	BB and KK	7.2	8.5	3.82 \pm 0.29	61; 3
5	BB and CP	11.5	1.1	2.84 \pm 0.22	116; 5
6	CP and KK	0.7	0.9	5.92 \pm 0.16	542; 14

because suitable and typical baboon sleeping sites are widely available throughout the Cape Peninsula, both within and outside of the home ranges of all troops. Instead, sleeping-site selection appears to be driven primarily by their proximity to human-modified habitats (Hoffman and O’Riain 2012). Discouraging baboons from using sleeping sites that are close to urban habitat (Fig. 3) should be a management priority given the large number of possible alternatives far from the urban edge and the lack of any natural predators that might otherwise influence sleeping-site selection. The increased spatial separation between baboons and humans at the beginning and end of each day will increase the ability of baboon monitors to achieve their overall goal of reducing spatial overlap between baboons and urban habitat, with subsequent reductions in human–baboon conflict.

Table 5. Measures of troop territoriality. $D \geq 1.0$ and $M \geq 0.08$ indicate the potential for territoriality. Troops are listed according to their geographical position from north to south.

Troop	D^\dagger	M^\ddagger
TK	0.73	0.14
SK	0.94	0.22
DG	1.30	0.21
RH	1.18	3.43
SWB	0.95	0.19
PR	1.64	0.34
KK	0.89	0.02
BB	1.24	0.52
CP	1.72	0.47

[†] Defensibility index (Mitani and Rodman 1979).

[‡] Fractional monitoring rate (Lowen and Dunbar 1994).

The results of field observations, territorial index calculations, and measures of range overlap for troops in the Cape Peninsula, all provide evidence for a degree of territoriality in chacma baboons, supporting the observations of Hamilton et al. (1976). The strongest evidence for territoriality was the aggressive interactions between the BB troop and its neighbors. Interestingly, the ability of the BB alpha male to single-handedly supplant two troops on separate occasions—

the KK troop comprising 49 individuals and the CP troop comprising 22 individuals—suggests that strength in intertroop encounters does not depend solely on troop size or the number of males present (Hamilton et al. 1975). Instead, the tendency for the BB troop to display overt spatial defense is most likely attributable to its home range encompassing a high-quality and monopolizable resource (sensu Strier 2007) in the form of a picnic area where humans and garbage bins are regularly raided for anthropogenic food sources. This same picnic area, which is the source of human–baboon conflict for the BB troop, provides a useful study site for future investigations into conflict-mitigation measures.

These findings are relevant to baboon management for they caution against simply removing troops that are experiencing high levels of human–baboon conflict. If troops aggressively defend access to high-quality anthropogenic food sources, then removal of chronic raiding troops, as has been done historically (Skead 1980), may simply allow excluded, and possibly less habituated, neighboring troops to move in, and discover and then monopolize the same resource, thus perpetuating the conflict. Evidence to support this statement comes from the Kommetjie region of the Cape Peninsula where the most recent troop removal was effected in 1990 by the local conservation authority (Beamish 2010). The removal of the Kommetjie troop resulted in short-term relief from human–baboon conflict, but the vacant home range was usurped about 8 years later (Kansky and Gaynor 2000) by a fission group from the neighboring DG troop. This fission group, currently known as the SK troop, now habitually raids the Kommetjie area, once again resulting in high levels of human–baboon conflict in the area (Nature Conservation Corporation, Baboon Hotline *personal communication*). Thus, the better long-term strategy to reduce human–baboon conflict in areas with multiple neighboring troops is to focus on the removal of, or on preventing access to, the anthropogenic food source(s) that are the primary drivers of the conflict itself (i.e., the baboon attractant), and not focus on the removal of whole troops. The latter approach has only proven successful when all the troops from entire geographical

regions have been removed simultaneously, such as was performed in the northern areas of Table Mountain National Park (Skead 1980). These large areas have remained devoid of troops for over 30 years with only occasional visits by lone dispersing males (Beamish 2010).

That the BB troop was the only one to display visible evidence of spatial defense should not be interpreted as a lack of territorial potential for the other troops, but rather may be a consequence of the widespread availability of sleeping sites (Hall 1963, DeVore and Hall 1965, Kummer 1968, Altmann and Altmann 1970, Anderson 1981) and/or the absence of predators (Anderson 1981). Furthermore, with a mean of ~7%, levels of home range overlap in the Cape Peninsula, were substantially lower than the range of 50 to 95% reported by Anderson (1982). Mean core range overlap was lower still (~0.3%). This minimal range overlap, particularly at the core level, suggests that range boundaries are well defined, a factor which may account for the general sparseness of territorial behavior observed among troops. However, the fractional monitoring rate of Lowen and Dunbar (1994) indicated territoriality to be an economically feasible option for all troops in the Cape Peninsula, apart from the KK troop. Thus, in addition to avoiding negative knock-on effects of troop removal, management should also view each troop as a variable that may affect the spatial ecology, and hence management, of neighboring troops.

Conclusions

We use baboon spatial ecology to understand the extent and severity of human–baboon conflict in the Cape Peninsula and to determine realistic and practical strategies for local baboon management within a metropolitan area. In so doing, it demonstrates how an enhanced understanding of wildlife spatial ecology can inform wildlife management and improve human–wildlife conflict-mitigation efforts.

Baboon troops with the least access to low-lying land and those that slept closest to the urban edge suffered the highest levels of human-induced injury and human-induced mortality. That two of the troops most impacted by human–baboon conflict are also presently the most actively managed by baboon monitors indicates that the ability of current management strategies to mitigate against human–baboon conflict is inadequate. However, the results caution against the renewed implementation of historically used management practices such as troop extirpation. Firstly, there is currently no numerical justification for troop removal because, despite the increased density of troops in human-modified habitats, there is no indication that this population is as yet overabundant. Secondly, evidence for intertroop territoriality suggests that the removal of nuisance troops would have limited success in reducing overall human–baboon conflict levels, and would simply create the opportunity for previously excluded troops to take advantage of the same conflict-causing resource.

Rather, the results indicate that landscape management that prioritizes the conservation of low-lying natural habitat, increased distance of sleeping sites to the urban edge, and decreased access to traditional conflict hot spots (i.e., picnic sites, waste depots, tourist centers) presents the least invasive and most sustainable ways of managing human–baboon conflict.

Preventing troops from consuming anthropogenic food sources should also be a chief management priority, for two reasons. Firstly, the only troop with no human–baboon conflict was also the only troop that did not forage on anthropogenic food sources. This result illustrates that reduced levels of human–baboon conflict are contingent upon preventing baboons from accessing food in human-modified habitats. Secondly, denying baboons access to anthropogenic food sources should improve their manageability by reducing the overall population density; troops that forage only on natural food sources will be forced to range over a large area of natural habitat to satisfy their nutritional requirements. As a result, the natural habitat of the landscape—much of which is currently devoid of baboons—will become more heavily and widely used and we predict that home ranges will continue to increase in size until each troop approaches the conservative mean density (2.3 baboons/km²) of those ranging entirely within Table Mountain National Park. This conservative density is comparable to the mean of baboon densities of 2.7 baboons/km² reported across South Africa (DeVore and Hall 1965, Stoltz and Saayman 1970, Whiten et al. 1987, Henzi et al. 1992) and thus presents a realistic long-term prediction for the density of the Cape Peninsula population in natural habitat. Furthermore, we predict that an added benefit of restricting troop diets to natural food sources will be a convergence of annual and seasonal ranging patterns that will make the population more predictable to manage and allow for the implementation of population-specific rather than troop-specific management plans.

Responses to this article can be read online at:
<http://www.ecologyandsociety.org/vol17/iss3/art13/responses/>

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LITERATURE CITED

- Altmann, S. A., and J. Altmann. 1970. *Baboon ecology: African field research*. University of Chicago Press, Chicago, USA and London, UK.
- Anderson, C. M. 1981. Intertroop relations of chacma baboons. *International Journal of Primatology* 2:285-310. <http://dx.doi.org/10.1007/BF02693480>
- Anderson, C. M. 1982. Baboons below the Tropic of Capricorn. *Journal of Human Evolution* 11:205-217. [http://dx.doi.org/10.1016/S0047-2484\(82\)80037-7](http://dx.doi.org/10.1016/S0047-2484(82)80037-7)
- Beamish, E. K. 2010. *Causes and consequences of mortality and mutilation in baboons of the Cape Peninsula, South Africa*. Dissertation. University of Cape Town, Cape Town, South Africa.
- Bulte, E. H., and D. Rondeau. 2005. Why compensating wildlife damages may be bad for conservation. *The Journal of Wildlife Management* 69:14-19. [http://dx.doi.org/10.2193/0022-541X\(2005\)069<0014:WCWDMB>2.0.CO;2](http://dx.doi.org/10.2193/0022-541X(2005)069<0014:WCWDMB>2.0.CO;2)
- Chapman, C. A., and R. W. Wrangham. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology* 31:263-273. <http://dx.doi.org/10.1002/ajp.1350310403>
- City of Cape Town. 2008a. *City of Cape Town, city statistics*. [online] URL: <http://www.capetown.gov.za/en/stats/Pages/CityStatistic.aspx>.
- City of Cape Town. 2008b. *City of Cape Town, indicator, population projection 2001 to 2021*. [online] URL: <http://www.capetown.gov.za/en/stats/Documents/Population.htm>.
- Cowling, R. M., I. A. W. MacDonald, and M. T. Simmons. 1996. The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* 5:527-550. <http://dx.doi.org/10.1007/BF00137608>
- Crook, J. H., and P. Aldrich-Blake. 1968. Ecological and behavioural contrasts between sympatric ground-dwelling primates in Ethiopia. *Folia Primatologica* 8:192-227. <http://dx.doi.org/10.1159/000155154>
- DeVore, I., and K. R. L. Hall. 1965. Baboon ecology. Pages 20-52 in I. DeVore, editor. *Primate behavior: field studies of monkeys and apes*. Holt, Rinehart and Winston, New York, New York, USA.
- Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation* 13:458-456. <http://dx.doi.org/10.1111/j.1469-1795.2010.00368.x>
- Distefano, E. 2005. *Human-wildlife conflict worldwide: a collection of case studies, analysis of management strategies and good practices*. Sustainable Agriculture and Rural Development (SARD), Food and Agricultural Organization of the United Nations (FAO), Rome, Italy. [online] URL: http://www.fao.org/sard/common/ecg/1357/en/hwc_final.pdf.
- Ellis, E. C., K. K. Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19:589-606 <http://dx.doi.org/10.1111/j.1466-8238.2010.00540.x>
- Else, J. G. 1991. Nonhuman primates as pests. Pages 155-165 in H. O. Box, editor. *Primate responses to environmental change*. Chapman and Hall, London, UK. http://dx.doi.org/10.1007/978-94-011-3110-0_8
- Environmental Systems Research Institute. 2002. *ArcView, version 3.3*. Redlands, California, USA.
- Hall, K. R. L. 1963. Variations in the ecology of the chacma baboon. *Symposium of the Zoological Society of London* 10:1-28.
- Hamilton, W. J., III, R. E. Buskirk, and W. H. Buskirk 1975. Troop-mobilizing behavior of adult male chacma baboons. *Folia Primatologica* 22:9-18.
- Hamilton, W. J., III, R. E. Buskirk, and W. H. Buskirk. 1976. Defence of space and resources by chacma (*Papio ursinus*) baboons in an African desert and swamp. *Ecology* 57:1264-1272. <http://dx.doi.org/10.2307/1935050>
- Henzi, S. P., R. W. Byrne, and A. Whiten. 1992. Patterns of movement by baboons in the Drakensberg Mountains: primary responses to the environment. *International Journal of Primatology* 13:601-629. <http://dx.doi.org/10.1007/BF02551256>

- Heydon, M. J., C. J. Wilson, and T. Tew. 2010. Wildlife conflict resolution: a review of problems, solutions and regulation in England. *Wildlife Research* 37:731–748. <http://dx.doi.org/10.1071/WR10006>
- Hill, C. M. 2000. A conflict of interest between people and baboons: crop raiding in Uganda. *International Journal of Primatology* 21:299–315. <http://dx.doi.org/10.1023/A:1005481605637>
- Hill, C. M. 2005. People, crops, and primates: a conflict of interests. Pages 40–59 in J. D. Paterson and J. Wallis, editors. *Commensalism and conflict: the human–primate interface*. The American Society of Primatologists, Norman, Oklahoma, USA.
- Hoffman, T. S. 2011. *The spatial ecology of chacma baboons (Papio ursinus) in the Cape Peninsula, South Africa: towards improved management and conservation strategies*. Dissertation. University of Cape Town, Cape Town, South Africa.
- Hoffman, T. S., and M. J. O’Riain. 2010. The spatial ecology of chacma baboons (*Papio ursinus*) in a human-modified environment. *International Journal of Primatology* 32:308–328. <http://dx.doi.org/10.1007/s10764-010-9467-6>
- Hoffman, T. S., and M. J. O’Riain. 2012. Landscape requirements of a primate population in a human-dominated environment. *Frontiers of Zoology* 9:1.
- IUCN (International Union for the Conservation of Nature and Natural Resources). 2010. *Red List of threatened species—version 2010.4*. Cambridge, UK. [online] URL: <http://www.iucnredlist.org>.
- Jenness, J. 2004. *Nearest features (nearfeat.avx) extension for ArcView 3.x, v. 3.8a*. Jenness Enterprises, Flagstaff, Arizona, USA. [online] URL: http://www.jennessent.com/arcview/nearest_features.htm.
- Jenness, J. 2005. *Repeating shapes (repeat_shapes.avx) extension for ArcView 3.x*. Jenness Enterprises, Flagstaff, Arizona, USA. [online] URL: http://www.jennessent.com/arcview/repeat_shapes.htm.
- Kansky, R., and D. Gaynor. 2000. *Baboon management strategy for the Cape Peninsula*. Final report. Table Mountain Fund Project number ZA 568, Cape Town, South Africa.
- Kaplan, B. S., M. J. O’Riain, R. van Eeden, and A. J. King. 2011. A low-cost manipulation of food resources reduces spatial overlap between baboons (*Papio ursinus*) and humans in conflict. *International Journal of Primatology* 32:1397–1412. <http://dx.doi.org/10.1007/s10764-011-9541-8>
- Kummer, H., editor. 1968. *Social organisation of Hamadryas baboons: a field study*. University of Chicago Press, Chicago, USA.
- Kummer, H., and F. Kurt. 1963. Social units of a free-living population of hamadryas baboons. *Folia Primatologica* 1:4–19. <http://dx.doi.org/10.1159/000164877>
- Lehmann, J., and C. Boesch. 2003. Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d’Ivoire. *Behavioural Ecology* 14:642–649. <http://dx.doi.org/10.1093/beheco/arg047>
- Lowen, C., and R. I. M Dunbar. 1994. Territory size and defendability in primates. *Behavioral Ecology and Sociobiology* 35:347–354. <http://dx.doi.org/10.1007/BF00184423>
- Macdonald, I. A. W., and R. M. Cowling. 1996. Guest editorial. *Biodiversity and Conservation* 5:525–526. <http://dx.doi.org/10.1007/BF00137607>
- Marais, E. 1939. *My friends, the baboons*. First edition. Robert M. McBride and Company, New York, New York, USA.
- Mascarenhas, A. 1971. Agricultural vermin in Tanzania. Pages 259–267 in S. H. Ominde, editor. *Studies in East African geography and development*. Heinemann Educational Books Ltd, London, UK.
- Mitani, J. C., and P. Rodman. 1979. Territoriality: the relation of ranging patterns and home range size to defensibility, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology* 5:241–251. <http://dx.doi.org/10.1007/BF00293673>
- Morris, B. 2000. Wildlife depredations in Malawi, the historical dimension. Pages 36–49 in J. Knight, editor. *Natural enemies: people–wildlife conflicts in anthropological perspective*. Routledge, London, UK.
- Richardson, D. M., B. W. van Wilgen, S. I. Higgins, T. H. Trinder-Smith, R. M. Cowling, and D. H. McKell. 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity Conservation* 5:607–647. <http://dx.doi.org/10.1007/BF00137612>
- Siex, K. S., and T. T. Struhsaker. 1999. Colobus monkeys and coconuts: a study of perceived human–wildlife conflicts. *Journal of Applied Ecology* 36:1009–1020. <http://dx.doi.org/10.1046/j.1365-2664.1999.00455.x>
- Sinclair, A. R. E., J. M. Fryxell, and G. Caughley, editors. 2006. *Wildlife ecology, conservation and management*. Second edition. Blackwell Publishing Ltd., Oxford, UK.
- Skead, C. J. 1980. *Historical mammal incidence in the Cape Province, Volume 1*. Department of Nature and Environmental Conservation, Cape Town, South Africa.
- South Africa. 2001. *Western Cape: hunting seasons, daily bag limits and hunting by the use of prohibited hunting methods*. Proclamation No. 49/2001. Nature Conservation Ordinance (Ordinance 19 of 1974). Provincial Gazette, Western Cape Province, South Africa.

Stoltz, L. P., and G. S. Saayman. 1970. Ecology and behaviour of baboons in the Northern Transvaal. *Annals of the Transvaal Museum* 26:99-143.

Strier, K. B., editor. 2007. *Primate behavioral ecology*. Pearson Allyn and Bacon, Boston, Massachusetts, USA.

Strum, S. C. 1994. Prospects for management of primate pests. *Revue d'Ecologie (La Terre et la Vie)* 49:295-306.

Strum, S. C. 2010. The development of primate raiding: implications for management and conservation. *International Journal of Primatology* 31:133-156. <http://dx.doi.org/10.1007/s10764-009-9387-5>

Swedell, L. 2011. African Papionins: diversity of social organization and ecological flexibility. Pages 241-277 in C. J. Campbell, A. Fuentes, M. C. MacKinnon, M. Panger, S. K. Bearder, and R. Stumpf, editors. *Primates in perspective*. Second edition. Oxford University Press, New York, New York, USA.

United Nations. 2010. *World Heritage List, Cape Floral Region Protected Areas, South Africa*. UNESCO World Heritage Centre, United Nations, Paris, France. [online] URL: <http://whc.unesco.org/en/list/1007>.

van Doorn, A. C. 2009. *The interface between socioecology and management of chacma baboons (Papio ursinus) in the Cape Peninsula, South Africa*. Dissertation. University of Cape Town, Cape Town, South Africa.

van Oosten, V. 2000. *The conflicts between primates and the human population in a protected area in north Cameroon*. MSc thesis. CML student report 133. Leiden University, Leiden, Netherlands.

Whiten, A., R. W. Byrne, and S. P. Henzi. 1987. The behavioral ecology of mountain baboons. *International Journal of Primatology* 8:367-389. <http://dx.doi.org/10.1007/BF02737389>

Woodroffe, R., S. Thirgood, and A. Rabinowitz, editors. 2005. *People and wildlife: conflict or coexistence?* Cambridge University Press, Cambridge, UK.

Appendix 1. Baboon ranging pattern and behavioral data collection, analysis and results.

Baboon ranging patterns

Data collection

To determine baboon ranging patterns we recorded Global Positioning System (GPS) data points for each troop. We collected GPS data points using handheld devices (Garmin eTrex) operated by field researchers, tracking collars and using a combination of both methods. Field researchers recorded the GPS coordinate of the centre point of the troop (visually estimated geometric centre) at 20-minute intervals between sunrise and sunset for an average of 109 days (± 28 days SEM, range: 71–170 days, $n=6$ troops) per troop. The terrain within these ranges was easily traversable on foot and visibility of baboons within all habitats was excellent. Tracking collars recorded the GPS point of a single troop member at 3-hourly intervals between sunrise and sunset for an average of 302 days (± 54 days SEM, range: 247–334 days, $n=3$ troops) per troop. Additionally, we increased the frequency of collar readings to 20-minute intervals for an average of 14 days (± 1 day SEM, range: 12–15 days, $n=3$ troops) during summer and winter. We tracked troops for full-days (sunrise to sunset with GPS readings every 20-minutes) and part-days. On part-days field researchers typically tracked baboons for half the day (sunrise to midday or midday to sunset) or for only a few hours during the day (e.g., when we had difficulty locating the troop), and tracking collars recorded GPS data points at 3-hourly intervals. We included only GPS data points that had an estimated level of accuracy of ≤ 10 m. We continued to collect data for each troop until either the number of new cells entered per month (see Hoffman and O’Riain 2012) reached an asymptote or until we had collected a full year of data. In total, we recorded 24,618 GPS data points for the population, with an average of 2735 ± 768 GPS data points SEM (range: 1668–5018, $n=9$ troops) recorded per troop. Finally, using the GPS data collected by field researchers and tracking collars, we identified all troop sleeping-sites, and categorized these sites as trees, cliffs or buildings.

Baboon Behavior

Data collection and analysis

We investigated the effect of human-modified habitat on baboon behavior by comparing the only two unmonitored troops of equal size ($n=16$; RH and BB) and similar composition that occupy markedly different habitats (natural versus urban). We compared 10 full-days of ranging and behavioral data recorded during the same season (winter). We did not study the troops simultaneously, but there were no significant differences in minimum temperature (Mann-Whitney $U=3551.0$, $p=0.059$) or rainfall (Mann-Whitney $U=3738.0$, $p=0.172$) between the data collection periods.

T Hoffman, along with 8 volunteers, collected the required spatial and behavioral data for BB. Volunteers commenced with behavioral data collection only when their records matched Hoffman’s with an accepted error level of $<5\%$ for behavioral recordings made over a full day of data collection. We supervised all volunteers on a daily basis to ensure that they adhered strictly to the data collection protocols. Researchers and volunteers collecting behavioral data wore identical field jackets and followed strict behavioral data collection protocols to record troop habitat use and diet. RH was studied as part of an ongoing doctoral thesis within the same research unit (BS Kaplan, UCT, unpubl. data), following identical data collection protocols as those described below.

For each troop we conducted instantaneous scans of individuals at 20-minute intervals. 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 centre (geometric centre) 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 randomized the direction of each transect by alternating the bearing (in the order of north, south, east and west) of each successive scan. Transects were not perfectly straight lines as care had to be taken not to walk directly towards baboons. When a baboon was on the transect line the observer deviated around the animal and immediately returned 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 versus leading edge). We recorded the GPS position of the centre point of the troop at the start of each scan and assigned a habitat category (natural habitat, urban habitat, agricultural habitat or invasive alien vegetation) to each GPS data point. We recorded behavioral data for male and female adults, sub-adults and juveniles. We classified behavior as foraging, socializing, resting or moving, as these activities constitute more than 95 % of a baboon's time budget (Dunbar 1992). In the case of foraging, which included all behavior related to food (searching, handling and feeding), we classified the food item as being from natural or urban food sources. We recorded each animal 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 a mean of 10 ± 1 (range: 1-16) animals per scan for RH and a mean of 5 ± 0.4 SE (range: 1-13) animals per scan for BB. We used Mann-Whitney U tests to investigate differences in the daily habitat use and diet of RH and BB and used one-way, single factor ANOVAs (with *post hoc* Tukey tests) to determine differences in percentage of scans allocated by RH and BB on a daily basis to foraging, socializing, resting and walking.

Results

The comparison of the two equal-sized, unmonitored troops (RH and BB) added statistical support to the assertion that ecological factors are important in explaining variation in ranging patterns and behavior. The home ranges of both troops in Pair 1 included urban and natural habitat, but the RH home range comprised eight times as much urban habitat (24.6 %) as the BB home range (3.4 %), and RH spent significantly more time in urban habitat than BB (Mann-Whitney $U=0.0$, $p<0.001$; Table A), and significantly less time in natural habitat (Mann-Whitney $U=0.0$, $p<0.001$). Furthermore, RH – who foraged on anthropogenic food sources significantly more than BB (Mann-Whitney $U=0.0$, $p<0.001$; Table A), and on natural food sources significantly less (Mann-Whitney $U=0.0$, $p<0.001$) – spent significantly less time foraging ($F_{1,18}=50.89$, $df=18$, $p \leq 0.001$; Table A) and significantly more time resting ($F_{1,18}=67.91$, $df=18$, $p \leq 0.001$). The troops spent a similar proportion of time socializing ($F_{1,18}=2.53$, $df=18$, $p=0.129$) and walking ($F_{1,18}=0.86$, $df=18$, $p=0.365$).

Table A. Mean daily percentage (\pm SEM) of habitat use, diet and activity budgets of two equal-sized troops (RH and BB) during winter ($n=10$ days). * indicate significant differences at $p<0.05$.

Troop	Habitat use (% per day)		Food items (% per day)		Activity (% per day)			
	Natural*	Human-modified* ^o	Natural*	Urban*	Forage*	Social	Rest*	Walk
RH	66.8 (\pm 7.4)	33.2 (\pm 7.4)	74.8 (\pm 7.3)	25.2 (\pm 7.3)	27.3 (\pm 3.2)	18.6 (\pm 3.2)	35.3 (\pm 3.2)	18.7 (\pm 3)
BB	94.5 (\pm 2.6)	5.5 (\pm 2.6)	99.0 (\pm 1.1)	1.0 (\pm 1.1)	55.0 (\pm 6.9)	14.3 (\pm 4.3)	14.4 (\pm 3.8)	16.3 (\pm 4.0)

^o Human-modified includes urban habitat