The spatial ecology of chacma baboons (*Papio ursinus*) in the Cape Peninsula, South Africa:

Towards improved management and conservation strategies

Tali Hoffman

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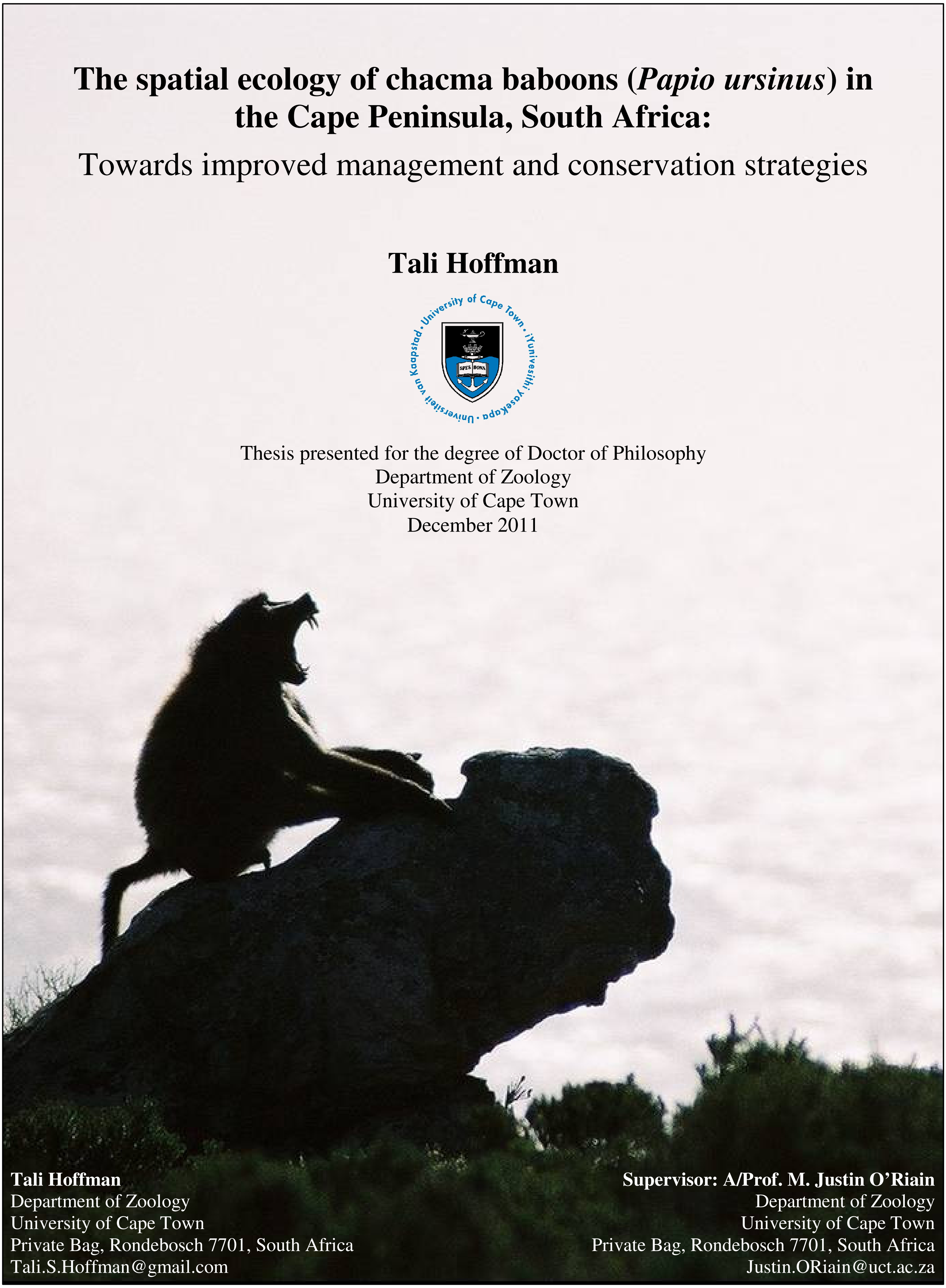

Tali Hoffman
Department of Zoology
University of Cape Town
Private Bag, Rondebosch 7701, South Africa
Tali.S.Hoffman@gmail.com

Supervisor: A/Prof. M. Justin O'Riain
Department of Zoology
University of Cape Town
Private Bag, Rondebosch 7701, South Africa
Justin.ORiain@uct.ac.za

The spatial ecology of chacma baboons (*Papio ursinus*) in the Cape Peninsula, South Africa: Towards improved management and conservation efforts.

ABSTRACT Competition for space between humans and wildlife is prevalent worldwide. In the Cape Peninsula, South Africa, extensive land transformation has geographically isolated, fragmented and reduced the size of the local chacma baboon population and is perceived to be a major driver of human-baboon conflict. However, no data on baboon landscape use exist to verify this perception. I studied the spatial ecology of this population, identifying baboon land use patterns, determining the drivers of intrapopulation variation in spatial ecology and investigating how spatial variables could inform baboon management efforts to reduce human-baboon conflict. I collected a full year of GPS locations for nine of the 12 resident troops and seasonal activity budget and diet data for four of the troops. Using hurdle models I ascertained that the key landscape features influencing baboon distribution patterns at the population-level were low altitudes, steep slopes and human-modified habitats. The combination of these variables provided baboons with access to high quality natural and anthropogenic food sources in close proximity to suitable sleeping sites. I found extensive intrapopulation variation in troop home range sizes (1.5-37.7 km^2), densities (1.3-12.1 baboons/km^2), day range lengths (1.65-6.58 km) and travel rates (0.19-0.77 km/hour) that could be explained by differences in troop size and habitat use. Larger troops had larger home ranges, while troops that spent more time in human-modified habitat had smaller home ranges, shorter day range lengths and spent less time feeding than troops in natural habitat. Further, I found that 1 km^2 of human-modified habitat could support nearly five times the number of baboons as the same area of natural habitat. Conservative (2.3 baboons/km^2) and generous (5.9 baboons/km^2) density estimates applied to a range of land availability scenarios suggested that the current population (460 baboons) has not reached saturation and could increase by 28-324 animals. Loss of access to low lying land and the proximity of sleeping sites to the urban edge correlated significantly with human-baboon conflict. Preventing further loss of low lying land within the home ranges of extant troops, and encouraging baboons to sleep farther from urban habitat, are thus essential to achieving a sustainable population that is not locked into high levels of conflict with humans. Evidence for intertroop territoriality indicated that reducing conflict through the culling of whole troops would only be successful when such troops have no immediate neighbours. In summary, the most sustainable way to manage baboons in the Cape Peninsula is through improved landscape conservation and resource management. More broadly, this study highlights the complexities of wildlife conservation at the interface of natural and human-modified habitats and shows how an understanding of wildlife spatial ecology can assist in improving wildlife management and conservation efforts.

I dedicate this thesis to my mother who, in teaching me the value of education, gave me the greatest education of all.

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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, and adhered to South Africa legal requirements. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to any of the funding organisations.

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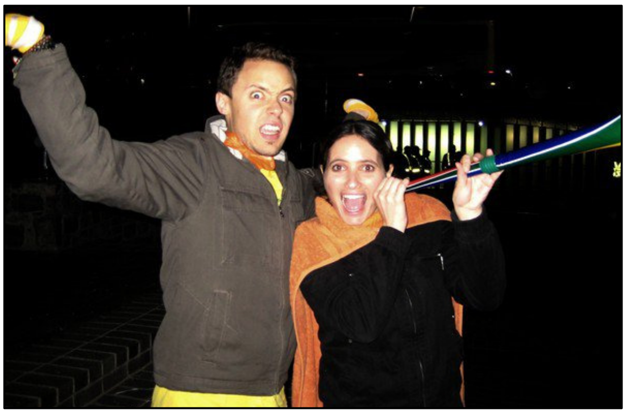
when times were tough, for listening with care to my ranting – particularly when you had no idea what I was talking about (which I suspect was often) – and for your undying support and encouragement I want to thank all my nearest and dearest ones. And I want to say a very special thank you to Alta de Vos, Ruth Narun, Claire Gregorowski, Ross Cowlin and Bentley Kaplan, who were the greatest rocks of all.

Next, to my family. Suffice to say, without the influence of my family, those near and far, I would never be who, or where, I am today. So to thank them for minutia seems arbritary when I have them to thank for absolutely everything. But I happen to like minutia. So I want to thank my mother, Michelle Hoffman, for being my biggest fan, my greatest support and my ultimate role-model. With your heart, your strength, your conviction, and your ability to rise up when others around you fall, you have been, and will always be, my inspiration and the exact person I hope to be when I grow up. This thesis is my gift to you. I want to thank my father, Jacob 'John' Hoffman for instilling in me a sense of self-worth, a conviction that education is important and a belief that I can achieve anything I set out to do. Your life and your passion live on in me. To my brother, Elan Hoffman, thank you for always reminding me to think and feel deeply but to not sweat the small stuff, to choose my life's direction while accepting that sometimes life might choose its own direction for me, and to set my goals as high as the clouds and then look for ways to achieve them. And finally, I thank my wonderfully quirky uncle, Richard Hoffman, for always being unquestionably ready to lovingly and willingly fight for my causes, celebrate my achievements, attend my talks and document my graduations as if I were his daughter proper. I love you all very much.



Finally, there were many things I was expecting and hoping to gain from this epic journey of a PhD, and I feel satisfied that all of those expectations were met. But what I am perhaps most grateful for are the many unanticipated things that cropped up along the way. Undoubtedly the most important of these was the wonderful surprise of finding love both where and when it was least expected. My final word of thanks is to Bentley, for showing me, at a time when I was least capable of seeing it, that life exists beyond this thesis, and that it is glorious.

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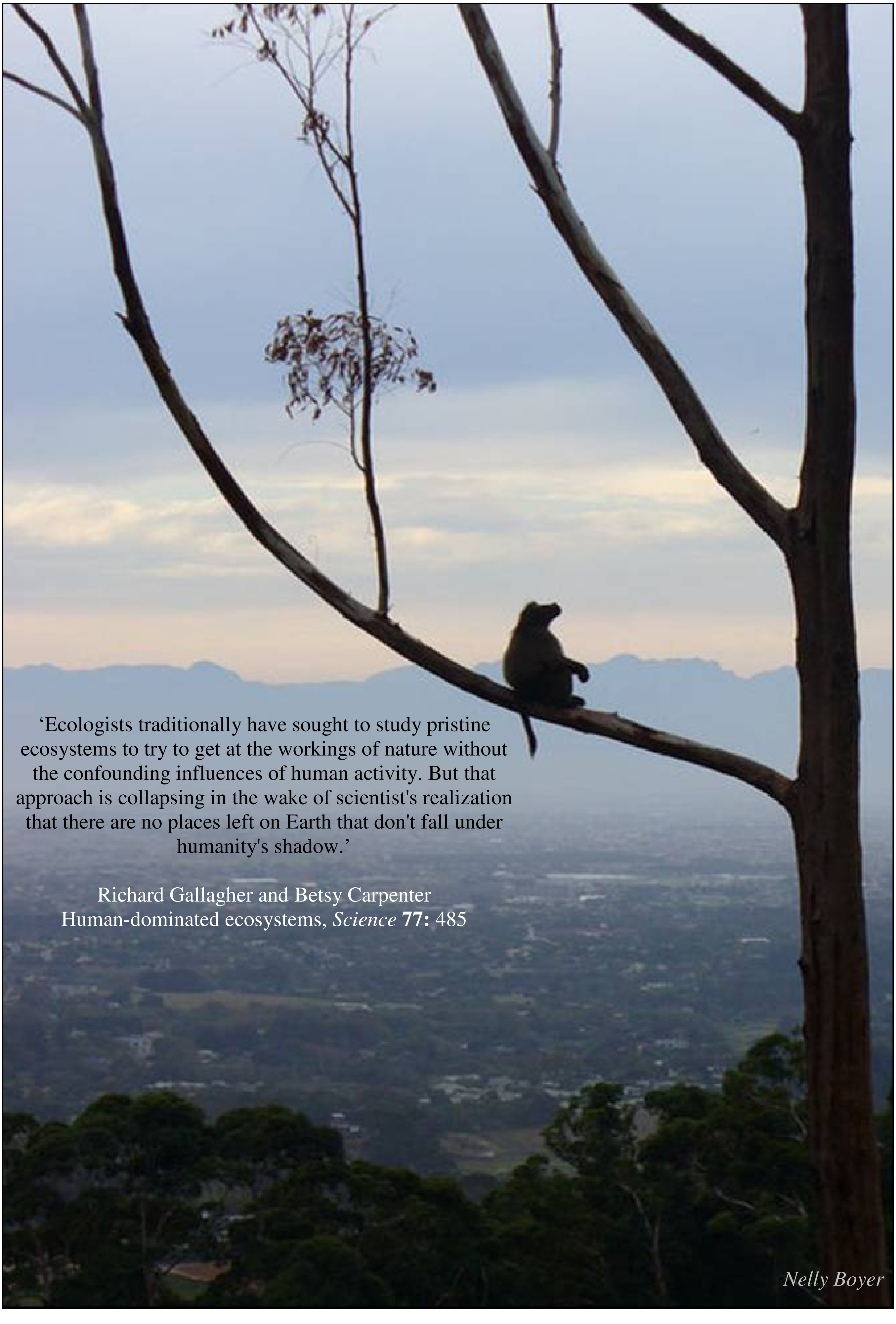
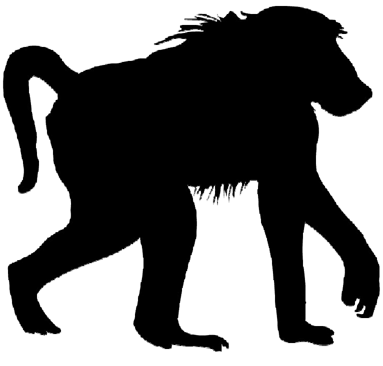


> ‘Ecologists traditionally have sought to study pristine ecosystems to try to get at the workings of nature without the confounding influences of human activity. But that approach is collapsing in the wake of scientist's realization that there are no places left on Earth that don't fall under humanity's shadow.’
>
> Richard Gallagher and Betsy Carpenter
> Human-dominated ecosystems, *Science* **77:** 485

Nelly Boyer

Chapter 1

Introduction



The human-wildlife interface

Humans have occupied almost every corner of the earth's surface for 10 000 years (Western 2001). However, the last three centuries have seen an unprecedented expansion of the human population and the transformation of global landscapes from predominantly wild to predominantly human-modified (Vitousek et al. 1997; Ellis et al. 2010). The proliferation of humans is credited to our ability to simplify ecosystems through habitat homogenisation, food web simplification, and nutrient input (Western 2001). However, the concomitant conversion, compression and fragmentation of natural land is considered the leading cause of extinction across all other species (Pimm and Raven 2000), with many wildlife adversely affected by the associated impacts including changes to habitat and resource availability (Menzel et al. 2005), geographic isolation (Cushman 2006), increased disease emergence (Daszak et al. 2001; Drewe et al. in press) and increased conflict with humans (Siex and Struhsaker 1999a; McLellan and Hovey 2001; Bulte and Rondeau 2005; Woodroffe et al. 2005).

Non-human primates (referred to hereafter as 'primates') present one of the greatest and most complex conservation challenges at the human-wildlife interface. The geographical overlap (sympatry) of humans and primates, which is widespread across Africa, Madagascar, Asia and Central and South America, is most likely attributable to an evolutionary convergence of ecological requirements (Sponsel et al. 2002). However, according to the most recent IUCN red data list, anthropogenic habitat disturbance is the primary cause for 92 % of all primate species being classified as endangered (IUCN 2010). Habitat loss associated with deforestation, agricultural encroachment and urbanisation poses a direct threat to specialist primates whose survival is reliant on access to habitat and food found only in narrow ecological niches (Emmons et al. 1983; Peres 1993; Jernval and Wright 1998). The effects of habitat change are less direct for generalist primates whose behavioural and dietary flexibility affords them the potential not only to benefit from, but also to thrive on anthropogenic habitat disturbance (Strum 2010). However, for generalists the feeding benefits associated with human-modified habitats most commonly come at the cost of human-primate conflict (Else 1991).

The generalist primates exhibiting the greatest sympatry with humans are members of the *Cercopithecus*, *Macaca,* and *Papio* genera (Hill 2005). Their success in human-modified habitats is attributed to their adaptability, intelligence, agility, dexterity and high levels of sociality and co-operation (Else 1991; Swedell 2011). Within this group, baboons (*Papio*) exhibit unrivalled levels of contact with humans (Swedell 2011) and are considered the most troublesome genus (Hill 2005). Although their notoriety may be more related to human perceptions than empirical data (Warren et al. 2007), there is abundant evidence throughout the agricultural areas of Africa that baboons – reported as pests in Uganda (Hill 2000), Nigeria (Pepeh 1996), Cameroon (van Oosten 2000), Kenya (Strum 1994), Tanzania (Mascarenhas 1971), Malawi (Morris 2000) and South Africa (Kansky and Gaynor 2000; Brown et al. 2006) – cause more crop damage than any other primate (Naughton-Treves 1996; Hill 2000) as well as all other wildlife species (Naughton-Treves 1998; Biryahwaho 2002). Although baboons are not currently listed as threatened or endangered (IUCN 2010), the high levels of human-baboon overlap and the associated conflict seen throughout Africa (Strum 1994; Hill 2005) are likely to increase as human populations continue to expand and land development proliferates. Consequently, over time the benefits afforded to baboons by habitat alteration are likely to be exceeded by the deleterious consequences of chronic competition for space and food that manifests as direct conflict with humans (Laurance et al. 2002).

Humans and baboons in the Cape Peninsula

The chacma baboon population (*Papio ursinus*) in the Cape Peninsula, South Africa provides one of the best examples of baboon coexistence with humans. The earliest records of baboon and human overlap in the Cape Peninsula date back to the 15th century with the arrival of Dutch settlers in South Africa (Goodwin 1952). Since then nearly half of the Cape Peninsula landscape has been transformed by a combination of urbanisation, farming and invasions by self-sown alien vegetation (Sinclair-Smith 2009). As a consequence of the altered landscape, this baboon population is now geographically isolated from all other populations, and all troops within it have contact with humans, albeit to different degrees, in both residential and tourist-frequented natural areas.

That baboons have persisted in this fragmented metropolitan landscape is attributable to them having retained access to large tracts of natural habitat, most of which now falls under the protection of the Table Mountain National Park (TMNP). Nonetheless, throughout their coexistence in the Cape Peninsula, the relationship between humans and baboons has been characterised by conflict. For humans this has translated into property damage, economic losses related to crop raiding and harassment by baboons for food (Kansky and Gaynor 2000). For baboons the conflict has resulted in troop extirpation (Skead 1980), the targeted removal of nuisance individuals and high levels of human-induced injury and mortality (Beamish 2010).

Over the last 15 years various management methods have been employed in an attempt to reduce this human-baboon conflict (HBC). Methods include sound aversion, localised installation of electric fencing and, most commonly, the herding of select troops away from human-occupied habitats by baboon monitors (Kansky and Gaynor 2000; van Doorn 2009). Additionally, in 1999 new legislation was introduced to protect baboons from human persecution and hunting (Cape Province 1999). That the baboon population has shown a steady increase in size over the last decade from 365 in 1998 (Kansky and Gaynor 2000) to 460 animals in 2011 (EK Beamish, University of Cape Town (UCT), unpubl. data) indicates that these management efforts have enjoyed some success. Yet levels of HBC remain high. In 2008 alone, there were 29 human-induced deaths (Beamish 2010), equating to a loss of 7 % of the total population, with troop-specific losses ranging from 5-27 % (Beamish 2010). Of further concern is that both the human population and the spatial extent of the city of Cape Town outside of the TMNP have doubled over the last 30 years (Sinclair-Smith 2009) putting more people in close contact with baboons, thereby increasing the potential for further HBC. Alarmingly there are no data available on the spatial ecology of the Cape Peninsula troops and thus all land transformation to date has proceeded without cognisance of its potential effect on these animals.

Spatial ecology, wildlife management and conservation

Mitigating against the negative effects of anthropogenic landscape transformation is inherently a spatial endeavour that involves identifying, managing, conserving and restoring wildlife habitats of the requisite quality and quantity (Cumming 2004; Mace et al. 2010). An understanding of the landscape requirements of animals has thus become increasingly important for wildlife conservation and management planning (Beckmann and Berger 2003; Friedmann and Daly 2004; Dickman 2010; Heydon et al. 2010).

Ecologists once sought to ignore or remove spatial patterns from their datasets as they were considered to obscure biological understanding (Liebhold and Gurevitch 2002). However, the last three decades have seen an increasing awareness among ecologists that spatial structure is a critical component of organismal and ecosystem ecology (Liebhold and Gurevitch 2002; Fortin and Dale 2005). Simultaneous technological advances have assisted this progression, with the development of Geographic Information Systems (GIS) providing ecologists with the means to quantify, analyse and display spatial data (Johnston 1998). Advances in spatial statistics have also enabled ecologists to address the analytical complexities associated with spatial scale and spatial autocorrelation that were previously unavoidable (Liebhold and

Gurevitch 2002). Consequently, spatial analysis is the most rapidly growing field in ecology (Fortin and Dale 2005) and is considered both pivotal to the generation of new ecological theory and relevant to ecological management and conservation (Perry et al. 2002).

Today the scientific literature is rich in studies that use spatial ecology to address animal management and conservation issues. Studies are conducted around the world on diverse taxonomic groups (e.g., amphibians: Ray et al. 2002; insects: Cabeza et al. 2010; reptiles: Pawara et al. 2007, mammals: McLellan and Hovey 2001; Nielsen et al. 2006, Scholes and Mennell 2008; birds: Heinänen et al. 2008). Every study presents a unique set of problems with its own particular challenges and constraints (Sinclair et al. 2006). However all studies support the assertion that an enhanced understanding of the ways in which wildlife respond to landscape changes will better equip biologists to manage and conserve wildlife in the face of landscape transformation (Collinge 2001).

Primate spatial ecology

Spatial ecology has been a central theme in primatology for more than seven decades (e.g., Carpenter 1940). Since then extensive variability in ranging patterns has been documented across the primate order (e.g., Clutton-Brock and Harvey 1977; Mitani and Rodman 1979; De Luca et al 2009) both among (interspecific) and within (intraspecific) species. At the broadest level the variation in spatial ecology can be explained by differences in ecological niche occupation (e.g., arboreal versus terrestrial or semi-terrestrial and diurnal versus nocturnal) and foraging strategies (e.g., frugivory versus folivory; Arrowood et al. 2003; Strier 2007) and the inherent constraints imposed on primates living under the different conditions. At a finer scale, ranging pattern variation stems from the intrinsic and extrinsic factors operating on primate groups.

For all primates, spatial ecological patterns are a function of ecological and social factors (Harvey and Clutton-Brock 1981) that operate on spatial and temporal scales. Ecological factors that affect ranging patterns and dictate the intensity to which certain areas of the landscape are used (e.g., DeVore and Hall 1965; Altmann and Altmann 1970; Barton et al. 1992) include: water availability (e.g., Altmann and Altmann, 1970; Chapman, 1988), sleeping site location (e.g., Zinner et al. 2001; Liu et al. 2004; Zhou et al. 2007), and the availability, distribution and quality of food sources (e.g., Clutton-Brock 1975; Ganas and Robbins 2005; Li and Rogers 2005; Riley 2008). Ranging patterns are further affected by climatic variability in rainfall (Isbell 1983; Olupot et al. 1997; Higham et al. 2009), temperature (Yang 2003) and day length (Li 2002; Hill et al. 2003), all of which have a direct bearing on primate biology (Hill et al. 2003, 2004; Dunbar 1993) and affect primates indirectly through their influence on natural resources (Bronikowski and Altmann 1996). At a community level, the ecological factors affecting primate spatial ecology are intraspecific relationships (Isbell 1983; Goodall 1986; Fashing 2001), interspecific associations (Holenweg et al. 1996), predation pressure (Boinski et al. 2000; Treves 2002; Matsuda et al. 2009), perceived predation risk (Cowlishaw 1997) and parasite avoidance (Freeland 1976; Hausfater and Meade 1982). Of these influential ecological factors, food availability and distribution offers the best explanation for the variation seen in primate ranging patterns (Clutton-Brock 1977; Bennett 1986; Riley 2008). On a spatial scale, primates who rely on widely dispersed food sources with unpredictable availability are predisposed to travelling farther each day and covering larger ranges than primates who feed on evenly distributed and reliably available food sources (Oates 1987). Similarly, on a temporal scale, seasonal shifts in food availability and distribution may result in primate troops travelling farther during periods of food scarcity than periods of food abundance (Isbell and Young 1993; Stevenson 2006; but see Buzzard 2006).

Primate spatial ecology is also influenced by troop size (Barton et al. 1992; Ostro et al. 1999; Ganas and Robbins 2005), troop spread (Cowlishaw 1998; Treves et al. 2001, Arrowood et al. 2003) and intragroup relationships (Robbins and McNeilage 2003). Troop living may confer the benefit of reduced predation risk to individuals, however intragroup feeding competition, which can hinder reproduction and compromise survival, is widely recognised as the greatest corresponding cost (Chapman and Chapman 2000; Ganas and Robbins 2005). As primate troop sizes increase so scramble and or contest competition increase (Isbell 1981; Isbell and Young 1993; Wrangham et al. 1993), forcing larger troops to cover larger areas to obtain enough food for all troop members (Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995). Thus, an increase in troop size should result in a corresponding increase in day range length and home range size (Chapman and Chapman 2000). This pattern has been widely, but not consistently, found in studies of primates (Gillespie and Chapman 2001). Troop size correlated positively with home range size and day range length in geladas (*Theropithecus gelada*; Iwamoto and Dunbar 1983), red colobus (*Procolobus badius*; Gillespie and Chapman 2001), Thomas's langurs (*Presbytis thomasi*; Steenbeck and van Schaik 2001), northern muriquis (*Brachyteles arachnoides hypoxanthus*, Dias and Strier 2003 – home range size only), and mountain gorillas (*Gorilla gorilla beringei*; Watts 1991, 1998; McNeilage 1995; Ganas and Robbins 2005). However, there are also cases where primates deviated from theory. Troop size did not correlate with day range length for patas monkeys

(*Erythrocebus patas*; Chism and Rowell 1988), blue monkeys (*Cercopithecus mitis*; Butynski 1990), northern muriquis (*Brachyteles arachnoides hypoxanthus*, Dias and Strier 2003), black and white colobus (*Colobus guereza*; Fashing 2001), redtail monkeys (*Cercopithecus ascanius*; Struhsaker and Leland 1988) or kipunji (*Rungwecebus kipunji*; De Luca et al. 2009). Furthermore, group size did not correlate with home range size for western chimpanzees (*Pan troglodytes verus*; Lehmann and Boesch 2003), or with either day range length or home range size for black and white colobus (*Colobus guereza*; Fashing 2001), and several Asian colobine species (Yeager and Kool 2000).

Shortcomings in the knowledge of primate spatial ecology

Typically, our knowledge of primate spatial ecology stems from studies of single troops (Strier 2007), and studies with large sample sizes of troops or that incorporate complete populations (e.g., Hamilton et al. 1976; Iwamoto 1978; Takasaki 1981) are rare (Bronikowski and Altmann 1996). However, within species, disjointed populations living under different ecological conditions may differ more from one another other in their ranging patterns and or social organisation than they do from closely related species (Dunbar 1993; Strier 2007). The same may be true for troops within the same population that occupy habitats with differential availability, distribution and quality of resources (e.g., Bronikowski and Altmann 1996), and particularly for species that are behaviourally adaptable. Thus, regardless of the intensity or duration of research, studies with small sample sizes are unable to assess the effects of local habitat differences, or take into account idiosyncratic differences among troops (Isbell and Young 1993). Consequently they may inadequately represent the variation displayed within populations and species (Bronikowski and Altmann 1996; Strier 2007), and may provide limited contributions to primate socioecological theory. Instead long-term studies of multiple troops within a population may be meaningful (Isbell and Young 1993). This thesis represents such a study.

The spatial ecology of baboons in the Cape Peninsula

There is currently little known about the spatial ecology of the Cape Peninsula baboon population. Hall (1962) and Davidge (1978) both published research on aspects of the ecology of troops from this population. However, their studies refer only to troops ranging in the southern-most section (Cape of Good Hope Section; CoGH) of the TMNP, a region of the Cape Peninsula that is predominantly covered by natural habitat and is home to just five of the 16 troops (Beamish 2010) present today. The remaining 11 troops range in a mix of natural, urban and agricultural habitats and their spatial and behavioural ecology is likely to differ markedly from those within the CoGH. In 2000, Kansky and Gaynor defined crude home range estimates for 10 troops based on ad hoc observations of troop presence. However, this approach is not recognised as a repeatable method for quantifying the spatial ecology of a wildlife species.

The absence of spatial data has greatly curtailed the efficacy of baboon management efforts in the Cape Peninsula. To date, most management decisions have been based on best guesses, public sentiments and the opinions of researchers both with and without relevant experience of the local baboon population. It is thus likely that until baboon habitat and land use patterns are incorporated into management plans, baboon management and conservation efforts will remain largely reactionary and serve only to address short term crises as they emerge.

Aims, objectives and chapter outline

The overarching aim of this research is to address the limited understanding of Cape Peninsula baboon spatial ecology by collecting and analysing a population-wide spatial dataset. I use this dataset to address the following key questions:

1. What are the land use patterns of this baboon population?
2. Is there intrapopulation variation in ranging patterns and behaviour and, if so, what explains this variation?
3. How can spatial variables inform baboon management and HBC mitigation efforts?

I organise my thesis into six chapters: this introductory chapter, a methods chapter, three data chapters, and a synthesis chapter. Each of the data chapters contains an introduction and rationale specific to the topic addressed within it so that each chapter can be read in isolation. I provide a summary outline of each chapter below.

In **Chapter 2** I describe the data collection methods, as well as analytical methods common to all chapters. I describe chapter-specific methods in the relevant chapters.

In **Chapter 3** I address key question 1, using models to determine the land use patterns of the Cape Peninsula baboons at a population-level. I assess the landscape features that are most influential in determining baboon distribution patterns (habitat, altitude, slope and water), and investigate the implications of these requirements for land development and baboon management and conservation efforts.

In **Chapter 4** I address key question 2. I analyse troop-level spatial patterns and assess the extent of intrapopulation variation in spatial ecology. I investigate the effects of troop size and human-modified habitat on ranging patterns and determine how ecological variables influence troop behaviour.

In **Chapter 5** I address key question 3. I combine aspects of the data from Chapters 3 and 4 to determine whether the baboon population is overabundant, and to investigate correlations between select spatial variables and levels of HBC across a range of troops. I then introduce new spatial variables to explore how patterns of baboon territoriality, sleeping site use and the spatial responses of troops to season and fire can improve baboon management plans and hence alleviate HBC.

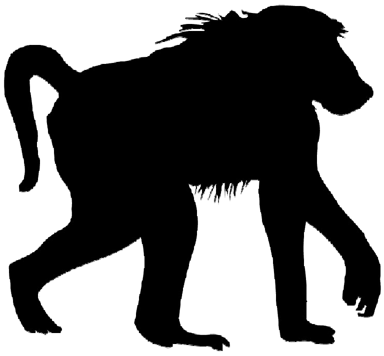
In **Chapter 6** I synthesise the main thesis findings and discuss the overarching management recommendations that emerged. I discuss the limitations of my study and give direction for future research.

Significance

The research is significant for at least four reasons and on multiple scales. First, the research stands to improve the management of this baboon population. By remedying the current paucity of information on baboon spatial ecology this research provides the first empirically grounded spatial recommendations for the short- and long-term management and conservation of baboons in the Cape Peninsula (Chapters 3, 5 and 6). In so doing, the population-level and landscape-level data presented equip all local environmental authorities with the information required to predict and plan for baboon responses to future land development and planned (clearing of alien vegetation; burning of senescent vegetation; plantation harvesting) and unplanned (wild fires) habitat changes. Second, the comprehensive spatial dataset established during this research provides essential baseline data for the design and implementation of future applied research projects for this population (Chapters 3, 4, 5 and 6). Third, by adding to the body of knowledge of baboon land use patterns, ranging pattern determinants, intrapopulation variation and spatial and behavioural adaptability (Chapters 3 and 4), this research provides one of the few population-level contributions to primate socioecological theory. Finally, the research offers an example of how spatial ecology can be used to improve the management and conservation of any wildlife species living in any human-dominated and or human-modified landscapes (Chapter 3, 5 and 6).

Chapter 2

Methods



STUDY SITE

The Cape Peninsula is located at the south-western most point of the African continent, in the Western Cape Province of South Africa (Fig. 2.1). It spans 470 km^2 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 home to the TMNP – one of eight areas of the Cape Floristic Region (CFR), a recognised world heritage site (United Nations 2010).

Landscape, ecology and climate

Summer drought, infertile soils, strong wind regimes and periodic fires (15-20 year intervals; van Wilgen 1982) are the primary drivers of the ecological patterns and processes of the Cape Peninsula (Cowling et al. 1996). The topography is dominated by the Peninsula Mountain chain which stretches from Table Mountain in the north to Cape Point in the south (33°55’-34°21’ S; 18°25’-18°28’ E). A narrow land mass with relatively low maximum altitudes (range: 0-1100 m; Cowling et al. 1996), more than half of the Cape Peninsula comprises natural habitat and has conservation status under the protection of the TMNP. The lower elevations are predominantly urbanised, some of the mid-elevations are used for agriculture and the higher elevations are almost exclusively indigenous fynbos vegetation that is only minimally fragmented by roads (Fig. 2.2). Fynbos (Fig. 2.2a), which dominates the Cape Peninsula flora, is a species-rich but nutrient poor, sclerophyllous shrubland that is a key component of the CFR (Simmons and Cowling 1996). The fauna is characterised by moderate species diversity but low endemism and numbers (Picker and Samways 1996) with chacma baboons being the only primate species present. The Cape Peninsula is devoid of natural baboon predators.

The regional climate is Mediterranean, with hot, dry summers and cool, wet winters - a climatic pattern that results in higher primary production in winter relative to summer (Cowling et al. 1996). Winds during both seasons frequently exceed gale force speeds with north-westerly winds dominating in winter and southerly- and south-easterly winds in summer. Average annual temperatures vary between 18-20 °C with little spatial variation across sites (Cowling et al. 1996). Rainfall does, however, show marked spatial variation, with exceptionally steep rainfall gradients that are influenced by altitude, aspect and other topographic features that trap or divert rain-bearing winds (Cowling et al. 1996).

Fig 2.1. Google Earth imagery of the Cape Peninsula (a) and showing its geographical position within the Western Cape Province, South Africa (b) and within the African continent (c).

Fig. 2.2. Photographs of the Cape Peninsula landscape showing indigenous vegetation (a), low lying urban habitat (b), invasive alien vegetation (c) and agricultural habitat which includes vineyards (d), pine and eucalyptus plantations (e) and an ostrich farm (f).

Human presence

Humans are believed to have been present in the Cape Peninsula for at least 200,000 years. The humans to settle in the area were the hunter-gatherer San who arrived ~20,000 years ago (Parliamentary Commissioner for the Environment 2003). The San were displaced by Khoikhoi pastoralists ~2000 years ago (Parliamentary Commissioner for the Environment 2003). Europeans arrived in 1652, and with them the Cape Peninsula landscape was gradually but substantially transformed for urban and agricultural land use practices (Parliamentary Commissioner for the Environment 2003).

Cape Town city is positioned at the northern edge of the Cape Peninsula, although its suburbs extend south along the coastline towards the CoGH and east across the Cape Flats (Fig. 2.1). Cape Town's population has grown substantially over the last five decades, from 500,000 people in the 1960s (Parliamentary Commissioner for the Environment 2003) to 3 million in 2001 (City of Cape Town 2008). The population is currently estimated to be 3.4 million (City of Cape Town 2008) and is projected to show an overall increase of 17 % by the year 2020 (Statistics South Africa 2007). The Cape Peninsula also serves as a major attraction to tourists, and with 1.8 million international tourists visiting in 2007 alone (City of Cape Town 2008), is considered the second greatest tourist attraction in South Africa after the Kruger National Park (Macdonald and Cowling 1996).

Humans have transformed 37 % of natural habitat in the Cape Peninsula through urbanisation 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). This extensive landscape transformation coupled with the rapid expansion of the human population explains why, despite much of the remaining natural habitat being protected by the TMNP, humans pose the most significant threat to the natural environment (Parliamentary Commissioner for the Environment 2003).

Food availability

The Cape Peninsula offers baboons a diversity of natural and anthropogenic food sources. Natural food sources include plant matter from natural vegetation 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*), 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 in backpacks, picnics and motor vehicles).

STUDY ANIMALS

Baboons

With a near continent-wide distribution in Africa baboons are among the most widespread of all primates. These large, semi-terrestrial monkeys occupy a diverse range of habitats including deserts, savannahs, grasslands and forests (Altmann and Altmann 1970; Estes 1991; Jolly 1993; Kingdon 1997; Swedell 2011). Their success is attributed to their agility, dexterity, high levels of sociality and co-operation, combined with dietary and behavioural flexibility (Else 1991; Bronikowski and Altmann 1996; Swedell 2011).

Fig. 2.3. Study animal: an adult male chacma baboon.

Baboons are not considered to be territorial primates (Stoltz and Saayman 1970; Mitani and Rodman 1979; Lowen and Dunbar 1994) although territoriality has been found in certain cases (e.g., Hamilton et al. 1976). As for other primates, baboon ranging patterns are largely a function of habitat quality and troop size (Swedell 2011) and in several studies baboons have been shown to conform to expected theoretical relationships among troop size and ranging variables (*sensu* Chapman and Chapman 2000). For example, Barton et al. (1992) showed that home range sizes and day range lengths are positively correlated with troop size and negatively correlated with habitat quality for yellow baboons (*P. cynocephalus*), and that across 18 populations of *Papio* troop size accounted for 48 % of the variation seen in day range length. Furthermore baboon troop sizes vary with habitat quality, with larger troops of baboons found in fertile regions like the Okavango Delta (Hamilton et al. 1976) compared with smaller troops found in more arid and seasonal environments like the Namib Desert (Hamilton et al. 1976) and the Drakensberg Mountains (Whiten et al. 1987; Henzi et al. 1992;

Henzi and Lycett 1995). Deviations from these theoretical expectations have been found however (e.g., Henzi et al. 1997b), suggesting that socioecological relationships are not fixed for baboons. Seasonal changes in resource availability also affect baboon range size, range occupancy and ranging patterns (e.g., Altmann and Altmann 1970; Bronikowski and Altmann 1996; Gwenzi et al 2007). Based on their research on yellow baboons, Bronikowski and Altmann (1996) suggested that baboons employ multiple and interrelated responses to ecological variability including troop size and behaviour changes and home range shifts.

Baboons in the Cape Peninsula

The Cape Peninsula is currently (August 2011) home to approximately 460 chacma baboons (EK Beamish, UCT, unpubl. data; Fig. 2.3) living in 16 troops. As a result of urban sprawl to the east, these troops form a geographically isolated population. At the onset of the study period (March 2006) the population comprised 354 animals (Beamish 2010) and was split into 12 troops ranging in size from 16-115 baboons (Fig. 2.4). The troops are distributed from the Tokai plantation in the southern suburbs of Cape Town down to the southernmost tip of the CoGH. The troops are able to range freely in approximately 250 km^2 of natural habitat, with urban habitat and neighbouring troops serving as the only major barriers to movement.

My overarching research objective was to research the spatial ecology of the 12 troops present when I began data collection in 2006. Several circumstances, however, precluded data collection for three troops: Klein Olifantsbos (KOB), Groot Olifantsbos (GOB) and John Travolta (JT; Fig. 2.4). KOB is considered to be a wild troop that is not habituated to human presence and thus the TMNP authority disallows any human access to this troop with the intention that they retain their fear of humans. GOB is a troop that regularly splinters into small raiding groups when it leaves the CoGH to raid in the villages of Scarborough and Misty Cliffs. While an important troop to study, this behaviour typically strands researchers with a random subset of the troop and I lacked both manpower and a sufficient number of tracking collars to track each sub-troop. JT was the smaller of the two Tokai troops (n=15) present in Tokai at the start of the study, and routinely raided the residential area of Zwaanswyk Road in upper Tokai. The large size of the erven (plots of land marked off for building purposes) in this area combined with high walls and electric fencing between neighbouring erven prevented me from following this troop on foot. To overcome these problems I, with assistance from my colleague Esme Beamish, collared two animals in the JT troop between August 2007 and October 2008. The first baboon remained collared for one month (August-September 2007), but we removed his collar when he sustained a neck injury during a fight with another baboon. We collared a second male in July 2008 but he was killed three months later after being struck by a motor car. These events prevented me from obtaining sufficient spatial data for this troop.

My nine study troops include Tokai (TK; Fig. 2.4), Slangkop (SK), Da Gama (DG), Red Hill (RH), Smitswinkel Bay (SWB), Plateau Road (PR), Kanonkop (KK), Buffels Bay (BB) and Cape Point (CP). The troops vary in size and demographic structure (Table 2.1).

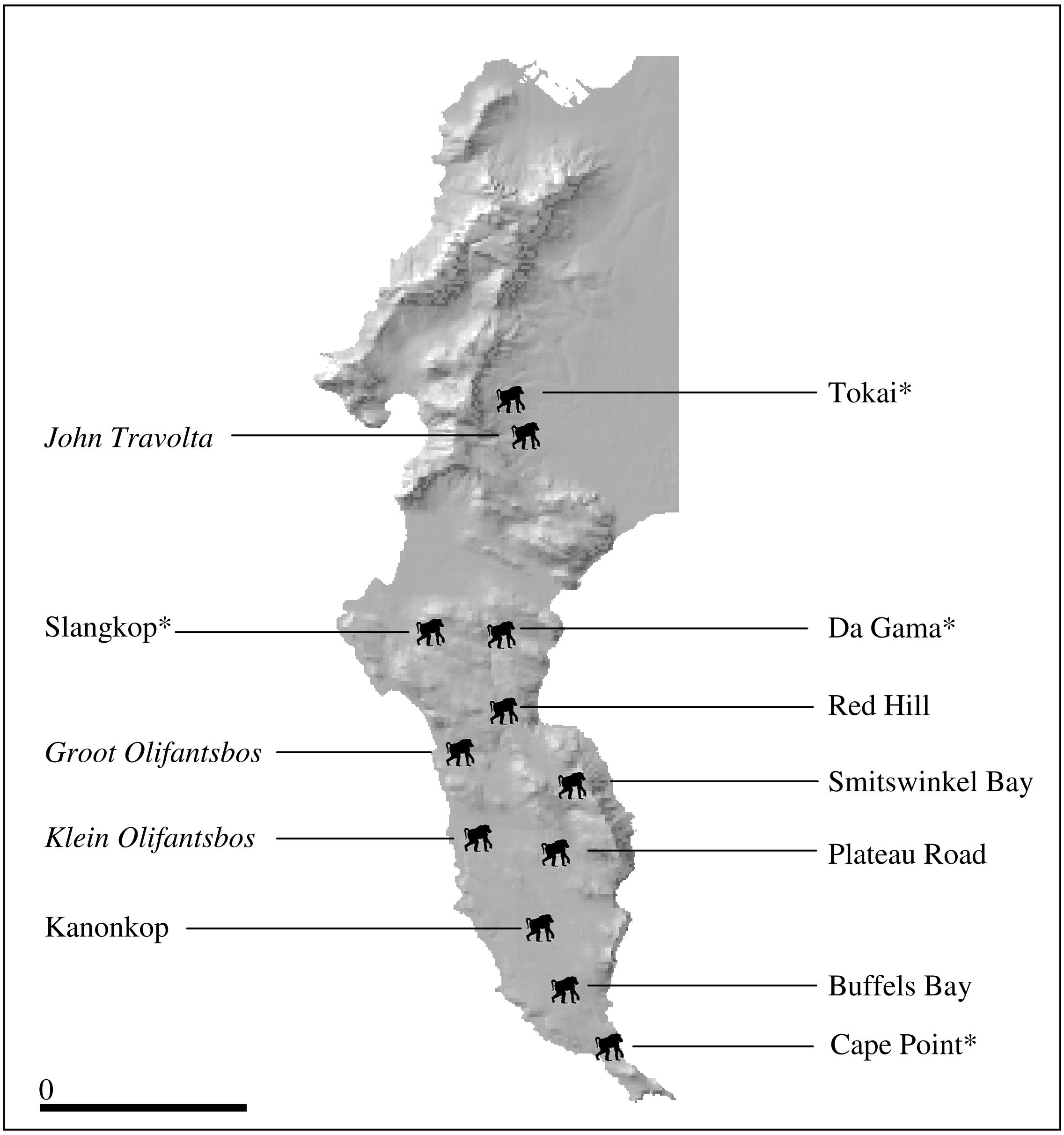


Fig. 2.4. A map of the Cape Peninsula illustrating the general locations of the 12 chacma baboon troops present at the time of data collection (baboon icons). Asterisks indicate the troops that are managed by baboon monitors, and italicised troop names indicate troops not included in this study.

The troops can be broadly categorised according to the land use category in which they interact with humans, the type of anthropogenic food sources available within their respective ranges, whether and when monitors are employed to reduce human baboon conflict (e.g. raiding) and the strategy employed by the monitors to reduce spatial overlap between humans and baboons. Three troops range within the CoGH, six troops range outside of it. All troops interact with humans albeit to different degrees and with different human demographics. All troops but one raid, with a variety of raiding behaviours presented. Four troops are managed by baboon monitors – people employed by the local management authorities to minimise HBC by herding baboons away from urban habitat (Kansky and Gaynor 2000; van Doorn 2009). Two different monitoring strategies are used. The first strategy requires constant herding of the troop within their home range to areas that have minimal overlap with urban and agricultural habitat and thus reduced scope for conflict (van Doorn 2009). The second strategy is less intrusive on baboon movement patterns and requires that monitors effectively 'hold the line' between a troop's home range and the adjacent urban habitat. In this case the monitors prevent the troop from entering the urban environment but have a negligible effect on troop movement beyond the urban edge. The choice of monitoring strategy is based on the spatial and ranging characteristics of the troop concerned in addition to financial constraints that limit the availability of monitors and logistical constraints that reduce the effectiveness of monitors to deter baboons.

Two of the study troops, PR and DG, were studied in 2004 and 2005 as part of a doctoral thesis within the same research unit (van Doorn 2009). The data collection methods for this thesis match mine – described below – and the data were made available to me so that I could include these two troops within my spatial analyses.

STUDY PERIOD

I commenced data collection in March 2006 and completed collection in August 2009. I included the spatial data collected during 2004 and 2005 as part of van Doorn's (2009) study in my analyses. Logistical and financial constraints prevented me from sampling all troops simultaneously, and in Table 2.1 I provide the time periods over which I studied each troop. Importantly there was no interannual variation in mean rainfall (*Kruskal-Wallis test*: $H_{(5,n=2191)}=6.6317$, $p=0.250$; Fig. 2.5), mean maximum (analysis of variance (ANOVA): $F_{5,2185}=0.8219$, df=2185, $p=0.534$; Fig. 2.6) or mean minimum temperatures (ANOVA: $F_{5,2185}=1.5676$, df=2185, $p=0.166$; Fig. 2.6) across all study years. Consequently, I did not consider climatic variables to be an important source of variation in comparisons between troops across different years.

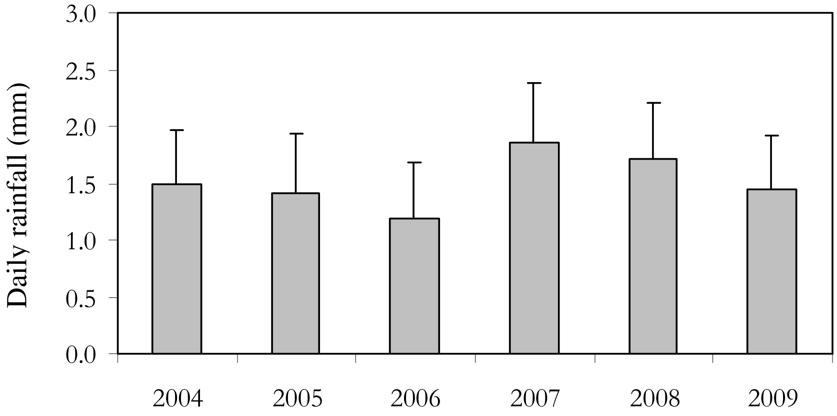


Fig. 2.5. Mean±SEM of the daily rainfall recorded during the study years. Rainfall did not differ significantly across the years.

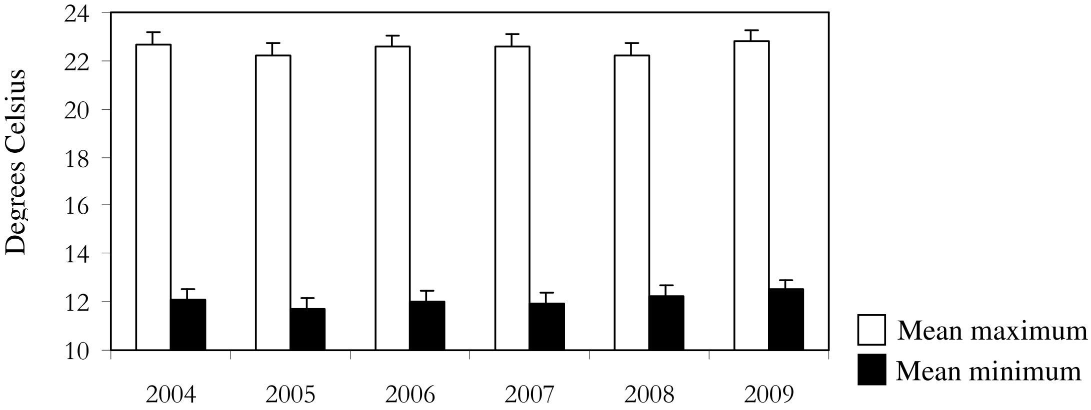


Fig. 2.6. Mean±SEM of the maximum and minimum temperatures recorded during the study years. Temperatures did not differ significantly across the years.

DATA COLLECTION

To determine baboon ranging patterns I recorded Global Positioning System (GPS) data points for each troop. I collected GPS data points using handheld devices (Garmin eTrex) operated by field researchers (as part of this study, and studies by Angela van Doorn and Matthew Lewis), tracking collars (see *Baboon Collaring* for details) and using a combination of both methods. Table 2.2 lists the GPS data collection methods employed for each troop.

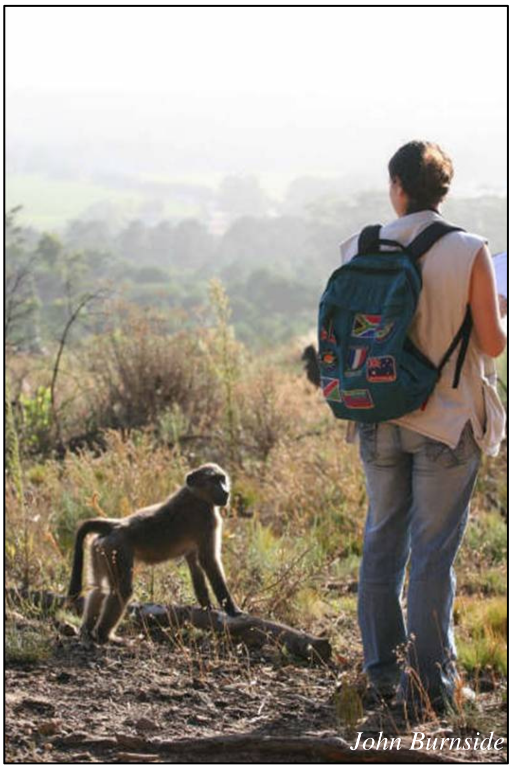


Fig. 2.7. Data collection by field researcher, TS Hoffman. All study troops were habituated to close (<10 m) observation when the study began.

Field researchers (Fig. 2.7) 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, I 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. I tracked troops for full-days (sunrise to sunset with GPS readings every 20-minutes; Table 2.2) 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.

Table 2.1. Details of data collection time periods, troop sizes at time of data collection and general locations of each troop as well as the land use category in which troops interact with humans, the type of anthropogenic food sources accessed and troop management details. Troops are listed chronologically by data collection time period.

Time period	Troop	Troop size	Location˜	Human interactions °	Raiding behaviour "	Management	
						Monitors	Monitor strategy
2004 - 2005	DG	36	Outside CoGH	U	B, H, U	Annual	Herd-and-hold
	PR	40	Outside CoGH	F, T, U	B, C	-	-
2006 - 2007	TK	115	Outside CoGH	F, U	B, C	Winter	Hold-the-line
2007 - 2008	CP	22	Inside CoGH	T	B, H, U	Annual	Herd-and-hold
	BB	16	Inside CoGH	T	B, H, U	-	-
	KK	49	Inside CoGH	T, U	N	-	-
2008 - 2009	SWB	26	Outside CoGH	T, U	B, H, U	-	-
	RH	16	Outside CoGH	U	B, H, U	-	-
	SK	24	Outside CoGH	U	B, H, U	Annual	Herd-and-hold

˜ CoGH=Cape of Good Hope Section of the Table Mountain National Park

° Human interactions: F=Farmers, T=Tourists, U=Urban residents

" Raiding behaviour: N=None; B=Bins; C=Crops; H=Humans, U=Urban (includes residential properties and restaurants)

Table 2.2. Details of GPS locations, collection methods, data type and principle investigator (PI) for each study troop. Troops are listed chronologically by data collection time period.

		Data collection days*													
		Summer Dec - Feb		Autumn Mar - May		Winter Jun - Aug		Spring Sep - Nov			GPS locations				
Time period	Troop	Full	Part	Full	Part	Full	Part	Full	Part	Total	Winter	Summer	Total	Collection method~	PIº
2004 - 2005	DG	24	2	23	24	13	32	6	10	*134*	921	1454	*4307*	FR	2
	PR	21	10	26	18	36	41	15	3	*170*	1921	1496	*5018*	FR	2
2006 - 2007	TK	15	17	16	18	24	32	15	-	*137*	1237	701	*2990*	FR	1
2007 - 2008	CP	18	58	-	91	13	60	-	90	*330*	621	819	*2282*	FR and C	1
	BB	24	5	24	4	11	3	-	-	*71*	321	353	*1882*	FR	1, 3
	KK	13	1	-	-	45	-	31	1	*91*	334	390	*2543*	FR	1, 3
2008 - 2009	SWB	12	77	-	91	14	38	-	92	*324*	433	664	*1907*	C	1
	RH	14	74	-	27	15	38	-	79	*247*	457	682	*1668*	C	1
	SK	15	70	-	91	15	53	-	90	*334*	589	537	*2021*	C	1

* Full = days where troops were tracked from morning to evening sleeping site with GPS data points recorded every 20-minutes; Part = days where troops were tracked baboons for ≤half the day or when GPS data points were recorded at 3-hourly intervals

~ FR=Field researcher; C=GPS tracking collar

º All students of the Baboon Research Unit, UCT. 1=Tali Hoffman; 2=Angela van Doorn; 3=Matthew Lewis

I included only GPS data points that had an estimated level of accuracy of ≤10 m. I continued to collect data for each troop until either the number of new cells (see *Data Analysis*) entered per month reached an asymptote or until I had collected a full year of data. I considered the asymptote to be reached when the number of new cells entered per month increased by <5 % for two months or more (Appendix 1; see Chapter 4). In total, I 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 (troop-specific details in Table 2.2).

Baboon collaring

Physical limitations imposed by the landscape (e.g., impassable mountain terrain and impenetrable vegetation) and threats to personal safety prevented me from following all troops on foot and necessitated the inclusion of tracking collars as a data collection technique (Fig. 2.8). I used tracking collars to collect datasets for four of the nine study troops (SK, RH, SWB and CP). I collared four baboons in total – two adult females and two incipient sub-adult males (Altmann 1980; Table 2.3). I only considered collaring adult females that were not visibly pregnant, lactating or weaning an offspring.

Table 2.3. Details of the collaring procedures used for each collared animal including capture methods and ratio of body weight to collar weight.

Troop	Collared individual*	Capture method for collar deployment	Capture method for collar removal	Baboon mass at collar deployment	Collar mass: body mass (%)
CP	AF	Darting	Darting	16 kg	3.8 %
SK	AF	Darting	Darting	20 kg	3.0 %
SWB	SAM	Darting	Cage Capture	23 kg	2.6 %
RH	SAM	Darting	Cage Capture	30 kg	2.0 %

* AF=Adult female; SAM=sub-adult male

Collaring procedures

Prior to collar deployment I spent time with each troop to establish which baboon was the most suitable candidate for collaring (sub-adult males and non-pregnant, non-lactating females). Target individuals were either cage captured and then immobilized using a pole syringe (Fig. 2.8; Table 2.3) or darted with a low impact 1.5 ml plastic dart with a pressurising chamber (Daninject or Telinject). Qualified veterinarians (Dr Hamish Currie, Dr Dave Zimmerman, Dr Markus Hofmeyr and Dr Mark Dittberner) experienced in large mammal immobilisation and capture, performed all darting and pole syringing procedures involving anaesthetic drugs. Each animal received a single intramuscular dose of Ketamine (2-5 mg/kg) and Medetomidine (0.02-0.07 mg/kg). Once immobilised, I fitted the collar while the veterinarian continued to monitor the baboon's vital signs. Once I had secured the collar the veterinarian administered Atipamezole (at 5x the Medetomidine mg dose) to reverse the effects of anaesthesia. I then placed the collared baboon in a holding cage to allow for a full recovery prior to releasing it in the immediate vicinity of its troop. I visited collared animals on a weekly basis to ensure that they were with their troop and thus that they were providing a reliable proxy for troop movement. Furthermore, I checked if the animals were injured in any way or showing signs of discomfort resulting from the collar. At the end of the data collection period I removed the collars from the animals following the same capture and immobilisation process described above.

Collar specifications

The tracking collars were designed specifically for baboons by Africa Wildlife Tracking. They were coloured to blend in with the grey colouration of baboon fur making them as inconspicuous as possible. The collar itself was made from strong and durable material that would neither break nor tear. The mass of each collar was approximately 0.60 kg and the mean mass of baboons wearing the collars was 22.3±5.8 kg SEM (range: 16-30 kg, n=4 baboons; Table 2.3). Thus collar mass expressed as a percentage of body mass was 2.8±0.7 % SEM (range: 2.0-3.8 %, n=4 baboons) which is within the tolerable weight limit (the total weight that can be added to an animal in the form of a transmitter without causing impediment to behaviour, survival or well-being), defined as ≤5 % for mammals and birds (White and Garrott 1990).

The tracking units were made with the latest GPS and Global System for Mobile Communication (GSM) technology. Once I had fitted the collar to the animals I could remotely adjust the frequency of collar readings (through cellular communication) allowing me to record both fine- and broad-scale movement patterns and to adjust the first and last readings of the day in accordance with day length changes throughout the year. The collars included a Very High Frequency (VHF) tracking component that could be used in the event of GPS failure, or to locate the animals during their routine checks. The potential of the collar battery to record approximately 2000 GPS data points enabled me to collect a minimum of one year's spatial data at the resolution I required for spatial analyses.

Effects of collars on collared animals

Upon recovery from the effects of anaesthesia the baboons would initially attempt to remove the collar and appeared to be agitated by the novel stimulus. However this behaviour typically only lasted for a few hours and baboons seldom handled the collar again after the first 24 hours. At no stage during the study period did any of the four collared baboons display any abnormal behaviour or sustain any injury related to the collar. Furthermore upon removal of the collar the attendant veterinarian inspected the neck of the animal and found none of the collared individuals to show any signs of chaffing or other injuries that could be related to the wearing of the collar. In 2008 the Cape of Good Hope Society for the Prevention of Cruelty to Animals (SPCA) in conjunction with the National SPCA conducted an independent assessment of the collared baboons and confirmed that the collars did not have any obvious adverse effects on the animals' behaviour or well-being. The research complied with protocols approved by the ethics committees of UCT and South African National Parks (SANParks).

Fig. 2.8. The procedure followed to collar baboons. Baboons identified as suitable for collaring (adult females and sub-adult males) were darted or cage captured and anaesthetised by a veterinarian (Dr Hamish Currie pictured; a). Once anaesthetised, the animal was weighed and measured and a GPS/GSM/VHF tracking collar was fitted to its neck (b). Care was taken to ensure that the collar was neither too tight to restrict breathing or movement, nor too loose that it might to fall off. Once the collar was fitted the anaesthetic drugs were reversed and the animal was placed in a cage to recover fully from the anaesthesia (c). Once recovered, the animal was released back into its troop (d) and frequently monitored to ensure the collar was not negatively affecting its welfare or behaviour.

DATA ANALYSIS

Prior to data analysis I tested whether the two data collection methods used (field researchers vs. tracking collars) produced comparable ranging patterns by analysing their estimates of (1) home range size and home range habitat cover and (2) troop day range length and travel rate. For (1) I followed the methods described in Chapter 4 to calculate the home range size and home range habitat cover for CP using field researcher data, and tracking collar data independently. I selected CP for this analysis as it was the only troop where both data collection methods were employed on a long-term basis (Table 2.2). My rationale for this analysis was that should the two data collection methods yield home ranges with significantly different boundaries, then I would expect a concomitant difference in the habitat composition of the respective home ranges. However, I found <5 % difference in the home range sizes calculated from the field researcher data compared to the tracking collar data. There was also <0.01 % difference in the composition of habitat cover within each home range estimate. For (2) I analysed 14 days of spatial data for SK when a field researcher (Tarryn Quayle, UCT, unpubl. data) and a tracking collar recorded GPS readings simultaneously at hourly intervals. I used *t*-tests to determine whether the two methods yielded significantly different measures of daily ranging patterns and found them to be comparable in their estimates of troop day range length (t=0.13, n=14 days, p=0.895; Fig. 2.9) and travel rate (t=-0.37, n=14 days, p=0.712; Fig. 2.10). Based on these analyses I concluded that troop ranging patterns were comparable despite differences in data collection methods.

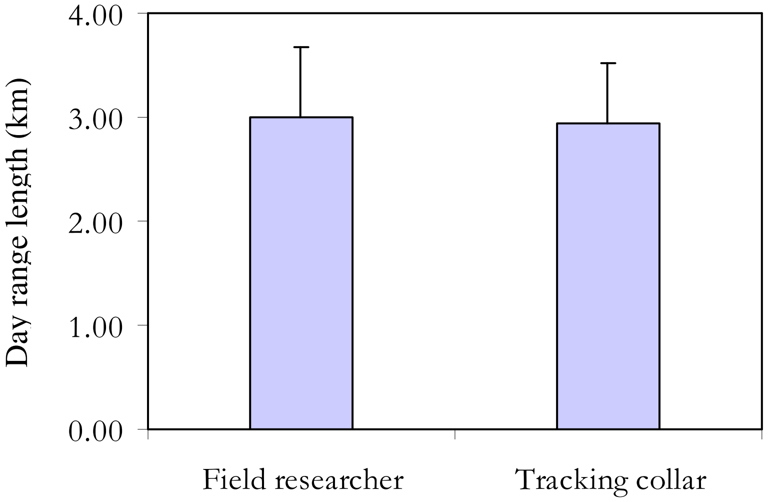


Fig. 2.9. Day range lengths for the SK troop calculated using data recorded by a field researcher and data recorded by a tracking collar.

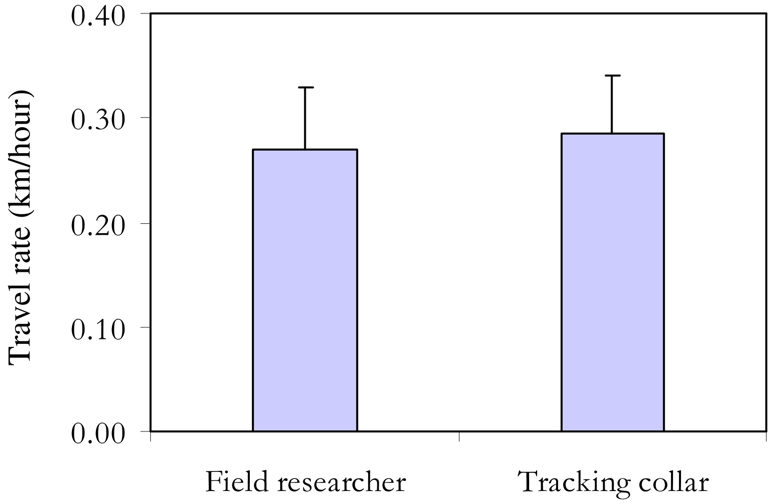


Fig. 2.10. Travel rates for the SK troop calculated using data recorded by a field researcher and data recorded by a tracking collar.

I describe chapter-specific analyses in the methods section of the relevant chapter. However, across all chapters, I analyse most of the spatial data using a matrix of grid cells spanning the full extent of the Cape Peninsula. Prior to analysis I assigned relevant explanatory topographic, habitat and management variables to each of these grid cells.

Cape Peninsula grid system

I used the Repeating_shapes extension to ArcView (Jenness 2005) to generate the Cape Peninsula grid system (Fig. 2.11), which comprised a matrix of cells that were 0.023 km^2 in area (150 m×150 m). Once created, I used an outline of the Cape Peninsula to clip the grid so that it did not extend beyond the coastline (Fig. 2.11b). This clipping process reduced the area of the cells bordering the coastline to <0.023 km^2. The grid size I used was smaller than those of Whiten et al. (1987; 1 km^2) and Henzi et al. (1992; 4 km^2) with the total area of each cell being sufficient in size to encompass the average troop spread of the largest troop (mean±SEM: 0.021±0.011 km^2, n=5 spreads).

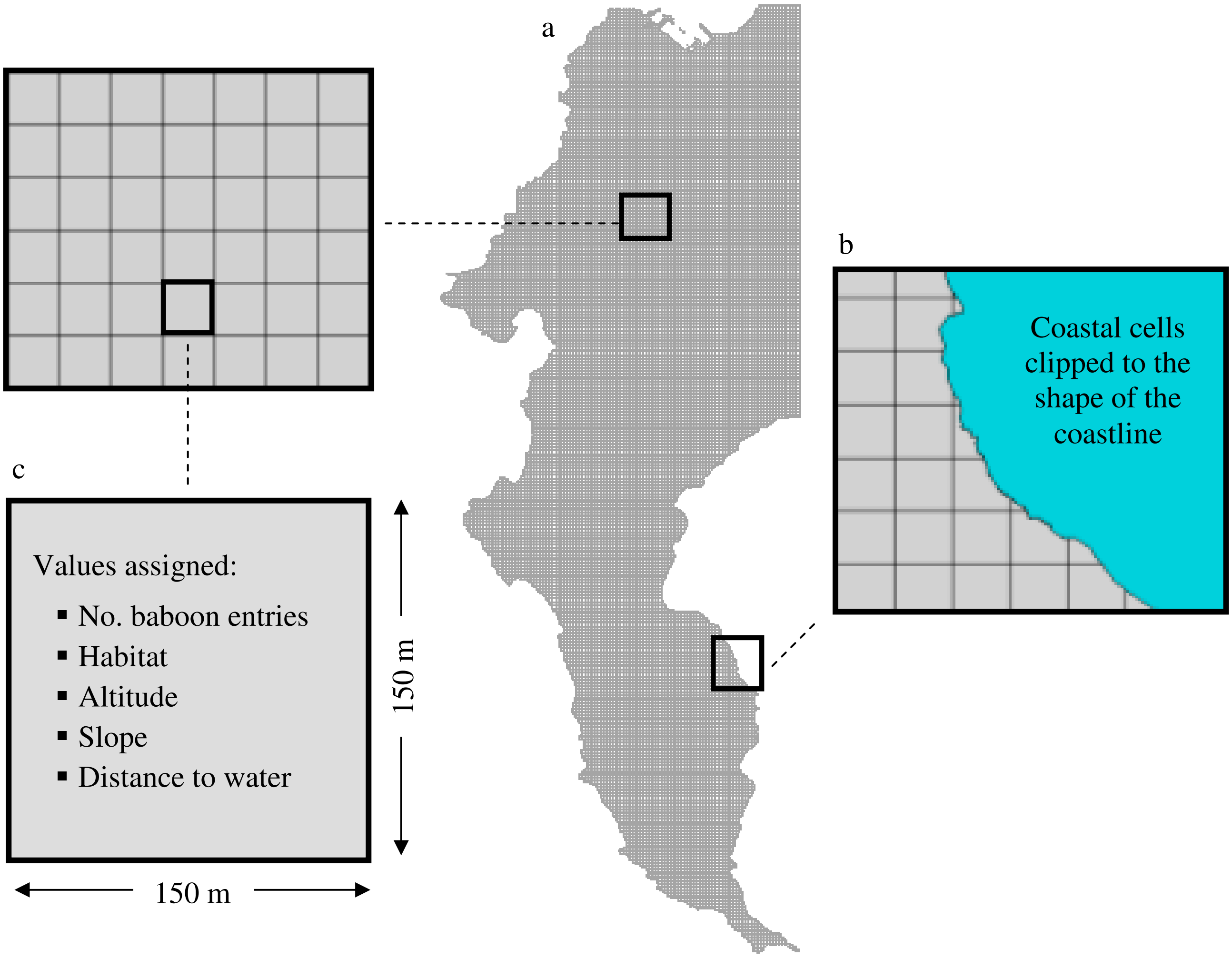


Fig. 2.11. The grid system used for data analysis that covers the full extent of the Cape Peninsula (a). Each cell within the grid system covers a 0.023 km^2 area, except for coastal cells that are clipped to the shape of the coastline (b). Each cell is classified according to its use by baboons, its habitat and its topography (c).

Topographic variables

I calculated the Mean_Altitude of each cell (Fig. 2.12a) using a 30 m digital elevation model (DEM; Environmental Systems Research Institute. 1998. CSDGM FGDC Metadata DTD 3.0.0 19981217). I used the same DEM to determine the Slope (Fig. 2.12b) of each cell, and calculated distances to permanent water sources (Distance_to_Water) using a shapefile (glcrveg; SANParks, unpubl. data) that details drainage systems in the region (Fig. 2.12c). I used a map of the spatial characteristics of annual rainfall patterns in the Cape Peninsula (raindatacont; SANParks, unpubl. data) to determine the mean rainfall for all grid cells. Despite spatial variation in rainfall patterns across the Cape Peninsula, all baboon home ranges fell within the 600-800 mm/year category with two exceptions: (1) a very small patch (five grid cells) within the SWB home range that fell within the 800-1000 mm/year category, and (2) the TK home range where the majority of cells fell within the range of 900-1200 mm/year, and five grid cells fell within the 1200-1300 mm/year range. Based on the homogeneity of rainfall patterns within the study area I excluded mean rainfall of grid cells from further analyses.

Habitat variables

I used GIS maps containing landscape information specific to the Cape Peninsula to categorise the habitat of each grid cell at both broad and fine levels. In addition, I used observer records of location-specific habitats, and information gleaned from digitisation of the Cape Peninsula using Google Earth imagery to verify the habitat categorisation of each cell. I used 2009 Google Earth imagery to coincide with my final data collection year. For each level of analysis I calculated the percentage cover of each habitat within every cell using the Intersect Function of the Geoprocessing Wizard in ArcView 3.3 (Environmental Systems Research Institute, Redlands, California). I converted the percentage values to categorical variables, assigning habitat categories based on the dominant habitat (>50 % of cover) within each cell.

Fig. 2.13 provides a schematic of the different habitat categories and sub-categories assigned to each cell. At the broadest level (broad-scale habitat) I divided cells into two mutually exclusive categories: natural and human-modified habitat (Fig. 2.14a). I then sub-categorised both of these habitats to include finer scale classifications (fine-scale habitat). The human-modified category comprised three mutually exclusive fine-scale categories: urban habitat, agricultural habitat, and invasive alien vegetation (Fig. 2.14b). Urban habitat consisted of all urban areas delineated in the City of Cape Town's (CoCT) Generalised Zoning shapefile, cells with human-made structures such as buildings, gardens and grass patches adjacent to buildings, and cells dominated in cover by roads and sports fields. Agricultural habitat included plantations – delineated using a shapefile (*lease_2006_06_28*; SANParks, unpubl. data) – and vineyards and an ostrich farm, which I mapped digitally using Google Earth.

I was unable to use existing datasets of the spatial characteristics of invasive alien vegetation because the measurements contained in those datasets were not comparable for different invasive alien species. However, on account of their marked structural differences, patches of invasive alien vegetation are clearly distinguishable from patches of indigenous vegetation in satellite imagery. So I conducted a digital survey using Google Earth to generate a current and comparable map of the range, extent and densities of all invasive alien species in the Cape Peninsula. I visited areas of the Cape Peninsula on foot to confirm the species of invasive alien vegetation located using the Google Earth survey. Following Campbell (1985) I determined the dominant invasive alien species, and the ground cover and plant height of that dominant species for every invasive alien vegetation patch, and subsequently ascribed those data to the relevant grid cells.

The natural habitat category comprised two fine-scale categories (Fig. 2.14): broad habitat unit (BHU: Mucina and Rutherford 2006) and structural vegetation (Cowling et al. 1996). The BHU (Fig. 2.14b), which is considered the most comprehensive classification system developed to date, distinguishes specific vegetation units, where a unit is 'a complex of plant communities ecologically and historically (both in spatial and temporal terms) occupying habitat complexes at the landscape scale' (Mucina and Rutherford 2006: pg 16). This system comprises recognisable vegetation complexes that are similar in their structure, nutrient levels and general ecological properties (Mucina and Rutherford 2006). I determined the structural vegetation of each cell (Fig. 2.14c) in accordance with the approach devised by Cowling et al. (1996) that divides fynbos into structural communities based on cover abundance, species dominance and structural characters. This vegetation definition is used most commonly in conservation management (Mucina and Rutherford 2006) and thus its use in these analyses allows patterns of habitat use by baboons to be identified at a level that is meaningful to environmental managers. Finally, because fynbos vegetation exists in a fire-driven ecosystem, I used datasets detailing the annual fire history in the Cape Peninsula from 1962-2009 to calculate the age of each natural habitat cell (Fig. 2.15a).

Land management and ownership

To incorporate a level of analysis that would be both relevant and meaningful to local environmental managers I used a shapefile containing erf information (*glerven_icmp*; SANParks 2006-2009) to identify the *land manager* (Fig. 2.15b) and *land owner* (Fig. 2.13c) of each cell.

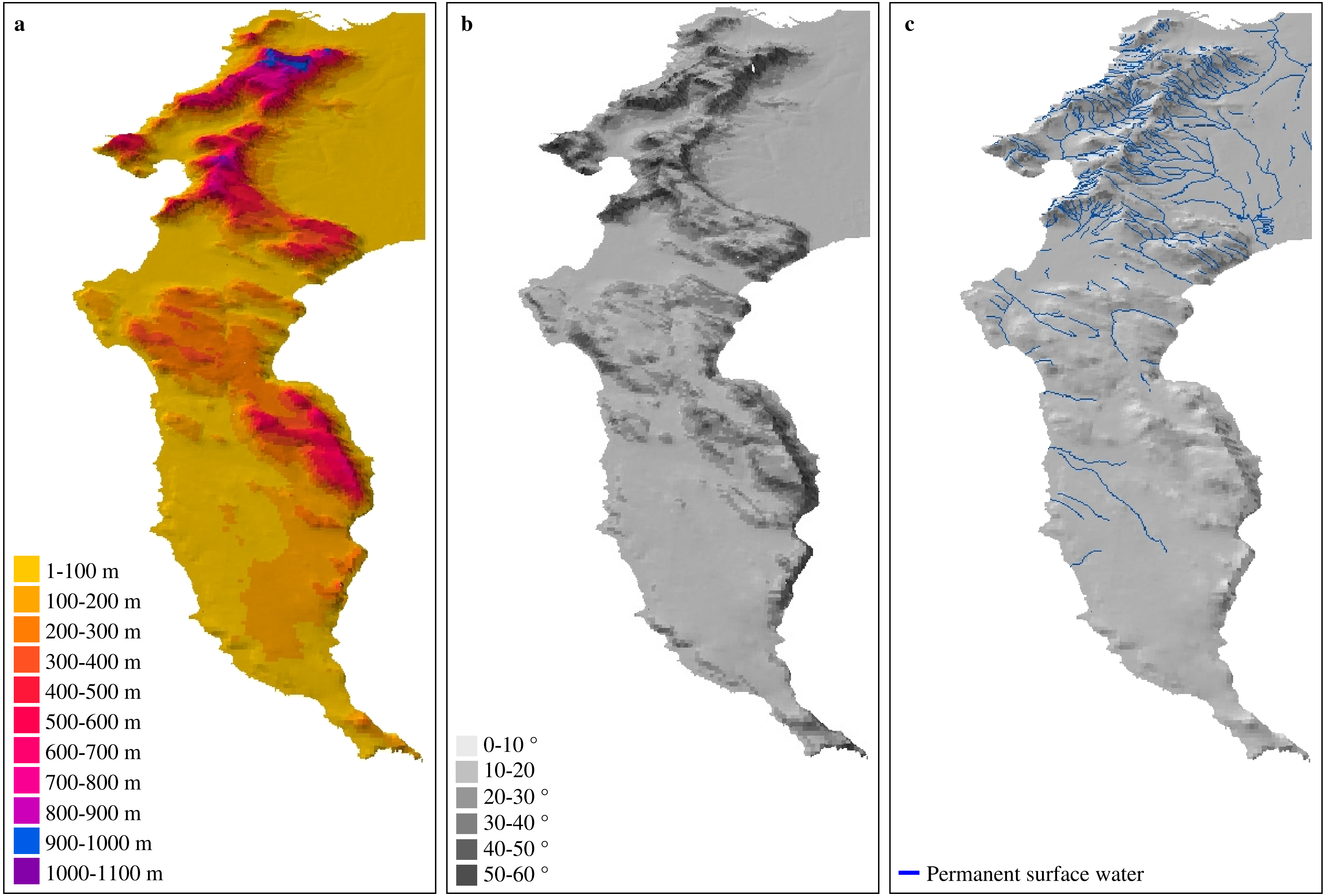


Fig. 2.12. 3D maps of the Cape Peninsula depicting (a) the altitude, (b) the slope and (c) the permanent surface water.

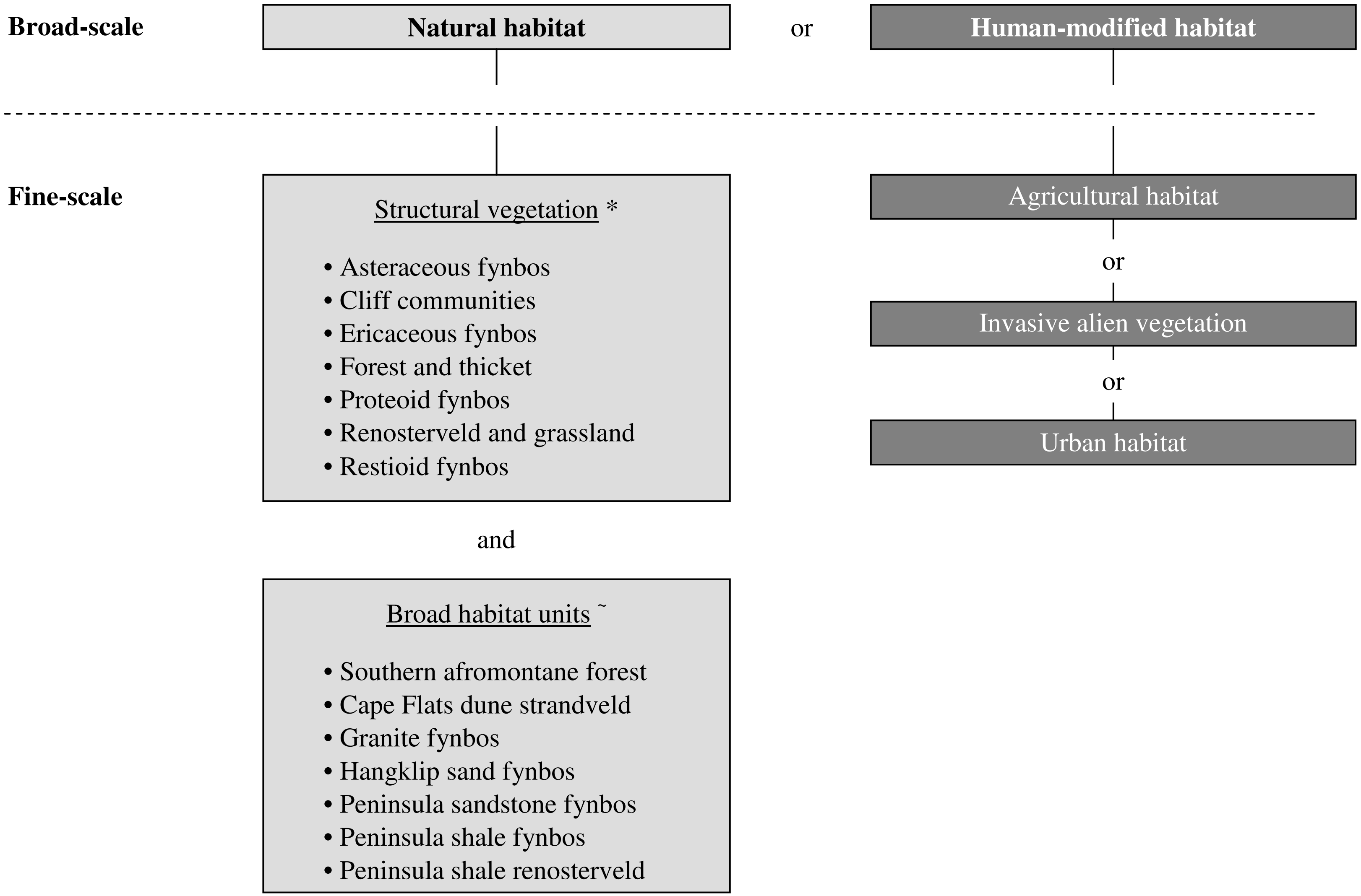


Fig. 2.13. Schematic of the categories used to assign broad- and fine-scale habitats to each cell. Cells broadly categorised as ‘natural habitat’ contain two different (but spatially overlapping) fine-scale habitats. I use ‘broad habitat units’ for analyses in Chapter 3 and ‘structural vegetation’ in Chapter 5. Cells broadly categorised as ‘human-modified habitat’ contain spatially distinct fine-scale habitats. Spatial representations of these categories are presented in Fig. 2.10. * adapted from Cowling et al. (1996); ˜ adapted from Mucina and Rutherford (2006).

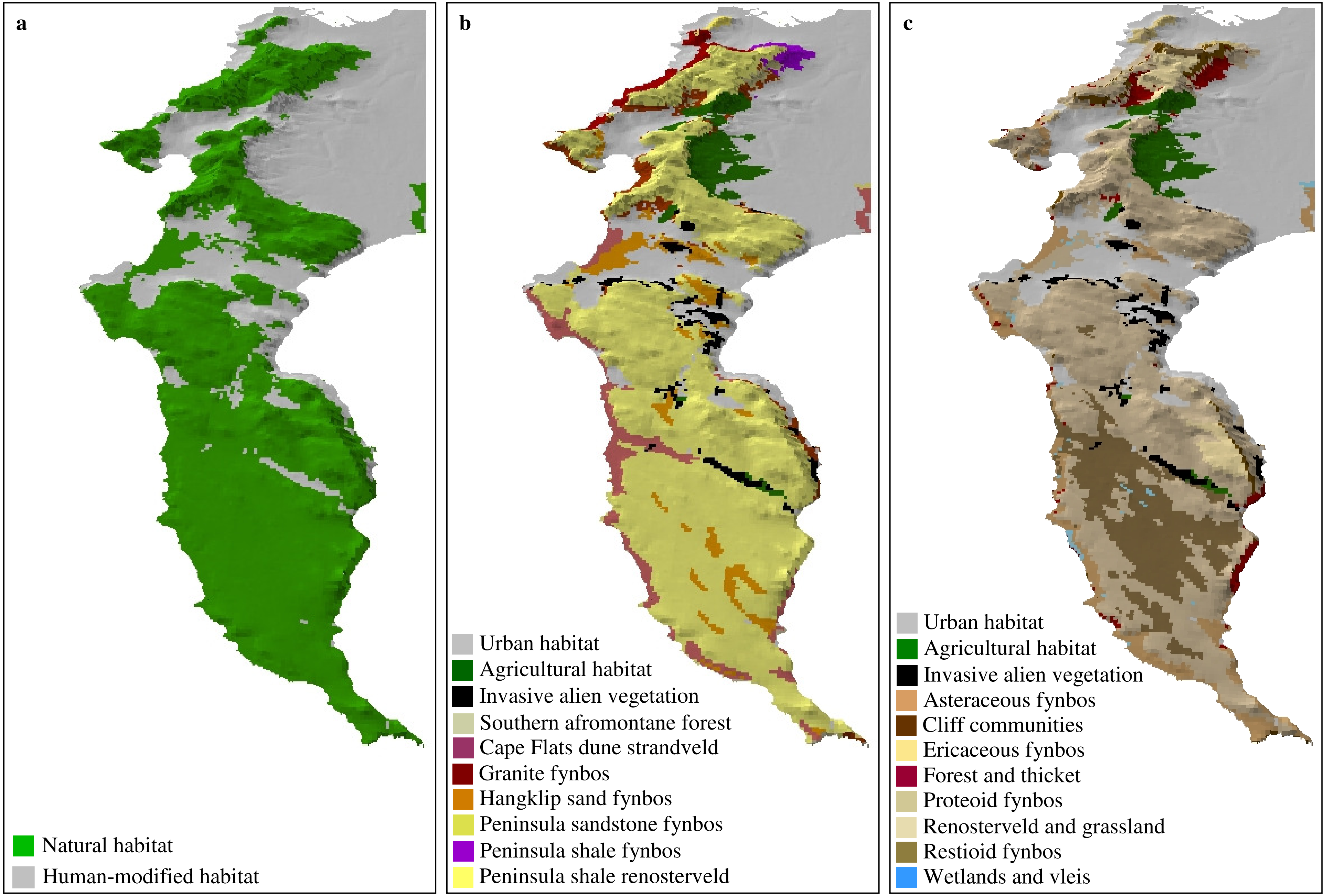


Fig. 2.14. 3D habitat maps for the Cape Peninsula including (a) broad-scale habitats, (b) fine-scale habitats with 'natural habitat' categorised as 'broad habitat units' and (c) fine-scale habitats with 'natural habitat' categorised as 'structural vegetation'.

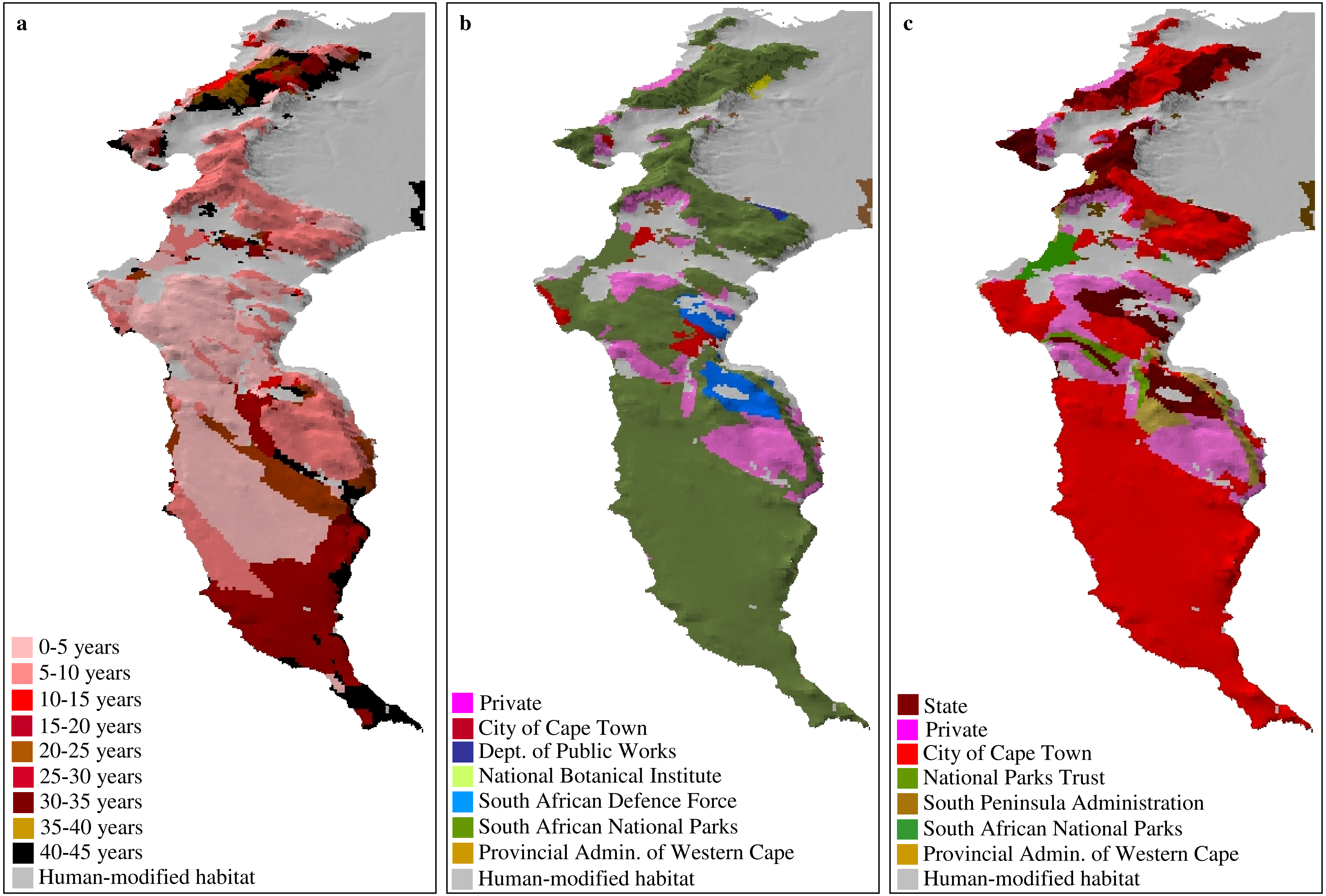
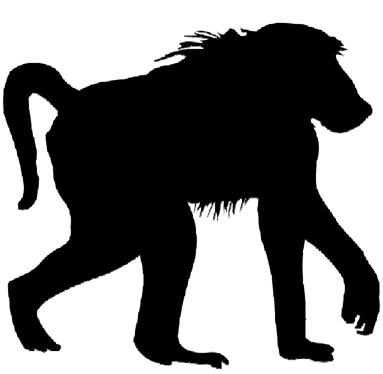


Fig. 2.15. 3D maps of the Cape Peninsula depicting (a) the age categories, (b) the managers and (c) the owners of all natural habitat.

Chapter 3

The land use patterns of the chacma baboon population of the Cape Peninsula



ABSTRACT As urban and rural land development become widespread features of the global landscape so an understanding of the spatial requirements of displaced and isolated wildlife species becomes increasingly important for conservation planning. In the Cape Peninsula, rapid human population growth and associated urban and rural land transformation, threaten the sustainability of the local chacma baboon population. In this Chapter I analyse spatial data collected from nine of the 12 extant troops to determine population-level patterns of landscape selection. I use hurdle models to ascertain the key landscape features influencing baboon occurrence and abundance patterns on two hierarchical spatial scales. Both spatial scales produced similar results that were ecologically reliable and interpretable. The models indicated that baboons were more likely to occur, and be more abundant, at low altitudes, on steep slopes and in human-modified habitats. The combination of these landscape variables provides baboons with access to the best quality natural and anthropogenic food sources in close proximity to one another and suitable sleeping sites. Surface water did not emerge as an influential landscape feature presumably as the area is not water stressed. The model results indicate that land development has pushed baboons into increasingly marginal natural habitat while simultaneously providing them with attractive, predictable and easily accessible food sources in human-modified habitats. The resultant competition for space between humans and baboons explains the high levels of human-baboon conflict and further erosion of the remaining fragments of land is predicted to exacerbate competition. This chapter demonstrates how the quantification of animal land use patterns can provide a mechanism for identifying priority conservation areas at the human-wildlife interface.

INTRODUCTION

The survival and long-term persistence of many wildlife species is dependent on access to habitat of requisite quality and quantity (Cumming 2004) and thus the primary goal of ecologists is to understand the ecological factors that determine species distribution and abundance patterns (McLoughlin et al. 2010). Furthermore as urban expansion and rural land development become more widespread on the global landscape (Western 2001), so the understanding of the spatial requirements of species becomes increasingly important for conservation planning and management (Beckmann and Berger 2003). This is especially so in the case of primates as habitat domination by humans (Cowlishaw and Dunbar 2000; Paterson and Wallis 2005), and the concomitant compression, fragmentation and conversion of primate habitats (Strum 2010), are the driving forces behind human-primate conflict and one of the greatest threats to primate survival (Laurance et al. 2002). The use of space has thus become a central theme in primate studies (Arrowood et al. 2003; Riley 2008), with conservationists relying on patterns of habitat use and minimum resource requirements for the effective conservation and management of various primate populations (Arrowood et al. 2003). This is particularly true for those inhabiting small, isolated and fragmented habitats (Robbins and McNeilage 2003).

Of concern to the sustainability of the isolated baboon population in the Cape Peninsula are the continued expansion of the human population and the increasing spatial extent of the city of Cape Town, both of which have doubled over the last 30 years (Sinclair-Smith 2009). In addition to exacerbating already high levels of HBC (Beamish 2010), further expansion of humans into natural areas of the Cape Peninsula may compromise baboon conservation in at least four ways. First, the spatial concentration of the baboon population may make it more susceptible to infectious disease (Wrangham 1974). Second, increasing overlap of baboons and humans could heighten the probability of bidirectional interspecies disease transmission (Pucak et al. 1982; Ravasi 2009; Drewe et al. in press). Third, the survivability and ecological role of future generations of baboons could be compromised if young baboons that grow up in troops heavily reliant on anthropogenic food sources do not learn the necessary skills for finding and processing indigenous food (Asquith 1989). Finally, as baboons become accustomed to obtaining food directly from humans and from human-modified habitats, so they may become increasingly aggressive towards humans, as observed for vervet monkeys in Amboseli National Park, Kenya (*Cercopithecus aethiops*: Lee et al. 1986) and macaques at Mt. Emei, China (*Macaca thibetana*: Zhao 1994).

The first step in avoiding the above negative scenarios is to encompass the land use patterns of baboons in the spatial planning processes of land development in the Cape Peninsula. Current knowledge of baboon land use patterns is speculative and anecdotal. Here I investigate the land use patterns of these baboons, pooling together spatial data from nine troops to determine population-level patterns of landscape selection. I use hurdle models (Cragg 1971) to ascertain the key landscape features influencing baboon distribution and abundance on two hierarchical spatial scales (Johnson 1980). I incorporate the foundations of primate ecological theory into the modelling process by selecting landscape variables that provide baboons access to the three resources critical to their survival: food (e.g., Clutton-Brock 1975; Barton et al. 1992; Riley 2008), sleeping sites (e.g., Crook and Aldrich-Blake 1968; Whiten et al. 1987; Rasoloharijaona et al. 2008) and water (e.g., Altmann and Altmann 1970; Chapman 1988). I address the following questions: (1) what are the key features influencing baboon landscape use and (2) what are the implications of baboon land use patterns for conservation in the Cape Peninsula?

METHODS

Study areas and datasets

Study areas

Confining studies to only one of the hierarchical scales at which landscape selection operates (Manly et al. 1993) may mask important aspects of landscape selection patterns (Dickson and Beier 2002). Consequently I analysed both first- and second-order landscape selection (Johnson 1980) which I selected based on their appropriateness for determining population-level management and conservation plans. I did not analyse data at the third- and fourth-orders of landscape selection (Johnson 1980) as these would be appropriate only for developing troop-level management plans which were beyond the scope of this study.

The study area for the first-order model covered the full extent of the Cape Peninsula (Fig. 3.1) - a 500.9 km^2 area spanning from the Cape Flats in the east to Cape Town in the north, Duiker Point in the west, and Cape Point in the south. To deduce patterns of landscape selection by baboons at the broadest level possible, this study area included land of all quality, irrespective of whether it was dominated by humans. For the second-order study area I include only land that was directly accessible to the respective troops that together comprise the population. The second-order study area is a more biologically meaningful area of analysis as it includes patterns of baboon philopatry and real spatial restrictions imposed by humans. I determined this area following this same procedure for each troop. I placed a circular zone (buffer) around each GPS location (Fig. 3.2). I defined the area contained within the outermost borders of the outlying buffers as the troops “accessible area”. I based buffer radius lengths on the mean day range length traversed by each troop during their study period (see Chapter 4), thereby representing a realistic measure of the area accessible to that troop within a day’s journey from their home range (given that they typically return to known sleeping sites within their range). Accessible areas that extended beyond the extent of the Cape Peninsula landscape were clipped to the coastline. Spanning 301.4 km^2, the study area for the second-order model included the combined extents of the accessible area for all troops (Fig. 3.1).

Model datasets

To produce tabular datasets for the models I assigned grid cells from the Cape Peninsula grid system described in Chapter 2 (Fig. 2.11) to the first- and second-order study areas and merged GPS data from the baboon population to the first- and second-order grids. The baboon GPS data comprised 1000 GPS data points from each of the nine study troops, randomly selected to control for intertroop differences in sample sizes and sampling regimes, as well as seasonal effects on baboon ranging patterns. I pooled the GPS data together to generate an ecologically meaningful population-level dataset. For both study areas I determined a use value for each entered grid cell by counting the number of GPS data points within it. I assigned a use-value of zero to non-entered cells.

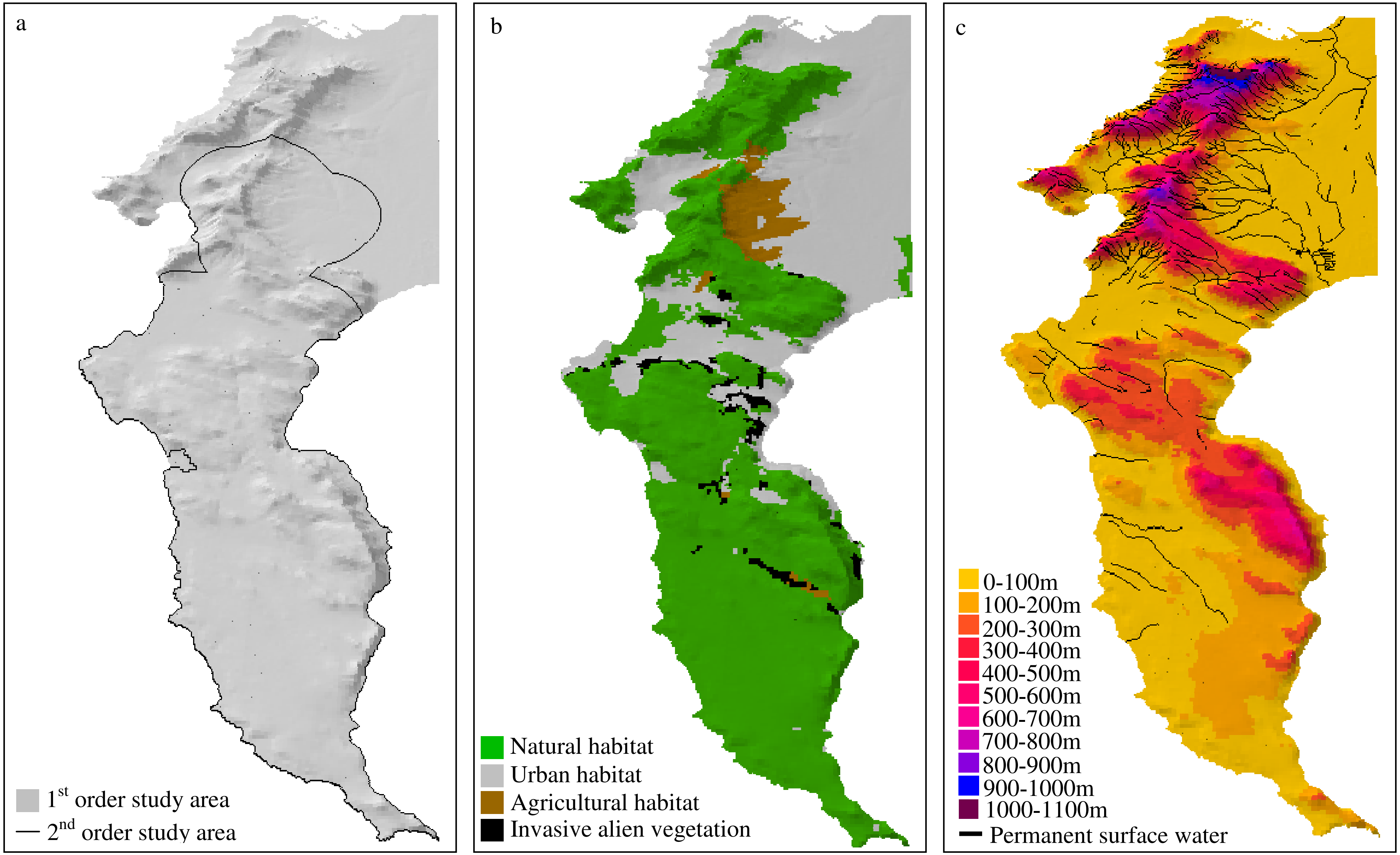


Fig. 3.1. (a) The first-order (entire grey area) and second-order (within the black outline) study areas used in the hurdle models. The predictor variables for both models included (b) broad-scale (natural habitat) and fine-scale habitat (urban habitat, agricultural habitat and invasive alien vegetation) and (c) topography (altitude, slope and permanent surface water).

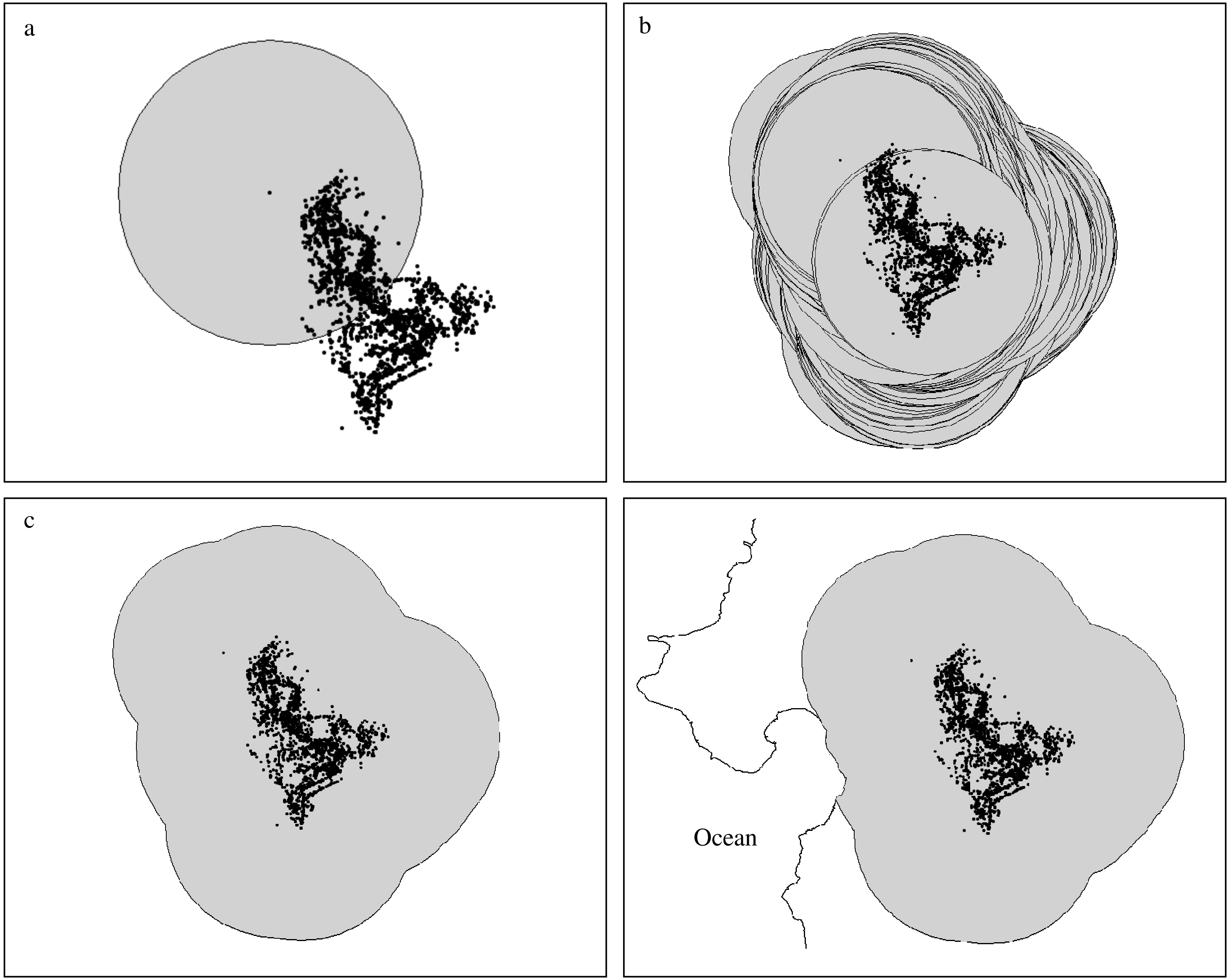


Fig. 3.2. A schematic representation of the steps followed to delineate the study area for the second-order hurdle models. (a) I centred a circle of fixed diameter (buffer) over a given GPS data point and then (b) repeated this process for all GPS data points collected throughout the study period. (c) I used the outermost extent of all buffers combined to produce an outline corresponding to the troops "accessible area". (d) If the accessible area extended beyond the Cape Peninsula landscape I clipped it to the coastline.

I used exploratory data analysis to identify ecological factors for inclusion in the models. For both model datasets I assessed over-dispersion by computing the ratio between the mean and variance of the data, where a variance much greater than the mean indicates over-dispersion (Potts and Elith 2006). I investigated zero inflation by calculating the percentage of zeroes present in each dataset. The variances of the count data were >20 x larger than their respective means for both datasets (Table 3.1) indicating over-dispersion. Zero-inflation was present in both datasets, with zeroes accounting for 91.5 % of the first-order study area and 85.5 % of the second-order study area. On account of the sampling regime the source of this zero-inflation was not related to design, survey or observer error (false zeroes; Zuur et al. 2009) but rather to the presence of structural (positive) zeroes resulting from cells being either suitable but not used, or unsuitable for use.

Table 3.1. Area, mean and range (minimum-maximum) of topographic predictor variables, and percentage cover of habitat variables within the first- and second-order study areas. Use values for the categorical predictors indicate the overall percentage of counts>0 for each habitat type.

		First-order study area		Second-order study area	
	Area	500.9 km^2		301.4 km^2	
Cell count details	Mean	0.39		0.66	
	Variance	8.27		13.9	
	% zeroes	91.5 %		85.5 %	
Predictor attributes*		Available	Used	Available	Used
	NAT	52.7 %	11.2 %	65.3 %	15.1 %
	UR	41.0 %	2.2 %	23.9 %	6.5 %
	AGR	4.7 %	27.5 %	7.8 %	27.8 %
	IA	1.7 %	29.9 %	2.9 %	30.0 %
		Mean ± SEM	Range	Mean ± SEM	Range
	Altitude	155.1 ± 2.4 m	0 - 1069.3 m	154.5 ± 2.5 m	0 - 911.81 m
	Slope	9.9.± 0.1 °	0 - 61.8 °	9.9.± 0.1 °	0 - 57.4 °
	Water	0.8 ± 0.02 km	0 - 10.2 km	1.1 ± 0.03 km	0 - 10.2 km

*NAT=Natural habitat; UR=Urban habitat; AGR=agricultural habitat; IA=invasive alien vegetation

Predictors

For both the first- and second order models I analysed cell use as a function of the following predictor variables: altitude (continuous), slope (continuous), the distance to permanent surface water sources (continuous) and habitat (categorical; Fig. 3.1). In Chapter 2 I describe how I assigned explanatory variables to each cell. Due to the complexity of ecological systems, ecological variables are frequently correlated with each other (multicollinear). Multicollinearity can lead to spurious model results, with Pearson r values as low as 0.28 having the potential to bias analyses (Graham 2003). I used Pearson correlations to test for multicollinearity among predictor variables, setting $|r|>0.28$ as my lower limit for multicollinearity (Graham 2003). Slope and altitude were positively correlated at $|r|>0.28$ in both the first- and second-order study areas (Table 3.2). Rather than minimising the biological importance of the models by excluding either variable (Graham 2003), I regressed altitude against slope and replaced slope with the residuals from the regression (Graham 1997). This procedure effectively removed the correlation between slope and altitude, with Pearson values of $r<0.001$ for both the first- and second-order models.

Table 3.2. Pearson correlations indicating multicollinearity among continuous predictor variables in the first- and second-order study areas. Correlation values of $|r|>0.28$ are in bold. All correlation values are significant at $p<0.05$ except for those italicised.

Study area	Predictors	Altitude	Slope	Water
First-order	Altitude	-	**0.62**	-0.09
	Slope	**0.62**	-	*-0.004*
	Water	-0.09	*-0.004*	-
Second-order	Altitude	-	**0.55**	-0.04
	Slope	**0.55**	-	0.11
	Water	-0.04	0.11	-

The study areas differed in their overall composition of habitats but were similar in their topographic profiles (Table 3.1). I used both broad-scale and fine-scale habitat variables. The broad-scale variable (Broad Habitat) categorised habitat as being natural or human-modified. The fine-scale variable (Fine Habitat) included the broad-scale natural category and the human-modified sub-categories, namely urban habitat, agricultural habitat and invasive alien vegetation. I did not include any fine-scale natural habitats (Fig. 2.14) because community-level diversity of the indigenous vegetation in the Cape Peninsula was too extensive to allow for meaningful population-level analyses. At the model building stage I determined which of these habitat variables would be most suitable for inclusion in the final models for each dataset by evaluating each in turn using the methods described under *Model evaluation* below. Once the final models were selected I evaluated each predictor in terms of its overall contribution to each respective model (Hilbe 2008). I used the habitat variable of 'natural' as the intercept category for both models.

Statistical methods

Modelling algorithms and model fitting

For all datasets I used hurdle models (Cragg 1971) to analyse cell use as a function of the predictor variables. Potts and Elith (2006) found that relative to four other regression models (Poisson, negative binomial, quasi-Poisson and the zero-inflated Poisson) the hurdle model had the greatest predictive performance when assessing the relationship between the abundance of an organism and its environment.

Hurdle models (also referred to as zero altered models; Heilbron 1989) are modified count models that separate data into two parts: one containing zero values and one containing positive counts (Potts and Elith 2006). As such, hurdles account for two ecological processes: the first is the process that causes an animal to be present at a site (occurrence; Zuur et al. 2009), and the second is the process that influences the numbers of animals found at a site, given that they occur there (abundance). Hurdle models model occurrence using binary (presence/absence) models with a binomial probability and model abundance (positive counts) using zero-truncated count models (Hilbe 2008). Quasi-likelihood removes the effect of zero-inflation in the binary models and the effect of over-dispersion in the zero-truncated models (Potts and Elith 2006; Hilbe 2008). The binary component is modelled using logit, probit or complementary log-log, and the count part using Poisson, geometric or negative binomial (Hilbe 2008).

Count data is typically modelled using the Poisson distribution, which assumes equality between means and variances (Maunder and Punt 2004). However, actual count data are often over-dispersed (mean≠variance) relative to the Poisson distribution (e.g., Bannerot and Austin 1983; Punt et al. 2000; Maunder and Punt 2004; Zuur et al. 2009). In this instance it becomes more appropriate to use the negative binomial distribution, which allows for a quadratic relationship between the mean and the variance (e.g., Punt et al. 2000; Maunder and Punt 2004). On account of the over-dispersion in both the first- and second-order datasets I fitted the positive counts models with negative binomial distributions.

I ran occurrence and abundance models at the first- and second-order. For occurrence models I used a binomial distribution with logit link, and for abundance models I used a negative binomial distribution with log link to ensure that the predicted values were always positive (Zuur et al. 2009). I conducted all statistical analyses using the R language and environment, an integrated software suite for statistical computing (Venables and Smith 2010). I fitted all models using the R package ‘pscl’ (Jackman et al. 2010).

Model selection

A good model is able to separate the information contained in a dataset from the noise of the dataset (Burnham and Anderson 2002). Selecting the best model is thus critical to the process of making valid inferences from biological data (Burnham and Anderson 2002). I evaluated a set of candidate models using Akaike Information Criteria (AIC), a parsimonious approach that covers model fit and parameter number (Heinänen et al. 2008), to choose a final and best approximating hurdle model at the first- and second-order.

Model evaluation

Once I had identified the final models, I evaluated them in the same manner proposed by Potts and Elith (2006) using correlation, calibration and error assessments. For correlations I determined both the Pearson correlation coefficient (r) and the Spearman rank correlation (r_s) for each model. Pearson’s r indicates the relative agreement between observed and predicted values; however, a perfect correlation (r=1) does not necessarily imply exact prediction, as all predictions may be biased in a constant direction (Potts and Elith 2006) and the intercept may thus not equal zero (Heinänen et al. 2008). Spearman’s r_s indicates similarity in the ranks of the predicted and observed values, with a high correlation coefficient meaning that the prediction order is correct (Potts and Elith 2006).

Calibration, which describes the numerical accuracy of a model, relates the level of agreement between the models predicted values and the actual observations (goodness-of-fit; Heinänen et al. 2008). I assessed model calibration with a simple linear regression between the observed and predicted values (Potts and Elith 2006). A lack of agreement can be partitioned into bias (indicated by the intercept term; b) and spread (indicated by the slope of the line; m), where a perfectly calibrated model has b=1 and m=0 (Pearce and Ferrier 2000). In a consistently biased model $b \neq 0$ and m=1, and in a model with both bias and predictions spread over a larger range of values than the observations, $b \neq 0$ and $\mathrm{m} \neq 1$ (Potts and Elith 2006).

I used the average error ($\mathrm{AVE}_{\mathrm{error}}$) and root mean squared error (RMSE) of the model residuals to assess discrepancies between predicted and observed values (Potts and Elith 2006). Both $\mathrm{AVE}_{\mathrm{error}}$ and RMSE depend on sample size (Potts and Elith 2006) and have the same dimensionality as the predictions (Heinänen et al. 2008). A positive $\mathrm{AVE}_{\mathrm{error}}$ indicates that the predictions are consistently lower than the observations, while the RMSE can be likened to the confidence interval of the predictions (Heinänen et al. 2008).

For visual evaluations of the models I generated graphs to assess whether any structure was present in the relationships between Pearson residuals and the fitted counts and continuous predictor variables. Using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California) I also mapped the predicted values of baboon occurrence and abundance and assessed these in relation to maps of the observed occurrence and abundance of baboons at the first- and second-order.

Spatial autocorrelation

Spatial autocorrelation deals with a lack of independence of data points and measures the degree to which a variable is correlated to itself in space (Cliff and Ord 1981). This phenomenon is pervasive in ecological datasets (Legendre 1993) and can stem from movement patterns of the study subject or underlying patterns of the landscape. Spatial autocorrelation can be problematic in analyses as it can lead to Type 1 statistical errors (false positives) and can result in inflated probabilities for predictor variables (Boyce et al. 2002).

The random selection of GPS data points for inclusion in the model datasets accounted for any spatial autocorrelation attributable to animal movement patterns. During the modelling process, once the models are fitted to the data, predictor variables should account for any autocorrelation caused by landscape patterns. If this is not the case, then spatial autocorrelation should be evident in the model residuals (Zuur et al. 2009). I used GeoDa

0.9.5-i (GeoDa Center for Geospatial Analysis and Computation, Arizona) to test for spatial autocorrelation in first- and second-order model residuals using Monte Carlo simulation (999 permutations) of Moran's *I*. Moran's *I* ranges from -1.0-1.0, with non-zeroes indicating that the abundance values produced for spatially connected grid cells are either more similar (positive autocorrelation) or more different (negative autocorrelation) than would be expected given a random association among the cells (Diniz-Filho et al. 2003). I calculated Moran's *I* using a weight matrix defined by k-nearest neighbours, defining the value for k by the number of cells within a 1 km radius from each cell (k=224).

Post-hoc analyses

To enhance the ecological interpretability of the model results I conducted several post-hoc analyses to investigate the spatial relationships between altitude and slope, and altitude and vegetation patterns. To this end I used ArcView 3.3 to delineate the Cape Peninsula landscape into 100 m altitudinal belts increasing from sea level to 1100 m (regional maximum). For each altitudinal belt I calculated the mean (±SEM) slope, as well as an average value of landscape productivity. I calculated the productivity averages using the Normalized Difference Vegetation Index (NDVI data produced by the South African National Botanical Institute; e.g., Pettorelli et al. 2005; Mueller et al. 2008) to assign a measure of productivity to each of the BHUs (Chapter 2) found in the Cape Peninsula (Mucina and Rutherford 2006), correcting the values for the effects of human-modified habitats (i.e. urban and agricultural habitats) on landscape productivity. To determine altitude-specific productivity patterns I averaged the productivity values of the BHUs contained within each altitudinal belt.

As a second analysis of the relationship between altitude and vegetation, I surveyed a section of the Cape Peninsula landscape to determine the effects of altitude on vegetation biomass. I assessed changes in biomass along three altitudinal transects running from sea level to 600 m above sea level (Fig. 3.3). At 100 m intervals (e.g., 0 m above sea level, 100 m above sea level, 200 m above sea level, etc.) along each transect I visually determined the growth form and canopy cover of the dominant vegetation (structural; Fig. 2.14c) within 10x5 m quadrates (*sensu* Campbell 1985). I selected these particular transects because they included an extensive and traversable altitudinal range relative to other regions of the Cape Peninsula, they covered an area of land stretching from sea level to mountain top that was undeveloped and dominated by natural habitat, and they fell within a large enough area to allow three replicate surveys to be conducted while controlling for geology, hydrology and invasive alien vegetation. Finally, using the first-order model results I calculated the absolute and cumulative areas of natural habitat remaining in the Cape Peninsula for each level of probability and each category of predicted abundance.

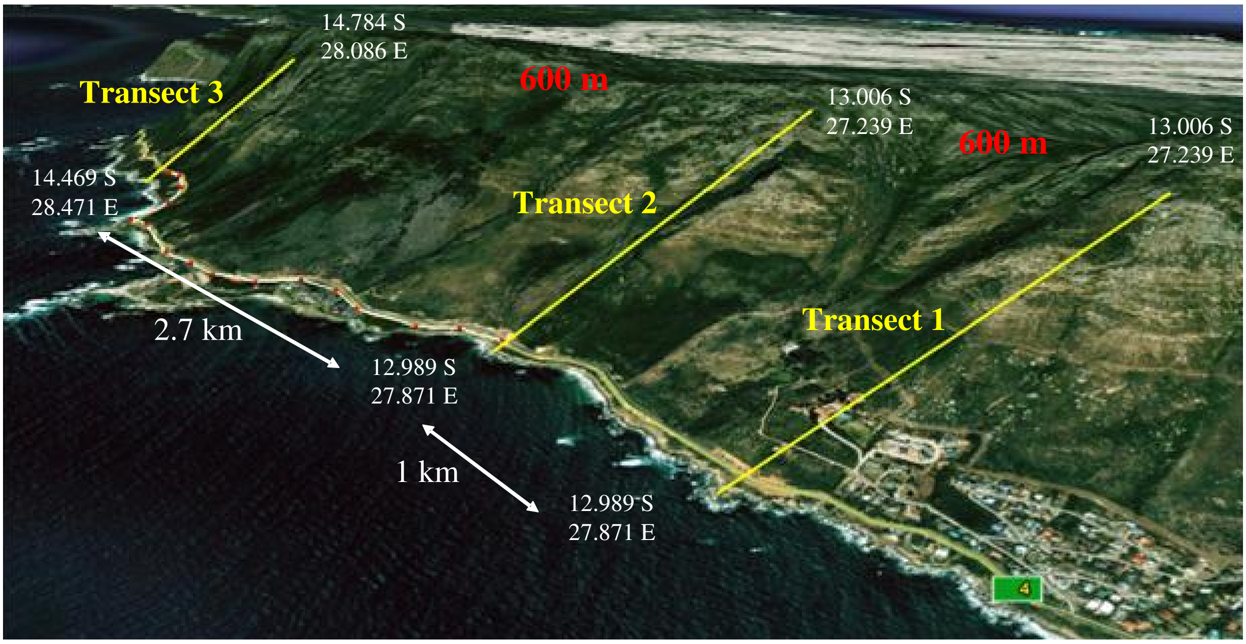


Fig. 3.3. An aerial photograph showing the altitudinal profile of the section of the Cape Peninsula in which I performed landscape surveys to quantify the relationship between altitude and vegetation biomass. The photograph shows the three transects used in the survey as well as the GPS coordinates of transect bases and summits, and the distances between them.

RESULTS

I selected the candidate models that included all topographic variables (altitude, slope and distance to water) and the Fine Habitat variable to be the final first- and second-order models as they had lower AIC values than all other candidate models (Table 3.3).

Table 3.3. Akaike Information Criteria (AIC) values of all candidate models, sorted in ascending order for both orders. Bold AIC values indicate the final models selected for each order.

First-order candidate models	AIC	Second-order candidate models	AIC
FH and ALT and SL and WAT*	**18661.30**	FH and ALT and SL and WAT	**17722.50**
BH and ALT and SL and WAT	19932.58	BH and ALT and SL and WAT	18273.88
ALT and SL and WAT	19994.88	ALT and SL and WAT	18306.76
FH and ALT and SL	20115.03	WAT	18550.09
WAT	20186.56	FH and ALT and SL	18898.74
FH and ALT	20294.06	FH and ALT	19209.22
FH and SL	20815.91	BH and ALT and SL	19437.55
FH	20887.12	FH and SL	19473.10
BH and ALT and SL	21372.21	ALT and SL	19506.23
BH and ALT	21601.21	FH	19520.14
ALT and SL	21784.91	BH and ALT	19768.53
BH and SL	21885.26	ALT	19816.75
BH	21920.86	BH and SL	19852.92
ALT	22063.51	ALT:SL (interaction term)	19914.12
ALT:SL (interaction term)	22071.54	BH	19932.16

* ALT=Altitude; BH=Broad habitat; FH=Fine habitat; SL=Slope; WAT=Distance to water

Both final models (Table 3.4) had consistently low levels of bias and were better calibrated than they were correlated. The amount of error around the predictions was low and when averaged across each study area was close to zero. However, even the small amounts of error might explain the low model correlation values which most likely resulted from error-related differences in observed and predicted values (Potts and Elith 2006). These errors, caused by variance in the models residuals, persist even under ideal sampling and analysis conditions (Tyre et al. 2001). Low but significant levels of spatial correlation were present in the residuals of the first-order (Moran's I=0.08, p<0.01) and second-order (Moran's I=0.08, p<0.01) final models. Despite having the higher AIC of the two final models, the first-order model was the better performer in all evaluation tests barring the Spearman Rank correlations (Table 3.4).

Table 3.4. AIC values and estimates of correlation, calibration and error used for the evaluation of the final first- and second-order hurdle models.

		Cell counts			Correlation		Calibration		Error	
Model	AIC	y	ŷ	ŷ-y	r	r_s	b	m	AVE_{error}	RMSE
First-order	18661.30	9000	9376	376	0.16	0.33	0.16	0.57	0.02	2.86
Second-order	17722.50	9000	9438	438	0.16	0.35	0.29	0.54	0.03	3.71

y=observed, ŷ=predicted; AIC=Akaike Information Criteria; b=intercept, m=slope; AVE_{error}=average error, RMSE=root mean square error.

Occurrence

The first- and second-order models detected the same relationships between baboon occurrence and the ecological predictors (Table 3.5 and 3.6). Habitat had the greatest influence on baboon occurrence, followed by distance to water, slope and then altitude. Relative to the topographic variables, the probability of baboon occurrence increased significantly with increasing distance to water, increasing slope and decreasing altitude (Fig. 3.4 and 3.5). Within the habitat predictor variable and relative to natural habitat (reference category), the probability of baboon occurrence increased significantly in agricultural habitat and invasive alien vegetation and decreased in urban habitat. The greatest difference between the two occurrence models was the magnitude of the coefficient estimate for urban habitat. Urban habitat had a stronger negative effect on baboon occurrence at the first-order compared to the second-order. This difference is minimally evident in the occurrence probability maps for the two orders (Fig. 3.6 and 3.7).

Abundance

The first- and second-order models found the same relationships between baboon abundance and the predictor variables (Table 3.5 and 3.6). Habitat had the greatest influence on baboon abundance, followed by slope and then altitude. Relative to the topographic variables, the predicted abundance of baboons increased significantly with increasing slope and decreasing altitude (Fig. 3.4 and 3.5). Relative to habitat, and compared to natural habitat, the predicted baboon abundance increased significantly in invasive alien vegetation and urban habitat. Distance to water and agricultural habitat had no significant influence on baboon abundance. The similarity of the results produced by the first- and second-order abundance models – in magnitude and significance – meant that that the same ecological conclusions could be drawn from both models. However, small differences in model performance abilities (Table 3.4), model dispersion parameters (theta) and model statistics (Table 3.5 and 3.6) meant that the models differed in their predictions of abundance relative to the predictor variables (Fig. 3.4 and 3.5). Consequently, the maps of predicted abundance differ noticeably, with the second-order model predicting a more generous abundance of baboons across the Cape Peninsula landscape than the first-order model (Fig. 3.6 and 3.7).

Table 3.5. Results of the first-order occurrence and abundance models including the coefficient estimates, standard errors (SEM), z-statistics and p values for each predictor. Habitat categories are italicised and significant values are in bold.

	Occurrence model coefficients				Abundance model coefficients			
Predictors	Estimate	SEM	z	$p(>\vert z\vert)$	Estimate	SEM	z	$p(>\vert z\vert)$
Natural habitat (intercept)	-2.484	0.058	-42.797	**<0.001**	-8.137	18.380	-0.443	0.658
Agricultural habitat	1.814	0.080	22.531	**<0.001**	-0.075	0.146	-0.512	0.609
Invasive alien vegetation	1.279	0.124	10.343	**<0.001**	0.962	0.223	4.320	**<0.001**
Urban habitat	-1.741	0.085	-20.469	**<0.001**	0.581	0.166	3.490	**<0.001**
Altitude	-0.004	0.000	-14.582	**<0.001**	-0.005	0.001	-5.949	**<0.001**
Slope	0.021	0.003	6.733	**<0.001**	0.052	0.007	7.745	**<0.001**
Distance to water	0.500	0.014	36.448	**<0.001**	-0.037	0.023	-1.619	0.105
Log (theta)					-10.450	18.380	-0.569	0.570

Pearson residuals: Min=-0.790; 1Q=-0.174; Median=-0.098; 3Q=-0.071; Max=56.745
Theta: count = 0.0003
Iterations: 36 in BFGS optimisation
Log-likelihood: -9316 on 15 Df

Table 3.6. Results of the second-order occurrence and abundance models including the coefficient estimates, standard errors (SEM), z-statistics and *p* values for each predictor. Habitat categories are italicised and significant values are in bold.

	Occurrence model coefficients				Abundance model coefficients			
Predictors	Estimate	SEM	z	*p*(>|z|)	Estimate	SEM	z	*p*(>|z|)
Natural habitat (intercept)	-2.329	0.060	-38.994	**<0.001**	-8.766	25.170	-0.348	0.728
Agricultural habitat	1.626	0.083	19.633	**<0.001**	-0.074	0.146	-0.511	0.609
Invasive alien vegetation	1.063	0.125	8.522	**<0.001**	0.962	0.223	4.319	**<0.001**
Urban habitat	-0.717	0.087	-8.214	**<0.001**	0.581	0.166	3.489	**<0.001**
Altitude	-0.004	0.000	-13.748	**<0.001**	-0.005	0.001	-5.953	**<0.001**
Slope	0.027	0.003	8.282	**<0.001**	0.052	0.007	7.749	**<0.001**
Distance to water	0.489	0.016	31.4	**<0.001**	-0.037	0.023	-1.615	0.106
Log(theta)					-11.080	25.170	-0.44	0.660

Pearson residuals:	Min=-0.796; 1Q=-0.221; Median=-0.171; 3Q=-0.125; Max=50.353
Theta:	count = 0
Iterations:	36 in BFGS optimisation
Log-likelihood:	-8846 on 15 Df

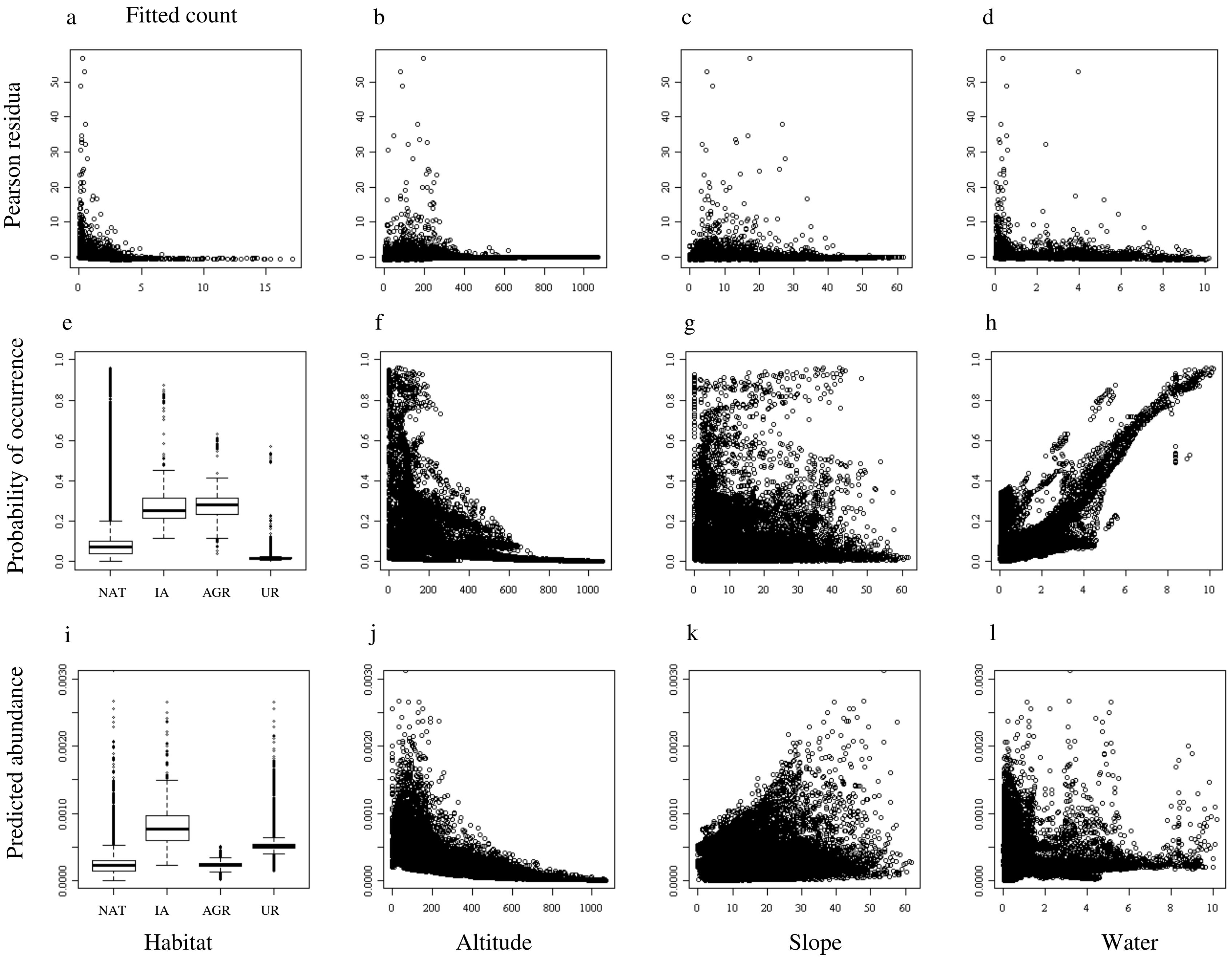


Fig. 3.4. Diagnostics (a-d) and results (e-l) for the first-order hurdle model. The diagnostics (a-d) include plots of fitted counts and predictors against Pearson residuals. The results in (e-h) show the probability of baboon occurrence relative to the predictor variables. The results in (i-l) show the predicted baboon abundance (count≥1) relative to the predictor variables. NAT=natural habitat, IA=invasive alien vegetation, AGR=agricultural habitat, UR=urban habitat.

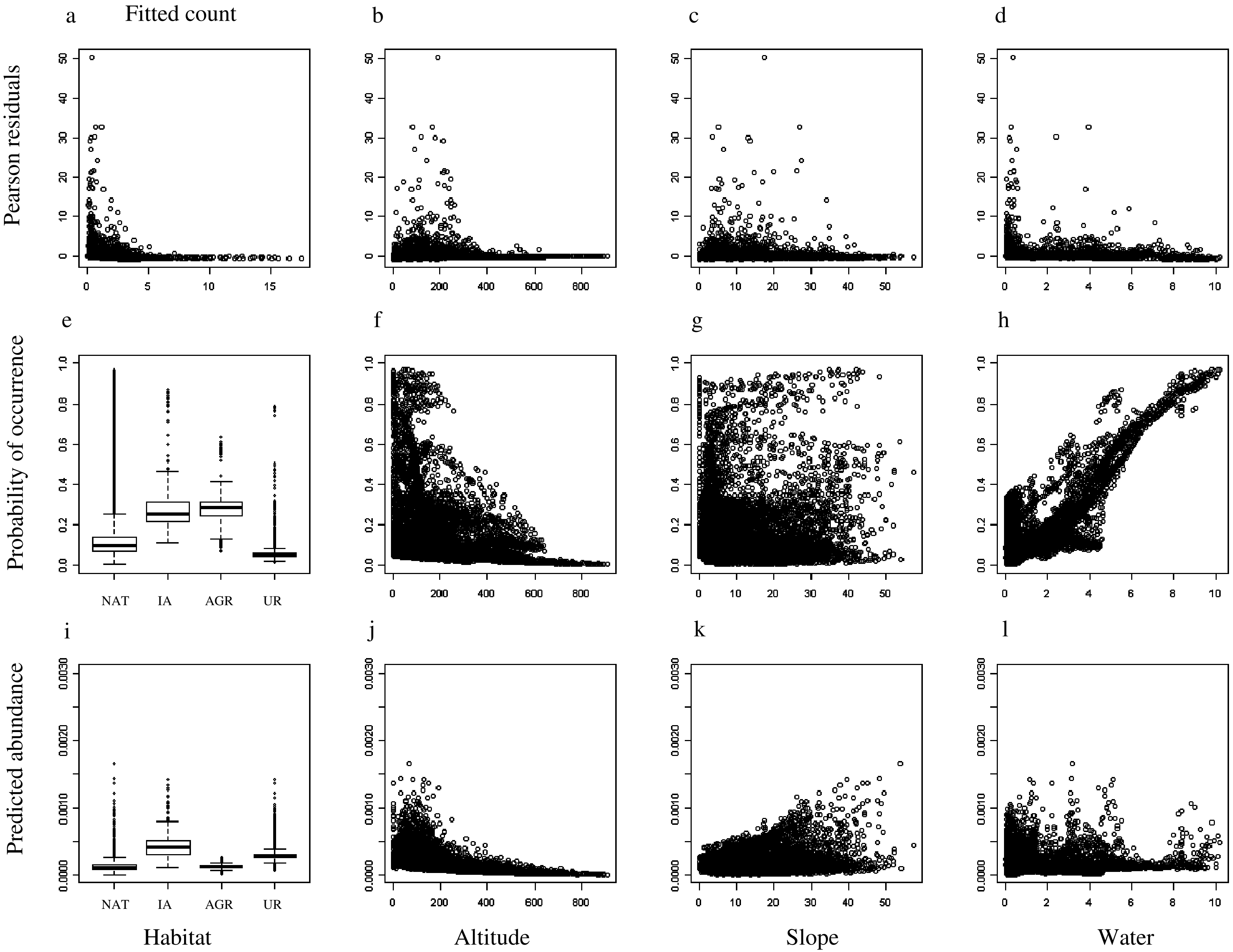


Fig. 3.5. Diagnostics (a-d) and results (e-l) for the second-order hurdle model. The diagnostics (a-d) include plots of fitted counts and predictors against Pearson residuals. The results in (e-h) show the probability of baboon occurrence relative to the predictor variables. The results in (i-l) show the predicted baboon abundance (count≥1) relative to the predictor variables. NAT=natural habitat, IA=invasive alien vegetation, AGR=agricultural habitat, UR=urban habitat.

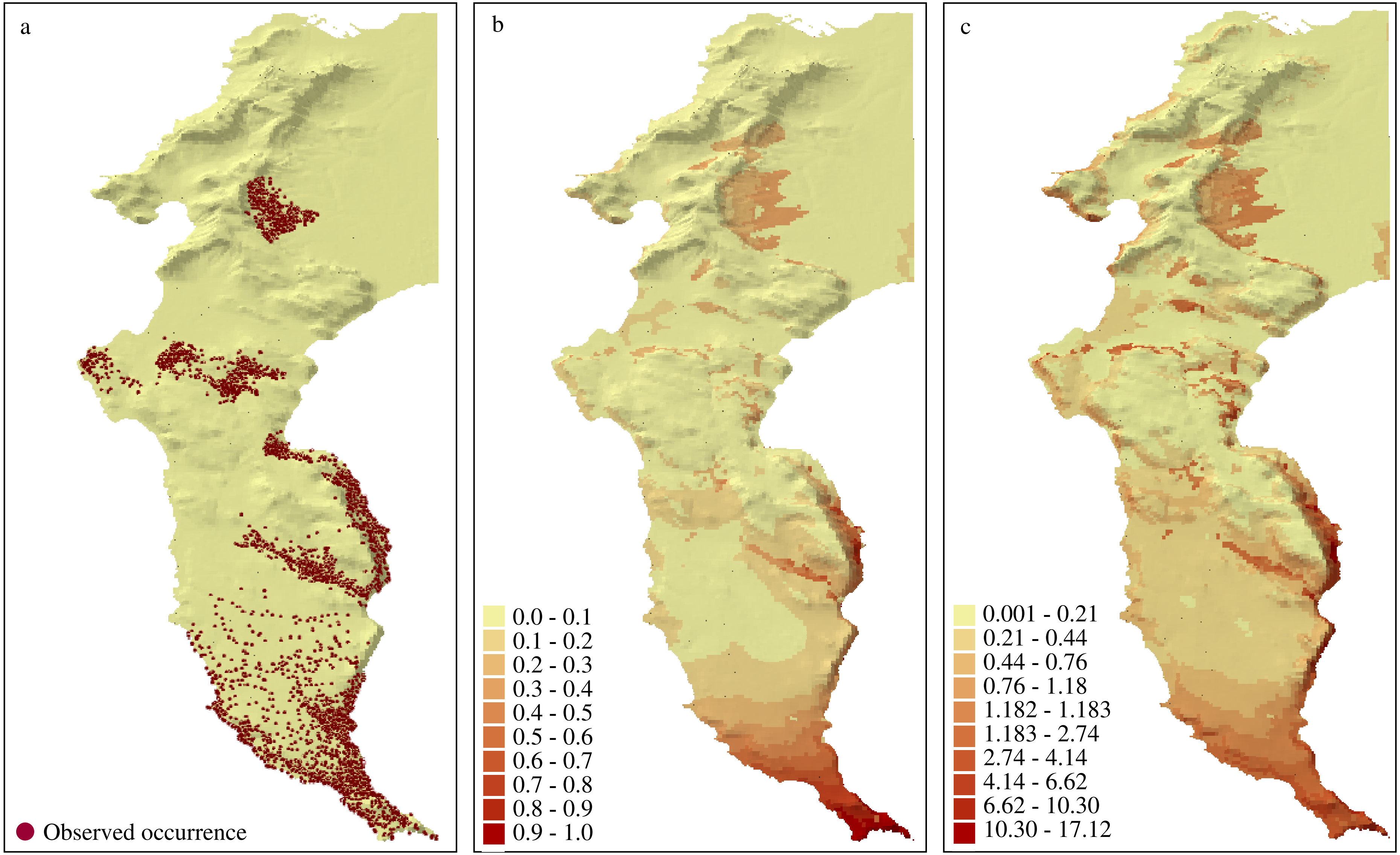


Fig. 3.6. 3D maps of the Cape Peninsula indicating observed baboon occurrence (a) plotted alongside predicted probabilities of occurrence (b) and predicted values of abundance (c) derived from the first-order model.

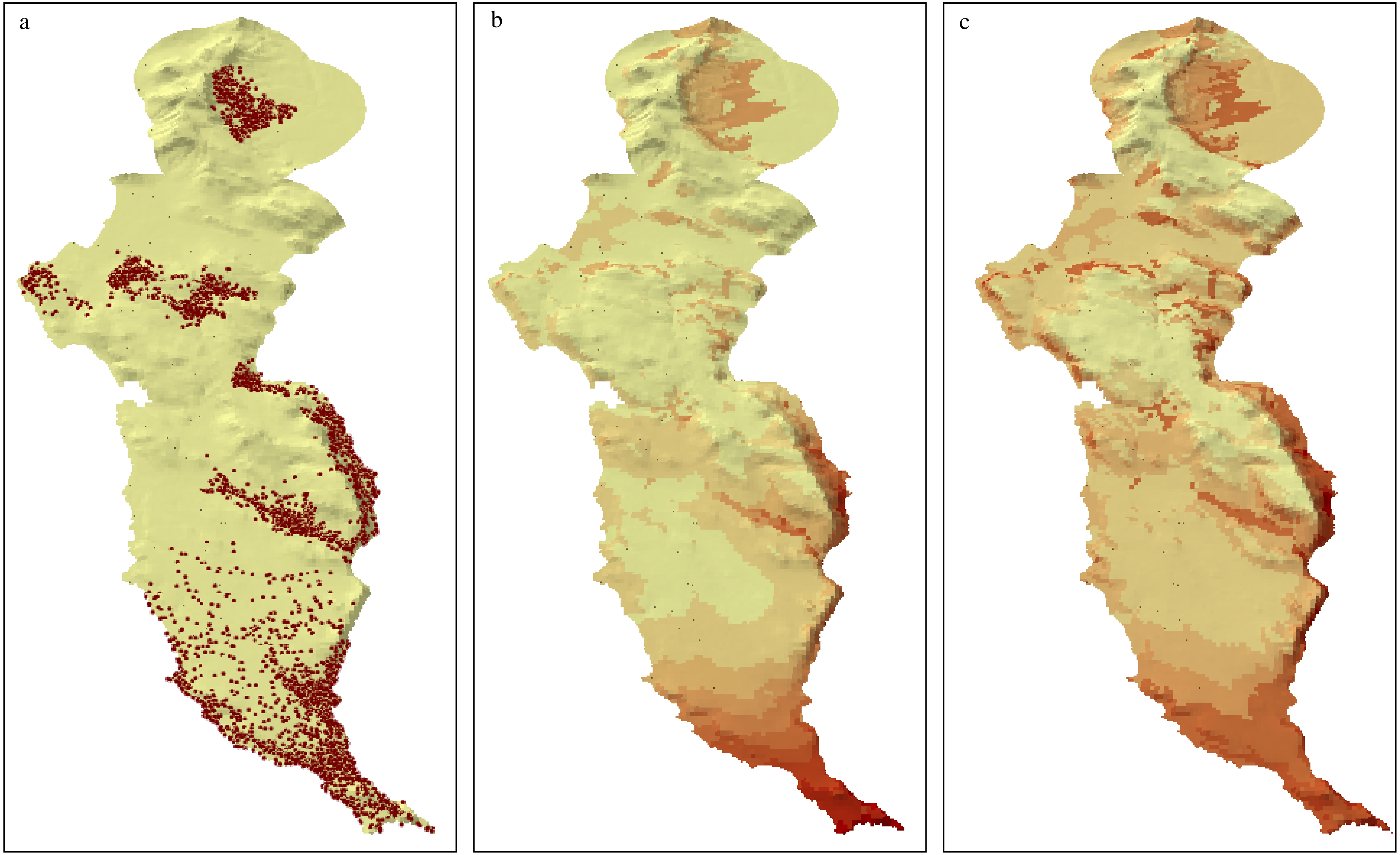


Fig. 3.7. 3D maps of the Cape Peninsula indicating observed baboon occurrence (a) plotted alongside predicted probabilities of occurrence (b) and predicted values of abundance (c) derived from the second-order model.

Post-hoc results

Vegetation productivity decreased as altitude increased (Fig. 3.8). Averaged across all vegetation types, productivity was highest between 100-200 m, decreasing steadily to 600 m where productivity levelled off. Landscape surveys of vegetation structure corroborated this productivity pattern. Across the three surveyed transects the largest plants were found in the lowest altitudinal belts (Table 3.7). Low trees (<10 m; Campbell 1985) and large shrubs (>2 m) dominated the lower elevations, with plant height decreasing at altitudes ≥400 m. Plant cover remained consistent at all altitudes despite the decrease in plant height. Slope was lowest in the lowest altitudinal belt (Fig. 3.9) and apart from a decrease at the 700-800 m belt, slope increased steadily to 900 m, decreasing thereafter.

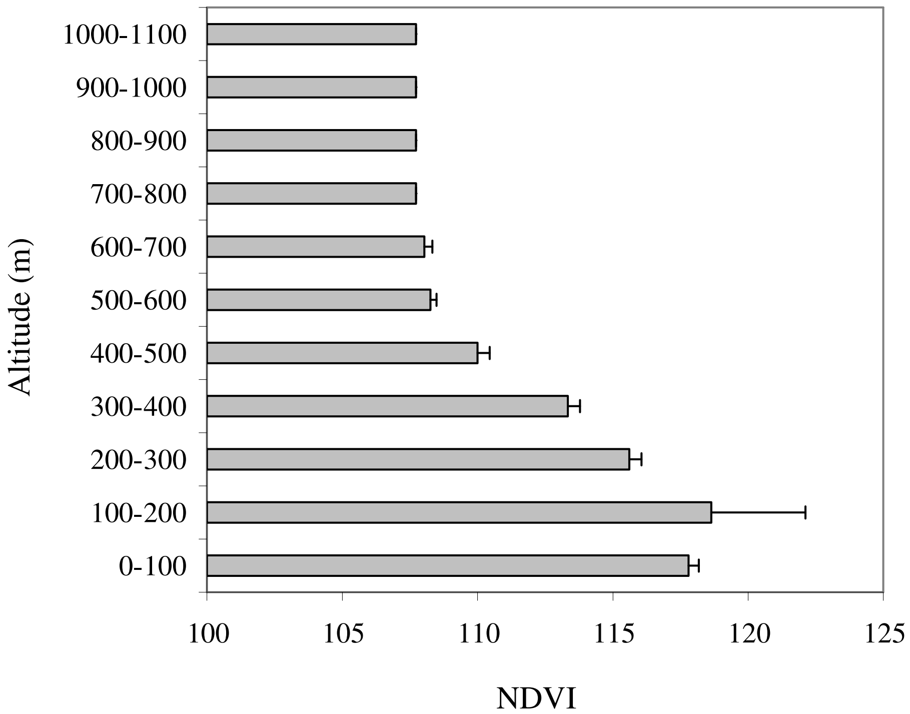


Fig. 3.8. Mean±SEM NDVI (Normalised Difference Vegetation Index) for all altitudinal belts in the Cape Peninsula.

Table 3.7. Vegetation height and cover (following Campbell 1985) of altitudinal vegetation transects. Data are sorted from highest to lowest altitudes.

	Transect 1		Transect 2		Transect 3	
Altitude	Height	Cover	Height	Cover	Height	Cover
500-600m	Shrubs 1-2m	75-100%	Shrubs 1-2m	75-100%	Shrubs 1-2m	75-100%
400-500m	Shrubs 1-2m	75-100%	Shrubs >2m	75-100%	Shrubs >2m	75-100%
300-400m	Shrubs >2m	75-100%	Shrubs >2m	75-100%	Low trees <10m	75-100%
200-300m	Shrubs >2m	75-100%	Low trees <10m	75-100%	Low trees <10m	75-100%
100-200m	Shrubs >2m	75-100%	Low trees <10m	75-100%	Low trees <10m	75-100%
0-100m	Shrubs >2m	75-100%	Low trees <10m	75-100%	Shrubs 1-2m	75-100%

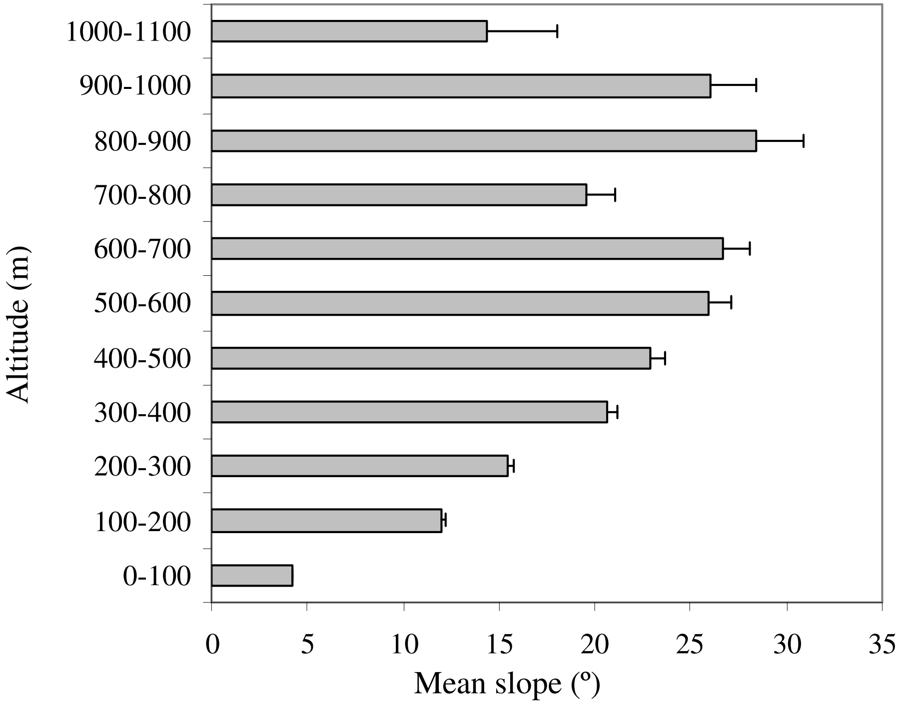


Fig. 3.9. Mean±SEM slope of all altitudinal belts in the Cape Peninsula.

There is only a minimal amount of natural habitat remaining that is consistent with the land use patterns of baboons (Table 3.8). Most of the natural habitat is available in areas that have a low probability of baboon occurrence (p<0.05) and low levels of predicted abundance (<5 GPS data points per cell).

Table 3.8. Remaining area of natural habitat at each level of occurrence probability and predicted abundance, and including cumulative totals. Data are sorted in decreasing order of probability, and decreasing values of abundance.

Occurrence Probability			Predicted abundance		
Probability	Undeveloped area (km^2)	Cumulative area (km^2)	Abundance	Undeveloped area (km^2)	Cumulative area (km^2)
0.9-1.0	0.6	0.6	15-20	0.0	0.0
0.8-0.9	1.8	2.3	10-15	0.0	0.0
0.7-0.8	1.5	3.8	5-10	1.1	1.1
0.6-0.7	1.8	5.6	1-5	20.2	21.3
0.5-0.6	2.9	8.5	0-1	242.9	242.9
0.4-0.5	4.5	13.0			
0.3-0.4	4.3	17.3			
0.2-0.3	7.8	25.1			
0.1-0.2	43.1	68.2			
0.0-0.1	196.1	264.2			

DISCUSSION

Ecological reliability and interpretability of models

While the complexity of biological systems inhibits the ability of ecological models to reflect all reality, a model that suitably approximates the information contained in empirical data allows interesting inferences about ecology to be made (Burnham and Anderson 2002). On account of their generalist nature (Swedell 2011), baboons are likely to have occurred throughout the Cape Peninsula prior to urbanisation, but with abundance being higher in more favoured habitat. The models reflect this pattern with the evaluation results and output maps showing that, despite being poorly correlated, both the first- and second-order models accurately predicted the current distribution of troops. Furthermore, both models predicted a higher abundance of baboons on land that is currently being used by troops that were not included in this study (*n*=3; Fig. 3.10) as well as historically recorded locations of extirpated troops (*n*=3). Also, in only small, non-contiguous patches did the models predict baboon occurrence or abundance patterns that are not supported by either historic records or current baboon distribution patterns. The model predictions deviated most notably for two of the baboon troops that are actively herded within their home ranges by baboon monitors (Fig. 3.10). Here, both the first- and second-order models predicted a lower probability of occurrence and a lower predicted abundance than I would expect given the troops ranging patterns (SK and DG troops: Chapter 4). This would suggest that the herding of baboons by monitors has affected their habitat use.

The low levels of positive spatial auto-correlation in the model residuals resulted from underlying landscape patterns, and may explain the average calibration of the models. Spatial correlation is almost always present in grid-datasets (Rahbek and Graves 2001; van Rensburg et al. 2002; Diniz-Filho et al. 2003) but as it does not bias regression coefficients (Hawkins et al. 2007) it does not affect the ecological interpretability of the models.

Key landscape features

Both models indicated that baboons are more likely to occur, and be more abundant, at low altitudes, on steep slopes and in human-modified habitats. These patterns are congruent with predictions based on baboon ecology as the combination of these variables provides baboons with access to food and sleeping sites – two resources critical to their survival.

Food

Optimal foraging strategies for primates simultaneously maximise nutrient gain (Oates 1987; Codron et al. 2006) and use of available time (Dunbar 1992; Dunbar et al. 2009). Accordingly, patterns of primate distribution and abundance across the landscape can be explained primarily by the distribution of the most lucrative foraging sites (Clutton-Brock and Harvey 1977; Bennett 1986; Riley 2008). Baboon occurrence and abundance in the Cape Peninsula converged with the areas of the landscape that have the most profitable food sources, namely lower altitudes (see Fig. 3.8) and human-modified habitats.

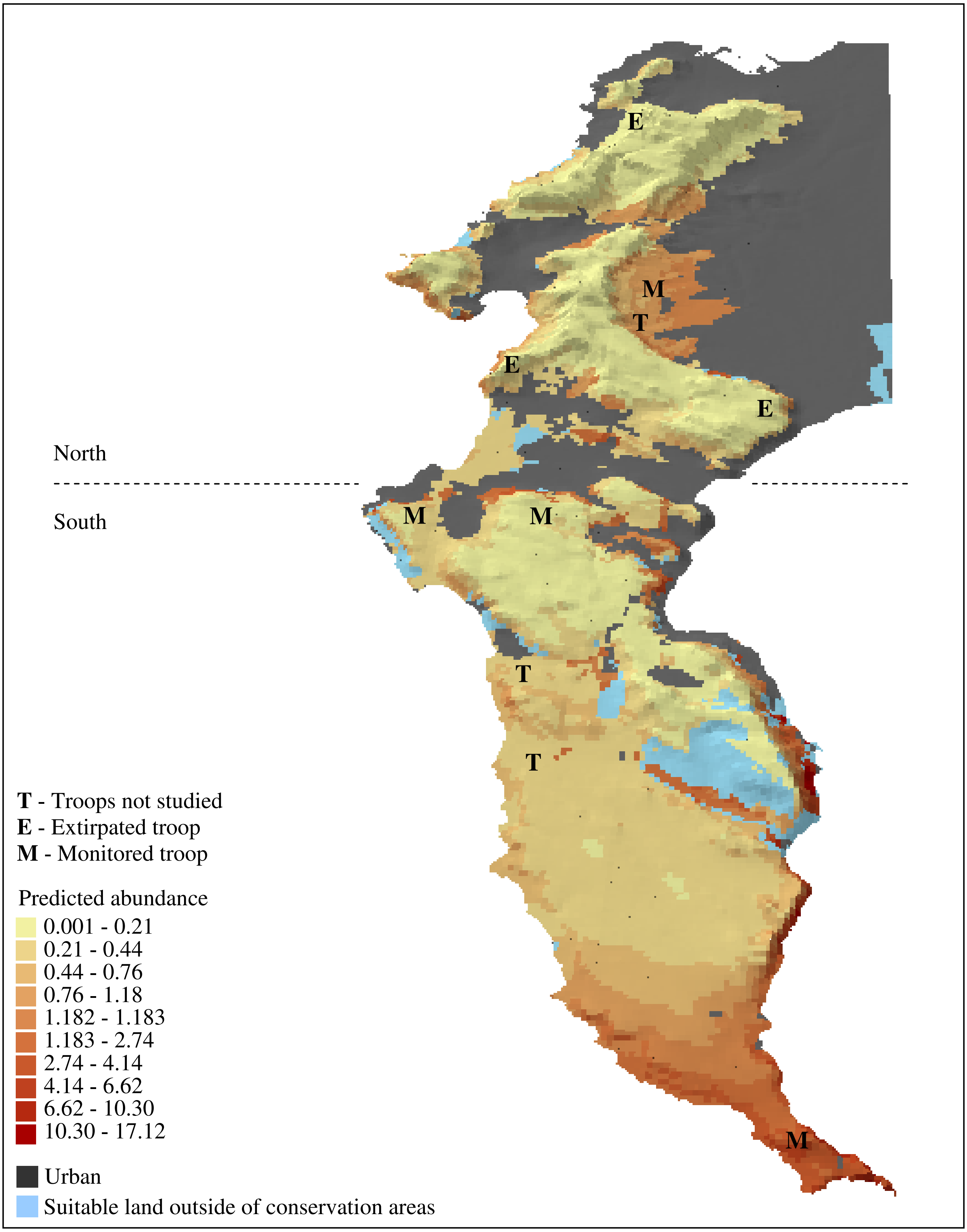


Fig. 3.10. The predicted abundance values from the first-order model overlaid with the extent of urban habitat in the Cape Peninsula, as well as the areas of land most suitable for baboons (probability of occurrence >0.5) that are not currently conserved within the Table Mountain National Park. Included on the map are the locations of troops not included in this study (T), troops extirpated prior to this study (E) and troops monitored during this study (M). A belt of urban habitat (dashed line), situated approximately half way down the length of the Cape Peninsula, serves to divide the baboons into northern and southern sub-populations.

Altitude and food

In the Cape Peninsula the benefits of foraging at low altitudes are threefold for baboons. First, as revealed by landscape surveys, the lower altitudes contain larger and more productive plants than the rocky mountaintops (Fig. 3.11). Second, baboons gain access to high-protein food resources along the coastline by consuming a variety of marine intertidal organisms. Not all local troops have access to the latter food source but troops that spend the majority of their time in the protein-poor indigenous vegetation (Cowling et al. 1996) routinely include marine-food sources in their diets (MC Lewis, UCT, unpubl. data). Third, most human-modified habitat is at lower altitudes and offers highly concentrated and predictable food resources.

Fig. 3.11. Typical altitudinal profile in the Cape Peninsula showing the relative increase of vegetation biomass with decreasing altitude.

Human-modified habitats and food

Anthropogenic habitat alteration can dramatically affect the quality, availability and distribution of food resources and the addition of anthropogenic food sources into primate diets can have a positive effect on both their abundance and fecundity (Altmann et al. 1978; Goodall 1983; Fa 1984; Strum 1991; Altmann and Alberts 2005; Higham et al. 2009). In addition to the food sources available in urban and agricultural habitats, humans in the Cape Peninsula have introduced many species of invasive alien plants (e.g., *Pinus*, *Acacia* and *Eucalyptus* spp.; Alston and Richardson 2006) which have both higher seed production and standing biomass than indigenous vegetation (van Wilgen and Richardson 1985; Honig et al. 1992). Human-modified habitats thus offer abundant, accessible and calorie-rich food sources that baboons favour over the low quality forage of local indigenous vegetation (van Doorn 2009; Hoffman and O'Riain 2010). That the models detected, on average, that baboons preferred human-modified habitats to natural habitat is thus unsurprising. There were, however, some interesting exceptions to this trend.

Urban habitat: - Baboons were less likely to occur in urban than in natural habitat despite the abundance of high quality food sources available in both houses and gardens. This is almost certainly a consequence of conflict with humans, with baboons suffering from harassment, injury and mortality when foraging in urban habitat (Beamish 2010). However, in time baboons are able to adapt to profitable foraging conditions by improving their raiding success while simultaneously minimising the costs associated with foraging in high risk habitats (Strum 2010). Indeed baboons in the Cape Peninsula manage to simultaneously mitigate against human threats while maximizing nutrient gain by spending minimal time raiding in urban habitat, acquiring human food quickly and returning thereafter to the relative safety of other habitats (van Doorn 2009). This raiding strategy would explain the low probability of occurrence predicted for urban habitat.

However, an additional explanation for these results may lie in the statistical procedure of the modelling process. In both the first- and second-order models the proportion of urban habitat used was much lower than what was available. When the amount of available urban habitat was decreased relative to the habitat use values (second-order model) the negative effect of urban habitat on baboon occurrence was reduced. This suggests a sensitivity of the occurrence models to large discrepancies between use and availability values. When these discrepancies are controlled, as they were in the abundance models, urban habitat was found to be favourable to natural habitat at both orders.

Agricultural habitat: - A similar pattern was found for agricultural habitat where the occurrence models determined that baboons preferred this habitat to natural habitat, but the abundance models found the preferences for the habitats to be similar. There are two possible – perhaps interacting – explanations for this pattern. Firstly, some crops (e.g., vineyards) have a distinctly seasonal growth cycle and are consequently not used consistently by baboons on an annual basis (Hoffman and O'Riain 2010). Secondly, agricultural habitats are the source of income for farmers who, across sub-Saharan Africa (Mascarenhas 1971; Strum 1994; Pepeh 1996; Hill 2000; Morris 2000; Kansky and Gaynor 2000; Oosten 2000; Brown et al. 2006) consider baboons to be pests capable of more crop damage than any other primates (Naughton-Treves 1996; Hill 2000; Tweheyoa et al. 2005) or indeed any other wildlife species (Naughton-Treves 1998; Biryahwaho 2002). Of the types of agricultural habitat in the Cape Peninsula, baboons are tolerated in pine and eucalyptus plantations (Hoffman and O'Riain 2010), but vineyard owners actively chase baboons when the vines are in fruit (Hoffman and O'Riain 2010), and livestock farmers routinely chase baboons off their property throughout the year (van Doorn 2009). Seasonal differences in crop use, and farm policing would not affect the presence-absence analyses of the occurrence models, but would reduce the significance of the overall patterns of baboon abundance in agricultural habitat.

Invasive alien vegetation: - Both the occurrence and abundance models revealed that baboons found invasive alien vegetation to be significantly preferential to natural habitat. This result is unsurprising given the 3-10 fold increase in above-ground biomass associated with invasive alien vegetation (Versfeld and van Wilgen 1986) and the resultant preference for foraging in this habitat (van Doorn 2009; Hoffman and O'Riain 2010). Furthermore, unlike urban habitat, baboons are able to exploit invasive alien vegetation without the cost of human harassment.

Sleeping sites

While food resources play a crucial role in determining primate spatial distributions, their availability to the animals is constrained by their proximity to other critical resources (Ober et al. 2005). In affording baboons safety from predators (DeVore and Hall 1965) and providing them with suitable vantage points for area surveillance (Anderson 1984), sleeping sites fundamentally affect baboon ranging patterns and dictate the intensity to which they use the landscape (Crook and Aldrich-Blake 1968; Rasmussen 1979; Davies 1984; Whiten et al. 1987; Zinner et al. 2001; Liu et al. 2004; Zhou et al. 2007). Baboons use a variety of sleeping sites including cliffs (Kummer and Kurt 1963; Crook and Aldrich-Blake 1968; Whiten et al. 1987), trees (DeVore and Hall 1965; Altmann and Altmann 1970), rocky outcrops (Altmann and Altmann 1970), and caves (Marais 1939; Hall 1963). In the Cape Peninsula baboons sleep primarily in trees and on cliffs (van Doorn 2009; Hoffman and O'Riain 2010, but see Chapters 4 and 5).

The baboons' use of trees as sleeping sites provides an additional explanation for the preference shown for invasive alien vegetation and agricultural habitat over natural habitat. Natural habitat in the Cape Peninsula is characterised by shrublands, grasslands and low trees (Campbell 1985; Cowling et al. 1996). By contrast both self-sown invasive alien vegetation and cultivated plantation trees (e.g., *Pinus and Eucalytus* spp.) are suitably sized for baboon sleeping site requirements (van Doorn 2009; Hoffman and O'Riain 2010). Furthermore, plantation trees have also been cultivated alongside vineyards and urban areas (Hoffman and O'Riain 2010) and, because of the high levels of disturbance at the urban/natural habitat interface and the significant source of alien propagules presented by suburban gardens (Alston and Richardson 2006), self-sown alien plants tend to invade and establish in close proximity to urban habitat. Thus the spatial distribution of tall trees in the Cape Peninsula provides baboons with suitable sleeping sites in close proximity to favoured foraging areas.

The importance of cliff sleeping sites was also detected by the models. Both models indicated that baboons are more likely to occur, and be more abundant, on steep slopes – the inaccessibility of which provides them with safe day-time and night-time refuges. Slope steepness has been found to be an important predictor of mountain gorilla distribution for the same reason (van Gils and Kayijamahe 2010). The coincident preference for steep slopes and low altitudes once again represents the importance of proximity of sleeping sites to favoured foraging areas. In the Cape Peninsula, slope steadily increases from the 100 m contour line (Fig. 3.9). Because urban development is constrained by the exposure and inaccessibility of high altitudes and steep slopes (Richardson et al. 1996) the spatial extent of urban habitat is restricted to the flat land below the 80 m contour line. Consequently steep cliffs, suitable as baboon sleeping sites, occur directly above favourable urban habitat in many areas.

Water

Given that water is a critical resource for baboons it is surprising that there was a significantly higher probability of baboons occurring far from permanent surface water sources than near to them. An explanation for this pattern emerges when results are considered in context with the hydrological attributes of the Cape Peninsula. With permanently flowing surface waters, the presence of freshwater wetlands and vegetation prone to seasonal water-logging (Cowling et al. 1996), the Cape Peninsula is not a water stressed environment. These factors explained the relative lack of importance of water in determining the ranging patterns of one of the local troops (TK: Hoffman and O'Riain 2010). For this same troop the high water content of vegetation explained the lack of 'drinking sessions' (*sensu* Altmann and Altmann 1970) where many baboons converge at a waterhole and drink simultaneously. These explanations seem equally applicable to all troops in the Cape Peninsula, especially given the results of the abundance models that indicated no significant relationship between baboon land use and surface water. Thus, rather than revealing an interesting ecological phenomenon where animals avoid water, the occurrence model results should rather be interpreted as an indication that permanent surface water need not be considered as a key landscape feature for baboons in the Cape Peninsula during years of good rainfall. However, permanent water sources may well become a good predictor of baboon occurrence during years of drought or below par rainfall, particularly during the dry summer season.

Conservation implications

It is possible, based on the inherent properties of the landscape, that the mountainous spine that runs the length of the Cape Peninsula has never provided sufficient food resources to support a large, spatially continuous baboon population. Baboons may have always been reliant on access to low land to obtain sufficient food, with high altitude areas acting as a demographic sink for the expanding population (e.g., Henzi et al. 1990). Thus, the rapid growth of the human population and extensive urbanisation over the last two centuries (Sinclair-Smith 2009) has not only isolated the local baboons from all other populations but has also annexed most of the low lying and more productive foraging areas. That baboons have persisted in this environment despite these challenges is testament to their ability to modify their foraging behaviour and coexist with humans. This coexistence, however, has come at a severe cost with whole troops having been extirpated (Skead 1980) and frequent cases of human-induced injury and mortality (Beamish 2010).

Currently, the most widely used method of baboon management is the employment of baboon monitors who attempt to reduce levels of HBC by herding troops away from the urban edge (van Doorn 2009). Because of the spatial attributes of urbanised areas, monitors must typically herd baboons away from favourable low lying land and up the mountain, into increasingly marginal habitat (Fig. 3.10). That monitored troops still suffer extraordinarily high levels of human-induced injury (Beamish 2010) is not attributable to atypical or errant baboon behaviour, but rather indicative of the intensity of the competition between baboons and humans for low lying land and the associated high quality natural and anthropogenic food resources. The inevitable persistence of this competition through time will forever compromise the ability to effectively manage baboons at the interface of natural and urban habitats.

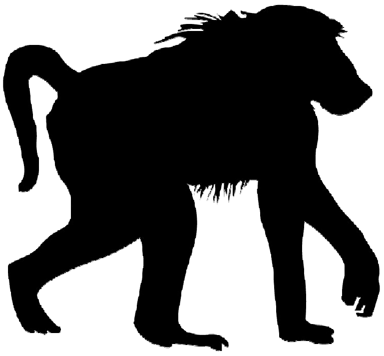
The implications of extensive land development for the future of baboon management and conservation are equally concerning. Currently, minimal amounts of the land considered to be ecologically suitable for baboons (probability of occurrence >0.5) remain undeveloped. This is most pronounced in the northern half of the Cape Peninsula (Fig. 3.10) where suitable natural habitat comprises non-contiguous islands made inaccessible to baboons by the sea of urbanisation surrounding them. The landscape of the southern half of the Cape Peninsula, where three-quarters of the current baboon population range, holds more promise with continuous stretches of ecologically suitable natural habitat still available. Of the natural habitat available in the southern Cape Peninsula, 87 % is conserved as part of the TMNP, with 13 % potentially subject to urban or agricultural transformation (Fig. 3.10). Transformation of this land will force baboons farther into the increasingly marginalised habitat of higher altitudes and will ultimately exacerbate levels of HBC, with inevitable deleterious consequences for baboons. If attempts to conserve the Cape Peninsula baboon population are to be effective, then mitigating against the development of the remaining natural fragments of the landscape must be addressed as a matter of urgency.

Conclusions

This study highlights the complexities of wildlife management and conservation at the interface of natural and human-modified habitats. This is particularly true for wildlife whose land use patterns are concurrent with those of humans, and whose ecological flexibility allows them to thrive in human-modified habitats. However, by enhancing our understanding of the fundamental drivers of human-wildlife conflict, the quantification of animal land use patterns can support and validate wildlife conservation efforts. Furthermore, an understanding of animal spatial ecology can assist in discriminating between the relative importance of landscape quality and landscape quantity, and can provide a mechanism for identifying priority conservation areas at the human/wildlife interface.

Chapter 4

Intrapopulation variation in the ranging patterns of chacma baboons in the Cape Peninsula



ABSTRACT Differences in group size and habitat quality 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 meta-analyses conducted within and across species. Studies with large sample sizes of groups or those which incorporate whole populations are rare but important for testing socioecological theory in primates. Here I quantify the ranging patterns of nine chacma baboon troops occurring within a single population and use generalized linear models to analyze the effects of troop size and human-modified habitat (a proxy for good quality habitat) on home range size and day range length. I also model the effect of human-modified habitat on baboon density. Intrapopulation variation in home range sizes (1.5-37.7 km^2), densities (1.3-12.1 baboons/km^2) and day range lengths (1.65-6.58 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, while troops that spent more time in human-modified habitat had smaller home ranges, shorter day range lengths and spent less time feeding. Further, I found that 1 km^2 of human-modified habitat could support nearly five times the number of baboons as the same area of natural habitat. Paired comparisons of two equal-sized troops and two troops occupying habitat extremes, highlight the dramatic effect of human-modified habitat on both spatial and behavioural ecology variables. In both comparisons the troops with greater access to human-modified habitat and the associated high quality human food sources had smaller home ranges, higher densities, shorter day range lengths, slower travel rates and spent more time resting. My findings confirm the ability of baboons, as behaviourally adaptable dietary generalists, to not only survive but to thrive in human-modified habitats with adjustments to their ranging patterns in accordance with current theory.

INTRODUCTION

Differences in group size (e.g., Barton et al. 1992; Ganas and Robbins 2005) and habitat use (e.g., Takasaki 1981; Izumiyama et al. 2003; Riley 2008) are frequently used to explain the extensive variability in ranging patterns found across the primate order (Clutton-Brock and Harvey 1977; Mitani and Rodman 1979; Chapman and Chapman 2000; De Luca et al. 2009). As primate group sizes increase so intragroup feeding competition increases (Isbell 1991; Isbell and Young 1993; Wrangham et al. 1993), forcing larger groups to cover larger areas as the individual group members strive to obtain enough food (Milton 1984; Chapman et al. 1995; Janson and Goldsmith 1995). Thus, if other variables are constant (e.g., habitat), an increase in group size should result in a corresponding increase in day range length (DRL) and home range size (Chapman and Chapman 2000).

Through differences in food availability and food distribution, habitat type also affects primate ranging patterns. Where food resources are widely dispersed with unpredictable availability, primates must travel far and cover large ranges to meet their nutritional requirements (Ganas and Robbins 2005; Li et al. 2005; Wieczkowski 2005). Conversely, when food resources are concentrated and have predictable availability, such as those found in some human-modified habitats (e.g., agricultural and urban habitat), primates may exhibit increases in group size (Fuentes et al. 2005; Hoffman and O'Riain 2010) and density (Brennan et al. 1985; Hoffman and O'Riain 2010), reductions in home range size and DRL (Saj et al. 1999; Hoffman and O'Riain 2010), disproportionate range use (Hill 2005; Riley 2008; Hoffman and O'Riain 2010), and reduced time feeding (Lee et al. 1986; Forthman-Quick and Demment 1988). This is particularly true for species (e.g., baboons) that are behaviourally adaptable and dietary generalists (Swedell 2011).

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

I investigate the effects of troop size and human-modified habitat on the ranging patterns of this geographically discrete population of baboons. The Cape Peninsula study site offers a useful setting for assessing the effects of troop size on ranging patterns as it contains multiple troops ranging in size from 16-115 individuals (Beamish 2010). While troop sizes vary considerably, they fall within the range of troop sizes reported elsewhere (Swedell 2011) and do not exceed the maximum ecologically tolerable size based on the mean annual rainfall and mean annual temperate of the study area (Dunbar 1992). This study site also offers the ideal setting for assessing the effects of human-modified habitat on primate ranging patterns as 37 % of the Cape Peninsula landscape has been transformed by human habitat modification (Richardson et al. 1996). Thus, along with natural habitat, local troops have varying levels of access to three types of broadly defined human-modified habitats – agricultural habitat, urban habitat and invasive alien vegetation – all of which have been shown to affect baboon ranging patterns locally (Hoffman and O'Riain 2010) and elsewhere across their distribution (Hill 2005 Strum 2010). Furthermore, because all troops live within one degree of latitude and longitude they are exposed to similar climatic conditions (Cowling et al. 1996) and hence any ranging pattern variation driven by differences in day length, temperature and rainfall (Isbell 1983; Li 2002; Hill et al. 2003; Yang 2003; Hill, 2006; Higham et al. 2009) is minimal. Finally, all troops experience similarly low levels of predation risk due to the absence of natural predators.

I determine the home range sizes, densities and DRLs of nine of the 12 troops present in the Cape Peninsula and quantify their use of natural and human-modified habitat. I investigate how ranging patterns are influenced by troop size (H1) and or by the human-induced habitat changes that have introduced high quality food into an otherwise nutrient-poor natural environment (H2; Bigalke 1979; Simmons and Cowling 1996). For H1 I predict, given the extensive heterogeneity in local habitat conditions, that the effect of habitat on baboon ranging patterns will be so great that it will mask the effects of troop size on home range size (Chapman and Chapman 2000), DRL (Chapman and Chapman 2000) and travel rate (Anderson 1982). For H2 I predict that troops with greater access to human-modified habitats will have smaller home ranges (Saj et al. 1999), higher densities (Brennan et al. 1985), shorter DRLs (Saj et al. 1999) and travel rates, and will forage less (Lee et al. 1986; Forthman-Quick and Demment 1988) than troops that occupy natural habitat, irrespective of troop size.

METHODS

Study site, study animals and spatial data collection

See Chapter 2.

Ranging patterns

I imported all GPS data points of troop locations into ArcView 3.3 and projected them in Transverse Mercator, spheroid WGS84, central meridian 19. I classed grid cells that contained one or more GPS data point as “entered cells”. Each troop’s home range included all entered cells, as well as those bounded on at least three sides by entered cells. I joined isolated cells to the nearest cluster of contiguous entered cells using the most direct route possible. I also classed cells that the troop was known to traverse (based on analyses of daily movement paths) as entered cells even if the frequency of data collection relative to travel speed meant that no GPS data points were recorded in them. I determined the percentage of home range cells that were not entered despite their inclusion in the home range area. I calculated the total home range size by summing the areas of all home range cells, and calculated the densities of baboons in each home range. I classified the habitat of each home range cell as natural habitat, urban habitat, agricultural habitat or invasive alien vegetation (see Chapter 2), and for each home range calculated the total cover (km^2) of each habitat.

I determined movement patterns for all troops from full-day journeys only (Altmann and Altmann 1970). For each troop I used the Nearest_features extension to ArcView (Jenness 2004) to calculate the DRLs for 11 randomly selected days in summer and winter, respectively. I did not include data from autumn and spring as I had previously found baboon ranging patterns in these seasons to be intermediate to the seasonal extremes of summer and winter (Hoffman and O’Riain 2010). I set the limit to 11 full-days per season to match the smallest seasonal sample recorded across troops (Table 2.2). I restricted my analyses to summer and winter as these were the seasons for which I had full-day records for all troops and thus allowed for a comparison across all nine study troops. To determine travel rates (TR) for each troop I followed a two-step process. First, I summed the distances between the three consecutive 20-minute scans taken per hour to calculate the TR for that hour. Next, I divided these hourly rates by the number of hours that I recorded data during long summer days (10 hours) or short winter days (7 hours) to calculate the mean TR for that day. I used one-way, single factor ANOVAs (and a *post hoc* Tukey test) to test for significant among-troop differences in DRLs and TRs. Finally, for each troop I averaged the 22 DRLs to determine a mean DRL for that troop, and averaged the 22 TRs to determine the mean TR for that troop.

Effects of troop size (H1) and human-modified habitat (H2)

I used generalized linear models (GLM; McCullagh and Nelder 1989) implemented in GenStat (13th edition; Payne et al. 2010) to assess the effects of troop size and human-modified habitat on home range size (Model 1) and DRL (Model 2). GLMs are a class of multivariate regression models that differ from classical linear models in that they do not require the error distribution of the response term to be normal (McCullagh and Nelder 1989). Instead, they use a link-function to relate the error distribution to a specific distribution function (e.g., normal, Poisson, gamma, binomial). Prior to running the models I used Spearman rank correlations to test for multicollinearity between the explanatory terms (*troop size* and *% use of human-modified habitat*) and found none (r_s=0.504, p=0.166). I fitted both GLMs with normal distributions and included constant terms. I used a logarithmic link-function for Model 1 (response term: *home range area*) and an identity link-function for Model 2 (response term: *DRL*). I constructed a third GLM (Model 3) to assess the effects of natural and human-modified habitat on home range density. Here I used troop size as the response term and the *area of natural habitat* (km^2) and *area of human-modified habitat* (km^2) within the home range as the explanatory terms. Prior to running this model I tested for multicollinearity between these explanatory terms and found none (r_s=-0.43, p=0.244). In this model the response term was a count (*number of baboons*) so I fitted the model with a Poisson distribution and used a logarithmic link-function. To give this model a simple and direct interpretation I did not include a constant term. For all three GLMs I used AIC (Heinänen et al. 2008) to select a final and best approximating model from a set of candidate models.

I further investigated the effect of human-modified habitat on ranging patterns and activity budgets by comparing two pairs of troops. First I compared the only two unmonitored troops of equal size (*n*=16; RH and BB; Pair 1) and similar composition that occupy markedly different habitats (natural versus urban). Next I compared the two troops occupying the most extreme habitat conditions from the least human-modified (KK) to the most human-modified (TK; Pair 2). For both pairs I compared 10 full-days of ranging and behavioural data recorded during the same season (winter). I did not study the troops simultaneously (Table 2.2), but there were no significant differences in minimum temperature (Pair 1: Mann-Whitney U=3551.0, p=0.059; Pair 2: Mann-Whitney U=3851.0, p=0.292) or rainfall (Pair 1: Mann-Whitney U=3738.0, *p*=0.172; Pair 2: Mann-Whitney U=3732.0, *p*=0.167) between the data collection periods for either pair.

I, along with 27 volunteers, collected the required spatial and behavioural data for TK, BB and KK. Volunteers commenced with behavioural data collection only when their records matched mine with an accepted error level of <5 % for behavioural recordings made over a full day of data collection. I supervised all volunteers on a daily basis to ensure that they adhered strictly to the data collection protocols. Researchers and volunteers collecting behavioural data wore identical field jackets and followed the behavioural data collection protocols described in Hoffman and O'Riain (2010) 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 I conducted instantaneous scans of individuals at 20-minute intervals. To obtain a representative measure of troop behaviour 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 behaviour and habitat of every baboon within a 90 ° arc centred on the transect trajectory. I randomised 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). I 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. I recorded behavioural data for male and female adults, sub-adults and juveniles. I classified behaviour as foraging, socialising, 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 behaviour related to food (searching, handling and feeding), I classified the food item as being from natural, urban or agricultural food sources. I 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. I recorded a mean of 11±1 (range: 1-34) animals per scan for TK, a mean of 10±1 (range: 1-16) animals per scan for RH, a mean of 5±0.4 SE (range: 1-13) animals per scan for BB and a mean of 15±1 (range: 1-39) animals per scan for KK. I used Mann-Whitney U tests to investigate differences in the daily habitat use and diet of RH vs. BB and TK vs. KK. I used one-way, single factor ANOVAs (with *post hoc* Tukey tests) to determine differences in percentage of scans allocated by RH vs. BB and TK vs. KK on a daily basis to foraging, socialising, resting and walking. Finally, for TK, BB and KK I recorded the GPS positions of all sleeping sites and categorised them as trees or cliffs. I determined the number of different sleeping sites used during the behavioural data collection period and calculated the mean (±SEM) distances between these sites.

RESULTS

Troop home ranges were distributed from Tokai in the north to Cape Point in the south (Fig. 4.1). I continued to collect data for each troop until either the cumulative frequency of new cells entered per month reached an asymptote (all except BB and KK; Appendix 1) or until I had collected a full year of data. I considered the asymptote to be reached when the number of new cells entered per month increased by ≤5 % for two months or more.

Ranging patterns

Home ranges of the 9 troops varied dramatically in size from 1.5-37.7 km^2 with a mean size of 11.0 km^2 (±6.8 km^2; Fig. 4.1; Table 4.1). Enclosed cells that were not entered accounted for 10.1-54.7 % of home ranges with a mean of 24.2 % (±8.7 %). The density of baboons within each home range varied from 1.3-12.1 baboons/km^2 with a mean population density of 4.7 baboons/km^2 (±2.5 baboons/km^2). Home ranges varied in their habitat compositions (Table 4.1; Appendix 2). Natural habitat was present in all home ranges covering 1.2-99.7 % of the areas, with a mean cover of 73.3 % (±19.7 %). Urban habitat was also present in all home ranges covering 0.3-29.4 % of the areas, with a mean cover of 11.2 % (±7.5 %). Four home ranges comprised between 6.9-12.9 % invasive alien vegetation with a mean cover of 10.1 % (±2.4 %). Three home ranges comprised between 0.2-93.6 % agricultural habitat with a mean cover of 33.1 % (±59.4 %). Troops differed in their use of natural and human-modified habitats, spending between 0.1-98.0 % of their time in natural habitat (mean use: 63.9±19.4 %; Fig. 4.2) and between 2.0-99.9 % of their time in human-modified habitat (mean use: 36.1±19.4 %).

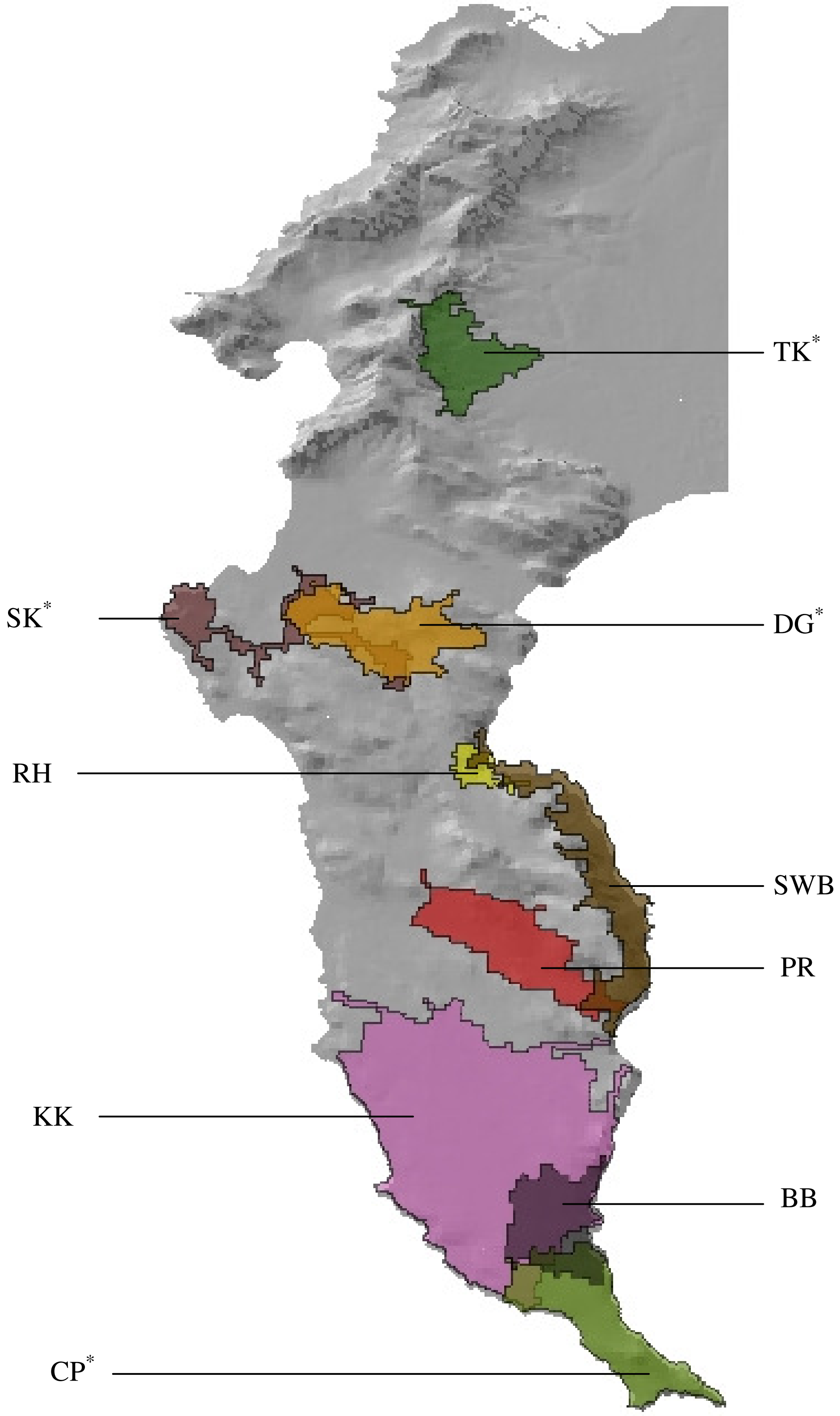


Fig. 4.1. A 3D map of the Cape Peninsula showing the home ranges of the nine troops in this study. Monitored troop are marked with an asterisk.

Table 4.1. Details of troop sizes and home ranges. Troops are tabled according to their geographical position from north to south.

		Home ranges				
Troop	Size	Area	Density	% cells not entered	% cover of natural habitat	% cover of human-modified habitat
TK	115	9.50 km^2	12.1 / km^2	12.6 %	1.2 %	98.8 %
SK	24	8.28 km^2	2.9 / km^2	25.8 %	71.2 %	28.8 %
DG	35	10.58 km^2	3.3 / km^2	20.0 %	71.5 %	28.5 %
RH	16	1.54 km^2	10.4 / km^2	10.1 %	75.4 %	24.6 %
SWB	26	9.26 km^2	2.8 / km^2	20.5 %	63.5 %	36.5 %
PR	36	9.05 km^2	4.0 / km^2	20.9 %	81.1 %	18.9 %
KK	49	37.65 km^2	1.3 / km^2	54.7 %	99.7 %	0.3 %
BB	16	5.63 km^2	2.8 / km^2	32.8 %	96.6 %	3.4 %
CP	22	7.46 km^2	2.9 / km^2	19.9 %	99.0 %	1.0 %

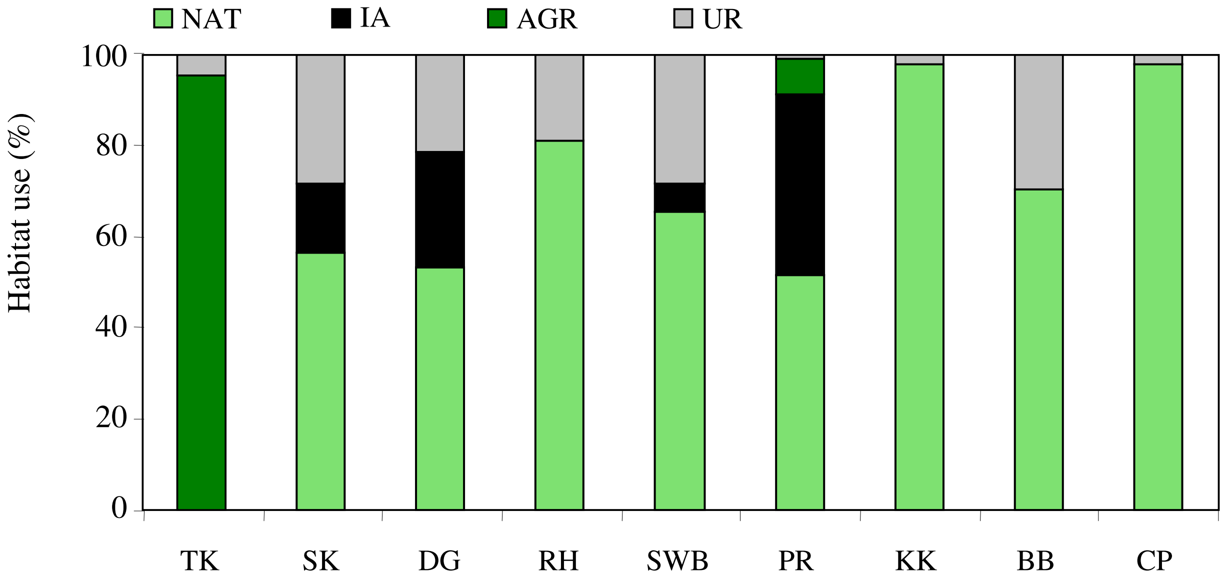


Fig. 4.2. Percentage use of each habitat for each troop. NAT=natural habitat; IA=invasive alien vegetation; AGR=agricultural habitat; UR=urban habitat. Troops are sorted geographically from north (left) to south (right).

DRLs varied from 1.67-6.58 km (mean: 3.99±1.04 km; Fig. 4.3) and differed significantly among troops ($F_{1,8}$=1351.99, df=8, $p \leq 0.001$; Table 4.2). TRs varied from 0.19-0.77 km/hour (mean: 0.42±0.12 km/hour; Fig. 4.4) and differed significantly among troops ($F_{1,8}$=1488.78, df=8, $p \leq 0.001$; Table 4.3). Tukey *post-hoc* tests on both DRL and TR revealed three significantly different groups of troops. Although the group compositions were not consistent between the two ranging variables, two patterns remained throughout. Firstly, for both ranging variables RH was significantly different from all other troops, with the shortest DRL and slowest TR. Secondly, KK and CP, the two troops who spent the most time in natural habitat (Fig. 4.2), were significantly higher than other troops for both ranging variables

Effects of troop size (H1) and human-modified habitat (H2)

The best AIC model for Model 1 (AIC=12.00; deviance=65.83; df=3) explained 89.8 % of the variance in the dataset. Home range size increased with troop size (Table 4.4; Fig. 4.5), and decreased with the % use of human-modified habitat (Fig. 4.6). The best AIC model for Model 2 (AIC=12.00; deviance=8.44; df=3) explained 44.4 % of the variance in the dataset. DPL was unaffected by troop size (Fig. 4.7) and decreased with the % use of human-modified habitat (Table 4.4; Fig. 4.8). The best AIC model for Model 3 (AIC=12.00; deviance=8.25; df=3) found that the number of baboons increased with the area of natural habitat in the home range (Table 4.4) and with the area of human-modified habitat in the home range, but that the latter could support nearly five times as many baboons as the former.

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 km^2), lowest density (1.3 baboons/km^2) and longest DPL (6.17 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 km^2), 3.5 times larger than the second largest home range (DG: 10.4 km^2) and three times larger than the population average (11.0 km^2). Conversely, the home range (9.5 km^2) of the largest troop (TK: 115 baboons) – which was dominated by human-modified habitat (98.8 %) – was smaller than the population average, the troop density (12.1 baboons/ km^2) was the highest locally and, despite its large size, the DPL and TR of TK were not significantly different from those of the two smallest troops (RH and BB; Figs 4.3 and 4.4).

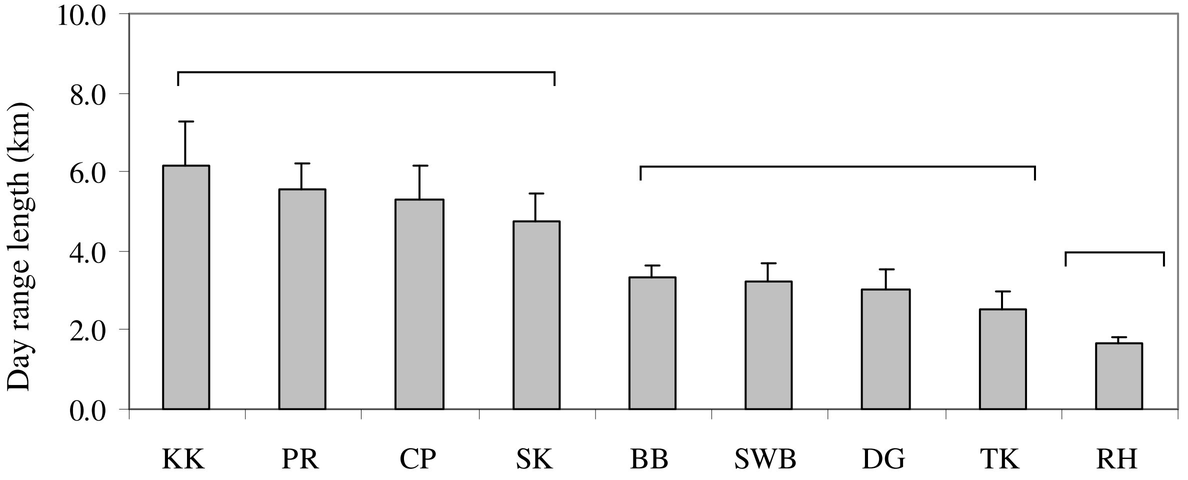


Fig. 4.3. Mean±SEM annual day range length for each troop (*n*=22 days per troop) sorted in descending order. Lines above the graph separate the troops into groups that are not significantly different but that differ significantly from the troops in other groups (see Table 4.2). The exceptions to the above include no significant differences between SK and BB, or between TK and RH.

Table 4.2. Results of Tukey *post-hoc* tests (MS=2.5607, df=214.00) determining among-troop differences in day range length. Bold values indicate significant differences at *p*≤0.05. Troops are tabled according to their geographical position from north to south.

Troop	TK	SK	DG	RH	SWB	PR	KK	BB	CP
TK	-	**<0.001**	0.976	0.563	0.863	**<0.001**	**<0.001**	0.799	**<0.001**
SK	**<0.001**	-	**0.003**	**<0.001**	**0.028**	0.633	**0.047**	0.059	0.951
DG	0.976	**0.003**	-	**0.038**	1.000	**<0.001**	**<0.001**	1.000	**<0.001**
RH	0.563	**<0.001**	**0.038**	-	**0.013**	**<0.001**	**<0.001**	**0.010**	**<0.001**
SWB	0.863	**0.028**	1.000	**0.013**	-	**<0.001**	**<0.001**	1.000	**<0.001**
PR	**<0.001**	0.633	**<0.001**	**<0.001**	**<0.001**	-	0.917	**<0.001**	1.000
KK	**<0.001**	**0.047**	**<0.001**	**<0.001**	**<0.001**	0.917	-	**<0.001**	0.640
BB	0.799	0.059	1.000	**0.010**	1.000	**<0.001**	**<0.001**	-	**0.001**
CP	**<0.001**	0.951	**<0.001**	**<0.001**	**0.000**	1.000	0.640	**0.001**	-

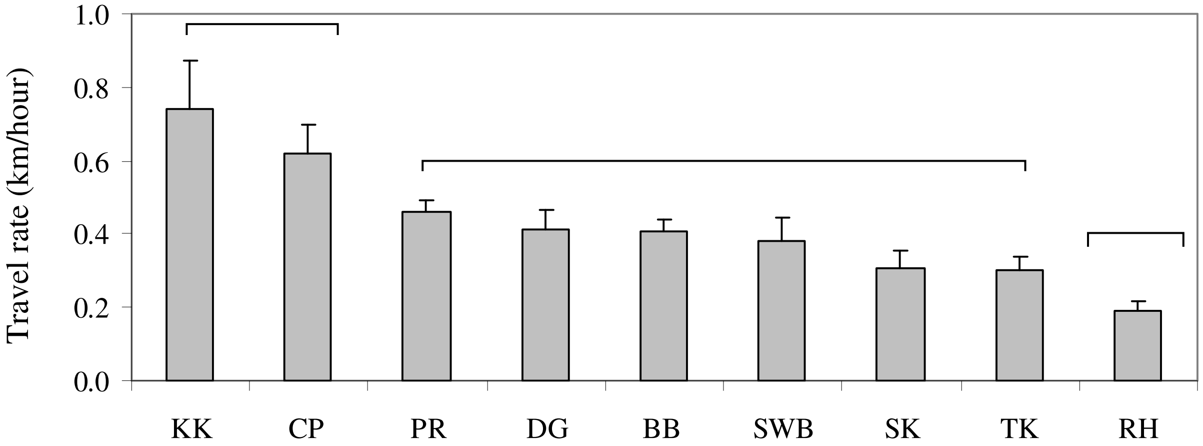


Fig. 4.4. Mean±SEM annual travel rate for each troop (*n*=22 days per troop) sorted in descending order. Lines above the graph separate the troops into groups that are not significantly different but that differ significantly from the troops in other groups (see Table 4.3). The only exception to the above is that TK and RH do not differ significantly from each other.

Table 4.3. Results of Tukey *post-hoc* tests (MS=0.0274, df=214.00) determining among-troop differences in travel rate. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

Troop	TK	SK	DG	RH	SWB	PR	KK	BB	CP
TK	-	0.275	0.9975	0.3691	0.729	**0.012**	**<0.001**	0.450	**<0.001**
SK	0.275	-	0.736	**<0.001**	0.9994	0.970	**<0.001**	1.000	**<0.001**
DG	0.9975	0.736	-	**0.042**	0.984	0.092	**<0.001**	0.875	**<0.001**
RH	0.3691	**<0.001**	**0.042**	-	**0.0017**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SWB	0.729	0.9994	0.984	**0.0017**	-	0.7248	**<0.001**	1.000	**<0.001**
PR	**0.012**	0.970	0.092	**<0.001**	0.7248	-	**<0.001**	0.9507	**0.0226**
KK	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-	**<0.001**	0.1799
BB	0.450	1.000	0.875	**<0.001**	1.000	0.9507	**<0.001**	-	**<0.001**
CP	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.0226**	0.1799	**<0.001**	-

Table 4.4. Results of the generalized linear models used to investigate the effects of troop size and human-modified habitat on home range size (Model 1) and day range length (Model 2), and the effect of habitat on troop size (Model 3). Bold values indicate significant differences at $p \leq 0.05$. The mathematical formulae are included for all models, with the sign of each parameter indicating the relationship (positive or negative) between each factor and the response terms (Y).

	Parameter	SE	*t*	*p*(*t*)
Model 1: Home range area (Y) = -1.86 + (3.37 * log troop size) + (-0.02 * use of human-modified habitat)				
Intercept	-1.86	0.83	-2.25	0.066
Troop size	3.27	0.51	6.44	**<0.001**
Use of human-modified habitat	-0.02	0.00	-7.79	**<0.001**
Model 2: Day range length (Y) = -1.38 + (4.90 * log troop size) + (-0.05 * use of human-modified habitat)				
Intercept	-1.38	2.73	-0.51	0.631
Troop size	4.90	2.08	2.35	0.057
Use of human-modified habitat	-0.05	0.02	-2.83	**0.030**
Model 3: Troop size (Y) = (0.11 * natural habitat cover) + (0.52 * human-modified habitat cover)				
Natural habitat cover (km^2)	0.11	0.00	35.71	**<0.001**
Human-modified habitat cover (km^2)	0.52	0.01	58.55	**<0.001**

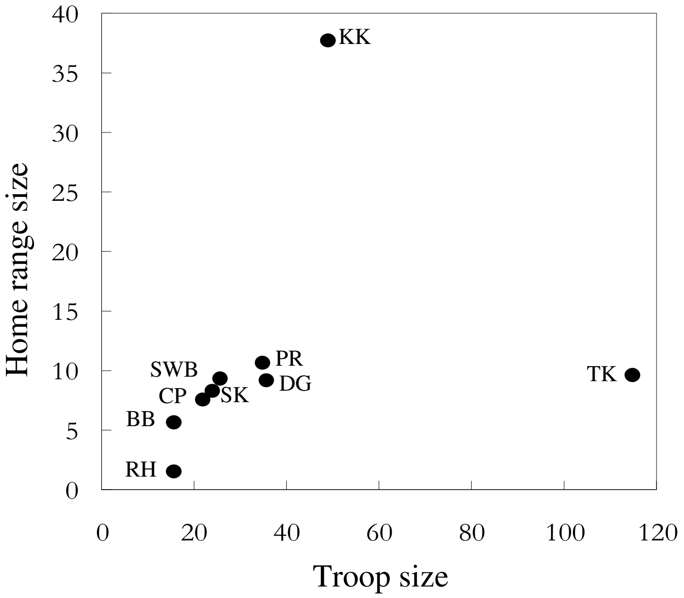


Fig. 4.5. XY scatter plot of the relationship between troop size and home range size.

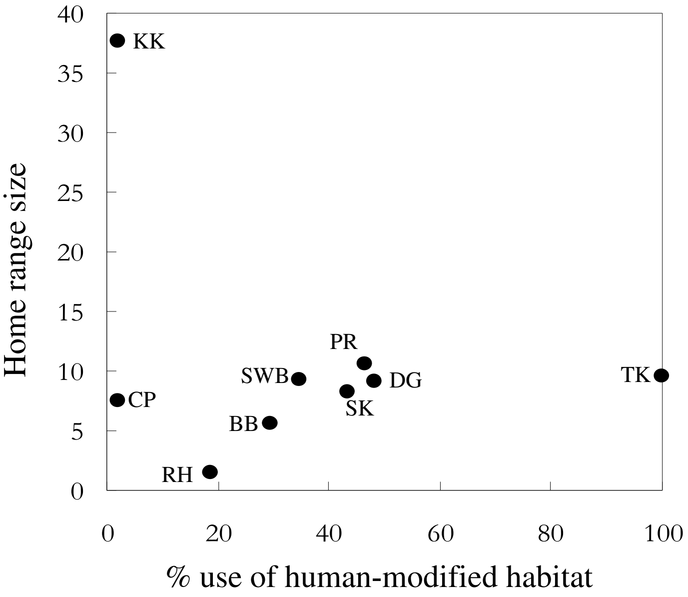


Fig. 4.6. XY scatter plot of the relationship between the % use of human-modified habitat and home range size.

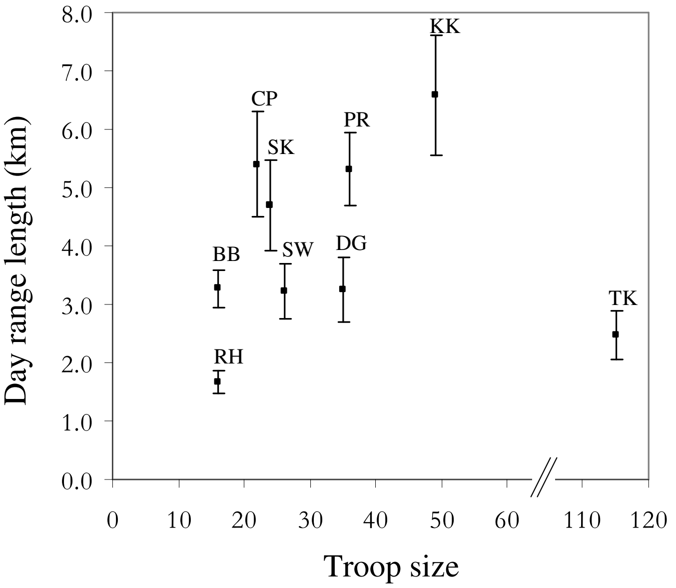


Fig. 4.7. XY scatter plot of the relationship between troop size and day range length (mean±SEM, n=22 days per troop).

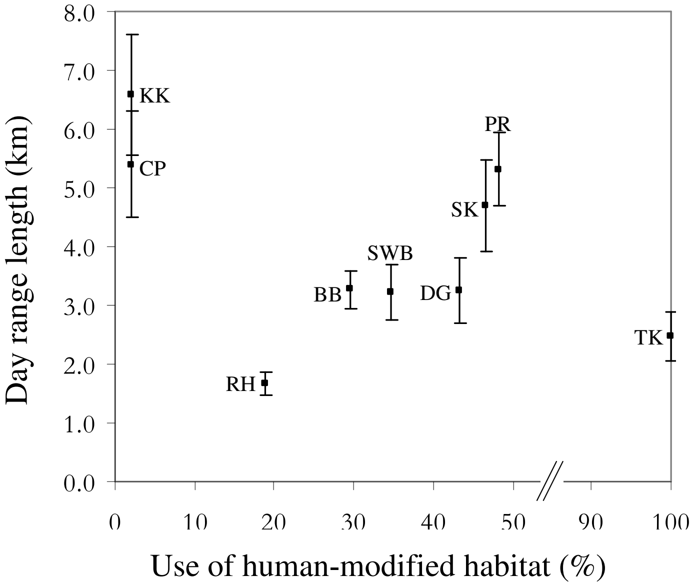


Fig. 4.8. XY scatter plot of the relationship between % use of human-modified habitat and day range length (mean±SEM, n=22 days per troop).

The comparison of the two equal-sized, unmonitored troops (RH and BB; Pair 1) and the two troops occupying the most extreme habitat conditions (TK and KK; Pair 2) added statistical support to the assertion that ecological factors are important in explaining variation in ranging patterns and behaviour. 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 4.5), and significantly less time in natural habitat (Mann-Whitney U=0.0, $p<0.001$). The RH home range (1.5 km^2) was 3.5 times smaller than the BB home range (5.6 km^2), and the RH density (10.4 baboons/km^2) was 3.5 times greater than the BB density (2.8 baboons/km^2). RH travelled significantly shorter distances ($t=4.47$, $n=10$ days, $p<0.001$; Fig. 4.3) at a significantly slower TR ($t=9.71$, $n=10$ days, $p<0.001$; Fig. 4.4) than BB. Furthermore, RH – who foraged on anthropogenic food sources significantly more than BB (Mann-Whitney U=0.0, $p<0.001$; Table 4.5), 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, $p\leq0.001$; Table 4.5) and significantly more time resting ($F_{1,18}=67.91$, df=18, $p\leq0.001$). The troops spent a similar proportion of time socialising ($F_{1,18}=2.53$, df=18, $p=0.129$) and walking ($F_{1,18}=0.86$, df=18, $p=0.365$). The comparison of the troops in Pair 2 revealed the most pronounced breakdown of troop size effects on baboon ranging patterns. Despite being twice the size of KK, TK – who spent significantly more time in human-modified habitat than KK (Mann-Whitney U=0.0, $p<0.001$; Table 4.6) and significantly less time in natural habitat (Mann-Whitney U=0.0, $p<0.001$) – travelled significantly shorter distances ($t=-3.37$, $n=10$ days, $p=0.003$; Fig. 4.3) at a significantly slower TR ($t=-4.50$, $n=10$ days, $p<0.001$; Fig. 4.4) than KK. Furthermore, TK – who foraged on anthropogenic food sources significantly more than KK (Mann-Whitney U=0.0, $p<0.001$; Table 4.6), and on natural food sources significantly less (Mann-Whitney U=0.0, $p<0.001$) – spent significantly less time walking ($F_{1,18}=36.36$, df=18, $p<0.001$; Table 4.6) and significantly more time resting ($F_{1,18}=13.19$, df=18, $p=0.002$) and socialising ($F_{1,18}=78.77$, df=18, $p<0.001$). The troops spent a similar proportion of time foraging ($F_{1,18}=0.86$ df=18, $p=0.367$).

TK slept in 11 sleeping sites, all of which were trees located within the Tokai plantation. The mean distance between sleeping sites was 1.0±0.1 km (Fig. 4.9). RH had one cliff sleeping site located near the centre of its range and directly above an urban residential area. KK had eight different cliff sleeping sites. Two were located along the eastern coast in its home range, and six along the western coast with a mean distance of 3.7±0.4 km between sites.

Table 4.5. Mean daily percentage (±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 $p<0.05$.

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

° Human-modified includes urban habitat

Table 4.6. Mean daily percentage (±SEM) of habitat use, diet and activity budgets of the two troops occupying the most extreme habitat conditions locally (TK and KK) during winter (*n*=10 days). * indicate significant differences at $p<0.05$.

	Habitat use (% per day)		Food items (% per day)		Activity (% per day)			
Troop	Natural*	Human-modified*°	Natural*	Anthropogenic*	Forage	Social*	Rest*	Walk*
TK	1.6 (±2.7)	98.4 (±2.7)	1.8 (±3.5)	98.2 (±3.5)	48 (±6.4)	23.1 (±3.2)	20.0 (±3.8)	8.9 (±3.1)
KK	100.0 (±0.0)	0.0 (±0.0)	100.0 (±0.0)	0.0 (±0.0)	52.0 (±5.6)	5.3 (±2.3)	9.4 (±4.3)	33.3 (±7.3)

° Human-modified includes agricultural habitat and urban habitat

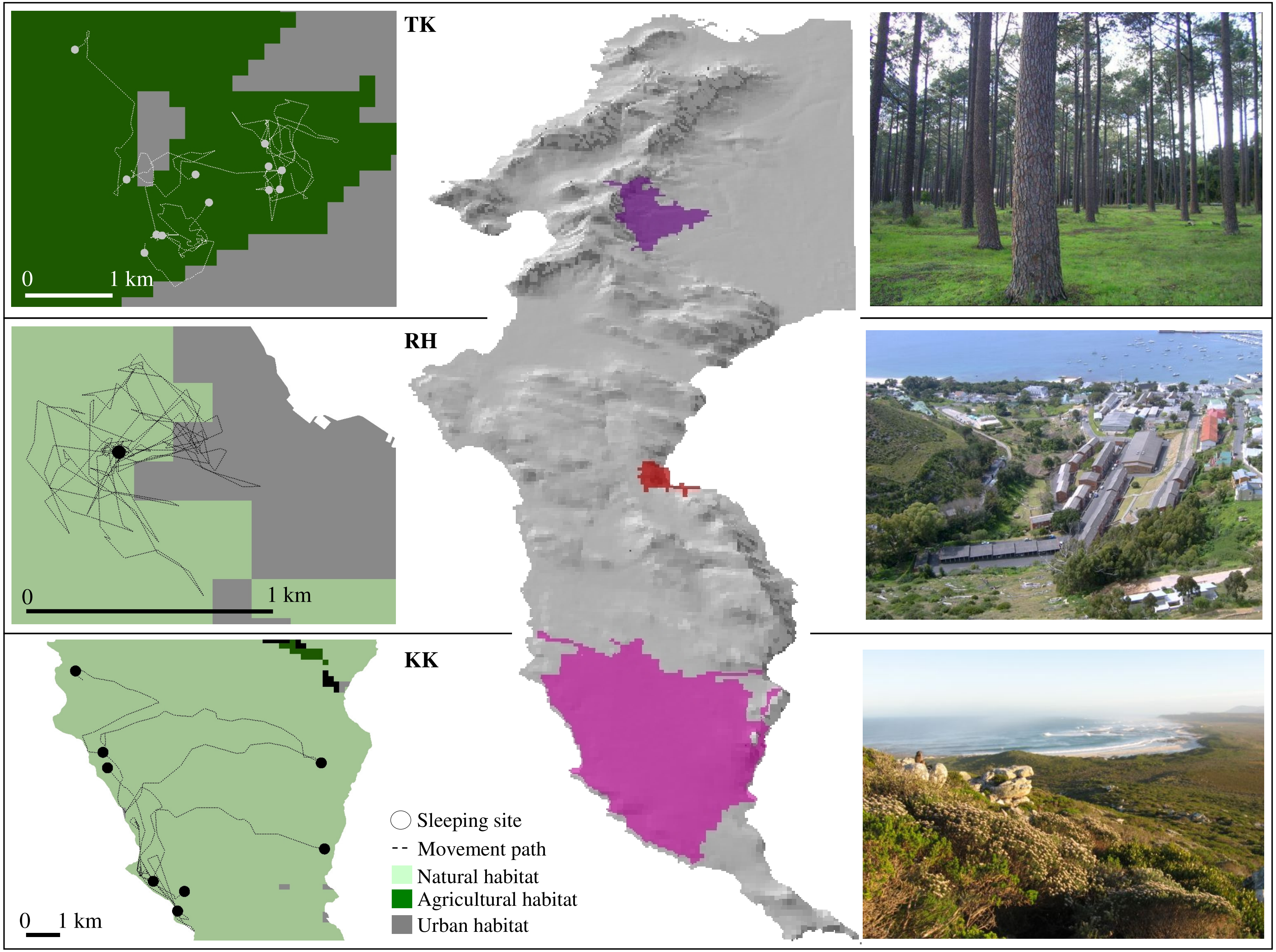


Fig. 4.9 A 3D map showing the home ranges of TK (purple), RH (red) and KK (pink) in the Cape Peninsula (central image) and the daily movement patterns and sleeping site distributions (left plates) recorded for each troop over a 10-day period. The plates on the right are photographs showing the broad habitat differences between the home ranges of the three troops.

DISCUSSION

The chacma baboon troops in the Cape Peninsula exhibit substantial intrapopulation variation in ranging patterns. This variation is expected (Bronikowski and Altmann 1996; Chapman and Chapman 2000) 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 and 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 km^2) equalled those previously reported across the entire chacma distribution, ranging from 1.9 km^2 (Limpopo (was Northern Transvaal), South Africa: Stoltz and Keith 1973) to 37.0 km^2 (Cape Peninsula, South Africa (C troop): Davidge 1978a) and among other primates, was most comparable to the variation reported for a wild population of Japanese macaques (*Macaca fuscata*, 0.24 26.7 km^2: Takasaki 1981).

Similarly to Takasaki (1981), but contrary to our first prediction (H1), I 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 including baboon monitors (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 (*sensu* Chapman and Chapman 2000). In accordance with my second prediction (H2) I found that human-modified habitat also significantly influenced baboon ranging patterns, with increased use of human-modified habitat corresponding to smaller home ranges and shorter DRLs. In support of these findings my third model revealed that 1 km^2 of human-modified habitat could support nearly five times the number of baboons as 1 km^2 of natural habitat.

The three troops (TK, RH, KK) occupying the extremes of habitat conditions from the most pristine to the most human-modified, consistently showed the most extreme ranging patterns. Furthermore, in all analyses of troop size and ranging patterns TK emerged as a consistent outlier. Primate species with access to high quality and predictably available resources, such as those found in some human-modified habitats (e.g., agriculture) typically show reductions in home range sizes and DRLs, and increases in group sizes and home range densities (Brennan et al. 1985; Saj et al. 1999; Fuentes et al. 2005). Thus it is unsurprising that the two troops (TK and RH) with the smallest home ranges, highest densities and shortest DRLs 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 longest DRL 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/km^2) comparable to that of troops occupying seasonally harsh environments like the Drakensberg mountains (0.95 baboons/km^2 (High troop): Whiten et al. 1987), while TK and RH occur at densities (TK: 12.1 baboons/km^2, RH: 10.4 baboons/km^2) most similar to troops found in fertile environments like the Okavango Delta (16.8 baboons/km^2 (G1 and H troops): Hamilton et al. 1976).

Two factors, namely concentrated food sources (Forthman-Quick and Demment 1988; Singh and Vinathe 1990; Riley 2007) 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 and 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. in press). Consequently, both TK and RH were able to satisfy their nutritional and resting requirements within very small areas. This resulted in high densities and short distances travelled daily and ultimately small home ranges. Similar effects on ranging patterns have been reported for baboons and other primates that have access to human-modified habitats (Brennan et al. 1985; Siemers 2000; Hill 2005) and anthropogenic food sources (Altmann and 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 and O'Riain 2010; van Doorn 2009). 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.

The proportion of time that primates spend feeding is a function of the richness, spatial proximity, and processing time of food sources (Altmann 1974). In the Cape Peninsula, baboons have altered their foraging behaviour and diet to include food items sourced from human-modified habitats. Of the two equal-sized, unmonitored troops, RH fed predominantly on anthropogenic food sources acquired through opportunistic raiding in residential urban habitat (e.g., bread, candy, fruit; Kaplan et al. in press). In contrast, BB had more limited access to anthropogenic food sources (from a picnic site used ephemerally by people) within its home range and fed predominantly on natural food sources. Of these two troops, RH spent less time foraging and more time resting. This reduction in time allocated to foraging is characteristic of primates that have access to concentrated and predictable food sources (Forthman-Quick and Demment 1988; Singh and Vinathe 1990; Riley 2007). The minimal time that RH allocated to foraging (27 %) as a result of its raiding proficiency is noteworthy, both locally and compared to naturally foraging chacma troops elsewhere (34 %: Davidge 1978b; 57 %: Dunbar 1992; 36 %: Gaynor 1994; 43 %: Hill et al. 2003), and is instead more comparable to provisioned baboon troops (Altmann and Muruthi 1988; Strum 2010). Interestingly, agricultural food sources did not have the same effect on baboon foraging time as urban food sources. Despite the remarkable differences in the ranging patterns and diets of TK and KK, the two troops devoted similar amounts of time to foraging. As suggested by Hoffman and O'Riain (2010) this similarity indicates that, despite their spatial concentration, the food sources in the TK home range may not be associated with a handling time or ingestion time low enough to reduce time spent foraging. That KK differed significantly from TK in all other aspects of behaviour, walking more and resting and socialising less, is a further indication that, compared to the TK home range, the environment occupied by KK was resource limited.

A final comparison among TK, RH and KK yields interesting insight into the relationship between troop size and habitat quality. Because females with access to habitats that have high quality food sources reproduce from a younger age and have shorter interbirth intervals than females who don't (Strum 2010), group growth rates and group sizes tend to correlate positively with habitat quality (Fuentes et al. 2005). Both the ranging patterns and behaviour of TK, RH and KK suggests that TK and RH have access to habitat of higher quality than KK. Yet, the sizes of these troops do not suggest the same relationship as KK was more than three times the size of RH, and TK was more than seven times the size of RH. Rather than indicate that troop size and habitat quality are not related in this population, these differences are likely the consequence of the combined influences of demographic processes and habitat effects. Population census data show that TK, who was first counted at 95 baboons (Kansky and Gaynor 2000), has grown at an average annual rate of 9.1 % over the last decade (Beamish 2010). Contrastingly, the KK troop has shown more stability over the same time period, growing at an average annual rate of 5.1 % (Beamish 2010). That RH is a much smaller troop than either TK or KK is attributable to RH establishing (after fissioning from the SWB troop) in 2007, less than one year before I began spatial data collection for this troop. However, the effects of habitat quality on troop size are still evident as RH has been growing at an average annual rate of 18.2 % (Beamish 2010) since its establishment, suggesting that – in the absence of a fission event – in time its troop size could surpass that of KK and approach that of TK. These results indicate that the effects of habitat on troop size may not be immediately discernible or accurately interpreted if long-term demographic data are not collected along with ecological data.

Conclusions

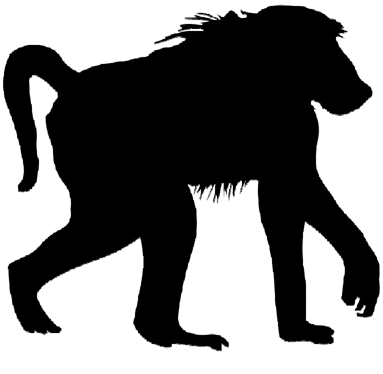
In summary, I found that ranging patterns of the chacma baboons in the Cape Peninsula were significantly affected by both troop size and human modified habitat. Despite extensive heterogeneity in habitat use, the ranging patterns of nine troops from this single population supported the theoretical expectation that larger troops will have larger home ranges. Furthermore, more time spent in human-modified habitat – with its availability and concentration of high-quality food sources - corresponded to smaller home ranges, shorter DRLs and higher densities.

The ranging patterns of baboons in predominantly natural habitat were comparable to those of troops occupying seasonally harsh environments like the Drakensberg Mountains. By contrast troops with access to human-modified habitats, where high quality and predictably available food sources were situated in close proximity to sleeping sites, had ranging patterns similar to those of troops occupying fertile environments like the Okavango Delta. Furthermore, comparisons of equal-sized troops and troops living under extreme habitat conditions revealed that troops with access to human-modified habitat exhibit increased home range densities, troop sizes and or growth rates and reduced home range sizes, DRLs, travel rates and time spent feeding than troops in natural habitat. Importantly human-modified habitats did not all confer comparable foraging benefits to baboons, and although spatially concentrated and predictably available, agricultural food sources did not lead to the same reduction in feeding time as did urban food sources.

The level of intrapopulation variation exhibited in the Cape Peninsula is testament to the exceptional adaptability and behavioural plasticity of baboons. However, it also cautions that studies focussed on only a small sample of troops within a population of adaptable and generalist species may underestimate the variability in their respective localities (Bronikowski and Altmann 1996). Finally, while the extensive variation highlights the aptitude of the Cape Peninsula population as a testing site for theoretical investigation and practical experimentation, it also intimates that baboon management strategies need to include both population-level and troop-specific patterns in order to be effective. The development of such comprehensive management plans forms the focus of the next chapter.

Chapter 5

Monkey management: Using spatial ecology to understand the extent and severity of human-baboon conflict in the Cape Peninsula



ABSTRACT Human-wildlife conflict poses one of the greatest threats to the persistence and survival of all wildlife. In the Cape Peninsula, HBC levels – measured here as human-induced injury and death – remain high despite substantial investment by conservation authorities in a variety of mitigation measures. Here I explore how spatial ecology can inform baboon management on the current and projected extent and severity of HBC and further propose mitigation. I apply conservative (2.3 baboons/km^2) and generous (5.9 baboons/km^2) densities to hypothetical landscape scenarios to estimate whether this baboon population is overabundant. I correlate conflict indices with spatial variables to explain intertroop differences in conflict levels. I investigate how an understanding of key elements of baboon ecology, including sleeping site characteristics, intertroop territoriality and the effects of season and fire on ranging patterns, can improve management. None of the estimated population sizes (488-799 baboons) indicated an overabundance of the current population (460 baboons). Conflict levels correlated positively with the loss of access to low lying land (Pearson r=0.77, p=0.015, n=9 troops) and negatively with the distance of sleeping sites to 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 the troops slept <500 m from the urban edge, resulting in increased spatial overlap and conflict with residents. Evidence for the potential for intertroop territoriality suggested that troop removal to mitigate HBC would only be a short-term solution as neighbouring troops are predicted to usurp the vacated home range and thus perpetuate the cycle of conflict. Certain troops showed a marked seasonal shift in home range use which equated to greatly increased spatial overlap between humans and baboons. However there was no clear ‘conflict season’ across all study troops suggesting that seasonal management plans should be troop-specific. Finally, because mature natural habitat was more attractive to baboons, baboon home ranges are predicted to expand and shift towards older vegetation patches following fires. Management authorities are thus advised to only burn portions of extant home ranges to avoid range expansion and ensure baboons can access adequate mature vegetation with higher standing biomass and productivity. Together the findings in this chapter suggest that an understanding of wildlife spatial ecology can be used to identify current and predicted landscape-level causes of HBC. This information can be used to formulate sustainable long-term landscape management and conservation plans so that less costly direct animal management is required.

INTRODUCTION

Conflict has characterised 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 brought competition between humans and wildlife for space and resources to unprecedented levels (Siex and Struhsaker 1999b; 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, repellents; 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).

In the Cape Peninsula, as the size of the human population and the extent of landscape transformation and fragmentation have increased, so too have levels of HBC (Beamish 2010). In Chapter 3 I argue that the convergence of human and baboon land use patterns is the primary cause of HBC. Additionally, in Chapter 4 I describe how the combination of baboon ecological flexibility (Hill 2000; Strum 2010) with access to human-modified habitats affects baboon ranging patterns and behaviour which, although energetically favourable for baboons, can increase HBC. A suite of management methods have been employed in an attempt to reduce local levels of HBC, including: troop extirpation (Skead 1980), legislation to protect baboons from hunting (Western Cape Province 1999), waste management, public education, assisted dispersal for adult males, the euthanasia of specific ‘problem’ individuals, the localised installation of electric fencing and the herding of select troops away from urban habitat by baboon monitors (Kansky and Gaynor 2000; van Doorn 2009). However, despite these efforts levels of HBC remain high, as indicated by the extent to which baboons suffer human-induced injury and mortality (Beamish 2010). It is thus evident that alternative and novel management techniques are required to reduce the frequency and severity of HBC, in addition to a better understanding of the fundamental drivers of this conflict.

Conflict despite mitigation efforts

My first aim in this chapter is to build on the findings of Chapters 3 and 4 to explain: (1) why conflict levels remain high despite current mitigation measures, and (2) why some troops experience higher levels of HBC than others. To do this I first investigate whether HBC levels could be attributable to an overabundance of baboons (i.e., has the population size exceeded was is sustainable given the habitat characteristics of the Cape Peninsula) 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 (Chapter 4). Second, I provide four spatial ecology variables that may prove useful in understanding why levels of HBC vary so dramatically between troops, namely: (1) the percentage of accessible area that is urbanised, (2) the percentage of home range area <100 m that is urbanised, (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 altitudes (Chapter 3) I predict that these analyses will reveal that troops with the least access to non-urbanised low lying land in their home ranges, and in the land immediately accessible to their home ranges, will experience the highest levels of HBC. Furthermore, based on the preference shown by baboons for human-modified habitat (Chapter 3) I predict that HBC levels will correlate with the extent of home range perimeter that abuts the urban edge and or the proximity of sleeping sites to the urban edge.

Using spatial ecology to inform conflict management

Wildlife management is synonymous with applied ecology (Sinclair et al. 2006) and thus, as a second aim of this chapter I investigate how ecological data can inform both current baboon management practices and lead to the development of novel management techniques. To this end I analyse key elements of baboon ecology including sleeping site characteristics and intertroop territoriality as well as the effects of season and fire on ranging patterns.

Sleeping sites

In Chapter 3 I argue that the distribution and characteristics of baboon sleeping sites are most likely a direct result of the proximity of these sites to the preferred forage of human-modified habitats. These sleeping patterns are problematic from a management perspective as the proximity of baboon sleeping sites to human-occupied areas increases the potential for interspecies disease transfer (Ravasi 2009; Drewe et al. in press) and compromises the ability of managers to effectively reduce raiding and minimise HBC. I analyse the characteristics and distribution of baboon sleeping sites and determine whether alternative sleeping site locations, with similar characteristics to those currently used by baboons, are available elsewhere in the Cape Peninsula at an increased distance from human-occupied areas.

Territoriality

Although baboons are typically considered to be non-territorial primates (Crook and Aldrich-Blake 1968; Stoltz and Saayman 1970; Mitani and Rodman 1979; Anderson 1982; Lowen and Dunbar 1994), their social organisation can be adapted to local conditions (Kummer 1968) and expression of territoriality can be flexible (Strier 2007). Furthermore, Hamilton et al. (1976) found evidence of strong spatial defence by chacma baboons in the Okavango Delta, Botswana and the Kuiseb Canyon, Namibia. The exhibition of territorial defence by Cape Peninsula troops would have direct management implications as it would suggest that the removal of ‘problem’ troops for the purposes of reducing HBC would simply serve to vacate a high conflict (i.e. high quality) site that previously excluded neighbouring troops could then usurp. In the event that the new troop experienced the same high levels of HBC and the troop removal process was repeated, this site could become a local population sink with threats to the sustainability of this geographically isolated population. Here I quantify patterns of community ecology, specifically seeking evidence of spatial (n=6 troops) and or temporal (n=3 troops) territoriality.

Seasonality

Baboon ranging patterns can be affected by seasonal shifts in food availability and distribution (Isbell and Young 1993; Stevenson 2006; but see Buzzard 2006) and annual variability in rainfall (Raemakers 1980; Isbell 1983; Higham et al. 2009), temperature (Yang 2003) and day length (Li 2002; Hill et al. 2003). Given the seasonality in the Cape Peninsula climate, with cool, wet winters and warm, dry summers with increased day length, it is important that management strategies are equipped to deal with any resultant seasonal variation in baboon ranging patterns. For this purpose I investigate differences in home range use and movement patterns during the seasonal extremes of winter and summer. Based on the findings of Hoffman and O’Riain (2010) I predict that troops will show an increased preference for low altitude areas in winter compared to summer, and as a result of the subsequent increase in proximity to low lying urban habitat I also predict that troops will show increased use of urban habitat during winter compared to summer.

Fire

The indigenous vegetation of the Cape Peninsula (fynbos) has burned periodically for approximately 100,000 years (van Wilgen 1982) with fire affecting plant growth, survival and reproduction and acting as an important structuring agent of vegetation communities (Bond and van Wilgen 1996; DeBano et al. 1998; Cowling et al. 2006). Fire frequency is important for vegetation recovery and regeneration, with time intervals between fires typically varying from 15-20 years (van Wilgen 1982). More frequent fires keep plant biomass low by eliminating most of the seed-producing shrubs, but in so doing compromise the regenerative ability of plants (van Wilgen and Kruger 1981). Less frequent burns (>30 years) are associated with hotter fires that reduce plant survival and pose a risk to adjacent urban habitat. Consequently, fire management is an important component of environmental management and in the Cape Peninsula it typically involves the control of natural and human-caused fires and the prescribed burning of select patches (DeBano et al. 1998). However, fire also affects wildlife both directly and indirectly (Whelan 1995) and thus understanding how fire affects animals in fire-prone ecosystems is another important aspect of fire management. Fire can even be used manipulate the distribution and characteristics of vegetation in order to create or maintain desired animal habitats (Hobbs and Gimingham 1987; Bond and van Wilgen 1996). There are currently no publications that describe how baboons respond to fire and post-fire conditions. Yet, in the Cape Peninsula, understanding how fire and the associated sudden changes in natural food availability might affect baboon ranging patterns is vital for preventing prescribed and unplanned burns from causing unexpected increases in HBC through dramatic home range shifts. To determine how fire may affect baboon spatial ecology I model the use of differently aged (i.e. time since burn) plots of vegetation by a baboon troop, predicting that the troop will show a preference for the higher biomass of older plots. In addition I conduct a vegetation survey in the same site to determine the relationship between vegetation age and vegetation biomass.

METHODS

Conflict despite mitigation efforts

Is this baboon population overabundant?

I applied two different density estimates to hypothetical scenarios of available land to explore the total number of baboons that the Cape Peninsula could support. I based the first density estimate on the mean density of the three troops (2.3 baboons/km^2; KK, BB, CP) ranging entirely within the CoGH. These troops forage predominately in natural habitat although two troops opportunistically access anthropogenic food sources at tourist nodes (BB: 1.2 %, CP: 0.2 % of winter diet). I based the second estimate on the mean density of the six troops ranging outside of the CoGH that have access to both natural and anthropogenic food sources (5.9 baboons/km^2; TK, SK, DG, RH, SWB, PR).

I applied these density estimates to eight hypothetical scenarios of land availability, each with a particular spatial extent and set of habitat conditions. The only restriction that pertained throughout all scenarios was that I denied baboons access to urban habitat, and to the island patches of natural habitat fully subsumed within urban habitat (Fig. 5.1a). To account for differences in the forage potential of different habitats, across all scenarios I applied the conservative density estimate to natural habitat, and the generous density estimate to agricultural habitat and invasive alien vegetation.

I divided the eight hypothetical scenarios of available land into two categories, Category (a) and (b), each comprising four scenarios respectively (Fig. 5.1). In Category (a) I 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. 5.1a). In Category (b) I included a less generous area of 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 (Fig. 5.1b) I limited the available land to that contained within, or directly adjacent to, the combined accessible areas of each troop (the area that could be reached by the troop within a mean day range length from its home range; Chapter 3).

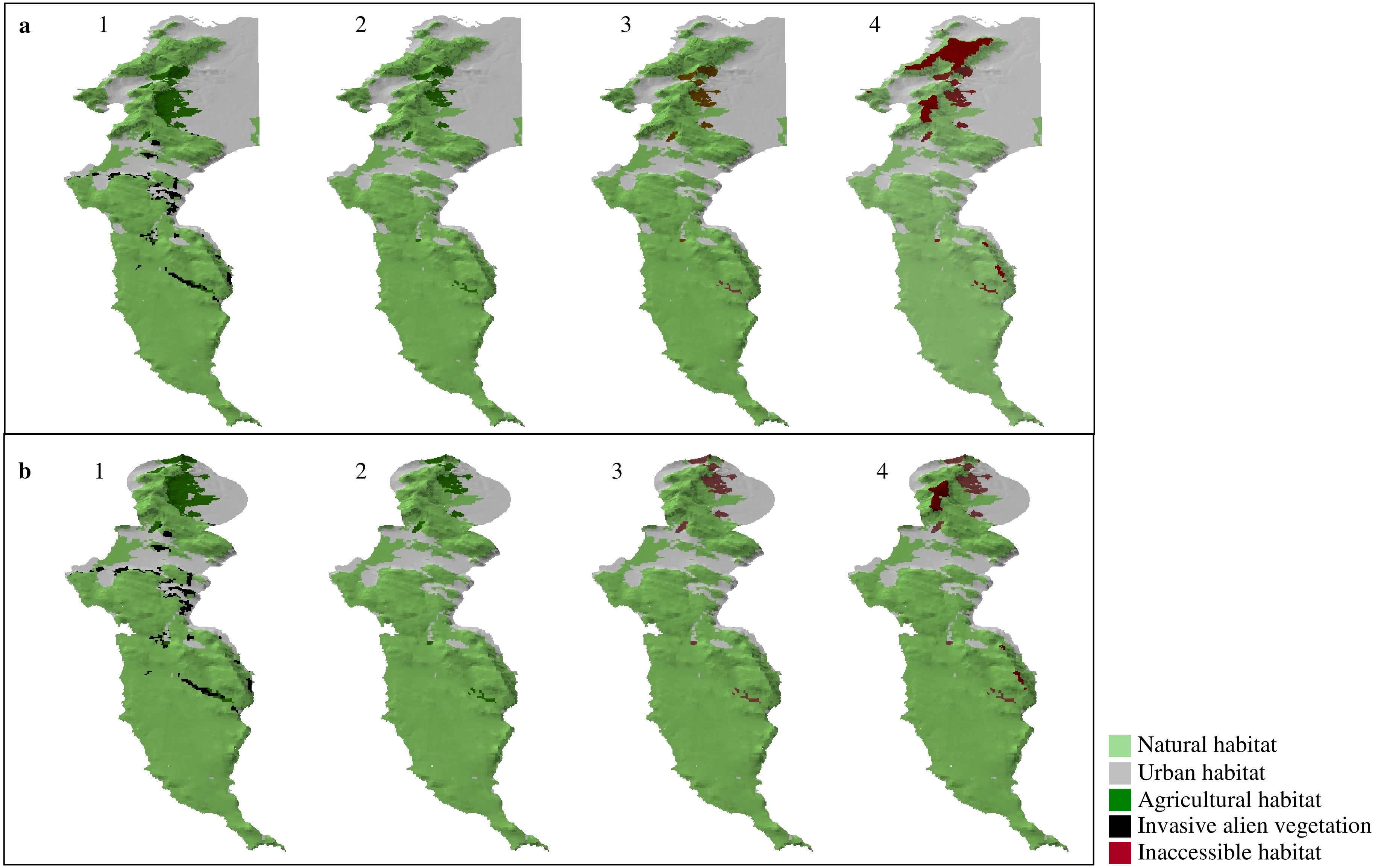


Fig. 5.1. 3D maps of the Cape Peninsula showing eight hypothetical scenarios of available land for baboons. I combined these scenarios with two baboon density estimates to explore the total number of baboons that the Cape Peninsula could support. In both (a) and (b) the total areas of available land decrease progressively from 1-4 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 one day journey. In all scenarios baboons are denied access to urban habitat. In both (a) and (b) the details of Scenarios 1-4 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).

In both Categories (a) and (b) the details of Scenarios 1-4 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. I derived Scenario 2 from Scenario 1 but here I included the planned landscape changes for the Cape Peninsula, with all invasive alien vegetation removed and the Tokai plantation restored to natural habitat. I derived Scenario 3 from Scenario 2 but here I 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). I derived Scenario 4 from Scenario 3 but, based on my understanding of the foraging behaviour of this population, here I included only natural habitat ≤600 m. I selected this value as this contour line was nearest to the highest altitude at which I recorded foraging behaviour for any troop (567.2 m; TK).

Can spatial ecology explain levels of HBC?

I calculated two indices of HBC for each troop using mortality and injury data recorded for the population from 2005-2007 (Beamish 2010). For the first conflict index (Index 1) I calculated the total number of baboons per troop that suffered either human-induced death or human-induced injury over the three year period. I 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 three year period.

To determine if spatial ecology variables provided explanations for the varying levels of HBC I 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 urbanised, (2) the percentage of home range area <100 m that was urbanised, (3) the percentage of home range perimeter abutting the urban edge and (4) the mean proximity of sleeping sites to urban habitat. I used the Cape Peninsula grid system (Chapter 2) to calculate (1) and (2), and the Clip function in the GeoProcessing wizard in ArcView 3.3 to measure (3). To calculate (4) I conducted the following for each troop: (a) I used the Nearest_features extension to ArcView (Jenness 2004) to calculate the mean distance of every sleeping site to its five nearest urban habitat grid cells and (b) 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.

Using spatial ecology to inform conflict management

Sleeping sites

For each troop I calculated the percentage of sleeping sites classified as buildings, trees or cliffs. I analysed all troop sleeping sites collectively to calculate the mean altitude and slope (±SEM) of the populations' cliff sleeping sites. To determine whether the use of buildings or trees was a function of choice or of limited cliff sleeping site availability I used ArcView 3.3 to identify grid cells across the Cape Peninsula that were ≥ 500 m from the urban edge, comprised natural habitat and were within the same range of altitude and slope values (mean±SEM) as known cliff sleeping sites. I based the urban edge proximity on the mean hourly travel rate of Cape Peninsula baboon troops (0.42±0.11 km/hour; Chapter 4) to ensure that I only identified suitable sleeping sites that were more than one hours mean travel time from the urban edge.

Territoriality

To determine whether community-level influences on troop-level ranging patterns may affect baboon management I investigated patterns of overlap and territoriality for neighbouring troops. I quantified the spatial association of neighbouring 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 3.3. I 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 2006). To quantify the temporal overlap of troops I analysed data collected over the same time periods and at synchronous time intervals for the neighbouring troops of KK, BB and CP. I used the Nearest_features extension to ArcView (Jenness 2004) to calculate the mean distance between these troops at any given time ($n=719$ GPS data points over 17 days for 3 troops).

I used two measures to assess primate territoriality: Mitani and Rodmans' (1979) defensibility index (D) and Lowen and Dunbars' (1994) fractional monitoring rate (M). Mitani and Rodmans' (1979) defensibility index (D) relates DRL to home range size, working on the assumption that home ranges are circular. I used the following formula to calculate D for all study troops: $D=d/(4A/\mathrm{pi})^{0.5}$ where d=mean DRL (km) and A=home range area (km^2). $D>1$ indicates that animals are territorial or that territoriality is economically feasible but not necessarily in operation, while $D<1$ 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 neighbouring 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 DRL (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 capable of territoriality and where $M<0.08$ primates can be considered incapable of territoriality. I 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, I recorded all intertroop interactions ad libitum.

Seasonality

I used multiple methods to analyse the influence of the seasonal extremes of winter (Jun-Aug) and summer (Dec-Feb) on baboon ranging patterns.

Home range use

To analyse patterns of home range use I used the same techniques described in Chapter 4 to calculate seasonal range sizes and cell use frequencies and conducted the same analyses for each troop. First, I assessed whether seasonal range shifting and or range expansion/contraction occurred by calculating the percentage of entered home range cells that were used in summer, in winter or in both seasons. Second, I investigated seasonal differences in repeated range use patterns by examining cell use over sequential pairs of full-days (Strier 1987; Kaplin 2001; Buzzard 2006). For each pairing I computed C-values as the ratio of b/a where b is the number of new cells entered on the second day of the sequential pair and a is the total number of cells entered on the second day. If all the cells entered on the second day are new then $C=1$, indicating a long-distance ranging pattern; if all the cells entered on the second day of the pair were also used on the first day then $C=0$, indicating a concentrated pattern of range use (Strier 1987). Both Kaplin (2001) and Buzzard (2006) considered $C\leq 0.77$ to indicate a concentrated ranging pattern. For the long distance ranging patterns Kaplin (2001) set the cut-off at $C\geq 0.90$ while Buzzard (2006) selected $C\geq 0.88$. I used $C\leq 0.77$ as the low cut-off for my data, but adjusted the high cut-off to $C\geq 0.85$ to include only the top 10 % of range use measurements. For each troop I calculated an average C value, as well the percentage of sequential full day pairs where C was ≤ 0.77 and ≥ 0.85. Finally, I used paired t-

tests to compare the mean altitudes of the grid cells entered in winter with those entered in summer, and the percentage daily use of urban habitat in winter compared to summer.

Movement patterns

I included only full-days of data into these analyses (Chapter 2). I used independent *t*-tests to investigate within-troop differences in winter and summer DRLs and travel rates. I used one-way ANOVAs to investigate among-troop differences in seasonal DRLs and travel rates. To assess the relationship between ranging patterns and climate, I obtained daily regional temperature and day length data from the South African Weather Service Climate Information Office for three weather stations in the Cape Peninsula. I analysed the ranging patterns of each troop against data recorded at its nearest weather station (Kirstenbosch WO: TK; Slangkop WO: SK, DG, RH; Cape Point WO: SWB, PR, KK, BB, CP). I used Spearman rank correlations to test for relationships between winter and summer DRLs and day length (e.g., Hill et al. 2003; day length data non-normal), and Pearson correlations to test for relationships between winter and summer DRLs and minimum temperature (e.g., Henzi et al. 1992). I did not collect data on days when it was raining heavily because of poor GPS functioning. Thus the movement data are biased towards days with light or no rainfall and so I did not test for correlations between DRLs and rainfall.

Fire

There were no fires in any of the troop home ranges during my study period, and hence I did not have the opportunity to compare baboon ranging patterns before and after a fire. I thus investigated the effects of fire on baboon ecology in two ways. First, following the methods described in Chapter 3, I developed a hurdle model for the KK home range to determine whether baboon ranging patterns were a function of vegetation age (i.e. time since last burn). I selected KK for this analysis as it was the only troop that foraged almost exclusively on natural vegetation (Chapter 4). All other troops had access to anthropogenic food sources which could mask the effects of fire on foraging and ranging patterns. Furthermore as a result of recent fires across a large portion of its home range – the most recent in 2006, one year prior to data collection for this troop – KK had access to a wider range of vegetation age classes (1-45 years) than any other troop. Using the model I analysed cell use within the KK home range as a function of the following predictor variables: altitude (continuous), slope (continuous), the distance to permanent surface water sources (continuous), habitat (categorical) and vegetation age (continuous). For the habitat variable I used fine-scale categories for both natural and human-modified habitats (Fig. 2.12b), the full list of which included urban habitat and the following BHUs: Peninsula sandstone fynbos, Cape Flats dune strandveld, Hangklip sand fynbos and beach.

Second, I determined the effect of vegetation age on vegetation biomass by assessing biomass differences among plots of known aged fynbos (i.e. time since previous burn; Fig. 5.2). In the biomass surveys I followed the methods of Campbell (1985) to assess the growth form and canopy cover of the dominant vegetation (structural; Fig. 2.14c) within 10x5 m quadrates set in plots of differing vegetation ages. I selected plots within the KK home range that fell on either side of the 2006 burn line so that I could compare immediately adjacent plots of immature and mature vegetation. This method allowed me to control for variation among plots in altitude, geology, hydrology and invasive alien vegetation. To factor out the effect of vegetation type on biomass in these surveys I conducted independent assessments within three of the structural vegetation units of the Cape Peninsula (Cowling et al. 1996; Mucina and Rutherford 2006; Fig. 2.14c) including restioid, proteiod and asteraceous fynbos plots. I surveyed the biomass of 10 quadrates of immature vegetation, and another 10 quadrates of mature vegetation for each of these vegetation types. Restioid fynbos plots were all located in Peninsula sandstone fynbos at an altitude between 100-200 m. Proteoid fynbos plots were all located in Peninsula sandstone fynbos at an altitude between 0-100 m. Asteraceous fynbos plots were all located in Cape Dune strandveld at an altitude between 0-100 m.

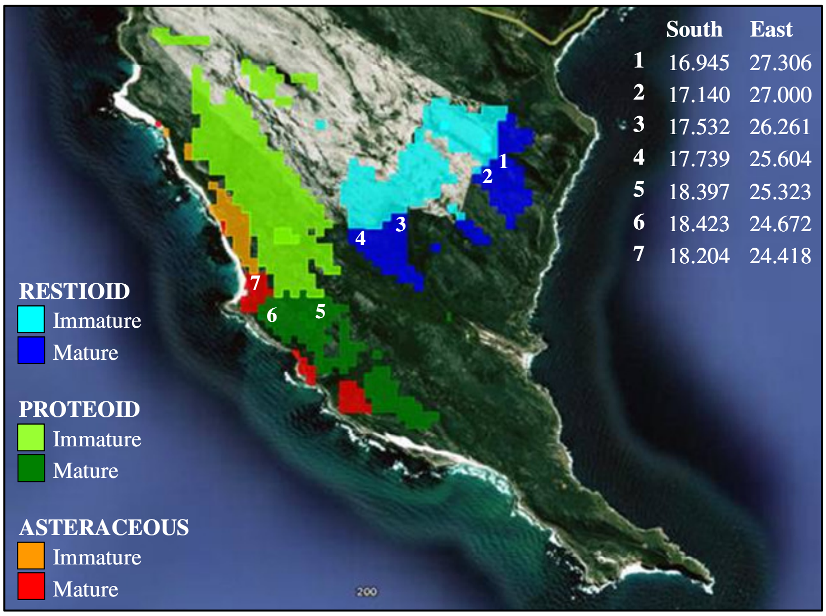


Fig. 5.2. An aerial photograph of the Cape of Good Hope Section of the Table Mountain National Park showing the approximate location (with GPS coordinates for each sample site) of seven sample sites used to determine the relationship between vegetation age and biomass. Sample sites are colour coded by vegetation type.

RESULTS

Conflict despite mitigation efforts

Is this baboon population overabundant?

The conservative and generous baboon density estimates applied to the hypothetical scenarios of available land in Category (a) yielded population sizes ranging from 586-799 baboons (Fig. 5.1; Table 5.1). The same two density estimates applied to the hypothetical scenarios of available land in Category (b) yielded population sizes ranging from 488-630 baboons.

Can spatial ecology explain levels of HBC?

The total number of baboons per troop experiencing HBC (Table 5.2) correlated positively with the percentage of each troop’s accessible area that was urbanised (Table 5.3). With troop size controlled, the mean annual percentage of each troop experiencing HBC correlated positively with the percentage of home range area ≤100 m that was urbanised, and negatively with the mean distance of troop sleeping sites to urban habitat. I found no significant correlations between the conflict indices and the percentage home range perimeter abutting the urban edge (Table 5.3).

Table 5.1. The estimated size of the Cape Peninsula baboon population under different scenarios of available land and habitat compositions. Baboon density in natural habitat is calculated at 2.3 baboons/km^2. Density in invasive alien vegetation and agricultural habitat is calculated at 5.9 baboons/km^2. See text and Fig. 5.1 for details.

		Habitat composition						
		Natural		Invasive alien vegetation		Agriculture		
		Density: 2.3 baboons/km^2		Density: 5.9 baboons/km^2		Density: 5.9 baboons/km^2		
Category	Scenario	Area (km^2)	Baboons	Area (km^2)	Baboons	Area (km^2)	Baboons	Estimated population size
A	Scenario 1	265.95	612	8.83	52.08	22.96	135	799
	Scenario 2	285.44	657	-	-	12.30	73	729
	Scenario 3	285.44	657	-	-	-	-	657
	Scenario 4	254.91	586	-	-	-	-	586
B	Scenario 1	197.35	454	8.80	51.94	21.00	124	630
	Scenario 2	216.82	499	-	-	10.34	61	560
	Scenario 3	216.82	499	-	-	-	-	499
	Scenario 4	212.26	488	-	-	-	-	488

Table 5.2. Measurements used to determine why some troops experience higher levels of human-baboon conflict than others, as well as the characteristics of the sleeping-sites used by each troop. Troops are ranked in descending order of the total number of human-induced deaths (HID) and injuries (HII) from 2005-2007.

	Conflict indices		Spatial variables				Use of sleeping site types*			Cliff sleeping sites	
Troop	Index 1: Total number of HID and HII	Index 2: Mean annual % HID and HII	% of accessible area that is urbanised	% of home range area <100 m that is urbanised	% home range perimeter abutting urban edge	Mean distance of sleeping sites to urban habitat	T	C	B	Mean altitude (m)	Mean slope (°)
DG	11	10.1 %	32.2 %	48.1 %	15.9 %	0.10 km	63 %	14 %	23 %	208.29	20.9
TK	9	2.5 %	38.7 %	14.6 %	21.6 %	1.14 km	100 %	0 %	+	-	-
SK	8	11.0 %	29.9 %	52.8 %	20.4 %	0.20 km	29 %	54 %	16 %	173.39	21.8
PR	7	6.0 %	5.3 %	1.4 %	0.0 %	0.25 km	84 %	16 %	+	230.40	27.4
RH	5	11.9 %	26.7 %	78.6 %	25.1 %	0.12 km	+	100 %	+	166.44	27.9
SWB	5	6.0 %	13.8 %	60.1 %	27.8 %	0.45 km		100 %	+	295.64	35.0
CP	4	5.2 %	0.1 %	0.7 %	0.0 %	1.99 km		100 %	+	96.57	19.1
BB	2	5.6 %	0.6 %	5.0 %	0.0 %	0.61 km	67 %	33 %	+	94.20	6.8
KK	0	0.0 %	1.3 %	0.6 %	0.0 %	2.17 km	16 %	84 %	+	71.62	16.6

* T=Tree; C=Cliffs; B=Buildings; No entry means that the sleeping site type was not available in the troops home range; + indicates that the sleeping site type was available but not used.

Table 5.3. Results of Pearson correlations testing for significant relationships between spatial variables and (a) total number of human-induced deaths (HID) and human-induced injuries (HII) per troop and (b) mean annual percentage of HID and HII per troop. Bold values indicate significant differences at $p \leq 0.05$.

	Count of HID and HII			% HID and HII		
Spatial variable	r	*p*	*n*	r	*p*	*n*
Urbanised % of accessible area	0.80	**0.010**	9	0.47	0.207	9
Urbanised % of home range <100 m	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	-0.17	0.655	9	-0.80	**0.001**	9

Using spatial ecology to inform conflict management

Sleeping sites

Troops slept in trees, on cliffs and on the rooftops of buildings (Table 5.2). 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 altitude of cliff sleeping sites was 167.07 m (±53.47 m SEM) and the mean slope was 21.91 ° (±5.86 ° SEM). Across the Cape Peninsula a total of 504 grid cells (11.6 km^2) situated ≥500 m from the urban edge comprised natural habitat and matched the altitude and slope characteristics of cliff sleeping sites used currently (Fig. 5.3).

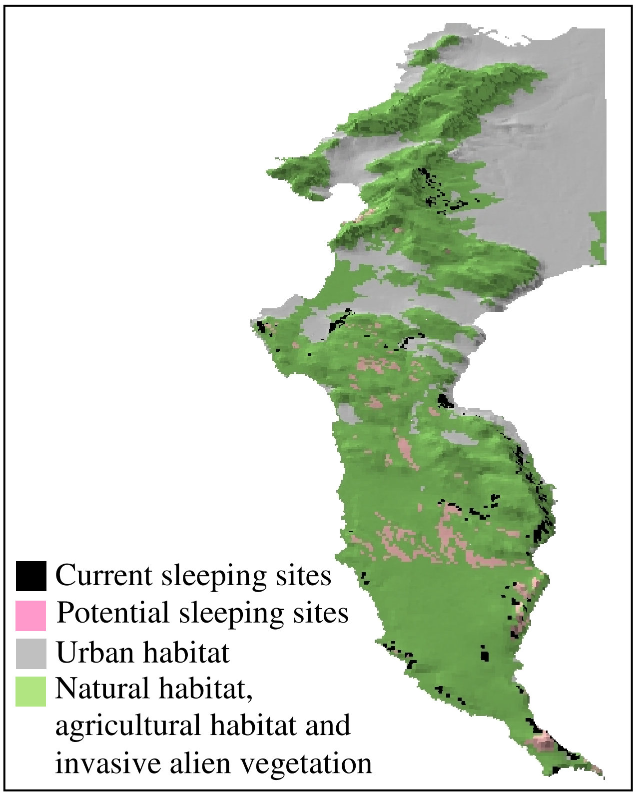


Fig. 5.3. A 3D habitat map showing the distribution of grid cells currently used as sleeping sites (black) and grid cells not used as sleeping sites (pink) that are ≥500 m from the urban edge and match the characteristics of used cliff sleeping sites.

Territoriality

TK was the only troop that was geographically isolated from all other troops by urban development. For all other troops the percentage of home range spatial overlap varied from 0.7-17.2 % with a mean overlap of 7.3 % (±4.9 %, n=6 pairs; Table 5.4). Core range overlap was restricted to five troops, with a mean overlap of 5.2 % (±4.8 %, n=4 pairs). Three troops that I collected fine-scale spatial data for simultaneously ranged at a mean distance of 4.19±1.79 km from one another. According to Mitani and Rodmans' (1979) defensibility index (D), five troops occupied ranges where territorial defence was economically feasible (although not inherently necessary; $D \geq 1$; Table 5.5). Once these values had been adjusted to include the fractional monitoring rate (M) put forward by Lowen and Dunbar (1994), all troops but one (KK) could be considered spatially capable of territoriality ($M \geq 0.08$).

Despite having only one adult male (vs. KK: n=6 adult males; CP: n=3 sub-adult males) and being numerically the smallest (BB: n=16 vs. CP: n=22; KK: n=49), BB displaced both CP and KK on separate occasions as they approached the picnic site portion of their home range (Appendix 2.8). The only animal from BB involved in the displacement was the single adult male whose aggression resulted in different responses from KK and CP. 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.

Table 5.4. Details of the spatial overlap of troop home ranges and the mean (± SEM) temporal proximity of neighbouring troops over a period of 17 days.

	Spatial overlap		Temporal overlap	
Troops	of home ranges	of core ranges	Mean proximity	n
BB and KK	7.2 %	8.5 %	3.82 ± 0.29 km	61 GPS points; 3 days
BB and CP	11.5 %	1.1 %	2.84 ± 0.22 km	116 GPS points; 5 days
CP and KK	0.7 %	0.9 %	5.92 ± 0.16 km	542 GPS points; 14 days
PR and SWB	3.1 %	-	-	-
RH and SWB	3.9 %	-	-	-
SK and DG	17.2 %	10.4 %	-	-

Table 5.5. Measures of troop territoriality. D≥1.0 and M≥0.08 indicate the potential for territoriality. Troops are tabled according to their geographical position from north to south.

Troop	D*	M°
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)

Seasonality

Home range use

Troops did not use their home ranges uniformly throughout the year (Fig. 5.4), but patterns were inconsistent across troops. In winter, troops used between 30.6-69.8 % of entered home ranges grid cells (mean: 51.4±9.0 %; Table 5.6), and in summer between 37.0-71.0 % of entered home ranges grid cells (mean: 51.3±7.0 %). Two troops (TK and KK) increased the use of their ranges in summer compared to winter; while all other troops showed the opposite pattern, using a smaller area of their range in summer compared to winter.

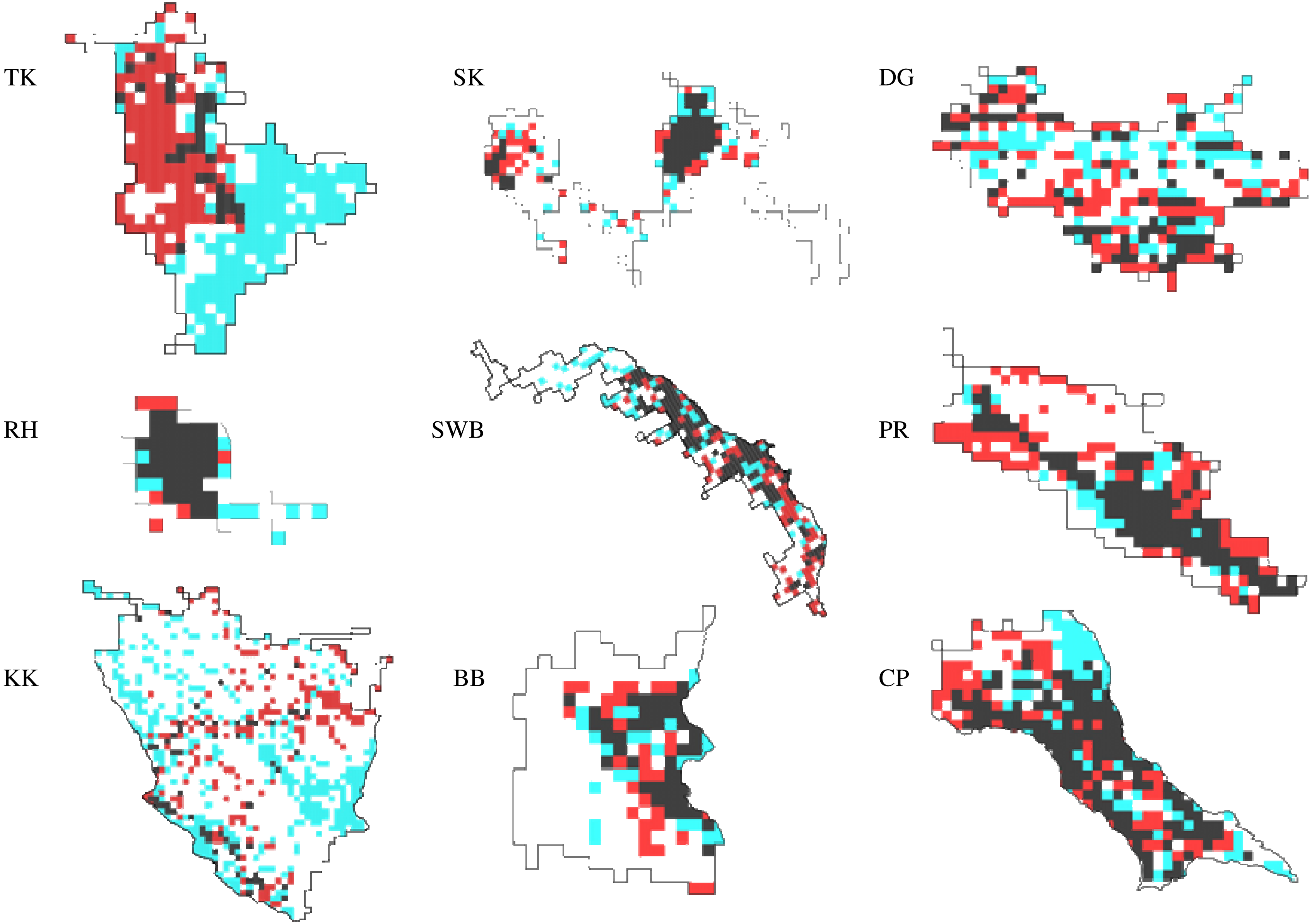


Fig. 5.4. Maps showing the seasonal range use patterns within the home ranges (black outlines) of all nine study troops. Red indicates cells used in summer, blue indicates cells used in winter, and black indicates cells used in both seasons. Troops are sorted geographically from north (top left) to south (bottom right). Home ranges are not drawn to scale.

Table 5.6. Details of seasonal range use patterns including percentage of home range (HR) used in each season, repeated use of cells in both seasons, and range use redundancy. For seasonal differences, ranges that were larger in summer relative to winter are indicated in bold and ranges that were smaller in summer compared to winter are italicised. For range use redundancy C≤0.77 indicates concentrated range use and C≥0.85 indicates long distance ranging patterns. The percentages of *C* values falling within those categories are also listed. Troops are tabled according to their geographical position from north to south.

	% of HR area used		Seasonal	Seasonal cell	Winter range use redundancy ~				Summer range use redundancy ~			
Troop	Winter	Summer	difference	use overlap	Mean *C*	*C≤0.77*	*C≥0.85*	Pairs	Mean *C*	*C≤0.77*	*C≥0.85*	Pairs
TK	40.9 %	50.4 %	**9.5 %**	8.4 %	0.74	50 %	35 %	20	0.79	33 %	47 %	15
SK	41.0 %	37.0 %	*4.0 %*	24.5 %	0.64	69 %	15 %	13	0.72	64 %	29 %	14
DG	55.1 %	46.8 %	*8.2 %*	24.2 %	0.84	20 %	60 %	5	0.69	55 %	18 %	11
RH	71.0 %	64.5 %	*6.5 %*	53.2 %	0.58	85 %	0 %	13	0.35	85 %	0 %	13
SWB	52.4 %	50.7 %	*1.7 %*	31.9 %	0.82	27 %	27 %	11	0.72	50 %	40 %	10
PR	68.2 %	46.9 %	*21.4 %*	38.1 %	0.71	54 %	31 %	13	0.84	20 %	73 %	15
KK	30.6 %	54.5 %	**23.9 %**	8.2 %	0.83	25 %	75 %	8	0.93	11 %	89 %	9
BB	41.0 %	38.2 %	*2.8 %*	23.6 %	0.75	50 %	33 %	6	0.70	38 %	25 %	8
CP	69.8 %	66.4 %	*3.5 %*	45.0 %	0.84	33 %	67 %	6	0.86	25 %	50 %	16

~ Strier (1987), Kaplin (2001) and Buzzard (2006).

Table 5.7. Analysis of seasonal ranging patterns including paired *t*-tests testing for statistical differences in seasonal urban use, altitude, day range lengths (DRL) and travel rates (TR), Spearman correlations testing for significant relationships between ranging patterns and day length, and Pearson correlation testing for significant relationships between ranging patterns and minimum temperature. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

	Seasonal altitude			Seasonal urban use			Seasonal DRL			Seasonal TR			Day length		Min temperature		
Troop	t	*p*	*n*	t	*p*	*n*	t	*p*	*n*	t	*p*	*n*	r_s	*p*	r	*p*	*n* (days)
TK	12.41	**<0.001**	151	3.99	**0.002**	12	2.46	**0.033**	11	0.44	0.671	11	0.72	**<0.001**	0.46	**<0.001**	24
SK	-1.58	0.117	101	5.21	**<0.001**	15	0.62	0.547	13	-2.21	**0.047**	13	0.10	0.643	0.10	0.651	26
DG	-0.21	0.827	176	0.45	0.684	12	1.71	0.115	12	1.48	0.168	12	0.38	0.054	0.40	0.055	26
RH	0.80	0.428	40	3.14	**0.010**	11	1.07	0.307	13	-3.19	**0.008**	13	-0.26	0.197	-0.22	0.267	27
SWB	-0.16	0.874	181	1.68	0.121	12	1.70	0.120	11	-2.67	**0.002**	11	-0.07	0.761	-0.34	0.108	23
PR	-3.47	**<0.001**	149	-1.00	0.336	14	2.85	**0.008**	26	-0.02	0.982	14	0.45	**0.015**	0.46	**0.013**	28
KK	-7.29	**<0.001**	240	1.88	0.088	13	-1.71	0.116	12	0.68	0.511	12	0.17	0.433	0.45	**0.027**	24
BB	-4.57	**<0.001**	68	1.11	0.287	14	-2.68	**0.027**	9	0.98	0.357	9	-0.17	0.399	-0.20	0.329	27
CP	0.52	0.602	211	-1.07	0.309	12	-3.75	**0.003**	22	0.98	0.349	12	0.05	0.818	0.03	0.873	25

All troops showed repeated use of areas of their home ranges in both winter and summer, although they differed substantially in this respect. Repeated use of cells in both seasons varied from 8.2-53.2 % (mean: 28.6±10.0 %; Table 5.6). Patterns of range use redundancy also differed seasonally. In winter five troops showed concentrated home range use ($C \leq 0.77$). On average none exhibited long distance ranging patterns ($C \geq 0.85$), but three troops had values in excess of $C \geq 0.85$ on 60-75 % of their sequential day pairs in this season. In summer five troops showed concentrated home range use ($C \leq 0.77$) while two troops exhibited long distance ranging patterns ($C \geq 0.85$). Additionally, two troops exhibited both concentrated and long distance ranging patterns in summer, although for both troops the latter accounted for the majority of their respective sequential day pairs.

During winter four troops (TK, PR, KK, BB) used grid cells with significantly lower altitudes than the grid cells used in summer (Fig. 5.5; Table 5.7). The altitudes used by all other troops were constant across seasons. Two troops (TK and SK) spent more time in urban habitat in winter than in summer (Fig. 5.6) and one troop (RH) spent more time in urban habitat in summer than in winter. Urban use for all other troops remained constant across seasons.

Movement patterns

Troop movement patterns varied seasonally but patterns showed little consistency across troops. Four troops exhibited significant seasonal differences in DRL (Fig. 5.7; Table 5.7), travelling farther in summer than in winter. All other troops travelled similar distances in both seasons. Three troops exhibited significant seasonal differences in travel rate (Fig. 5.8), all travelling faster in winter than in summer. All other troops travelled at similar rates in both seasons. In tests of the effects of climate on ranging patterns, the DRLs of only two troops correlated positively with day length. Furthermore the DRLs of three troops correlated positively with minimum temperature.

Among troops, winter DRLs ($F_{1,8}$=718.93, df=8, $p \leq 0.001$), winter travel rates ($F_{1,8}$=672.14, df=8, $p \leq 0.001$), summer DRLs ($F_{1,8}$=839.99, df=8, $p \leq 0.001$) and summer travel rates ($F_{1,8}$=947.15, df=8, $p \leq 0.001$) varied significantly. Across the seasons there were no consistent patterns of intertroop variation in DRLs (Tables 5.8 and 5.9) or intertroop variation in travel rate (Tables 5.10 and 5.11).

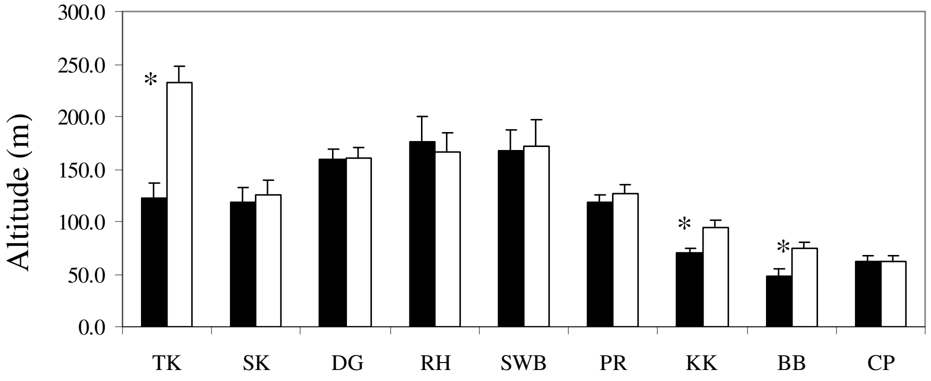


Fig. 5.5. Mean±SEM altitude of grid cells used by each troop in winter and summer. Asterisks indicate troops with significant seasonal differences (see Table 5.7). Troops are sorted geographically from north (left) to south (right).

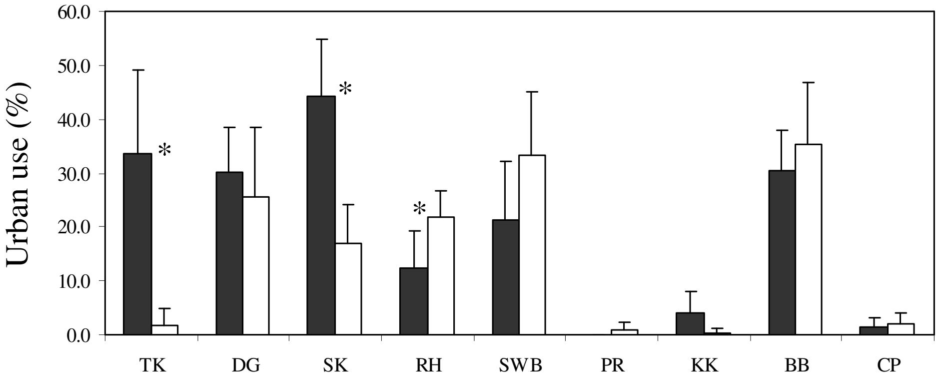


Fig. 5.6. Mean±SEM percentage daily use of urban habitat by each troop in winter and summer. Asterisks indicate troops with significant seasonal differences (see Table 5.7). Troops are sorted geographically from north (left) to south (right).

■ Winter ☐ Summer

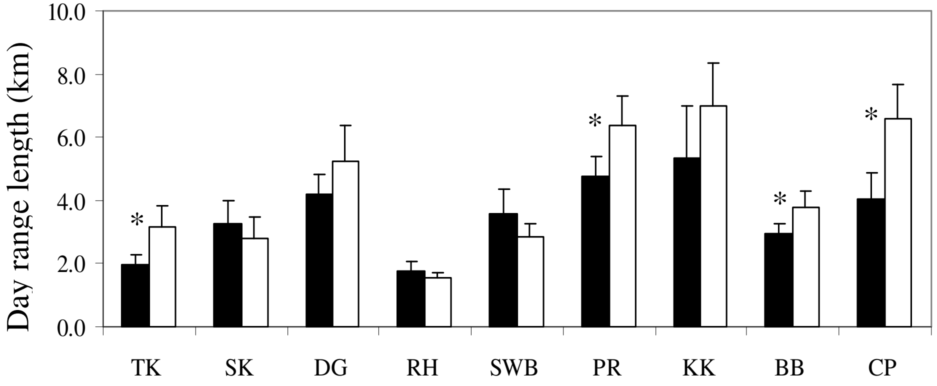


Fig. 5.7. Mean±SEM day range lengths for each troop in winter and summer. Asterisks indicate troops with significant seasonal differences in day range lengths (see Table 5.7). Troops are sorted geographically from north (left) to south (right).

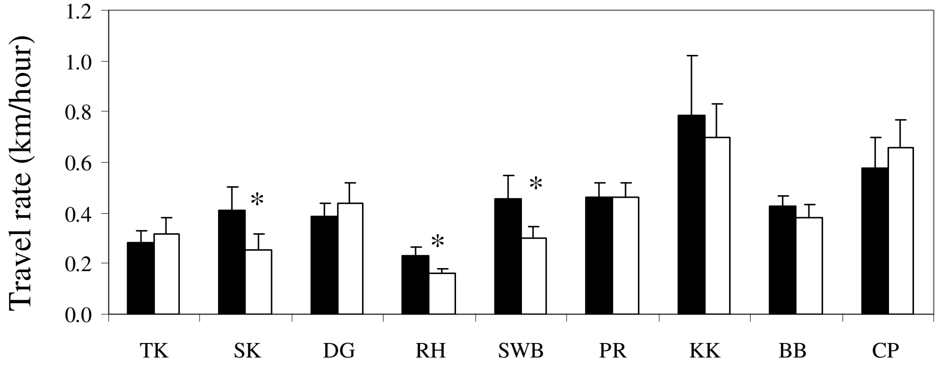


Fig. 5.8. Mean±SEM travel rate for each troop in winter and summer. Asterisks indicate troops with significant seasonal differences in travel rates (see Table 5.7). Troops are sorted geographically from north (left) to south (right).

Table 5.8. Results of Tukey post-hoc tests (MS=1.9732, df=104.00) determining differences among troops in winter day range lengths. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

Troop	CP	BB	KK	PR	SWB	RH	DG	SK	TK
CP	-	0.628	0.394	0.935	0.996	**0.003**	1.000	0.896	**0.014**
BB	0.628	-	**0.003**	**0.042**	0.977	0.442	0.472	1.000	0.732
KK	0.394	**0.003**	-	0.981	0.070	**<0.001**	0.545	**0.010**	**<0.001**
PR	0.935	**0.042**	0.981	-	0.466	**<0.001**	0.981	0.132	**<0.001**
SWB	0.996	0.977	0.070	0.466	-	**0.040**	0.981	1.000	0.130
RH	**0.003**	0.442	**<0.001**	**<0.001**	**0.040**	-	**0.001**	0.126	1.000
DG	1.000	0.472	0.545	0.981	0.981	**0.001**	-	0.783	**0.007**
SK	0.896	1.000	**0.010**	0.132	1.000	0.126	0.783	-	0.329
TK	**0.014**	0.732	**<0.001**	**<0.001**	0.130	1.000	**0.007**	0.329	-

Table 5.9. Results of Tukey post-hoc tests (MS=2.4476, df=101.00) determining differences among troops in summer day range lengths. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

Troop	CP	BB	KK	PR	SWB	RH	DG	SK	TK
CP	-	**0.004**	0.999	1.000	**<0.001**	**<0.001**	0.448	**<0.001**	**<0.001**
BB	**0.004**	-	**0.000**	**0.006**	0.928	**0.030**	0.431	0.861	0.992
KK	0.999	**<0.001**	-	0.983	**<0.001**	**<0.001**	0.110	**<0.001**	**<0.001**
PR	1.000	**0.006**	0.983	-	**<0.001**	**<0.001**	0.600	**<0.001**	**<0.001**
SWB	**<0.001**	0.928	**<0.001**	**<0.001**	-	0.479	**0.008**	1.000	1.000
RH	**<0.001**	**0.030**	**<0.001**	**<0.001**	0.479	-	**<0.001**	0.513	0.221
DG	0.448	0.431	0.110	0.600	**0.008**	**0.000**	-	**0.003**	**0.034**
SK	**<0.001**	0.861	**<0.001**	**<0.001**	1.000	0.513	**0.003**	-	1.000
TK	**<0.001**	0.992	**<0.001**	**<0.001**	1.000	0.221	**0.034**	1.000	-

Table 5.10. Results of Tukey post-hoc tests (MS=0.0334, df=104.00) determining differences among troops in winter travel rates. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

Troop	CP	BB	KK	PR	SWB	RH	DG	SK	TK
CP	-	0.502	0.144	0.800	0.781	**<0.001**	0.195	0.322	**0.004**
BB	0.502	-	**<0.001**	1.000	1.000	0.162	1.000	1.000	0.622
KK	0.144	**<0.001**	-	**0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
PR	0.800	1.000	**0.001**	-	1.000	**0.030**	0.972	0.997	0.244
SWB	0.781	1.000	**0.001**	1.000	-	0.055	0.988	0.999	0.341
RH	**<0.001**	0.162	**<0.001**	**0.030**	0.055	-	0.452	0.203	0.998
DG	0.195	1.000	**<0.001**	0.972	0.988	0.452	-	1.000	0.915
SK	0.322	1.000	**<0.001**	0.997	0.999	0.203	1.000	-	0.712
TK	**0.004**	0.622	**<0.001**	0.244	0.341	0.998	0.915	0.712	-

Table 5.11. Results of Tukey post-hoc tests (MS=0.0189, df=101.00) determining differences among troops in summer travel rates. Bold values indicate significant differences at $p \leq 0.05$. Troops are tabled according to their geographical position from north to south.

Troop	CP	BB	KK	PR	SWB	RH	DG	SK	TK
CP	-	**0.001**	0.997	**0.016**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**
BB	**0.001**	-	**<0.001**	0.878	0.948	**0.010**	0.985	0.492	0.982
KK	0.997	**<0.001**	-	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
PR	**0.016**	0.878	**0.001**	-	0.100	**<0.001**	1.000	**0.005**	0.170
SWB	**<0.001**	0.948	**<0.001**	0.100	-	0.222	0.275	0.995	1.000
RH	**<0.001**	**0.010**	**<0.001**	**<0.001**	0.222	-	**<0.001**	0.708	0.135
DG	**0.003**	0.985	**<0.001**	1.000	0.275	**<0.001**	-	**0.022**	0.407
SK	**<0.001**	0.492	**<0.001**	**0.005**	0.995	0.708	**0.022**	-	0.976
TK	**<0.001**	0.982	**<0.001**	0.170	1.000	0.135	0.407	0.976	-

Fire

The third-order model for KK had low levels of bias (*b*=1.30, *m*=0.09) and was better calibrated than it was correlated (Pearson r=0.15; Spearman r_s=0.37). The error around the predictions (average error=0.43, root mean square error=6.79) was low. The model revealed that vegetation age did not have a significant influence on baboon occurrence, but did have a significant positive influence on baboon abundance (Table 5.12). Vegetation age was less influential than the predictor variables of habitat, distance to water and slope, but more influential than altitude. Landscape surveys showed that across all vegetation types, plots of mature vegetation were larger in size and more widespread in canopy than immature vegetation (Table 5.13).

Table 5.12. Results of the third-order occurrence and abundance models for KK including the coefficient estimates, standard errors (SEM), z-statistics and *p* values for each predictor. Habitat categories are italicised and significant values are in bold.

	Occurrence model coefficients				Abundance model coefficients			
Predictors*	Estimate	SEM	z	*p*(>lzl)	Estimate	SEM	z	*p*(>lzl)
PSF (intercept)	-0.502	0.148	-3.398	**0.001**	-1.192	0.389	-3.067	**0.002**
Beach	-1.407	0.487	-2.889	**0.004**	-0.502	0.637	-0.787	0.431
CFDS	0.757	0.231	3.279	**0.001**	0.317	0.212	1.495	0.135
HSF	0.602	0.181	3.333	**0.001**	1.069	0.216	4.942	**<0.001**
Urban habitat	1.210	1.122	1.078	0.281	1.748	0.798	2.190	**0.029**
Altitude	-0.006	0.001	-4.38	**<0.001**	-0.012	0.002	-8.124	**<0.001**
Slope	0.043	0.013	3.454	**0.001**	0.096	0.014	6.829	**<0.001**
Dwater	0.172	0.045	3.855	**<0.001**	0.227	0.057	3.953	**<0.001**
Age	0.013	0.007	1.737	0.082	0.024	0.008	2.888	**0.004**
Log (theta)					-1.528	0.397	-3.851	**<0.001**

Pearson residuals:	Min=-0.723; 1Q=-0.603; Median=-0.547; 3Q=0.361; Max=7.804
Theta:	count = 0.217
Iterations:	23 in BFGS optimisation
Log-likelihood:	-2394 on 19 PDF

* PSF=Peninsula Sandstone Fynbos, CFDS=Cape Flats Dune Strandveld, HSF=Hangklip Sand Fynbos

Table 5.13. Growth form and canopy cover of immature and mature plots of Asteraceous, Proteoid and Restioid fynbos.

Growth form of dominant stratum	Asteraceous		Proteoid		Restioid	
	Immature	Mature	Immature	Mature	Immature	Mature
<25cm	10 %	0 %	80 %	0 %	100 %	0 %
25-50cm	90 %	0 %	20 %	0 %	0 %	0 %
50-100cm	0 %	100 %	0 %	80 %	0 %	100 %
100-200cm	0 %	0 %	0 %	20 %	0 %	0 %
Canopy cover of dominant stratum	**Asteraceous**		**Proteoid**		**Restioid**	
	Immature	Mature	Immature	Mature	Immature	Mature
0-25%	0 %	0 %	0 %	0 %	0 %	0 %
25-50%	0 %	0 %	10 %	0 %	30 %	0 %
50-75%	0 %	0 %	50 %	0 %	60 %	0 %
75-100%	100 %	100 %	40 %	100 %	10 %	100 %

DISCUSSION

Conflict despite mitigation efforts

Is this baboon population overabundant?

An overabundance of baboons cannot explain the high levels of HBC in the Cape Peninsula as none of the predicted baboon population sizes, 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 a1; Fig. 5.1) showed that the current population size (460 baboons; EK Beamish, UCT, unpubl. data) could increase by 324 baboons. At the opposite extreme, the scenario that set the greatest restrictions on available land and denied baboons access to any human-modified habitats (Scenario b4), still allowed for an increase of 28 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 as they fail to take into account the full ecological complexity of the local landscape. The inclusion of this level of complexity, however, would require detailed research that focuses on the nutritional composition of all baboon dietary items and that includes investigations into the nutritional variation found across natural habitats, plant ages, altitudes and seasons (see Chapter 6). Furthermore, these density estimates cannot be used to predict any oscillatory patterns of population size that could result from changes in foraging conditions, nor how these changes may impact upon the levels at which the population size self-regulates. Despite these shortcomings, these population estimates offer management two important insights. First, they serve as a precautionary forecast of the size towards which this baboon population will tend under different landscape management regimes. Second, they emphasize that, with the possible exception of the most conservative of land availability scenarios (b4), management efforts will not need to engage in any direct regulation of baboon numbers.

Can spatial ecology explain levels of HBC?

The loss of access to low lying land as a result of urbanisation, and the mean proximity of sleeping sites to urban habitat provided the best explanations for why levels of HBC 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 altitudes (Chapter 3), provides important support for the statements made in Chapter 3 that further development of both the low altitude areas of home ranges and the land immediately accessible to baboons from their home ranges will exacerbate levels of HBC 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 urbanised proved to be the primary determinant of HBC levels, it was not the only determinant. Two troops (TK and PR) whose home ranges comprised predominantly agricultural and natural habitat suffered the 2nd and 4th highest numbers of human-induced deaths and injuries respectively. Even two of the three troops (BB, CP) ranging entirely within the protected natural habitat of the CoGH who had only minimal (<1 % of home range) access to urban habitat suffered HBC. Importantly the only troop with no recorded HBC was KK. 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 HBC, ostensibly any troop that consumes anthropogenic food sources is at risk of suffering from HBC.

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

Using spatial ecology to inform conflict management

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 as well as the effects of season and fire on baboon ecology yielded interesting insight into how HBC can be mitigated in the Cape Peninsula.

Sleeping sites

Baboons are known to utilise 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 tree and cliff sleeping sites.

What is concerning from a management perspective is that four troops with access to all sleeping site types 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 – SK on the rooftop of a confectionary factory (Compass Bakery) alongside hot air vent (Appendix 2.2) and DG atop and inside sections of a residential apartment block (Appendix 2.3). These patterns of sleeping site use are not a consequence of limited sleeping site availability as 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, as argued in Chapter 3, sleeping site selection appears to be driven primarily by their proximity to human-modified habitats. Discouraging baboons from using sleeping sites that are close to urban habitat (Fig. 5.3) 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 HBC.

Territoriality

The results of field observations, territorial index calculations and measures of range overlap for troops in the Cape Peninsula, all provide evidence for territorial potential for chacma baboons, supporting the observations of Hamilton et al. (1976). The strongest evidence for territoriality was the aggressive interactions between BB and its neighbours. Interestingly, the ability of the BB alpha male to single-handedly supplant two troops on separate occasions – one comprising 49 individuals (KK) and the other 22 individuals (CP) – suggests that strength in intertroop encounters does not depend solely on troop size nor the number of males present (Hamilton et al. 1975). Instead, the tendency for BB to display overt spatial defence is most likely attributable to its home range encompassing a high-quality and monopolisable resource (*sensu* Strier 2007) in the form of a picnic area where humans and bins are regularly raided for anthropogenic food sources. This same picnic area, which is the source of HBC for BB, 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 HBC. 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, neighbouring troops to move in, monopolise the same resource and perpetuate the same high levels of 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 one of the local conservation authorities (W Peterson, pers. comms.). The removal of the Kommetjie troop resulted in short-term relief from HBC but the vacant home range was usurped circa.

eight years later (Kansky and Gaynor 2000) by a fission group from the neighbouring DG troop. This fission group, currently known as the SK troop (Chapter 4, Fig. 4.1), now habitually raids the Kommetjie area, once again resulting in high levels of HBC in the area (Nature Conservation Corporation 2011). Thus, the better long term strategy to mitigate against HBC in areas with multiple neighbouring troops is to focus on the removal, or the prevention of access to, the anthropogenic food source(s) that are the primary drivers of the conflict itself (i.e. the baboon attractant) and not 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 the TMNP (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 BB was the only troop to display visible evidence of spatial defence 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 50-95 % 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 behaviour 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 KK. 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 neighbouring troops.

Seasonality

The Cape Peninsula troops did not use their home ranges uniformly throughout the year. However, seasonal ranging patterns varied widely among troops, proving it difficult to make generalisations about seasonal effects on landscape use and to determine seasonal management plans to reduce HBC. Two troops expanded their ranges in the cold, wet winter months. This type of wet season range expansion has been reported by Gwenzi et al. (2007) who found that four out of five troops in the Chimanimani highlands in Zimbabwe expanded their home ranges in the wet season. As primate home ranges may increase in size in response to food scarcity (Clutton-Brock and Harvey 1977) the seasonal size discrepancy suggests that food resources in the Cape Peninsula are scarcer during winter than summer. However, three other troops contracted their ranges during the cold, wet winter suggesting that, in fact, winter is the season of plenty. To complicate matters further, four troops barely shifted their ranges at all (<5 %) suggesting that resource availability is comparable in both seasons.

Season also had a varied effect on the DRLs, travel rates and range use redundancy patterns of troops. I found that the DRLs of two troops only showed an expected positive relationship with day length (e.g., Hill et al. 2003) while an increase in minimum temperature led to an increase in DRL for three troops only (e.g., Henzi et al. 1992). I found more variation still in the seasonal use of altitudes and urban habitats. Contrary to my expectations only three troops occupied significantly lower altitudes in winter compared to summer. An increased use of urban habitat was also not seasonally dependent for most troops with only two troops increasing their use of urban habitat during winter and one increasing its use of this habitat in summer.

The ability of baboons to adapt to ecological conditions (Chapter 4) precluded overarching and consistent interpretations of the effects of season on baboon spatial ecology. Differences in diet, landscape management methods, and the troop-specific – and mostly unique – combinations thereof, all contribute to the substantial variation in these seasonal results. These combined influences also elucidate why season alone cannot explain why baboon managers receive more than double the number of negative reports about baboons from local residents in winter compared to summer (Nature Conservation Corporation 2011). There are, however, two ways in which these seasonal patterns can be used to inform management. The first is to consider that the diet, habitat and management influences currently operating on each troop will remain as they are for the foreseeable future. In this case, while it is not possible to make population-level recommendations for seasonal baboon management, it is possible to devise troop-specific plans that incorporate the predominant seasonal ranging patterns of each troop (summarised in Table 5.14).

Table 5.14. Summary table of the spatial ecology variables relevant to the seasonal management of baboons. Only statistically significant results are tabled. Troops are tabled according to their geographical position from north to south.

Troop*	Largest seasonal range (>5% difference)	Greatest use of low altitudes	Greatest use of urban	Winter ranging pattern	Summer ranging pattern	Furthest travel distance	Fastest travel rate
TK	Summer	Winter	Winter	Concentrated	-	Summer	-
SK	-	-	Winter	Concentrated	Concentrated	-	Winter
DG	Winter	-	-	-	Concentrated	-	-
RH	Winter	-	Summer	Concentrated	Concentrated	-	Winter
SWB	-	-	-	-	Concentrated	-	Winter
PR	Winter	Winter	-	Concentrated	-	Summer	-
KK	Summer	Winter	-	-	Long distance	-	-
BB	-	Winter	-	Concentrated	Concentrated	Summer	-
CP	-	-	-	-	Long distance	Summer	-

* - indicates that there was no significant difference between the seasons.

The second way to use these seasonal data to inform management is to consider a scenario where troops are no longer able to access human-modified habitats, but are allowed to range freely in natural habitat. In this case, it becomes possible to develop a population-level seasonal management plan that can be modelled on the seasonal ranging patterns of KK – the troop that currently has the least access to human-modified habitats, feeds only in natural habitat and is not actively managed by baboon monitors. Under these conditions winter becomes the season when baboons will spend an increased amount of time at low altitudes, occupying smaller areas and covering shorter distances. The greatest management challenge in winter will thus be the protection of the urban edge so as to decrease the potential of urban raids by baboons while they are in closer proximity to urban habitat. By contrast, in summer, baboons will most likely shift to long-distance ranging patterns and cover larger areas of their home ranges. Thus in summer, management efforts may need to be widespread within baboon home ranges rather than concentrated, with a greater proportion of the urban edge requiring protection.

Fire

Although fynbos foliage is of low nutritive quality (Bigalke 1979), macronutrient (potassium, calcium, magnesium, phosphorus and sulphur) concentration in the fruits, seeds, pods and flowers of plants is relatively high (Cowling and Richardson 1995). Older fynbos plants typically have higher biomass and nutrient loads due to the presence of large seed-reproducing shrubs (van Wilgen 1982) with biomass increasing in annual increments between 1000-4000 kg/ha (Kruger 1977) in the first few years after a fire. As I predicted, the results from the KK home range model coupled with those of vegetation surveys indicated that baboons will be more abundant on mature plots of vegetation compared to immature plots as they offer higher vegetation biomass. Thus a fire which results in a decrease of vegetation biomass in a troop's home range may lead to an adjustment of baboon ranging patterns as they track patches of older vegetation within their home ranges or outside of their home ranges if none exist within them. The latter may lead to post-fire home range expansions and or substantial home range shifts towards areas that contain older plants.

Not all fires may yield this same response from baboons as the effects of fire on vegetation biomass can vary depending on fire frequency, season, intensity and spatial extent (Bond and van Wilgen 1996). Also, the effects of fire on baboon ranging patterns may be offset immediately after the fire event should relatively nutritious post-fire forage result from the recycling of above-ground vegetation biomass into new growth (Cowling and Richardson 1995). That this was not seen in this study may be a function of the timing of the study period relative to the timing of the fire (one year later). Additionally, it may be a consequence of the variability of post-fire nutrient availability – the characteristics, extent and duration of which is dependent on a complex interaction of a number of factors including fire intensity, soil properties and pre-fire vegetation (Cowling and Richardson 1995).

Before more detailed management recommendations can be made with reference to fires, more research should be conducted to determine how baboons respond spatially to different kinds of fires (e.g. intensity, frequency), and whether baboons show the same level of dietary switching, group fragmentation and ranging pattern shifting in response to fire as do other behaviourally flexible primates (e.g., *Macaca fascicularis*: Berenstein 1986). However, until such information is available the data presented here indicate that managers should strive to not burn entire troop home ranges during prescribed burns, and should allow sufficient time between burn intervals for vegetation biomass to regenerate.

Conclusions

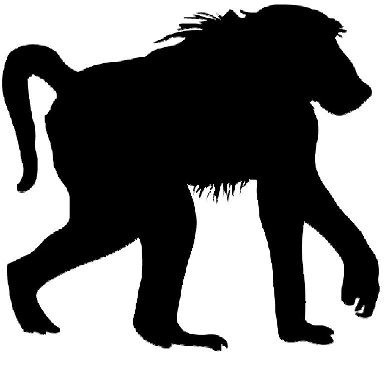
This study uses baboon spatial ecology to understand the extent and severity of HBC in the Cape Peninsula and to determine realistic and practical strategies for local baboon management. In so doing it demonstrates how an enhanced understanding of wildlife spatial ecology can inform wildlife management 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 HBC are also presently the most actively managed by baboon monitors indicates that the ability of current management strategies to mitigate against HBC 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 as, despite the increased density of troops in human-modified habitats, there is no indication that this population is overabundant. Secondly, evidence for intertroop territoriality suggest that the removal of nuisance troops would have limited success in reducing HBC, and could simply create the opportunity for previously excluded troops to take advantage of the same conflict-causing resource with little long term change to local levels of HBC. Instead, the results indicate that landscape management that prioritises the conservation of low lying natural habitat, increased distance of sleeping sites to the urban edge, the improved management of conflict hotspots (i.e. picnic sites, waste depots, tourist centres) and the planning of prescribed vegetation burns, presents the least invasive and most sustainable way of managing HBC.

Preventing troops from consuming anthropogenic food sources should also be a chief management priority for two reasons. First, the only troop with zero levels of HBC was also the only troop that did not forage on anthropogenic food sources. This result illustrates that reduced levels of HBC are contingent upon preventing baboons from accessing food in human-modified habitats. Second, denying baboons access to anthropogenic food sources should improve their manageability by reducing the overall population density via the following mechanism: troops foraging 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 I predict that home ranges will continue to increase in size until each troop approaches the conservative mean density (2.3 baboons/km^2) of those ranging within the CoGH. This conservative density is comparable to the mean of baboon densities reported across South Africa (2.7 baboons/km^2; 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, I 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.

Chapter 6

Synthesis: Mapping the way forward for baboon management and conservation in the Cape Peninsula



Managing wildlife in the face of anthropogenic habitat transformation is inherently a spatial endeavour that involves identifying, restoring, managing and conserving wildlife habitats of the requisite quality and quantity (Cumming 2004; Mace et al. 2010). An understanding of the landscape requirements of animals has thus become increasingly important for wildlife conservation and management planning (Beckmann and Berger 2003; Dickman 2010; Heydon et al. 2010). In this study I researched the spatial ecology of the Cape Peninsula baboons to provide data that could enhance our understanding of their landscape preferences and thereby improve baboon management and conservation approaches, with the ultimate objective of achieving a sustainable baboon population that is not in conflict with its human neighbours. In addition I provide information relevant to current and future landscape transformation and their potential impacts on this baboon population including: urbanisation, clearing of invasive alien vegetation, burning of indigenous vegetation and plantation harvesting. These research objectives are subsumed within three separate but related data chapters, the content of which is summarised by the following three questions:

1. What are the land use patterns of this baboon population? (Chapter 3),
2. Is there intrapopulation variation in ranging patterns and behaviour? (Chapter 4),
3. Can spatial variables inform baboon management and HBC mitigation efforts? (Chapter 5).

Throughout the thesis I discuss the results in context with our current knowledge of baboon socioecology and apply the findings to current baboon management strategies and policies. In this chapter I synthesise these discussions and make specific recommendations for improved landscape conservation and resource management. I discuss the limitations of my study and provide possible directions for future research in the Cape Peninsula. Finally, I summarise the value of this research to the broader theory of primatology and spatial ecology and to the practice of human-wildlife conflict mitigation and animal conservation.

Synthesis of thesis findings

The first instances of conflict between humans and baboons in the Cape Peninsula are likely to have resulted from little more than competition for low lying land (Chapter 3). Higher vegetation biomass and productivity at low altitudes (Chapters 3) explains the preference for such land by humans (agriculture) and baboons (foraging) respectively. In addition, Cape Peninsula baboons are known to supplement their diet with nutrient-rich marine intertidal organisms (Hall 1961; MC Lewis, UCT, unpubl. data) that are only found along the coast (i.e.

at low altitude) coinciding with the location of prime residential real estate. Thus humans initially displaced baboons into increasingly marginal high lying land and subsequently extirpated troops from entire regions of the Cape Peninsula when levels of conflict were deemed unacceptably high. Subsequent legislation preventing the hunting of baboons (Western Cape Province 1999) saw a steady increase in both the number of troops and the total baboon population from 365 baboons in 10 troops in 1998 (Kansky and Gaynor 2000) to 460 baboons in 16 troops in 2011 (EK Beamish, UCT, unpubl. data). These increases, when coupled with rapid urban expansion, may explain why HBC levels have remained high despite management authorities investing in costly conflict mitigation measures (e.g., baboon monitors).

Two other related factors have enabled baboons to thrive in the face of intense landscape competition, namely: 1) dietary and behavioural flexibility and 2) access to anthropogenic food sources. Most human-modified habitats, including urban habitat, agricultural habitat and invasive alien vegetation are characterised by highly concentrated food sources that baboons favour over the indigenous forage available in natural habitat (Chapter 4). Furthermore, there are abundant natural (e.g., cliffs) and artificial (e.g., buildings) sleeping sites in close proximity to the urban edge (Chapter 3 and 5) providing baboons with refuges in close proximity to their favoured foraging areas.

Together these changes are associated with a reduction in home range size and a concomitant increase in baboon density, and decreases in DRL and time spent feeding (Chapter 4). Indeed the effects of this habitat modification on baboon spatial ecology have been so remarkable that in some measures of ranging patterns, intrapopulation variation equals the variation that exists between geographically disparate populations of chacma baboons. Thus, for example, troops that occupy natural habitats in the Cape Peninsula exhibit ranging patterns comparable to those of troops in seasonally harsh environments like the Drakensberg, while troops that access human-modified habitats have ranging patterns similar to those of troops occupying fertile environments like the Okavango Delta.

The increased spatial proximity of humans and baboons and the ability of the latter to adapt to novel environments is also a major driver of the high levels of HBC in the Cape Peninsula (Chapter 5). Nearly all troops experience high conflict levels, although those with the least access to low lying land and those that sleep closest to the urban edge suffer the most human-induced injury and mortality. Worryingly, it is likely that levels of HBC will continue to increase as the baboon population grows while more natural land is usurped for transformation to urban habitat and agricultural habitat.

Despite the implementation of various management methods since 1998, levels of HBC remain high (Beamish 2010). The spatial data presented in this thesis can explain the limitations of the more commonly used management strategies and offer both guidance for the improvement of current strategies and recommendations for alternative strategies.

Assessment of management strategies

Baboon monitors

Baboon monitoring is the principle conflict mitigation method used in the Cape Peninsula (Kansky and Gaynor 2000; van Doorn 2009) and is popular as a concept (i.e., baboon chasers) to reduce crop raiding throughout Africa (Naughton-Treves 1997; Hill 2000; Osborn et al. 2005). However, as shown in Chapter 5, this method offers only a limited solution to reducing conflict levels for Cape Peninsula troops. Troops, such as DG and SK, which have been managed daily by monitors for the longest time (since 1998), and at the greatest intensity in terms of monitor numbers (teams of 2-3 men), still experience the highest levels of conflict. This suggests that while monitors may mitigate HBC they do not prevent it and furthermore they do not reduce HBC to levels below those of unmonitored neighbouring troops. During my data collection period (2006-2009), three of the nine study troops had monitors who used the ‘herd-and-hold’ strategy (van Doorn 2009). This strategy involves the herding of a troop to areas within its home ranges where monitors can most successfully hold it (i.e., blockade) and hence prevent it from entering nearby urban habitat. Thus, for example, SK was typically herded to a small portion (32 %, 2.7 km^2) of its total home range (8.3 km^2; Fig. 6.1) which bordered a major road and a low income, densely populated residential area (Ocean View). The rationale for this holding location was that it provided two relatively impervious boundaries to the troop (risks from vehicles and dogs respectively) and thus facilitated the task of the monitors to hold the troop in this specific area.

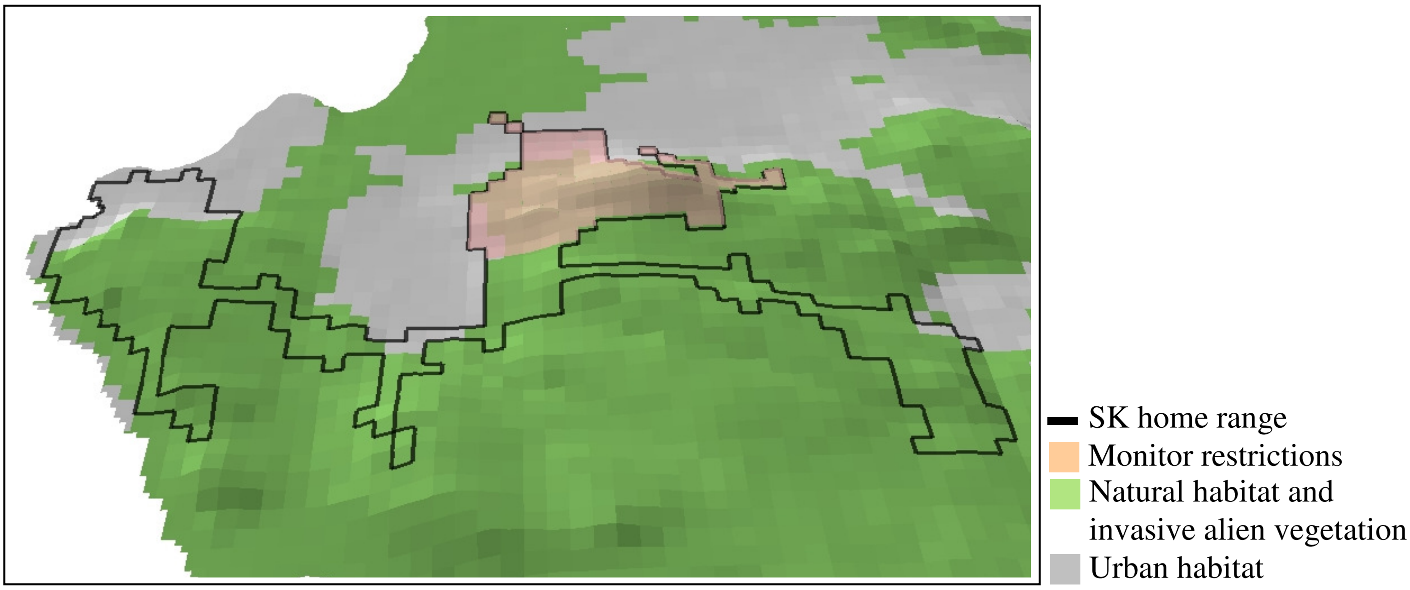


Fig. 6.1. A 3D habitat map showing the full extent of the SK home range (black outline) and the section of the home range to which the troop was restricted on days with monitors (pink cells).

In her study on the effects of the herd-and-hold strategy on another local baboon troop (DG), van Doorn (2009) found that while monitors significantly reduced troop raiding levels, their unsystematic and often aggressive herding technique led to significantly constrained foraging behaviour and increased the potential for elevated stress levels in troop members. Furthermore by restricting the troop to only a small portion of their home range the monitors prevented the troop from tracking seasonal variation in the availability of natural food items (Chapter 5) and further denied them choice in home range use for thermoregulatory, water and sleeping site purposes. In response to van Doorn's findings a second monitor strategy, 'holding the line', was proposed by the Baboon Research Unit (BRU, UCT) in 2009. This strategy is less intrusive for it requires that monitors hold the line between a troop's home range and the adjacent urban habitat but allows the baboons the freedom to make their own spatial and temporal choices within all other habitats in their home range. This strategy was first tested on SWB in June 2009 by the residents of Simon's Town in consultation with the BRU. A comparison of troop movement patterns (determined using tracking collar data) six months before and after this strategy was adopted suggests that there is considerable merit in the hold-the-line strategy versus the herd-and-hold strategy (Fig. 6.2). Not only was the hold-the-line strategy 100 % successful at keeping the troop out of the residential area of Simon's Town – with an associated 18 % increase in use of natural habitat, and a 23 % decrease in use of urban habitat (Table 6.1) – but there was no interference by humans on troop movement patterns beyond of the urban edge.

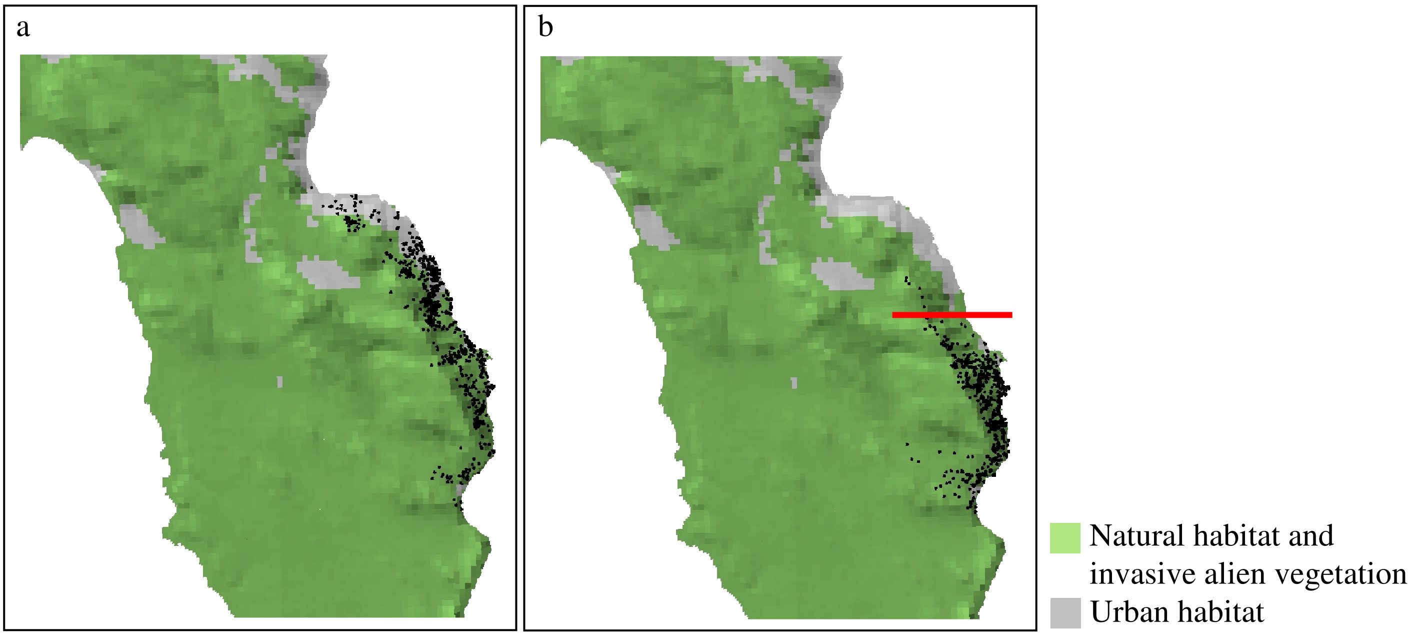


Fig. 6.2. GPS locations of SWB recorded by a tracking collar six months before (a) and six months after (b) the introduction of baboon monitors. The solid red line in (b) denotes the urban edge which baboon monitors were instructed to prevent the baboons from crossing using a variety of noise aversion methods.

Table 6.1. Habitat use by the SWB troop six months before, and six months after the introduction of baboon monitors using the 'hold-the-line' strategy.

Habitat	Before monitors	After monitors
Natural	64.0 %	81.6 %
Agriculture*	0.2 %	4.5 %
Invasive alien	8.1 %	9.5 %
Urban	27.6 %	4.5 %

* Ostrich farm

Based on the above findings the management authorities have embraced the hold-the-line strategy but there are a number of important challenges to overcome before it can be applied to other troops in the Cape Peninsula. The success of the hold-the-line strategy for SWB was greatly facilitated by the linear shape of the troop's home range (confined to land between a high mountain range and the coastline; see Appendix 2.5) which resulted in a short urban edge that was relatively easy to defend. For troops with less linear home ranges where the urban edge is considerably longer (Chapter 5), the task of holding the line would require more resources (i.e., number of monitors) than are currently available. Alternatively the same number of monitors would need to be more effective at deterring baboons from urban habitat (e.g., through noise aversion). Techniques to improve monitor effectiveness are currently being investigated (BS Kaplan, PhD thesis, UCT) but until these results are obtained the costs of herding baboons needs to be considered and the herd-and-hold strategy avoided whenever possible.

I endorse the hold-the-line strategy for another important reason. In her thesis van Doorn (2009) recommended that if herding persists then monitors should only herd troops a maximum distance of 200 m from the urban edge and should not attempt to hold them in any particular portion of their home range. While this represents an improvement as it allows troops more freedom of movement within their home ranges, it still exacts a significant spatial cost to the baboons as the greater the size of the urban edge buffer, the less ecologically viable land will be available to them. Thus, using SK as an example again, if a buffer of 200 m is set around the urban edge, then baboons will be denied access to 8.9 km^2 of low lying (mean altitude: 105.41 m), ecologically viable land (Fig. 6.3) within the total area of land currently accessible to them. In addition, because the buffer will effectively close existing corridors to other tracts of natural habitat, the troop will lose an additional 5.1 km^2. If the width of the buffer is reduced to 100 m, the troop would regain access to an additional 2.5 km^2 of ecologically viable land, but the connectivity of the natural habitat would still not be restored (Fig. 6.3). If, however, the monitors were capable of holding the line on or very near to the urban edge, then the troop would not only retain access to the greatest possible amount of ecologically viable land in the full 40.0 km^2 area of natural habitat, but they could range and forage within it in an unconstrained manner and under minimal human-induced stress. Thus, if effort is to be placed on improving the effectiveness of baboon monitors while minimising their effect on baboons, I recommend that the focus should be on determining the best way to replace the herd-and-hold strategy with the hold-the-line strategy.

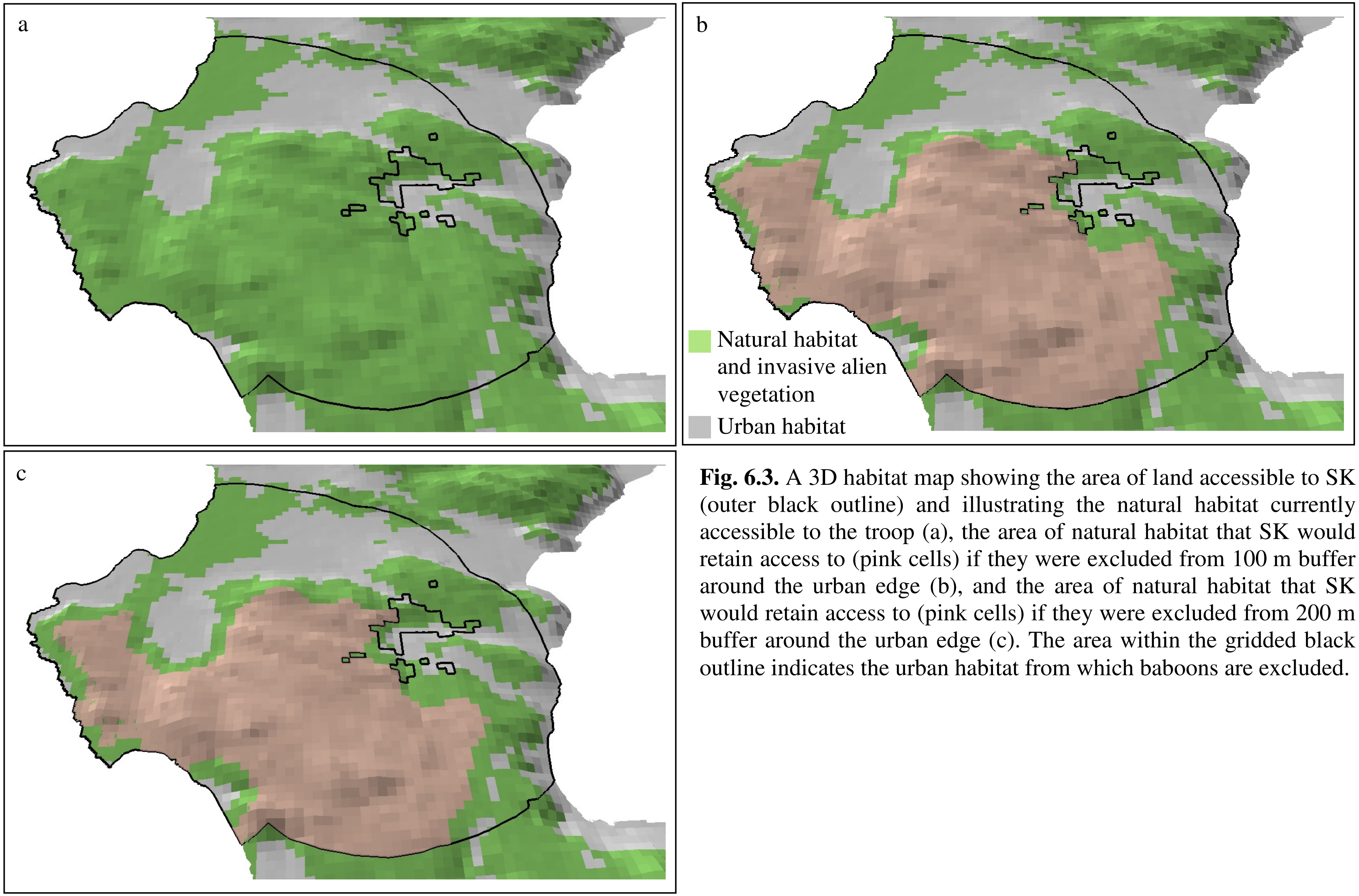


Fig. 6.3. A 3D habitat map showing the area of land accessible to SK (outer black outline) and illustrating the natural habitat currently accessible to the troop (a), the area of natural habitat that SK would retain access to (pink cells) if they were excluded from 100 m buffer around the urban edge (b), and the area of natural habitat that SK would retain access to (pink cells) if they were excluded from 200 m buffer around the urban edge (c). The area within the gridded black outline indicates the urban habitat from which baboons are excluded.

Troop culling

My findings caution against the use of troop culling as a long term solution to reducing HBC levels. Patterns of territoriality suggest that the removal of troops whose home ranges overlap with a high-quality and monopolisable food resource (e.g., picnic sites) would simply create the opportunity for neighbouring troops to expand their home ranges into the vacated area and in so doing, come into contact with the same resource that served as the original driver of the HBC. For example, the removal of DG, arguably the troop with the highest levels of HBC, would almost certainly result in the SK troop expanding its home range into the vacated home range area, thereby perpetuating the cycle of conflict.

History has shown, however, that troop extirpation can be successful at reducing HBC when there are either no other neighbouring troops or when all the troops from entire geographic regions are removed. Thus, following the extirpation of all troops from Table Mountain, Kalk Bay and Chapmans Peak (Fig. 6.4) in the 1980's and 1990's, HBC levels dropped to zero in all adjacent residential areas with only the occasional dispersing male providing temporary and infrequent conflict. Currently there is only a single troop in the Cape Peninsula which currently has no immediate neighbours – RH (isolated since SWB was excluded from urban habitat by monitors in 2009). Removal of this troop would thus be predicted to result in an immediate localised reduction of HBC (Fig. 6.5).

At a regional level the removal of the entire northern subpopulation would in all probability eliminate HBC for half of the Cape Peninsula as the north/south divide, formed by a broad urban belt (Fig. 6.4), represents an effective barrier to the northward movement of troops in the southern population. However, given that baboons are an integral part of the local biodiversity and are thus considered important to ecological processes in indigenous vegetation, the removal of baboons from entire sections of the TMNP may have long-term adverse effects on the general ecology of this large portion of the CFR. Clearly conservation and management authorities will have to weigh up the tangible costs of HBC with the assumed benefits of baboons to ecosystem functioning in fynbos. Given that the latter aspect of baboon ecology is little understood there is an urgent need to obtain such information to effect informed conservation decisions.

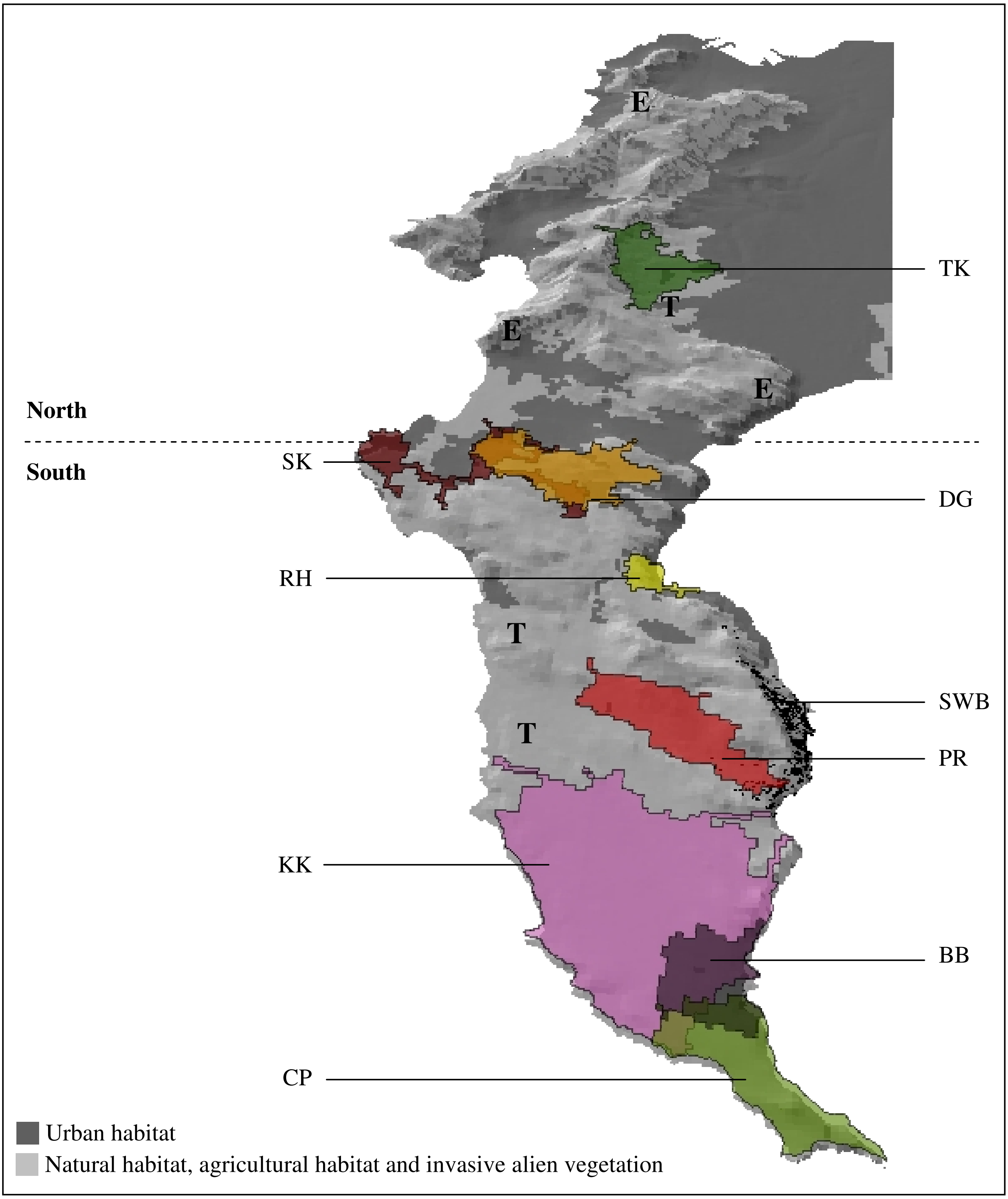


Fig. 6.4. A 3D map of the Cape Peninsula showing the home ranges of all study troops indicating the isolation of RH since the SWB troop (black GPS points) was excluded from urban habitat by monitors in 2009. Included on the map are the locations of troops not included in this study (T) and troops extirpated prior to this study (E) A belt of urban habitat (dashed line), situated approximately half way down the length of the Cape Peninsula, divides the baboons into northern and southern sub-populations.

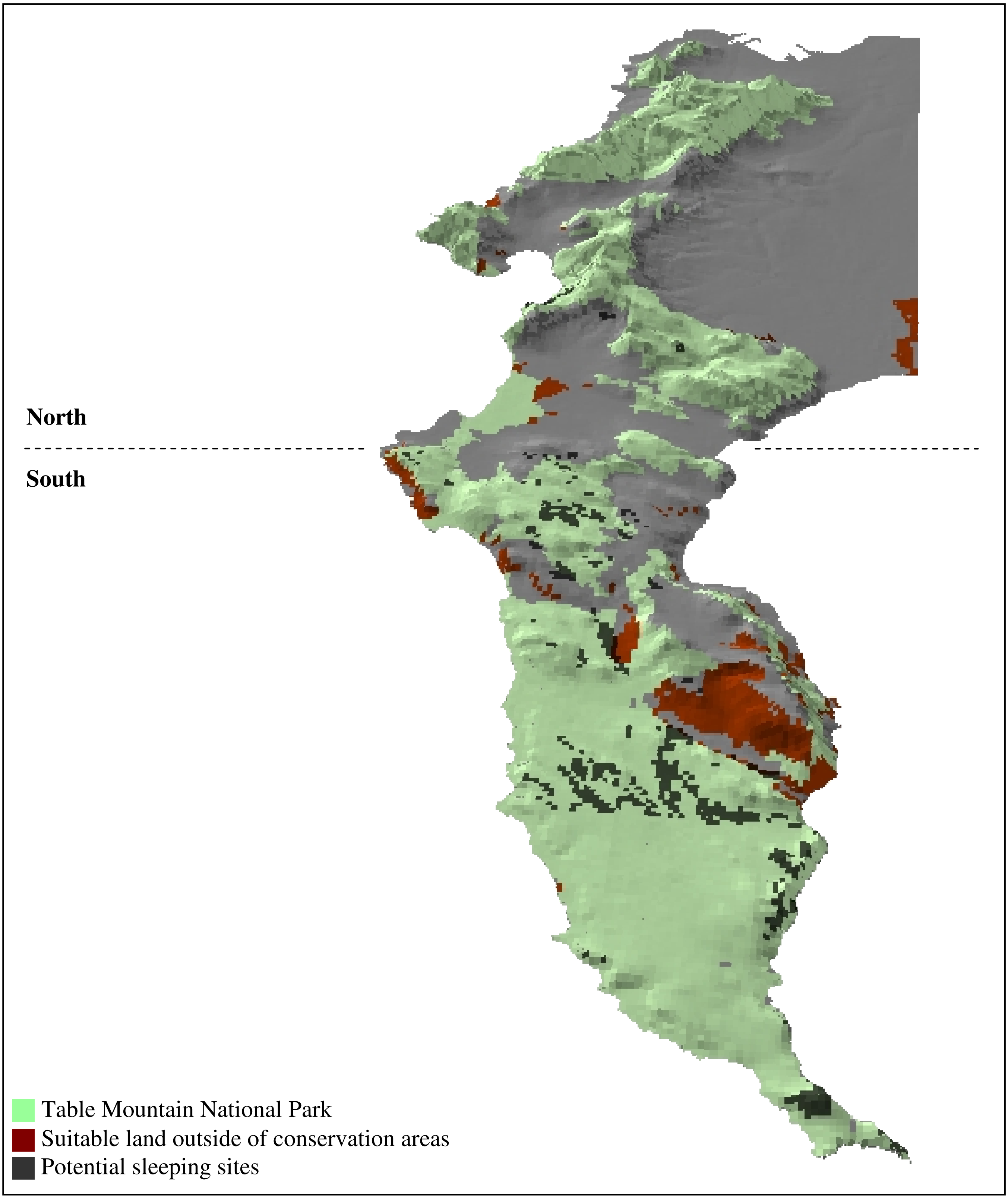


Fig. 6.5. A 3D map showing the natural habitat conserved within the Table Mountain National Park and the ecologically suitable natural habitat that falls outside of conservation areas. The map also shows the location of potential baboon sleeping sites (yellow cells) that are ≥500 m from the urban edge and match the characteristics of used cliff sleeping sites. A belt of urban habitat (dashed line), situated approximately half way down the length of the Cape Peninsula, serves to divide baboons into northern and southern sub-populations.

Recommended alternative management strategies

Landscape conservation

Ensuring that baboons retain access to existing tracts of natural habitat is a critical first step for preventing further escalation of HBC conflict in the Cape Peninsula. However, much of this natural habitat comprises small, non-contiguous islands surrounded entirely by human-modified habitat. This is particularly true in the northern half of the Cape Peninsula where land development is extensive (64 %) relative to the southern half (17 %) and the natural habitat is more fragmented (Fig. 6.4). In these fragmented areas troops would have to traverse large portions of human-modified habitat to reach other patches of natural habitat. Given the preference baboons show for human-modified habitats (Chapter 3), such traversing would likely result in an increase in the frequency and or spatial extent of HBC. Thus, although in Chapter 5 I provided scenarios of hypothetically available areas of land that included these natural habitat islands (to determine density estimates for the Cape Peninsula; see Scenarios 1-4), here I suggest that the most suitable management approach is to consider the scenarios that deem these islands unavailable to baboons (Scenarios 5-8).

By contrast, the southern half of the Cape Peninsula, currently home to 75 % of extant troops and ~65 % of the total number of baboons (Beamish 2010), includes more continuous stretches of ecologically suitable undeveloped land (Chapter 3). Of this land, 87 % is conserved as part of the TMNP, with 13 % potentially subject to urban and or agricultural development. The fragments that comprise it are located predominantly at low altitudes (mean: 127.56 m; range: 0-625.33 m), providing troops with access to relatively fertile patches of indigenous vegetation (Chapter 3) and – in many cases – with unimpeded access to the coast. Furthermore, the range of slopes in this landscape (0-57.36 °) provides suitable baboon sleeping sites. Development of this land would result in baboons losing access to 26 % of currently used home range cells and 12 % of core range cells forcing them farther into the increasingly marginalised habitat of higher altitudes. The loss of this land to development is predicted to exacerbate levels of HBC and this must to be conveyed to developers, land use planners, conservation authorities and residents in the affected areas so that they can factor in this consequence when deciding on the overall costs of a given development.

Conserving this undeveloped land requires the involvement of their various landowners (Norton 2000), the list of which includes: private owners (62 % of land), the State (23 %), the

CoCT (15 %) and the Provincial Administration of the Western Cape (0.2 %). Currently both the CoCT and Provincial Administration of the Western Cape have accepted the GPS data from this thesis and incorporated digital images of the quantified baboon home ranges into the development plans for the Strategic Environmental Management Department of Environmental Affairs and Development Planning in the Western Cape and the City of Cape Town. While the inclusion of these maps into land development planning processes may not prevent further erosion of natural habitats, it will trigger baboon specific "Environmental Management Plans" and initiate an assessment of the possible impacts of such development on the affected troop(s). This process will further allow for all interested and affected parties to provide input on the implications of such a development on the troop(s). However, because most of this undeveloped land is owned by private parties, it is vital that the responsibility of landscape conservation is not left entirely to environmental authorities. Rather, a great deal of effort should be placed on encouraging and or providing incentives for private landowners to participate in the conservation process. This can be achieved using a variety of methods including one or a mix of voluntary, property-based, price-based or regulatory mechanisms (Gunningham and Young 1997; Elmendorf 2003). Finally, conservation of the land owned by the remaining parties could be achieved by entrusting the management of those portions of land to SANParks, as per the arrangement between the CoCT and TMNP managers.

Resource management

The ranging patterns of primates are principally determined by the availability and distribution of their critical resources, namely food (Clutton-Brock 1975; Barton et al. 1992; Ganas and Robbins 2005; Riley 2008), sleeping sites (Crook and Aldrich-Blake 1968; Whiten et al. 1987; Zhou et al. 2007) and water (Altmann and Altmann 1970; Chapman 1988). In conjunction with landscape conservation, informed management of these resources offers conservation authorities the most sustainable means for altering the spatial ecology of the Cape Peninsula troops to reduce HBC.

Managing food resources should be the first step of the resource management process. Density estimates (Chapter 5) suggest that restricting baboons to a diet of natural food sources will reduce the population density in the long-term and make troop movement patterns more predictable and hence more manageable on both an annual and seasonal basis. Currently the only troop (KK) with no HBC is also the only troop to forage exclusively on natural food sources. This strongly suggests that preventing baboons from accessing anthropogenic food sources is the best long-term solution to reducing HBC levels. To prevent baboons from accessing food in urban habitat, CoCT management should focus on creating bylaws that force urban residents to reduce the incentives for baboons to enter residential areas (e.g., baboon proof bins, no planting of fruiting trees). Invasive alien vegetation and commercial plantations should be restored to natural habitat (as currently planned for commercial plantations), and baboons should be prevented from accessing other agricultural food sources (e.g., grapes, ostrich feed). To simultaneously ensure the viability of baboon forage in natural habitat, during prescribed fire events managers should strive to burn only portions of an entire home range at one time and allow sufficient time between burn intervals for vegetation biomass to regenerate (Chapter 5).

Managing baboon sleeping sites is an imperative second step of the resource management process. To reduce the spatial proximity of baboons and humans, baboons should be actively discouraged from using tree and building sleeping sites in or near the urban edge. Here again, the removal of invasive alien vegetation and plantation harvesting should assist this process. Baboons should instead be encouraged to use the natural (cliff) sleeping sites that are located more than an hours travel distance from the urban edge and which are widely available in the Cape Peninsula (Fig. 6.5).

With regards to water management, permanent surface water need not be considered as a key landscape feature for baboons in the Cape Peninsula during years of good rainfall. However, during years of drought or below average rainfall it is possible that baboons will be attracted to permanent water sources within low lying urban and agricultural habitats. Under such environmental conditions managers could utilise artificial watering points to encourage movement away from human-modified habitats.

These resource management endeavours, if successful, will improve both the immediate and long-term manageability and conservation of baboons in the Cape Peninsula. Keeping baboons out of human-modified habitats should result in an immediate decrease in levels of HBC with associated benefits for both baboons and humans. On a longer time scale, the ranging patterns of troops should exhibit less habitat-related variation as troop home ranges begin to comprise more comparable habitat compositions. This will improve the ability of managers to generate population-specific, rather than troop-specific management plans. Furthermore, the population should become more manageable as the mean density and population growth rate decrease over time in response to dietary changes. Lastly, decreasing the amount of time that baboons spend in urban habitat will come with two additional and important management and conservation benefits. First, time spent in indigenous vegetation should reduce the probability of bidirectional interspecies disease transmission between baboons and humans (Pucak et al. 1982; Ravasi 2009; Drewe et al. in press). Second, young baboons will have the opportunity to learn the requisite skills for finding and processing indigenous food (Asquith 1989) thereby enhancing the ecological role of baboons in Cape Peninsula fynbos vegetation.

Shortcomings of this study and directions for future research in the Cape Peninsula

In this thesis I quantified the spatial ecology of the Cape Peninsula baboons by assessing habitat use, ranging patterns and activity budgets across nine troops. However, I did not conduct detailed foraging and dietary analyses of individual troop members, and therefore what remains lacking is information regarding the quantity and quality of natural food sources that would be required to sustain a viable baboon population that is not in conflict with humans. A concern might thus remain that certain troops are locked into conflict with humans because an insufficiency of natural food sources obligates them to access anthropogenic food sources. However, despite the absence of such nutritional data, the spatial and behavioural ecology of the naturally-foraging KK troop (this thesis; M.C. Lewis, UCT, unpubl. data), as well as this troops demographic patterns (Beamish 2010), indicate that while baboons retain access to both low-lying natural land and protein-rich marine food sources, there is no evidence to suggest that they will become food-stressed in the absence of raiding.

A further limitation of my thesis is the lack of practical solutions that can be readily implemented for reducing HBC in the Cape Peninsula. Clearly there is a need to develop sustainable solutions to HBC, that employ a variety of tools not tested in this thesis (e.g., electric fencing, sound aversion) to discourage baboons from entering human-modified habitat.

Finally, though much effort has been put into researching the ecological aspects of baboon management in the Cape Peninsula (Ravasi 2009; van Doorn 2009; Beamish 2010; this thesis), comparably little attention has been paid to the human aspects of the same problem. Yet, the way that locals perceive human-wildlife conflict determines their responses to it and their willingness, or lack thereof, to participate in mitigation programs (Hockings and Humle 2009). Thus, determining human attitudes and desires regarding HBC is vital for ensuring the effectiveness and sustainability of all baboon management and conservation efforts.

Advancing the study of primate spatial ecology

Spatial ecology has been a focus of primatological studies for many decades, and ranging patterns have been documented for most genera in the primate order. However, spatial research is logistically difficult and requires substantial investments in both labour and time. Consequently, with only a few exceptions, primate spatial studies have been restricted to small sample sizes. While these studies provide detailed information on the ecology of their respective study groups, they are prone to underestimating the range of spatial and behavioural variation across geographic regions (Chapter 4). This is particularly true for adaptable, generalist species that are increasingly affected by anthropogenic change and its marked impacts on the quality and quantity of available food. My findings suggest that the optimal scale at which to study primate spatial ecology is at the population-level. This level is appropriate for accurately assessing the extent and causes of ranging pattern variation for any given primate population, while simultaneously controlling for any variation linked to geographical differences (e.g., latitude and climate). Furthermore, population-level studies are fast becoming an increasingly realistic option for primatologists given the vast improvements to remote tracking technology (e.g., GPS tracking collars) in recent years. Importantly I found that data from this technology can produce ranging patterns comparable to those produced from data collected by field researchers (Chapter 2). Thus primatologists now have unprecedented flexibility when selecting data collection methods for population-level field studies.

My research provides support for theories that have until recently been tested almost exclusively using data from meta-studies (e.g., Majolo et al. 2008; Bettridge 2010). Population-level analyses are an important contribution to theories tested using meta-analyses because they are not confounded by phylogenetic and geographical variation (see above). Thus this study provides important support for the theoretical prediction that troop size and habitat type will affect primate ranging patterns and behaviour. In the Cape Peninsula larger troops have larger home ranges, while troops that spend more time in human-modified habitat (with predictable sources of high quality food) have smaller home ranges, shorter day range lengths and spend less time feeding than troops in natural habitat. Interestingly, and contrary to my prediction, I found troop size to have a significant positive effect on home range size despite the extensive heterogeneity of broad scale habitat types in the study area, and despite the potentially confounding influence(s) of baboon monitors.

Advancing research of human-wildlife conflict and practice of animal conservation

My findings also have application beyond the field of primatology. Ostensibly the most important of these lies in the realisation that in the Cape Peninsula specifically and the Western Cape generally, mountains have provided an important refuge for many wildlife species including baboons. Over time many of these high lying areas which are not suitable for agriculture or urbanisation have achieved official conservation status. There are two consequences of this. Firstly many of these parks are essentially natural islands within a sea of transformed land and thus the populations therein will require active management to reduce the effects of inbreeding, overpopulation and overexploitation of resources. Secondly conflict with humans has become focussed along the low lying boundaries of these parks as they represent both the edge to isolated and expanding wildlife populations and the site of higher primary production of plants (Chapter 3). Currently there are no management plans for these surviving, disconnected populations of wildlife and this thesis provides a starting point by identifying suitable methods and analyses for understanding the spatial ecology of species on these islands, and for devising management plans to ensure viable meta-populations throughout the region.

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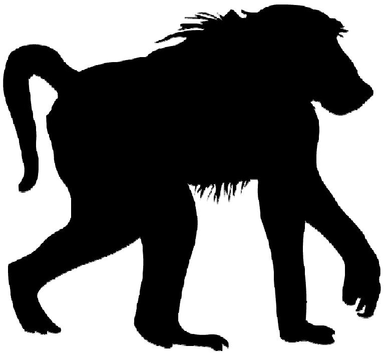

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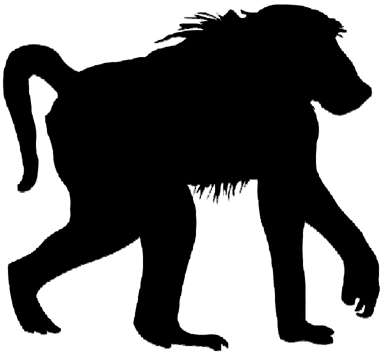

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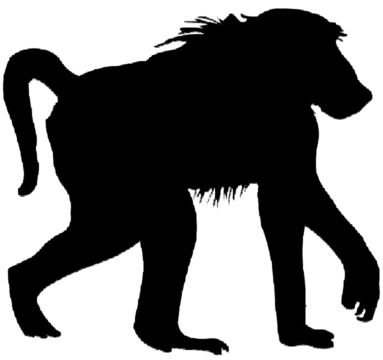
LIST OF ACRONYMS

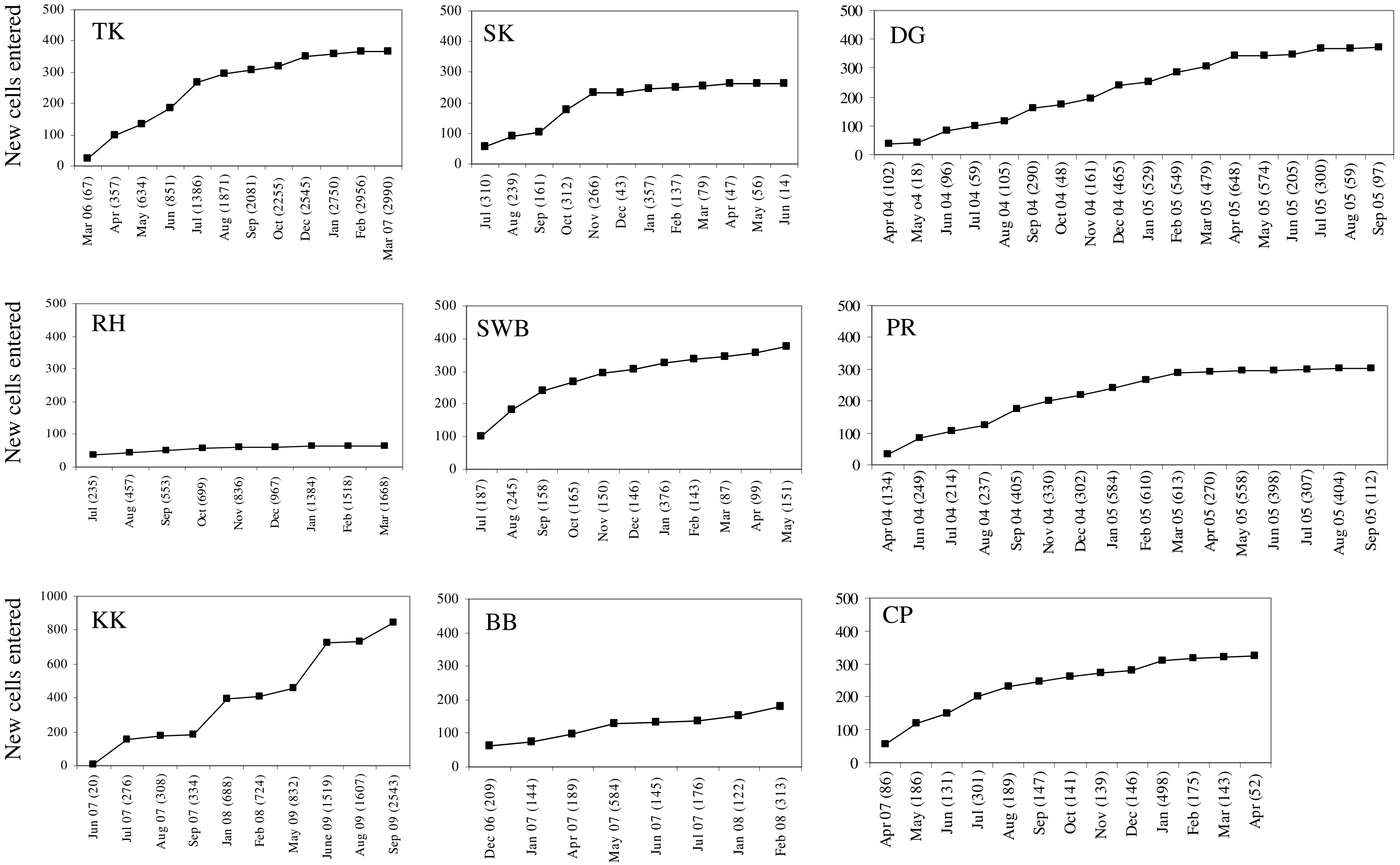
ANOVA	Analysis of Variance
BHU	Broad Habitat Units (Mucina and Rutherford 2006)
BRU	Baboon Research Unit
CFR	Cape Floristic Region
CFR	Cape Floristic Region
CoCT	City of Cape Town
CoGH	Cape of Good Hope Section of the Table Mountain National Park
DRL	Day Range Length
GIS	Geographic Information System
GPS	Global Positioning System
GSM	Global System for Mobile Communication
HBC	Human-Baboon Conflict
SANParks	South African National Park
TMNP	Table Mountain National Park
TR	Travel Rate
UCT	University of Cape Town
VHF	Very High Frequency

Baboon troops

BB	Buffels Bay
CP	Cape Point
DG	Da Gama
KK	Kanonkop
PR	Plateau Road
RH	Red Hill
SK	Slangkop
SWB	Smitswinkel Bay
TK	Tokai

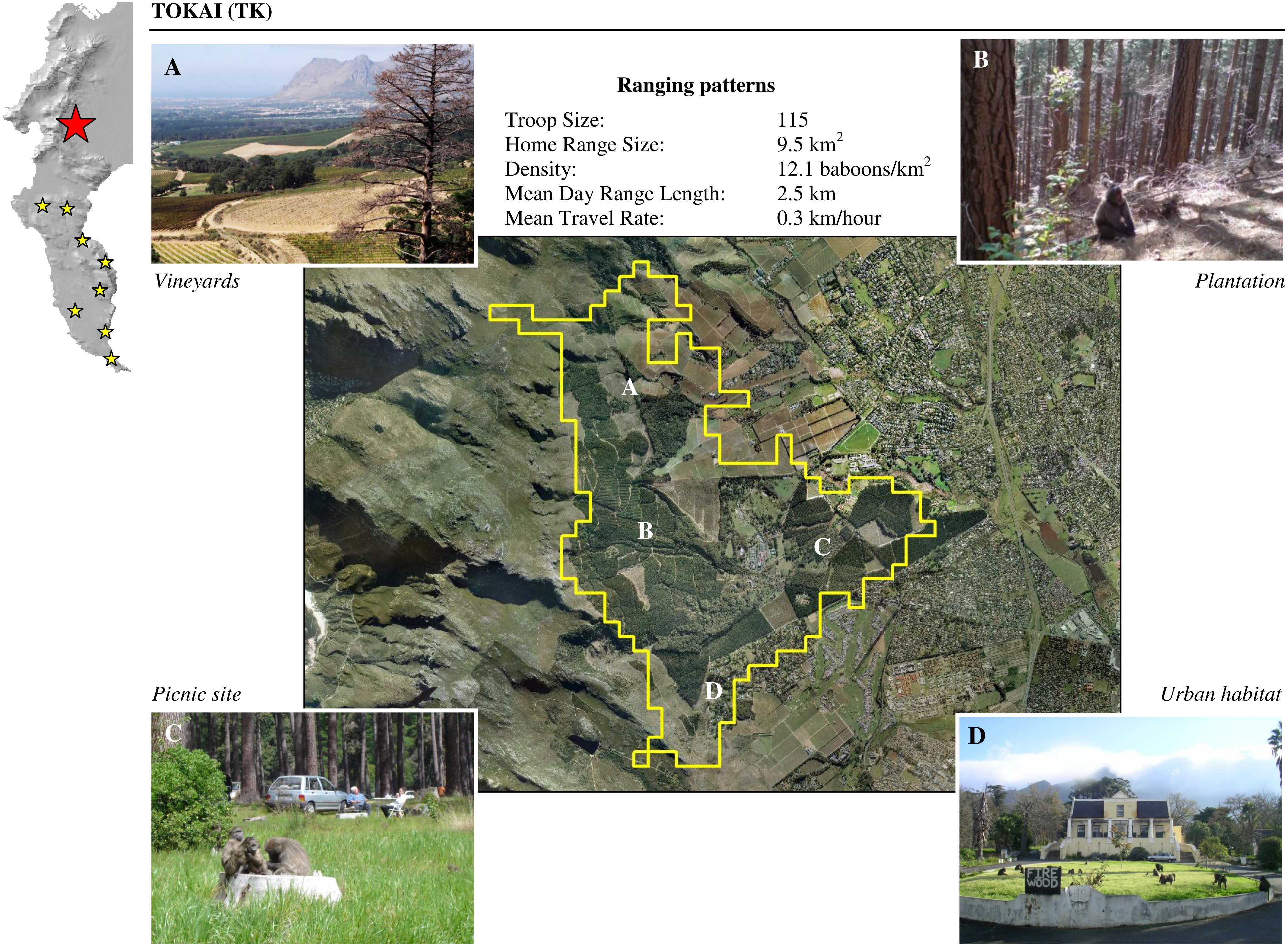
Appendices





Appendix 1. XY line plots of the cumulative number of new cells entered per month of data collection for the nine study troops. .For direct comparison, all graphs are set to the same scale on the Y-axis. This was not possible for KK, as its home range was exceptionally large.

TOKAI (TK)

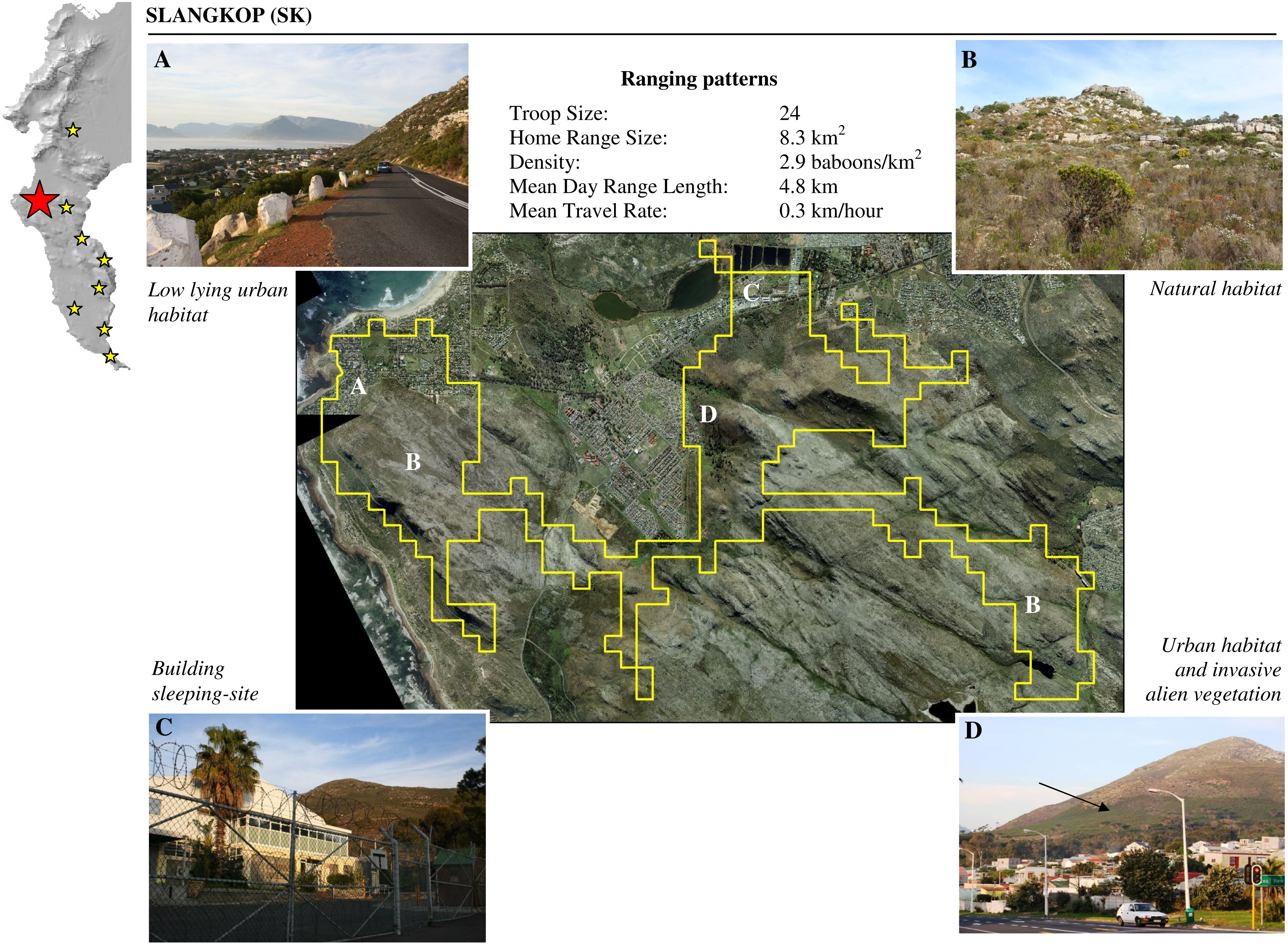


Ranging patterns

Troop Size:	115
Home Range Size:	9.5 km^2
Density:	12.1 baboons/km^2
Mean Day Range Length:	2.5 km
Mean Travel Rate:	0.3 km/hour

Appendix 2.1. (Top left) The location of the TK troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The TK home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

SLANGKOP (SK)



Ranging patterns

Troop Size:	24
Home Range Size:	8.3 km^2
Density:	2.9 baboons/km^2
Mean Day Range Length:	4.8 km
Mean Travel Rate:	0.3 km/hour

Low lying urban habitat

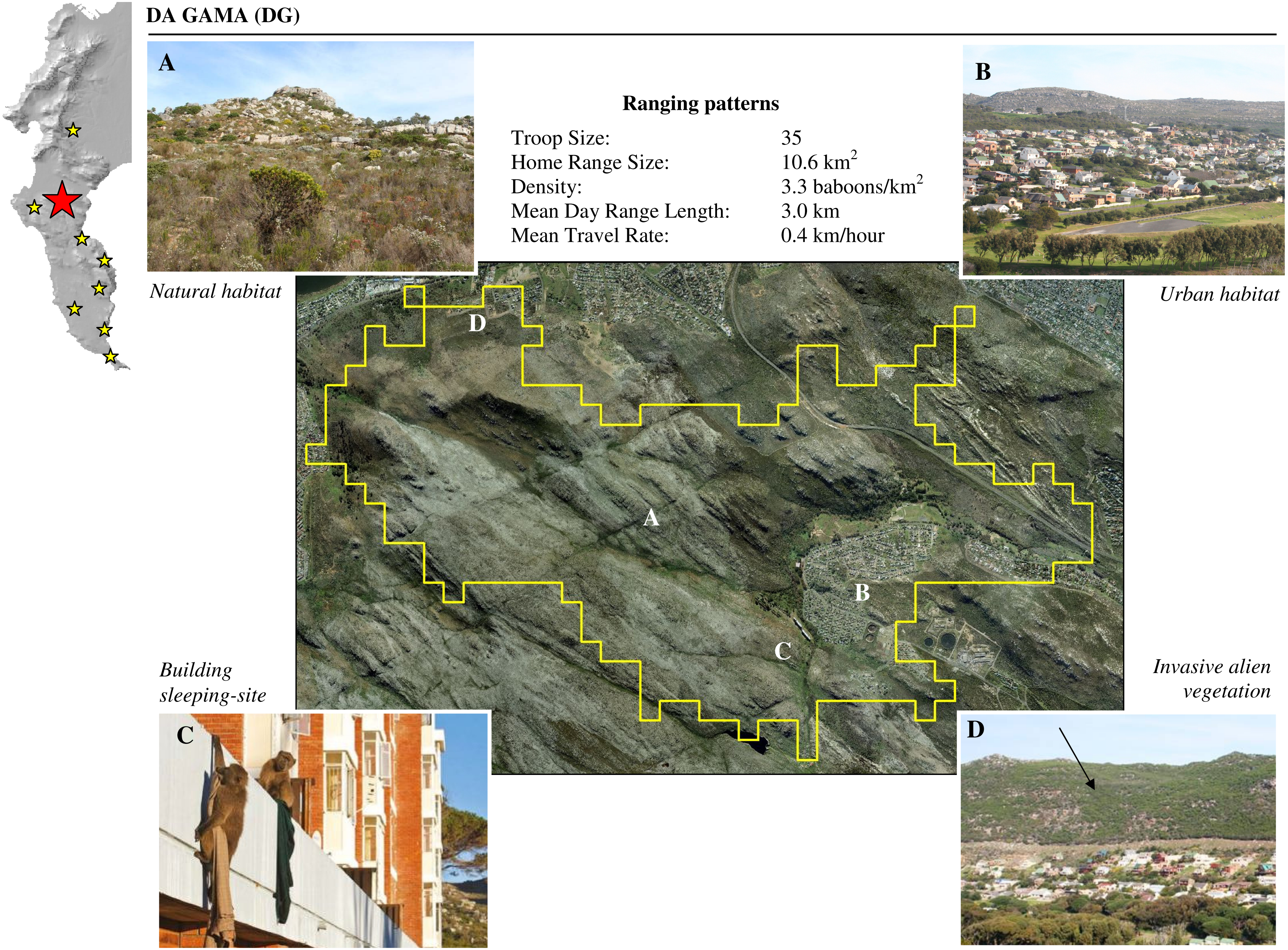
Natural habitat

Building sleeping-site

Urban habitat and invasive alien vegetation

Appendix 2.2. (Top left) The location of the SK troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The SK home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

DA GAMA (DG)



Ranging patterns

Troop Size:	35
Home Range Size:	10.6 km^2
Density:	3.3 baboons/km^2
Mean Day Range Length:	3.0 km
Mean Travel Rate:	0.4 km/hour

Natural habitat

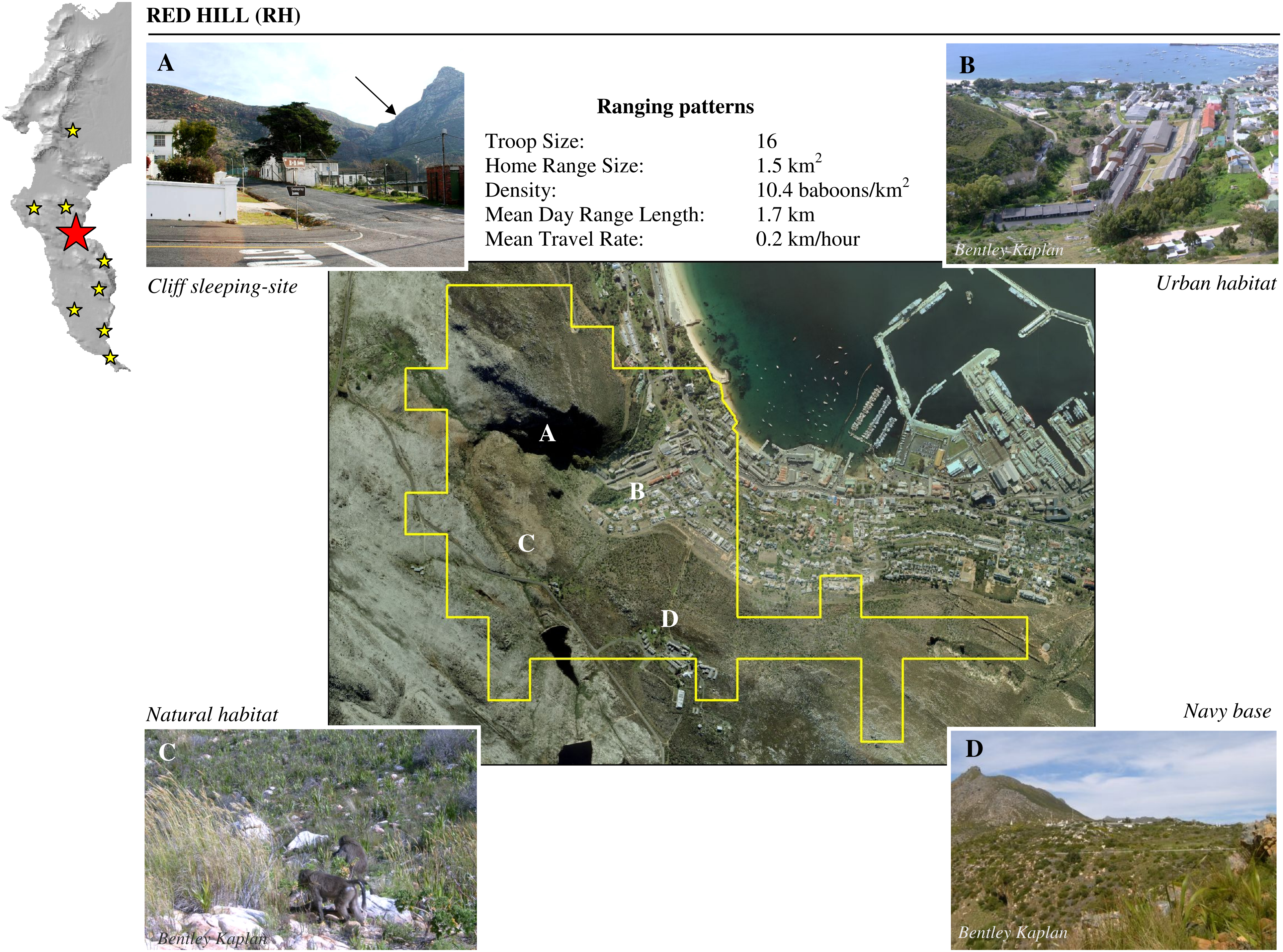
Urban habitat

Building sleeping-site

Invasive alien vegetation

Appendix 2.3. (Top left) The location of the DG troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The DG home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

RED HILL (RH)

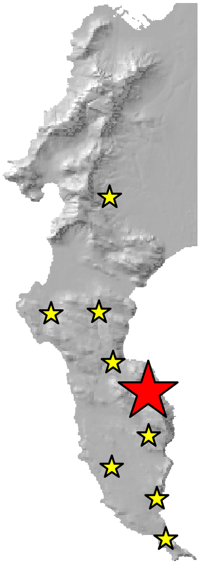


Ranging patterns

Troop Size:	16
Home Range Size:	1.5 km^2
Density:	10.4 baboons/km^2
Mean Day Range Length:	1.7 km
Mean Travel Rate:	0.2 km/hour

Appendix 2.4. (Top left) The location of the RH troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The RH home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

SMITSWINKEL BAY (SWB)

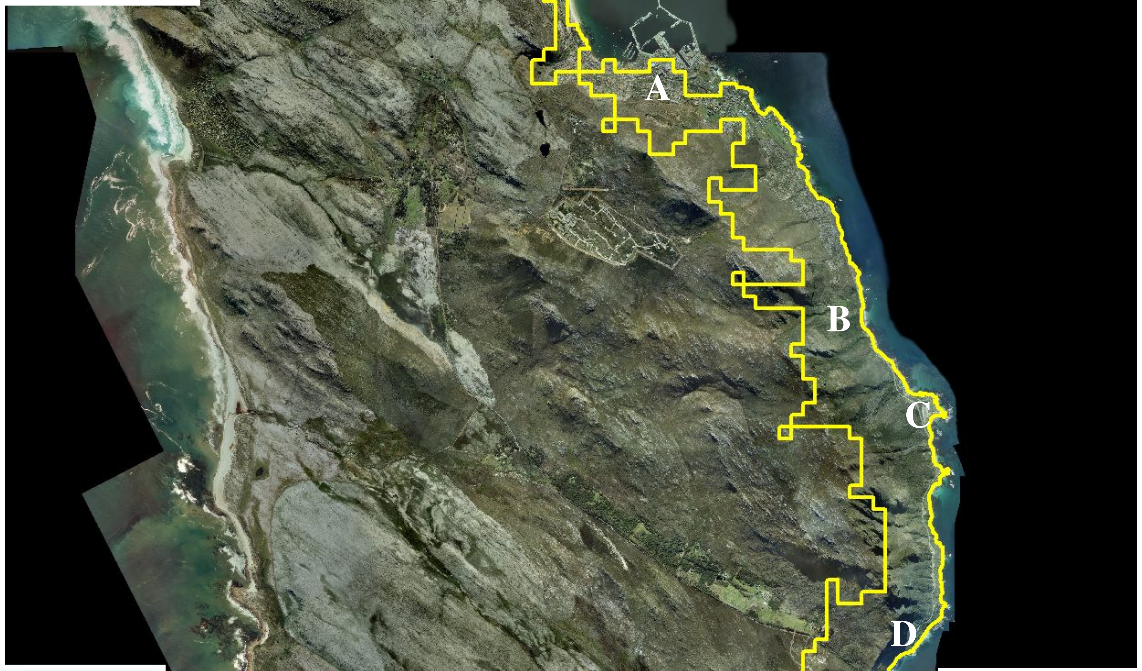


Urban habitat

Ranging patterns

Troop Size:	26
Home Range Size:	9.3 km^2
Density:	2.8 baboons/km^2
Mean Day Range Length:	3.3 km
Mean Travel Rate:	0.4 km/hour

Coastal road running the length of the low lying land in the home range

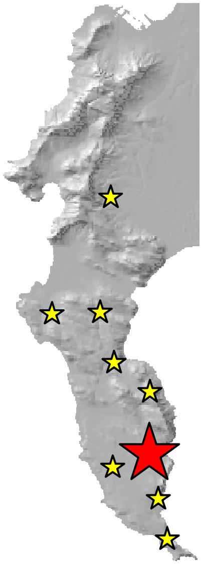


Millers Point caravan park

Smitswinkel Bay

Appendix 2.5. (Top left) The location of the SWB troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The SWB home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

PLATEAU ROAD (PR)



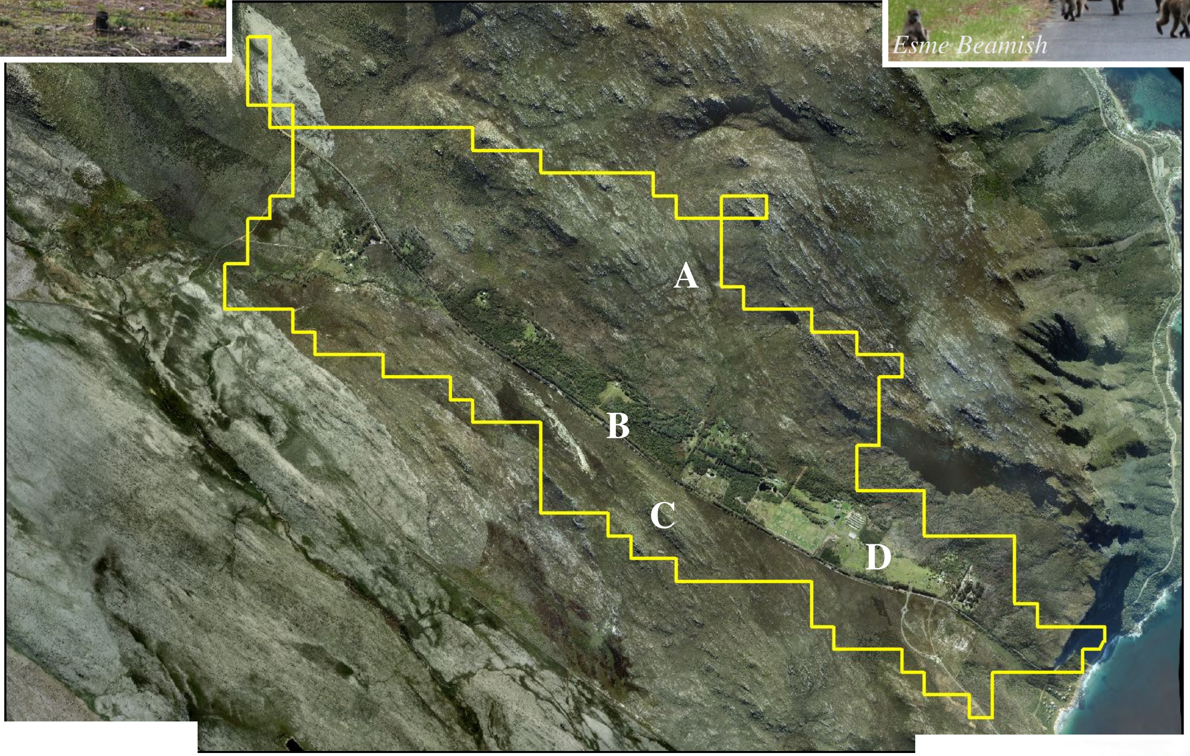
Natural habitat

Ranging patterns

Troop Size:	36
Home Range Size:	9.1 km^2
Density:	4.0 baboons/km^2
Mean Day Range Length:	5.6 km
Mean Travel Rate:	0.5 km/hour

Esme Beamish

Invasive alien vegetation along the road

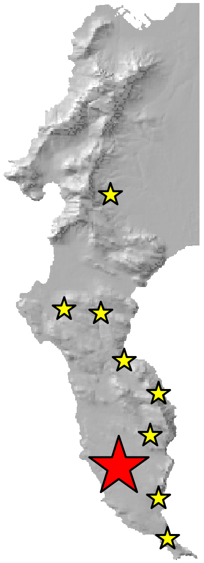


Road marking the border of Cape of Good Hope Section of Table Mountain National Park

Ostrich farm

Appendix 2.6. (Top left) The location of the PR troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The PR home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

KANONKOP (KK)

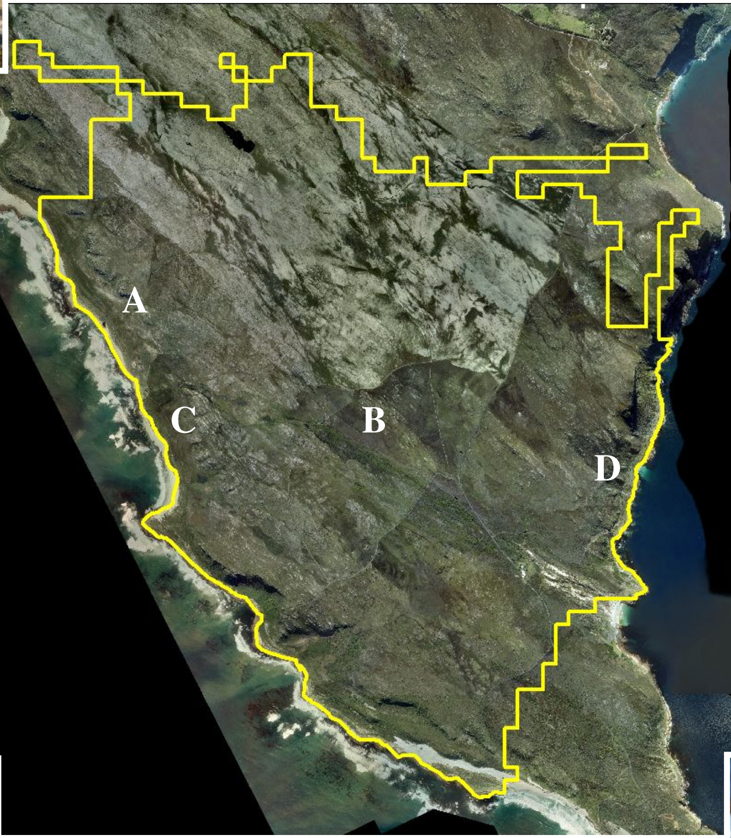


Natural habitat

Ranging patterns

Troop Size:	49
Home Range Size:	37.7 km^2
Density:	1.3 baboons/km^2
Mean Day Range Length:	6.2 km
Mean Travel Rate:	0.7 km/hour

Recently burned wetland vegetation

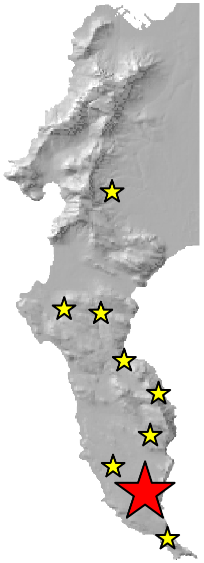


Urban habitat

Mussel beds

Appendix 2.7. (Top left) The location of the KK troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The KK home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

BUFFELS BAY (BB)



Rachel Schill

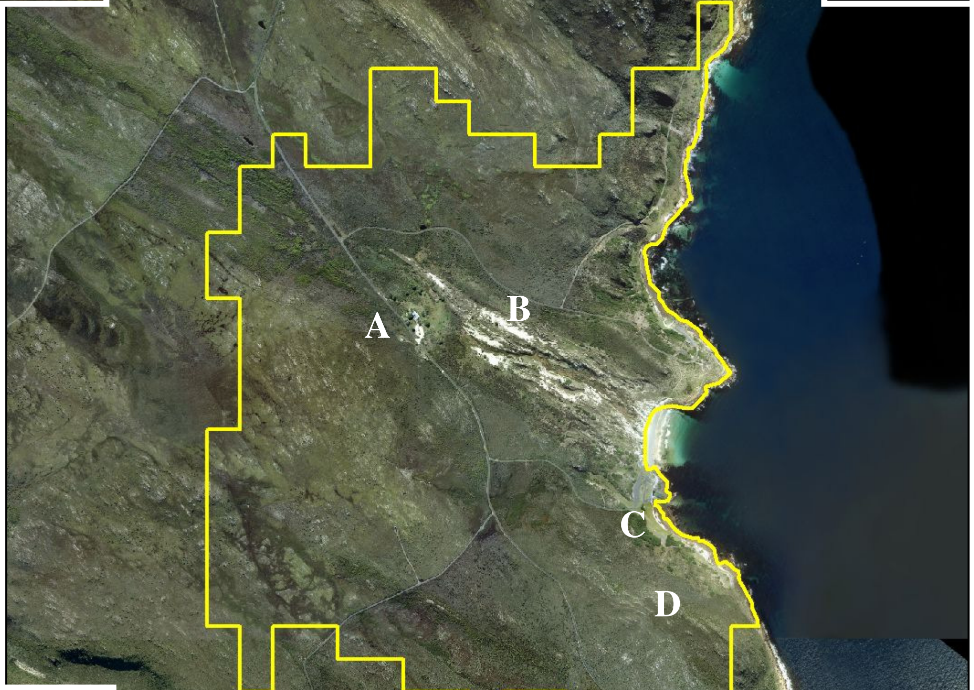
Tree sleeping-site at Buffelsfontein Visitors Centre

Ranging patterns

Troop Size:	15
Home Range Size:	5.6 km^2
Density:	2.8 baboons/km^2
Mean Day Range Length:	3.3 km
Mean Travel Rate:	0.4 km/hour

Leslie Steele

Dune vegetation

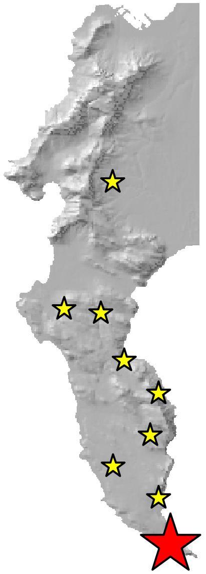


Picnic site

View of picnic site from cliff sleeping-site

Appendix 2.8. (top left) The location of the BB troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The BB home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.

CAPE POINT (CP)



Rachel Schill

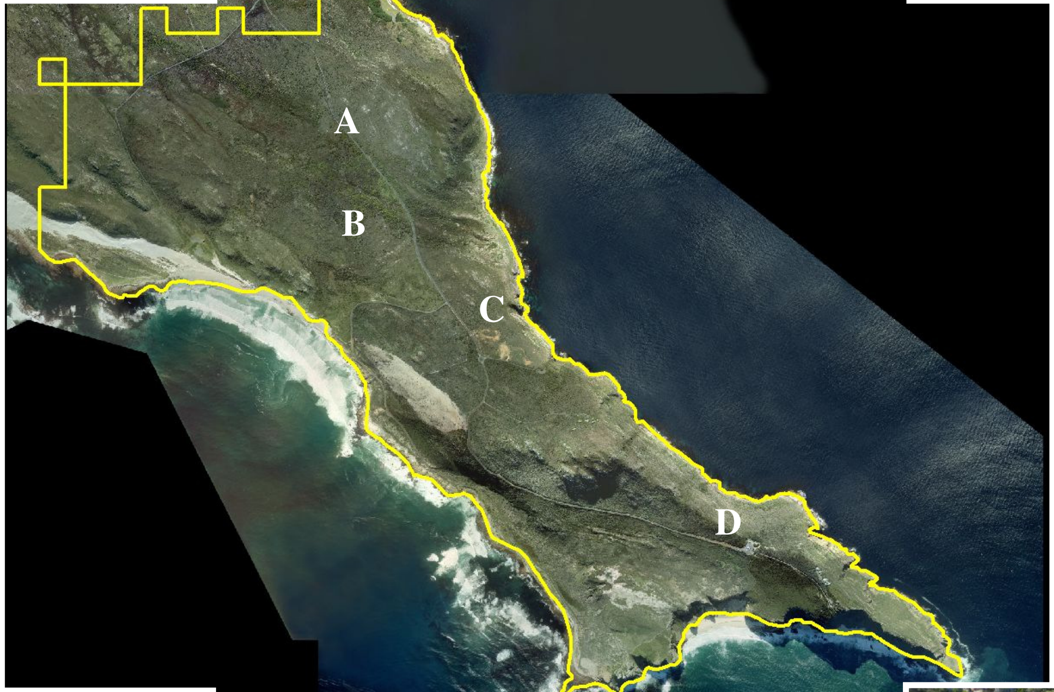
Road with tourists

Ranging patterns

Troop Size:	22
Home Range Size:	7.5 km^2
Density:	2.9 baboons/km^2
Mean Day Range Length:	5.3 km
Mean Travel Rate:	0.6 km/hour

Rachel Schill

Natural habitat



Cliff faces

Denise Thompson

Cape Point restaurant

Appendix 2.9. (top left) The location of the CP troop (red star) relative to other troops (yellow stars) in the Cape Peninsula. The CP home range (yellow outline) overlaid onto an aerial photograph (central image) with photographs taken within this home range.