Behavioural and physiological responses of chacma baboons (*Papio ursinus*) to wildfire in the Cape Peninsula of South Africa

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Table of Contents

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Plagiarism declaration

I know that plagiarism is wrong. Plagiarism is using another's work and to pretend that it is one's own.

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Abstract

In an ecological context, ‘flexibility’ refers to an animal’s ability to respond immediately to environmental stimuli through physiological and behavioural adjustments. Specifically, primates exhibit a high degree of ecological flexibility, which allows them to persist through environmental changes that vary in duration and predictability. To cope with the variability of conditions within their habitats, baboons have evolved flexibility in ranging behaviour, social behaviour, and diet. Natural disasters are predicted to increase across the globe, and many parts of the world are experiencing longer wildfire seasons and higher wildfire frequencies than ever before. The aim of this study is to use an existing data set to assess how baboons responded, behaviourally and physiologically, to an extensive wildfire. I compare home range use, activity budgets, faecal glucocorticoid concentrations, and urinary C-peptide concentrations three months after the fire to the same three months in the previous year for the same 16 adult females.

In the months following the fire, the baboons had a larger spatial range compared to the same months in the year prior. The additional area incorporated unburnt areas into their home range, which were preferentially used over burnt areas. Behavioural adjustments included notably less time spent engaging in social behaviours than in the year prior. Perhaps most surprisingly, post-fire physiological indicators did not suggest high levels of psychological, energetic, or nutritional stress, as glucocorticoid concentrations were significantly lower post-fire compared to the year prior, while C-peptide concentrations were not significantly different between the two periods. The troop appears to have benefited from a surfeit of exotic pine seeds that were released by pine trees as a result of the fire. This unexpected nutritional windfall, in addition to the inclusion of vineyards within their ranging patterns, may explain why there were no physiological indicators of nutritional stress despite the loss of most above ground biomass. Despite suffering the loss of 12 troop members in the fire and injury to a further 12 individuals, adult females in the Tokai troop were able to adjust to a severe and extensive change to their home range. Although primate ecological flexibility has been widely documented, this is the first study to explore the behavioural and physiological responses of baboons to extensive habitat changes resulting from a wildfire, and the potential implications for the management of wildlife on the urban edge.

Introduction

Behavioural flexibility

A common goal of ecologists and evolutionary biologists is to understand variation in behaviour and the subsequent consequences for evolutionary fitness (Krebs & Davies 1997; Sih et al. 2004; Alcock 2009). In a variable and transforming world, animals that can adapt to changes in their surroundings are likely to exhibit higher survival and reproductive success (Bürger & Lynch 1995; Kinnison & Hairston 2007; Coppens et al. 2010). When environmental change occurs slowly, over many generations of a given species, that species can adapt through evolutionary change (Stockwell et al. 2003; Hoffmann & Sgrò 2011; Rezende & Diniz-Filho 2012). When abrupt environmental change takes place, individuals of some taxa are able to rapidly respond through behavioural flexibility (Beever et al. 2017).

In an ecological context, 'flexibility' refers to an animal's ability to respond immediately to environmental stimuli through physiological and behavioural adjustments (Gordon 1991; Hadfield & Strathmann 1996). Flexible behaviour allows for prompt and reversible coping mechanisms to specific local conditions, and is often manifested in temporal changes in the behaviour of individuals (Coppens et al. 2010; van Buskirk 2012). Animals across numerous taxa exhibit varying levels of behavioural flexibility, including but not limited to, insects (ants: Gordon 1991; mayflies: Tikkanen et al. 1996), reptiles (turtles: Hays et al. 2006), fish (salmon: Dill 1983), birds (Webster & Lefebvre 2001; Sol et al. 2002), and a range of diverse mammals including bats (Ratcliffe & Dawson 2003), rodents (Rymer et al. 2013), and non-human primates (van Schaik 2013).

The role of innovative actions and consequential learning in behavioural flexibility cannot be ignored. Species that exhibit flexible behaviour often display innovative behaviours (Sol et al. 2002; Reader & MacDonald 2003; Tebbich et al. 2010; Huebner & Fichtel 2015). In discussion of non-humans, innovative behaviours are defined as actions that provide a solution to a novel problem or a novel solution to an old problem (Kummer & Goodall 1985). Most simply, behaviours that result in favourable outcomes are more likely to be repeated (Miller & Escobar 2002). Learning from novel actions can facilitate behavioural flexibility through various cognitive mechanisms as animals accumulate experience of environmental stimuli through their lives (Dukas 2004; Magistretti 2006; Mery & Burns 2010; Shettleworth 2010). Across various taxa, high levels of innovation, learning, and associated behavioural flexibility are linked with bigger brains relative to body size (Reader & Laland 2002; Reader & MacDonald 2003; Sol et al. 2005; Deaner et al. 2007; Reader et al. 2011). This phenomenon is exemplified by primates, whose behavioural flexibility is irrefutable (Reader & Laland 2002; Reader & MacDonald 2003; Deaner et al. 2007; Reader et al. 2011).

Baboon behavioural flexibility

Primates exhibit a high degree of ecological flexibility, which is reflected in their wide variety of habitats, life history traits, social systems, mating strategies, predator avoidance tactics, and diets (Jones 2006; Campbell et al. 2011; Mitani et al. 2012). Baboons (genus *Papio*) are one of the most successful primate taxa, thriving in a diverse range of habitats and climates across latitudes throughout sub-Saharan Africa (Jolly 1993; Swedell 2011). The wide geographical and environmental range that baboons occupy suggests on its own that baboons are highly adaptable. Within their various habitats across their near-continental range, baboons persist through environmental changes that vary in duration and predictability, including daily temperature fluctuations, seasonal differences in weather conditions and food availability, and habitat transformations resulting from climate change or human-induced landscape changes (Alberts & Altmann 2006). To cope with the variability of conditions within their habitats, baboons have evolved flexibility in locomotion (arboreal and terrestrial), diet (omnivorous), mating systems (polygyny and polygynandry), and social systems (single-male, multi-male, and multi-level societies) (Alberts & Altmann 2006; Swedell 2011).

Perhaps the most prominent example of behavioural flexibility in baboon troops is shown in foraging behaviour and diet. Food has been shown to influence many aspects of ecology, including distribution, movement, behaviour, and social organisation (Lambert 2011; Chapman et al. 2012). The combination of selective (particular species and/or plant parts) and generalist foraging strategies (feeding on plants, invertebrates, small vertebrates, and anthropogenic food) found in baboons results in high dietary flexibility (Alberts & Altmann 2006). Opportunistic foraging occurs throughout the year based on seasonally available resources, resulting in a highly varied diet (Alberts & Altmann 2006; Swedell 2011). Baboons engage in ‘handoff foraging’, characterised by tracking and exploiting fluctuating food sources as they become available (Alberts et al. 2005; van Doorn et al. 2010). ‘Fallback foods’, those that are readily available in the environment but nutritionally poor, can be relied on if higher quality food is not obtainable (Post 1981; Altmann 1998; Alberts et al. 2005; van Doorn et al. 2010; Lambert 2011). In addition, baboons may exploit ‘high return’ foods more during periods of low natural food availability (Dunbar 1983; Forthman-Quick & Demment 1988; Naughton-Treves et al. 1998; Alberts et al. 2005; van Doorn et al. 2010). Anthropogenic food, despite often high risks associated with its acquisition, is an example of this. All of these feeding strategies are evident in baboons and contribute to their ability to maintain a nutritionally balanced diet in diverse habitats (Johnson et al. 2013).

When shifts in foraging behaviour and diet composition mirror fluctuating food availability, resultant changes in ranging behaviour are often seen. In periods of low food resource availability, baboon troops may allocate more time to traveling and exhibit associated home range expansions (Whiten et al. 1987; Barton et al. 1992). Troops that exploit anthropogenic food sources typically travel shorter distances daily and occupy smaller home ranges than naturally foraging troops (Altmann & Muruthi 1988; Strum 2010; Hoffman & O'Riain 2012a). Within home ranges, baboon troops may use specific areas more intensely than others, subject to variation in climatic variables, habitat quality, predator activity, sleeping site availability, and the availability of food and water (Altmann & Altmann 1970; Hamilton 1986; Whiten et al. 1987; Barton et al. 1992; Henzi et al. 1992; Cowlishaw 1997a, 1997b; Zinner et al. 2001; Hill et al. 2003; Higham et al. 2009; Hoffman & O’Riain 2011; Pebsworth et al. 2012). This adjustment of space use resulting from fluctuating ecological and social factors illustrates the profound scope of behavioural and spatial flexibility in baboons.

In addition to diet and spatial adaptability, baboons demonstrate social flexibility. The list of suggested evolutionary agents that have potentially shaped group living in primates is long (Schülke & Ostner 2012). For baboons, one of the most prominent benefits of social living is protection from predation (Hill & Lee 1998; Janson 1998), although group living most certainly also increases access to mates, allows for information sharing, and facilitates food detection (Terborgh & Janson 1986; van Schaik & Hörstermann 1994; Chapman & Chapman 2000; Wilson 2000; Sussman & Garber 2011). Group composition and social structure vary among baboons, most likely as a result of variation in ecological and environmental factors such as habitat quality, resource availability, and predator pressure (Swedell 2011). Regardless of the social system, social bonds are important within baboon troops (Silk 2007). It also appears that individuals understand and monitor the social relationships among other group members, in respect to both the nature and quality of the bond (Cheney & Seyfarth 1992; Tomasello & Call 1997; Bergman et al. 2003; Crockford et al. 2007; Cheney & Seyfarth 2008). Female baboons in particular have been shown to benefit from social bonds, with more socially integrated females displaying enhanced birth rates, personal longevity, and infant survival, as well as reduced competition and lower risk of infanticide (Palombit et al. 1997; Silk et al. 2003, 2009, 2010; Silk 2007; Cheney & Seyfarth 2009; Schülke & Ostner 2012; McFarland et al. 2017). Growing literature suggests that social bonds can also indirectly enhance the fitness of female baboons by reducing chronic stress levels through focused grooming coping mechanisms (Engh et al. 2006; Crockford et al. 2008; Wittig et al. 2008; Cheney & Seyfarth 2009).

It is also important to note that living in social groups increases opportunities for innovation and social transmission of information within troops, as shown in the behavioural and cultural variations across populations (Castro & Toro 2004; Caldwell & Whiten 2011; Fuentes 2011). Social information can be attained easily from other group members, allowing individuals to make more informed decisions regarding their environment (Laland 2004; Dall et al. 2005), which in turn may allow animals to better cope with habitat changes.

The extent to which baboons successfully adjust to sudden and unexpected environmental change can be inferred based on measurable proxies. Glucocorticoid metabolites in faecal samples can be used to measure physiological stress, as they play a crucial role in response to stressors (Norris & Carr 2013). Glucocorticoids mediate the immediate effects of acute stressors by redirecting energy away from non-essential functions (Sapolsky et al. 2000) to increase the availability of glucose (Felig & Frohman 2001) and trigger various features of the immune system (Dhabhar 1998). Increases in glucocorticoid concentrations also elicit the release of oxytocin, which stimulates the desire for social bonding and physical contact (Uvnäs-Moberg 1997), therefore encouraging individuals to take active measures to alleviate the stress (Sapolsky et al. 2000; Goymann & Wingfield 2004; Cheney & Seyfarth 2009). However, persistent stressors can induce deleterious chronic stress responses if homeostasis cannot be reached (Sapolsky 1985, 2004; Sapolsky & Mott 1987; Sapolsky et al. 2000). Numerous environmental and social conditions have been shown to influence glucocorticoid concentrations. Psychological stressors, such as social instability, aggression, threat of infanticide, mother-infant conflict, and coping behaviours, have been shown to increase glucocorticoids in non-human primates (Alberts et al. 1992; Champoux et al. 2001; Beehner et al. 2005; Crockford et al. 2008; Ostner et al. 2008a, 2008b; Wittig et al. 2008). Glucocorticoid production can also be stimulated by metabolic stressors, including injury, temperature extremes, or nutritional stress (Selye 1936; Barton & Whiten 1993; Huber et al. 2003; Foerster & Monfort 2010; Rasooli et al. 2010). Hence, glucocorticoid concentrations can be a physiological indication of the condition of individual animals in regards to exposure to psychological or energetic stressors.

Urinary C-peptide can be used as a biomarker for variation in body condition, nutritional status, and energetic balances (Hoogwerf & Goetz 1983). Because C-peptide is a direct by-product of insulin synthesis and excreted in urine without further processing (Rubenstein et al. 1969), it has proven a reliable indicator for individual energy balance across various non-human primate taxa (see Girard-Buttoz et al. 2011 for summary). High C-peptide concentrations specify a positive energy balance (energy intake exceeds output), whereas a low C-peptide concentration suggests a negative energy balance (energy output exceeds input) (Sherry & Ellison 2007). Periods of food restriction, as well as decreases in body mass, body mass index, and body fat, have all shown decreases in urinary C-peptide secretion for captive (Sherry & Ellison 2007; Deschner et al. 2008) and wild primates (Thompson & Knott 2008; Thompson et al. 2009; Girard-Buttoz et al. 2011). Therefore, C-peptide concentrations can be utilised to explore an individual's variation in energetic and body condition.

The various ecological strategies and physiological adjustments that allow baboons to cope with potentially stressful environmental changes at both population and genus scales suggests that they have been shaped by selection for flexible characteristics driven by environmental change (Strum 1987; Alberts & Altmann 2006). This supports the hominid 'variability selection' hypothesis, which proposes that continuously changing environments of the East African paleo-environment selected for flexible, generalist animals (such as baboons and humans) that could exploit new ecological opportunities when presented with unexpected changes and resource uncertainty (Potts 1996; Potts 1998a, 1998b).

Cape Town's baboon population

Chacma baboons (*Papio ursinus*) are one of the last remaining medium-sized mammals living on the south-western tip of the Western Province of South Africa – the Cape Peninsula. Recent genetic assessments suggest that chacma baboons have lived in the Cape Peninsula for almost 2 million years (Sithaldeen et al. 2015). Today, increasing human population (Statistics South Africa 2017), landscape transformation, and habitat fragmentation (Sinclair-Smith 2009) occur across much of the peninsula. Consequent to the growing human numbers and urban sprawl, the Cape Peninsula baboon population experiences high levels of human-baboon conflict (Hoffman & O'Riain 2011, 2012b; Beamish & O'Riain 2014). All troops within the Cape Peninsula have contact with humans in residential areas or tourist-frequented natural areas (Hoffman 2011). Various methods of management to reduce spatial overlap of humans and baboons are in progress, and include sound aversion, electric fencing, and herding by specialised baboon field rangers (van Doorn 2009; CapeNature 2012; Fehlmann et al. 2017). As a result of vast landscape transformation, many troops on the peninsula reside in severely altered habitats. Here, baboon troops appear to have a propensity for favouring these transformed habitats (Hoffman & O'Riain 2012b). The cultivated pine plantations in the Cape Peninsula offer cool, shaded microclimates, abundant food sources such as pine seeds, and seemingly endless potential sleeping site locations in the upper branches of large exotic trees (Hoffman & O'Riain 2011; Johnson et al. 2013).

It has been shown that the Cape Peninsula's marked seasonal extremes in day length, climate, and natural food availability result in marked seasonal variation in activity budgets and home ranges of local baboons (Davidge 1978a, 1978b; van Doorn et al. 2010; Hoffman & O'Riain 2012a; Lewis & O'Riain 2017). Additionally, physiological biomarkers such as glucocorticoids and C-peptides show discernible seasonal variation in accordance with seasonal fluctuations in availability of natural food items in other baboon populations (Weingrill et al. 2004; Gesquiere et al. 2008; Thompson et al. 2008). These responses to temporal variation in their environment suggest that Cape Peninsula baboons already exhibit ecological flexibility as they cope with extreme seasonal changes.

Fire as an inevitable stochastic event

We are currently experiencing rapid and unpredictable changes across our global climate (Etterson & Shaw 2001; Alley et al. 2003). A worrying complication of these changes is that species are being forced into novel environments that they are ill-adapted to (Friedlingstein 2008; Chen et al. 2011; Sih et al. 2011). Stochastic events such as natural disasters, which are predicted to increase in the future due to climatic change (IPCC 2014), will only exacerbate this mismatch of species' evolutionary adaptations and current environment.

Fire has been shaping the Earth's atmospheric and terrestrial systems for millions of years (Scott 2000; Bowman et al. 2009; He et al. 2016). However, today wildfires are the product of both natural and anthropogenic sources. Although fire can play an essential ecological role (Keywood et al. 2013), its dynamic nature also poses a potential threat to wildlife and society (Bowman et al. 2011; Moritz et al. 2014). Wildfires have become a bigger threat in recent decades, as many parts of the world have experienced longer fire seasons (Pechony & Shindell 2010; Jolly et al. 2015) and higher large-wildfire frequencies since the 1960's (Aravena et al. 2003; Gillett et al. 2004; Pausas 2004; Westerling et al. 2006). Wildfires are influenced by the weather, available fuel, and the landscape (Moritz et al. 2005; Whitlock et al. 2010), with weather being the most important driver at regional scales (Bessie & Johnson 1995; Littell et al. 2009; Abatzoglou & Kolden 2013). Currently, we are faced with rising global temperatures (Hansen et al. 2010; IPCC 2014) and more extreme weather patterns (Meehl et al. 2000; Mitchell et al. 2006; IPCC 2014), including severe and widespread droughts (Dai 2013). Climatic change models predict a generally warmer and drier climate (Liu et al. 2010; de Groot et al. 2013; Flannigan et al. 2013) – conditions that are favourable for an increase in both the occurrence and intensity of fires (Pechony & Shindell 2010; Carvalho et al. 2011).

Although global reports show significant fire season lengthening in many areas of the world, Mediterranean forests, woodlands, and scrublands are being particularly targeted (Wilson et al. 2010; Jolly et al. 2015). Mediterranean-type ecosystems (MTEs) are characterised by fire-prone vegetation and experience wet, cool winters and dry, warm summers. MTEs occur along the west coast of North America, central Chile in western South America, the Mediterranean basin, southern and western Australia, and the southwest region of South Africa (Dallman 1998; Olson et al. 2001). Notably, wildfire frequencies have increased significantly in most of these areas (Piñol et al. 1998; Aravena et al. 2003; Gillett et al. 2004; Pausas 2004; Westerling et al. 2006). It has been shown that climatic control on fire occurrence in these areas lies close to 'tipping points' and they are extremely sensitive to change (Batllori et al. 2013). Specifically in southwest South Africa, fire potential is projected to increase within its Mediterranean biome (locally recognised as the fynbos biome (Rebelo et al. 2006; Underwood et al. 2009)) through the end of the century, with high levels of agreement between climate models (Liu et al. 2010; Moritz et al. 2012).

That being said, fire is an important ecological process for fynbos vegetation (van Wilgen & Forsyth 1992; Cowling et al. 1996). Along with summer drought, infertile soils, and strong winds, wildfires every 15-20 years drive the ecological patterns and processes of the Cape Peninsula (van Wilgen 1982; Kruger & Bigalke 1984; Cowling et al. 1996). Like many other plant communities in fire-prone environments globally (Dixon et al. 1995; Keeley & Fotheringham 1997), most fynbos germination is stimulated by smoke-related chemical cues from burning vegetation (de Lange & Boucher 1990; Brown 1993), resulting in high seedling establishment following burns (van Wilgen & Forsyth 1992). Thus, the fynbos of the Cape Peninsula is well adapted to, and in fact depends on, periodic fires (Bond & van Wilgen 1996).

However, fire frequency has increased significantly on the Cape Peninsula since the 1970's (Forsyth & van Wilgen 2008; van Wilgen 2009, 2013). Although most fires within this period were recorded as having unknown origins, they are almost certainly generated by humans (Forsyth & van Wilgen 2008). Today, wildfires in the Cape Town area are mostly initiated by human negligence and arson (Western Cape Government, 2017; WoF 2018). To exacerbate the situation, high fuel loads are provided by exotic vegetation such as *Acacia* spp., *Eucalyptus* spp., and *Pinus* spp. in the area (Richardson & Brown 1986; van Wilgen 2009; WoF 2018). While many species of fynbos vegetation are fire-resilient (van Wilgen & Forsyth 1992), not all are; many iconic *Protea* spp. (Kruger & Lamb 1979; van Wilgen 1982) and threatened *Erica* spp. are adversely affected by frequent burning (Richardson et al. 1996; Forsyth & van Wilgen 2008).

As with the Cape Peninsula flora, local animals are negatively impacted by fires to varying degrees. Wildfires can adversely affect wildlife both directly, through injuries, and indirectly with the rapid change in above ground biomass (Kraaij & van Wilgen 2014). Direct fire mortality, although not common for most animals, is frequently seen in tortoises in the peninsula (Stuart & Meakin 1983). While species richness may not be affected, bird composition does shift depending on the intensity of fynbos damage, as many nectarivores require mature vegetation (Fraser 1989). Small mammals such as rodents show population declines, but typically return to pre-fire abundances six months to two years after the fire (Fraser 1990; Midgley & Clayton 1990). Interestingly, instead of migrating out of the area small mammals typically remain in their home range and utilise small unburnt patches in the landscape (Midgley & Clayton 1990). Thus while local wildlife may be able to cope with fire as an ecological process, the frequency and intensity of the current fire regime presents novel challenges.

The Muizenberg Fire and the Tokai troop

On 2 March 2015, a fire was ignited on the fynbos-dominated Muizenberg Mountains of the Cape Peninsula. For the next six days, through gale force winds and record-breaking temperature highs, the Muizenberg Fire burned 5 120 hectares across the centre of the peninsula (Golby 2015). Homes, hotels, businesses, roads, and popular recreational areas were damaged or destroyed by the fire. In addition to the urban damage, wildlife was also affected. Tortoises, rodents, porcupines, and small antelope are just a few examples of animals that were killed by the fire. Four baboon troops came face to face with the flames, causing troop members to flee into the trees in response to the approaching fire. The flames proceeded to trap troop members in the canopy, resulting in 12 baboon deaths (18% of the troop) and at least 12 burn injuries (E. Beamish, unpublished data). The Tokai area, where the troops reside, suffered significant habitat alteration, with the ground transformed to an ashy powder, and although most large trees were left standing, significant bark charring and canopy destruction had occurred. For weeks afterwards, smoke rose from ground crevices, signifying the considerable damage to the root systems of standing trees. Public concern for the welfare of the wildlife included calls to establish feeding stations to combat potential food shortages. Wildlife management agencies urged against this out of concern that it would encourage reliance on human-derived food resources (O'Riain, personal communication). At the time, managers were not certain, however, that there was enough food and hence baboon rangers carefully monitored the troops' behaviour to infer whether they were foraging successfully.

One of the troops that sustained fire-induced injuries, mortality, and habitat loss was the Tokai troop. Perhaps one of the best-studied troops in the Cape Peninsula population (Hoffman 2011; Hoffman & O'Riain 2011; Johnson et al. 2013), the Tokai troop had been subject to years of behavioural observation as part of the Tokai Baboon Sociality Project. The project aimed to examine the relationship between social bonds and measures of both health and reproductive success in the troop. Data collection included focal follows, instantaneous scans, ad libitum data, and GPS positions of the troop, as well as faecal and urine samples. The fire necessitated a 31-day break in data collection due to safety concerns, following which data collection continued using the same protocols. Thus although these data were not collected for the purposes of understanding how fire impacts baboon behavioural and spatial ecology, they clearly can be used to assess how fire impacts baboon ecology using a before and after approach. Although many baboon troops have been studied in the Cape Peninsula (Hall 1962; Brown 1964; Davidge 1978a, 1978b; van Doorn et al. 2010; Hurn 2011; Kaplan et al. 2011; Drewe et al. 2012; Hoffman & O'Riain 2012a, 2012b, 2012c; Beamish & O'Riain 2014; Fehlmann et al. 2017; Lewis & O'Riain 2017), and primate ecological flexibility has been widely documented (Jones 2006; Campbell et al. 2011; Mitani et al. 2012), nothing to my knowledge has been recorded on the behavioural and physiological responses to a large scale stochastic event such as a fire.

Objectives, hypotheses, and rationale

The aim of this study is to use an existing data set to assess how baboons responded, behaviourally and physiologically, to an extensive fire. I compared home range use, activity budgets, faecal glucocorticoid concentrations, and urinary C-peptide concentrations three months after the fire (with data collection beginning 25 days after the fire was extinguished; referred to as "post-fire") to the same three months in the previous year (referred to as "year prior"). These timeframes were chosen in an attempt to control for seasonal effects on behaviour and physiological biomarkers since, as previously discussed (see 'Cape Town's baboon population'), extreme seasonal shifts in natural food availability, day length and weather have been shown to significantly impact baboon troops on the Cape Peninsula (Davidge 1978a, 1978b; van Doorn et al. 2010; Hoffman & O'Riain 2012a; Lewis & O'Riain 2017). Therefore, a comparison of data from the summer months directly before the fire (December, January, and February) to the autumn/winter months directly after the fire (April, May, and June) would be unsound for this study troop. It should be noted that any yearly variation in temperature and precipitation remains a limitation of this study; however, this potential impact is still not as impactful as the variation in temperature and precipitation between summer (directly before the fire) and autumn/winter (directly after the fire).

Based on our current knowledge of how a large scale reduction in food availability would influence ranging behaviour and activity budgets I predicted that after the fire the: 1) home range would shift to areas not previously used and home range size would increase in size (Hoffman & O'Riain 2011, 2012a; Lewis & O'Riain 2017) and 2) percentage time spent travelling and socialising would increase while time spent resting and feeding would decrease (Dunbar & Sharman 1984; Dunbar 1992; Alberts et al. 2005; Engh et al. 2006; Silk et al. 2006a, 2006b; Silk 2007). Using our current knowledge of how primates in general and baboons in particular respond to traumatic events and reduced food availability I predicted that after the fire: 3) mean glucocorticoid concentrations would increase (Champoux et al. 2001; Engh et al. 2006; Crockford et al. 2008; Gesquiere et al. 2008; Wittig et al. 2008); and lastly 4) mean C-peptide concentrations would decrease (Thompson & Knott 2008; Thompson et al. 2009; Girard-Buttoz et al. 2011; Lodge 2012).

This study capitalises on a unique opportunity to explore the impact of a sudden environmental disaster on baboons by using the fine-scale behavioural and physiological data collected as part of an ongoing long-term research project on baboon sociality. The significance of the insights gained from this study is twofold. Firstly, by identifying and quantifying behavioural and physiological differences after the fire compared to the year prior, I make a significant contribution to our understanding of how wild baboons responded to a sudden distressing event. Secondly, findings from this study are valuable in the future management of baboon troops affected by environmental disasters. As formerly outlined, fire is an unavoidable natural process that is predicted to become more impactful globally and locally due to climatic and anthropogenic factors. In Cape Town's fire-prone environment, where baboon troops are intensively managed, it would be especially advantageous for conservation bodies and management entities to understand how fire affects baboon behaviour and physiology, as well as the behavioural and spatial modifications that baboons make to cope with these changes.

Methods

Study site

The Cape Peninsula is located in the south-western most corner of South Africa (Figure 1). The region's Mediterranean climate is marked by warm, dry summers and cool, wet winters (Kruger 1979), generating higher levels of primary productivity in winter than summer (Cowling et al. 1996). The peninsula is known for its roughly 50 km-long mountainous spine, most of which falls within Table Mountain National Park (TMNP) – a protected area managed by local conservation authorities. The Cape Peninsula is part of the Cape Floristic Region, a biodiversity hotspot of global significance (Mittermeier et al. 1998; Myers et al. 2000). The Cape Floristic Region is dominated by fynbos, an endemic, species-rich vegetation type (Simmons & Cowling 1996). Living on acidic and nutrient-poor soils (Rebelo et al. 2006), the small-leaved evergreen shrubs that distinguish many fynbos communities provide low-quality forage for generalist herbivores (Campbell 1986; Glyphis & Puttick 1988; Coetzee et al. 1997). As a result, animal species diversity is moderate with few endemic mammal species (Fraser 1994; Picker & Samways 1996). Since the early 1900's there have been no natural predators of baboons on the Cape Peninsula (Skead 1980; Stuart et al. 1985), with humans responsible for most injuries and deaths (Beamish & O'Riain 2014).

The study troop resides within the Tokai Forest section of the TMNP (34°03'17 S, 18°23'59 E), which during the study period was dominated by exotic pine and eucalyptus plantations (Hoffman & O'Riain 2011). The Tokai Forest area receives 1 000 to 1 500 mm annually, with a mean annual temperature ranging from 18 °C to 20 °C (Cowling et al. 1996). Elevation in the study site spans 90 to 540 m above sea level. Higher elevations (>250m) are largely comprised of indigenous fynbos vegetation, while lower elevations are urbanised. The mid-elevation mountainside is covered almost exclusively by alien vegetation, including a historic arboretum of exotic plants (mostly *Eucalyptus* spp., and *Quercus* spp.), commercial plantations of mature pine trees (*Pinus radiata*) and eucalyptus (*Eucalyptus* spp.), and private vineyards. Horse riding, cycling, and hiking are all permitted in Tokai Forest, and consequently baboons are frequently exposed to diverse human activities. Intermittent commercial harvesting of pine plantations within small patches of the study site began in 2007 and was ongoing during the study (see TMNP 2009, 2011 for more information).

During the last year of the study the Muizenberg Fire (see above) engulfed the study site from 2 to 4 March 2015 (Golby 2015; Figure 2). Within the study site, multiple man-made structures were destroyed, and most vegetation was affected. Small fires continued to smoulder throughout the area for months after the initial burn. Many unpredictable tree-falls occurred in the weeks following the fire due to significant root damage. The area was closed to the public for health and safety reasons and to minimise ecological impacts associated with human activities (TMNP 2015). Harvesting of burnt pine trees became a priority, and thus harvesting effort increased in the months following the fire with large numbers of workers, heavy machinery and trucks entering the area each day.

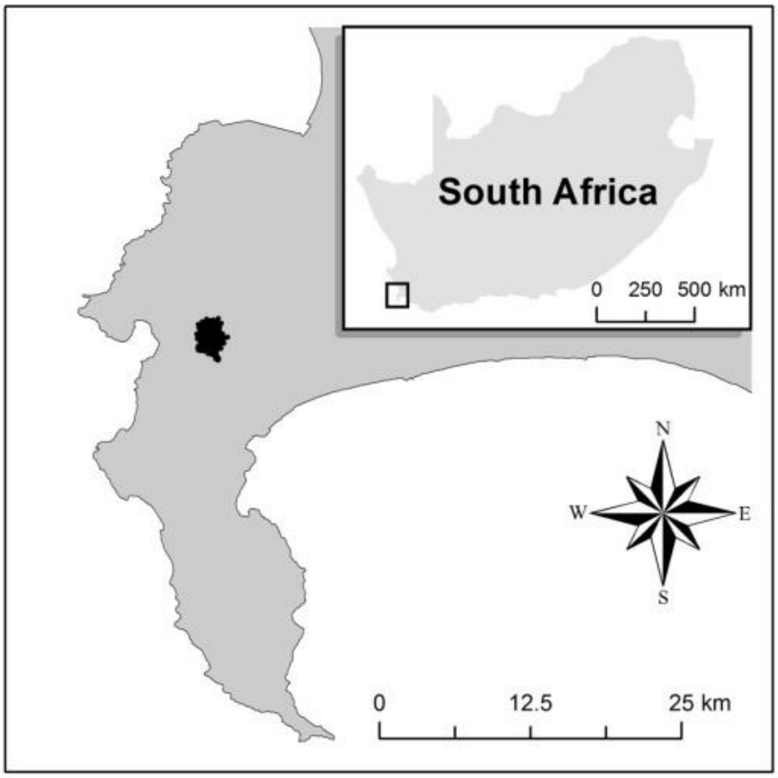

Figure 1. Map of the Cape Peninsula, with study site location shown.

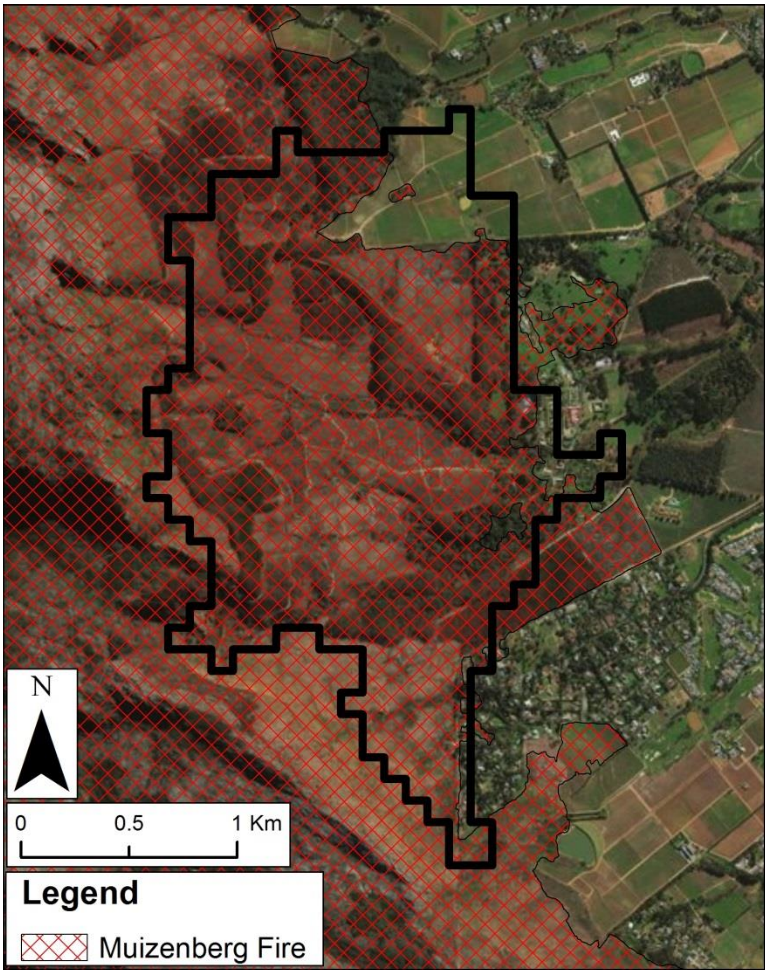

Figure 2. Map of the Tokai Forest area, showing the area burned by the Muizenberg Fire. The black outline indicates the study troop's total home range across both post-fire and year prior sampling periods.

Study subjects

The study troop, known as the Tokai or MT1 troop, was one of four troops in the Tokai area (Richardson 2014; Chowdhury & Swedell 2016; E. Beamish, personal communication). During the study period the year before the fire, the troop comprised approximately 65 individuals (E. Beamish, unpublished data), including 22 adult females and 5 adult males. The Muizenberg Fire resulted in the death of 12 baboons within the troop: four adult females and eight subadults or juveniles. Only adult female baboons were included in these analyses, as this was the only category for which there were detailed behavioural data. The study troop exclusively sleeps in the abundant exotic eucalyptus and pine trees found throughout the area. Due to frequent interactions with recreational users of Tokai Forest, all baboons in the troop were well-habituated to human presence (<10 m distance) prior to the onset of the study. There was no discernible effect of researcher presence on the behaviour of the baboons.

Because of proximity to suburban properties, picnic sites, school campuses, and commercial areas, troops in the Tokai area are actively herded away from the urban edge by baboon field rangers (Kansky & Gaynor 2000; Hoffman & O'Riain 2012a, 2012c; Fehlmann et al. 2017). Shouting, chasing, and the shooting of paintball guns are all used as deterrents (CapeNature 2012; Richardson 2012). Living in the peri-urban environment, the troop does occasionally gain access to anthropogenic food sources, including crops (grapes and barley within vineyards), waste in rubbish bins, fruiting trees in domestic gardens, animal feed on small holdings, and a variety of human-derived foods within houses (van Doorn et al. 2010; Hoffman & O'Riain 2011; Kaplan et al. 2011; Johnson et al. 2013; Fehlmann et al. 2017).

Data collection

Data were collected by the Baboon Sociality Project from August 2012 to June 2015, however the focus of the project during the first two years was not aligned with the interests of this study. Therefore, a subset of the project data is used in this study, containing only data from 2014 and 2015 (for more details see "Data analyses" section). The Muizenberg Fire caused the suspension of data collection from the 1st of March to the 1st of April 2015. Data collection terminated at the end of June 2015 in accordance with the conditions of the research permit. Consequently, only 3 months of post-fire data were collected.

Data collection included locating the troop at their sleeping site every morning and following them for 8.3 ± 3.2 hours or until visual contact with the troop was lost for more than two hours. Most of the study area was easily traversable on foot and visibility was generally adequate for the purposes of behavioural observations. Behavioural and hormonal data were collected on individually identifiable adult female baboons, while spatial data were recorded for the troop as a whole. All research methods used were approved by the Queens College and Duke University Institutional Animal Care and Use Committees, as well as South African National Parks (SANParks; permit: CRC/2015/001-2010) and CapeNature (permit: AAA007-00090-0056).

Spatial data

Troop ranging patterns were recorded by noting geographic coordinates of the troop position every 60 minutes or when the troop had travelled a minimum of 200 meters from the previous recording. The troop position was visually estimated as the geometric centre of the troop spread (as per Hoffman & O'Riain 2011). Coordinates were recorded by placing a location marker on the Google Maps application on observers' tablets (Google 2014).

Focal follows

Focal follows were conducted using the behavioural recording programme Noldus Pocket Observer (Eckhardt & Waterman 2004) on a Nexus 7 tablet. We followed focal females at a distance of 10-20 meters and recorded behavioural states during 15-minute continuous focal observations. Behaviours were defined according to a predetermined ethogram which included eight behavioural states: moving, stationary, feeding, foraging, resting in contact, grooming self, and grooming with another (see Appendix 1 for general definitions). Focal follows were paused when clear observations of the female could not be made, and resumed as soon as adequate visual contact was regained. Focal follows paused for longer than 15 minutes were abandoned.

A random list generator was used to determine the order in which to observe females each day. The list was then divided randomly between all observers to reduce observer bias. Observers aimed to complete their list in the exact order prescribed; however, if the next specified female could not be located within ~15 minutes, the observer continued onto the next female on the list, ideally completing the skipped individual as soon as possible thereafter. If the list was completed before the end of the day, a second randomized list was produced. Completed focals were tallied weekly to ensure equal sampling effort for all females each month.

Inter-observer reliability (IOR) tests were performed at regular intervals to ensure consistency of behaviour coding and timing, and reduce the possible effects of observer bias. New observers were required to achieve an accepted error level of <10% over at least 10 focal follows before recording data. Errors of up to 10 seconds were not flagged as disagreements when calculating agreement scores.

Faecal collection and processing

Faecal samples from adult female baboons were collected opportunistically in plastic bags. Samples were collected after the individual had moved away from the defecation location. Faecal samples contaminated with urine were not used, as urine contains much higher concentrations of metabolites (Bahr et al. 2000). As with behavioural samples, the aim was to acquire equal numbers of samples from all females each month.

Immediately after collecting the faecal matter it was kneaded for approximately one minute to achieve a homogeneous paste (as per Beehner & Whitten 2004). To avoid bacterial growth, samples were processed as follows no longer than five hours after collection. Faecal matter was dried in an oven (at 100 °C for ~3.5 hours), then ground into a fine powder by rubbing it between two metal sieves. The powder was subsequently stored in a freezer in airtight plastic tubes with silica beads (as per Beehner & Whitten 2004).

The preserved samples were exported to the Smithsonian Conservation Biology Institute's Endocrine Research Laboratory in Front Royal, Virginia, USA. In the lab, faecal GC metabolites were extracted from 0.20 ± 0.02 g of faecal powder (as described by Foerster and Monfort 2010). A ^{125}I double-antibody radioimmunoassay (MP Biomedicals, Orangeburg, NY, USA) was performed to quantify GCs (as described by Wasser et al. 2000). This process has been successfully used for a wide range of non-human primates (Wasser et al. 2000; Heistermann et al. 2006; Beehner & McCann 2008; Gesquiere et al. 2008), including chacma baboons (Crockford et al. 2008). The antiserum cross-reacts 100% with corticosterone, 0.34% with desoxycorticosterone, 0.10% with testosterone, 0.05% with cortisol, 0.03% with aldosterone, 0.02% with progesterone, 0.01% with rostenedione, and 0.01% with 5α-dihydrotestosterone.

Urine collection and processing

Urine samples from adult female baboons were collected opportunistically with modified insect net poles wrapped with plastic bags when the individuals were in their sleeping trees in the mornings, or alternatively, pipetted off rocks or leaves after an individual had moved away from a urination location. Urine samples contaminated with faeces were not used, as faecal matter significantly decreases C-peptide levels (Higham et al. 2011). The aim, again, was to acquire equal numbers of samples from all females each month.

About 2 ml of urine was collected in a plastic sample tube, and immediately placed in a storage vial with ice for the remainder of the field session (but no longer than 12 hours, as per Higham et al. 2011). Sample tubes were later stored in the freezer until transport on dry ice no more than six months later (as per Higham et al. 2011) to the Smithsonian Conservation Biology Institute in Front Royal, Virginia, USA.

At the lab, the samples were lyophilized for long-term storage. Urinary CPs were quantified using a commercially available C-Peptide ELISA kit (IBL International GmbH, Hamburg, Germany). To control for differences in urine concentration, the urinary CPs were indexed to urinary creatinine (Cr) and expressed as ng C-Peptide/mg Cr (as in Bahr et al. 2000, Girard-Buttoz et al. 2011).

Data analyses

Well-documented seasonal differences in the behaviour and movement patterns of Cape Peninsula troops reduce the utility of comparisons of months directly before (summer) and after (autumn/winter) the Muizenberg Fire (Davidge 1978a, 1978b; van Doorn et al. 2010; Hoffman & O'Riain 2011; Lewis & O'Riain 2017). Further, since baboons engage in different behaviours throughout the day, with resting and social grooming behaviours biased toward the beginning and end of each day (Hall 1962; Altmann & Altmann 1970; Davidge 1978a; van Doorn 2009), and data collection frequently ended around 15:00, seasonal changes in day length would generate diurnal behaviour biases that would prohibit sound comparisons across seasons (Hill et al. 2003, 2004). Therefore, to alleviate this seasonal confounding, I compared the same 16 adult females in the same months (April, May, and June) in the year before (2014) and the year of (2015; post-fire) the Muizenberg Fire. I considered these comparisons to be the best option given the data available and the massive impact of seasonality for this troop.

Data analysed in this study were collected by 13 observers and were recorded for 88 days from 1 April 2014 to 30 June 2014, and 87 days from 1 April 2015 to 30 June 2015. All statistical analyses were conducted in R, version 3.2.5 (R Core Team 2016). In cases where the assumptions of data normality and homoscedasticity were not met, nonparametric tests were used to determine differences between post-fire and the year prior data.

Home range & spatial use

GPS points indicating troop location (post-fire: n = 287; year prior: n = 302) were mapped within the study area, and straight travel paths were assumed between consecutive points. All GPS coordinates were converted into decimal degrees and rounded to 9 decimal places before being imported into ArcGIS Desktop (version 10.4; ESRI 2016) and projected into WGS 1984, UTM Zone 34S. GPS data points that were recorded less than 60 minutes apart were excluded from analyses.

The troop's home range and areas used during the post-fire and year prior sampling periods were determined following methods previously used for Peninsula troops (Hoffman & O'Riain 2011; Lewis & O'Riain 2017): a grid was superimposed over the study area to examine the potential influence of environmental factors on cell use frequency. The Repeating Shapes extension in ArcGIS (Jenness 2012) was used to position the grid of 100 x 100 meter cells over the study area (Hoffman & O'Riain 2011). The grid was then cropped along any impenetrable borders of the area (e.g. electrified fences).

Home ranges were estimated by including: entered cells; cells completely enclosed by entered cells; cells that were bordered on three sides by entered cells; and cells that were bordered on two opposite sides by entered cells. Entered cells included cells that contained GPS points or travel paths. These criteria were based on those used for previous studies of Peninsula baboon home ranges (Hoffman & O'Riain 2011; Lewis & O'Riain 2017). The cell accumulation curve for the estimated home range plateaued in week 11 for both post-fire and year prior periods, suggesting that our effort provided a reliable estimate of the area used by the troop per sample period (Figure 3). For modelling of cell use drivers, cell use was defined as the number of GPS points in each cell. To control for the smaller area within cropped cells the observed frequency of cell use (Obs_i) was adjusted by the area of the cell ($Area_i$; in m^2) using the formula:

$$Adj_i = Obs_i \div Area_i \times 10000$$

where Adj_i is the adjusted frequency for cell i. Adj_i was then rounded to the nearest whole number.

Environmental variables known to influence baboon spatial use were assessed per grid cell (as in Hoffman & O'Riain 2011, 2012a; Lewis & O'Riain 2017), using the "Spatial Join" analysis tool in ArcGIS. Variables included distance to sleeping sites, distance to freshwater sources, distance to the urban edge, elevation, slope, habitat type, and for the post-fire sampling period, percent of cell that was burned (Figure 4). All distances were measured in ArcGIS using Euclidean distance, and were calculated from the middle of the cell (using the "Feature to Point" data management tool) to the nearest feature of the variable in question (using the "Near" analysis tool). Sleeping site locations were determined by the first GPS points of each day, with the post-fire and year prior sampling periods analysed separately due to differences in used sleeping sites for each period. Freshwater sources included all watercourses and dams in the area including small non-perennial streams detected during data collection (modified from CoCT 2017a). The urban edge was marked according to satellite imagery. Elevation and slope were derived from a 10-meter digital elevation model (CoCT 2017b) and recorded per cell as the average elevation/slope by first using the "Raster to Point" conversion tool, and later specifying for mean value in the "Spatial Join" tool. Due to difficulties in obtaining habitat data at the correct scale, I created my own habitat shapefile based on personal knowledge of the study area using roads and paths seen on satellite imagery as reference points. Habitats included pine plantation, cleared plantation, eucalyptus plantation, grassland, shrubland, mixed other (including mainly mixed forest and riparian thicket), urban, and vineyard. Each cell within the home range was assigned habitat based on the vegetation that comprised the majority of the cell. Post-fire cells were assessed for the 'percentage of cell burned' which was calculated from a fire scar shapefile (SANParks 2017) using the "Identity" analysis tool, the "Calculate Geometry" and "Field Calculator" options of the attribute table, and the "Join" tool.

The environmental variables were assessed for multicollinearity using a Pearson's correlation matrix using the "Hmisc" R package (Harrell & Dupont 2008). Variables with correlation coefficients ($|r|$) > 0.7 were defined as collinear (Dormann et al. 2013). Elevation, slope, and distance to urban edge were all collinear for my study site (Appendix 2). Therefore, a principal component analysis (PCA) was performed with the "ade4" and "factoextra" R packages (Chessel et al. 2004; Kassambara & Mundt 2016, respectively) to derive an uncorrelated index using the three variables as loadings (Dormann et al. 2013). All three variables were log transformed prior to the PCA to correct non-normal distributions. The resultant index was characterized by the Principal Components of the PCA and considered as potential variables for inclusion in the cell use models.

The three principal components (PC1, PC2, and PC3) generated through the PCA carried 83%, 12.3% and 4% of the total inertia, respectively (Appendix 3). Therefore only PC1, which explained most of the variation, was retained. The relative contribution of the three environmental variables to PC1 was relatively even and going in the same direction, indicating that an increase in one of the covariates is associated with a similar increase in the other two (Appendix 3). In this case, it shows that higher elevations has steeper slopes, and are located farther away from the urban edge.

Sparse Spatial Generalised Linear Mixed Models (SGLMMs) using the "ngspatial" R package (version 1.2-1; Hughes & Xiaohui 2018) were used to examine the post-fire and year prior relationships between home range cell use frequency and environmental variables. The sparse SGLMM is an extension of the generalized linear model (GLM), and accounts for the spatial confounding of areal data through Moran eigenvectors that incorporate spatial autocorrelation patterns (Hughes & Haran 2013). The frequency of cell use for both post-fire and year prior periods was found to have a negative binomial distribution using the "fitdistrplus" R package (Delignette-Muller et al. 2014; Appendices 4-5). Therefore, the SGLMMs were run specifying a negative binomial distribution for the response variable – a newly added feature of the ngspatial package. For both post-fire and year prior SGLMMs, the default setting (q = 50) was used for the number of Moran eigenvectors (Hughes & Xiaohui 2018), and a Moran's I test was used through the "spdep" R package (Bivand & Piras 2015) to test for spatial autocorrelation. Both the post-fire and year prior SGLMMs showed no significant spatial autocorrelation in the residuals (*p* > 0.2 in each case). Numbers of model iterations were increased as needed in order to achieve Monte Carlo standard error-to-estimate ratios indicative of model convergence for all predictor variables (Jones et al. 2006, Hughes & Xiaohui 2018). All environmental variables used were standardised before running the model to allow for direct comparison of effect sizes of predictor variables.

Multiple models were analysed to determine which collinear predictor variables (elevation, slope, and distance to urban edge), or principal components incorporating these, produced the best model when all other variables were held constant. These models, which included all non-correlated predictor variables and one of the correlated predictor variables to be tested, were compared using Deviance Information Criterion (DIC) values. Ultimately, final SGLMMs were run to test which environmental factors best explained the variation in use of home range cells. Predictor variables with highest posterior density intervals that contained 0 were then removed, as their estimate could not be confidently resolved.

Final SGLMMs were run using PC1 (encompassing elevation, slope, and distance to urban edge) instead of a single representative variable to facilitate our interpretation of baboon habitat choice. However, model testing proved that using any one of the collinear variables, or PC1, resulted in similar model fits (Appendix 6). PC1 was selected because it represented all three environmental variables without impairing model structure. Distance to water was removed from both post-fire and year prior models, as its highest posterior density intervals contained 0 in both cases.

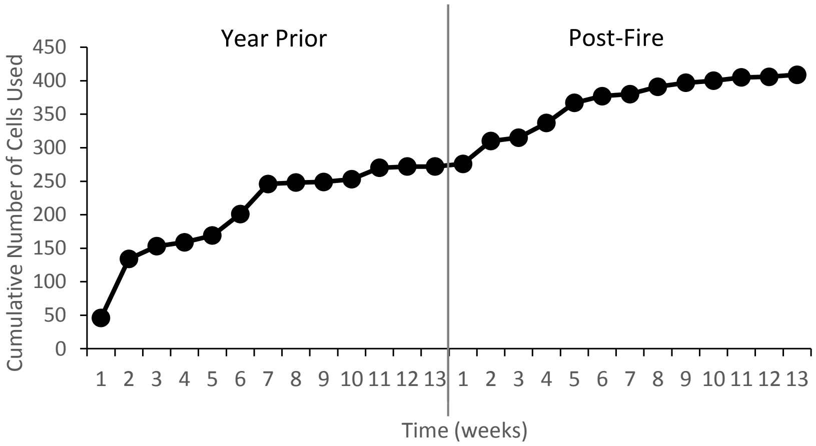

Figure 3. Cumulative number of grid cells used by the Tokai troop after each week of the year prior and post-fire sampling periods.

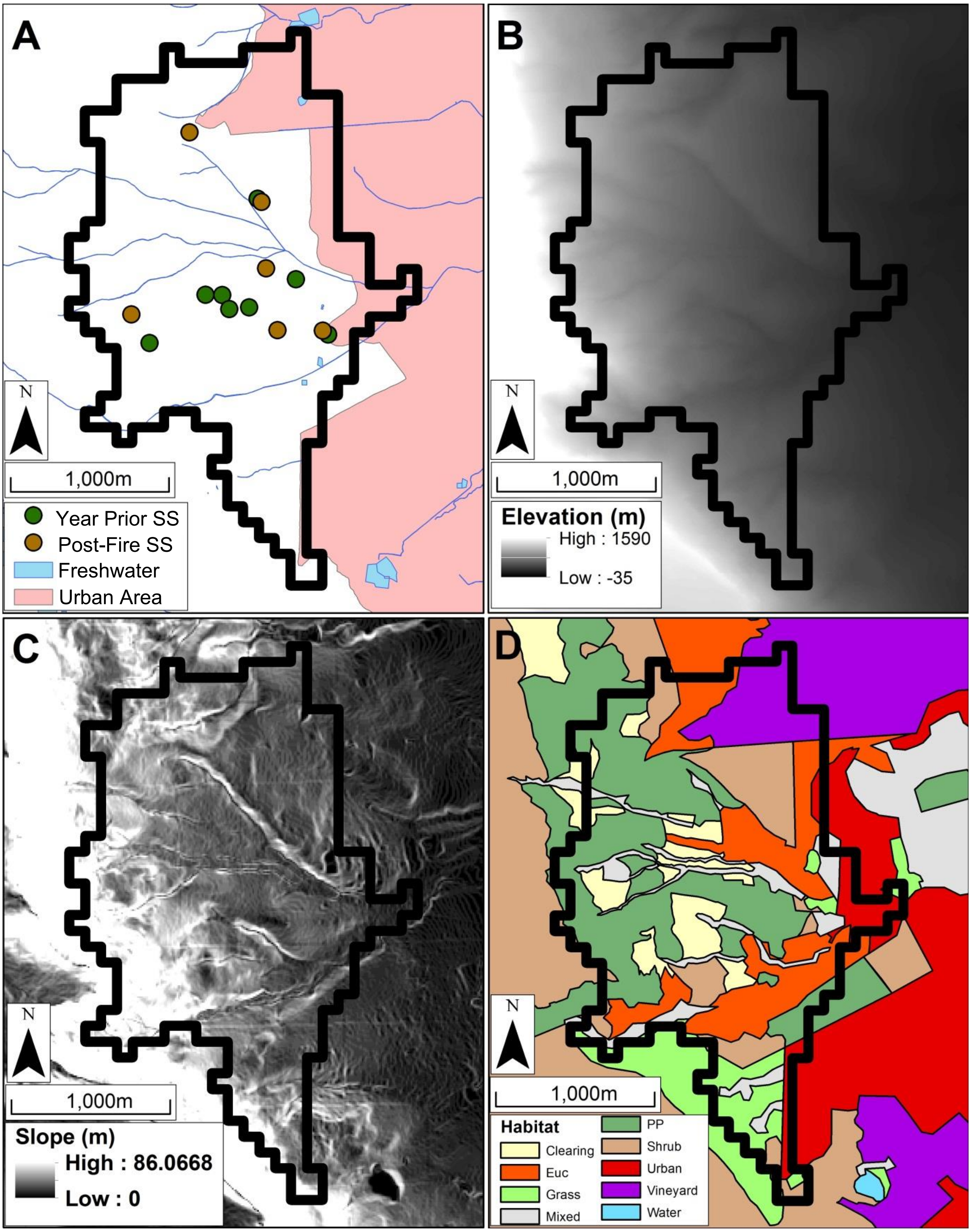

Figure 4. Maps showing the environmental variables used as predictor variables in the sparse SGLMM: sleeping sites ("SS"), freshwater sources, and urban area (A); elevation (B); slope (C); and habitat type (D; with "Clearing" indicating cleared plantation, "Euc" indicating Eucalyptus plantation, "Grass" indicating grassland, "Mixed" indicating mixed other, "PP" indicating pine plantation, and "Shrub" indicating shrubland). The black outline indicates the total home range across both post-fire and year prior sampling periods.

Activity budget

Behavioural observations used in this study (total hours post-fire: *n* = 181; total hours year prior: *n* = 123) equated to approximately 11 ± 1 (SD) hours per adult female during the post-fire period and 8 ± 1 (SD) hours during the year prior. Behavioural states were combined into four main categories: moving, resting, feeding, and social behaviour, as these activities are known to constitute >95% of baboon time budgets (Dunbar 1992). Moving included traveling by walking, running, and/or climbing. Resting included stationary states (i.e., standing, sitting, or lying) as well as self-grooming. Feeding included foraging (actively searching for food using hands) and consuming food (handling and masticating food items). Lastly, social behaviour included grooming and resting in contact with another adult.

Thus for each female, proportion of time per category was determined for post-fire and year prior periods by dividing time spent per category by total time observed. The overall proportion of time engaged in each category per female (Obs_{prop}) was calculated by:

$$Obs_{prop} = (Obs_F + \ldots + Obs_F) \div Obs_{Total}$$

where Obs_F is the observed time (in seconds) the female spent performing behaviours in the category, and Obs_{Total} is the total observed time (in seconds) of the female for all behaviour categories.

To reveal changes in behaviours, methods were followed from previous studies on similar troops (van Doorn et al. 2010; Lewis & O'Riain 2017). Wilcoxon paired tests were performed to compare the proportion of time spent engaged in a behaviour category post-fire and year prior using the "stats" R package (R Core Team 2016). Holm corrections were applied to p-values (Holm 1979) to adjust for multiple comparisons, as a test was completed for each behaviour category. Although activities within the activity budget are not independent of each other (for instance, more time spent on one category inadvertently means less time is available to be spent on the other categories), the comparison of the same behaviour category between sampling periods are independent.

Faecal glucocorticoid and urinary C-peptide concentrations

Faecal samples used (total post-fire: *n* = 419; total year prior: *n* = 388) averaged to 26 ± 7 (S.D.; range: 14 – 42) samples per adult female post-fire, and 19 ± 3 (S.D.; range: 13 – 23) samples per adult female for the year prior. Urine samples used (total post-fire: n = 55; total year prior: n = 53) averaged to 3 ± 2 (S.D.; range: 0 – 7) samples per adult female post-fire, and 3 ± 2 (S.D.; range: 1 – 6) samples per adult female for the year prior. Glucocorticoid concentrations and C-peptide concentrations were averaged for each female over the post-fire and year prior periods. A Wilcoxon paired test was performed using the “stats” R package (R Core Team 2016) to determine differences between the post-fire and year prior concentrations.

Results

Home range & spatial use

From both post-fire and year prior GPS locations I calculated a total home range of 4.04 km^2, with 1.32 km^2 of the range used exclusively post fire (Figure 5). During the year prior sampling period the group's range spanned 2.72 km^2 while post fire the troop used 3.71 km^2, an increase of 0.99 km^2. When controlling for troop size, which decreased during the fire, this resulted in an increase in area used per capita – year prior and post-fire values were 0.04 km^2 and 0.06 km^2 used per baboon, respectively. The extent of spatial overlap between the two periods was 2.39 km^2. Year prior cell use frequency varied from 0 to 30 GPS points per cell, with 90.9% of cells (n = 250) containing fewer than 3 points per cell (Figure 5). Post fire, the cell use frequency varied from 0 to 12 GPS points per cell, with 93.0% of cells (n = 347) containing fewer than 3 points per cell (Figure 5). In the year before the fire, the troop utilised eight distinct sleeping sites – four of which were in close proximity to each other (shown in Figure 4A). Six sleeping sites, including this cluster of four, were completely destroyed in the fire. After the fire, the remaining two sites continued to be used and four new sites were added, resulting in six total sleeping sites used (shown in Figure 4A).

The final SGLMMs performed well, as there were strong correlations between observed and predicted values generated for both post-fire and year prior cell use (Table 1). This indicates that the fitted values from the SGLMMs, and the ranks of these fitted values, were similar to the observed values (Potts & Elith 2006).

The model output for the year before the fire indicated that, during this time, cell use frequency was highest at lower elevations, milder slopes, and closer to the urban edge (all variables incorporated within PC1), while cell use frequency decreased with increasing distance to the nearest sleeping site (Table 2). Also, cells dominated by grassland habitat had higher cell use frequencies than cells dominated by pine plantation.

The post-fire model output indicated that, unlike the year before the fire, post-fire cell use frequency was highest at higher elevations, steeper slopes, and greater distances to the urban edge, and similarly to the year before, cell use frequency decreased with increasing distance to the nearest sleeping site (Table 3). After the fire, habitat did not significantly explain variation in use of home range cells. However, whether or not land was burned did significantly explain cell use variation, for cell use frequency significantly decreased as percentage of cell burned increased.

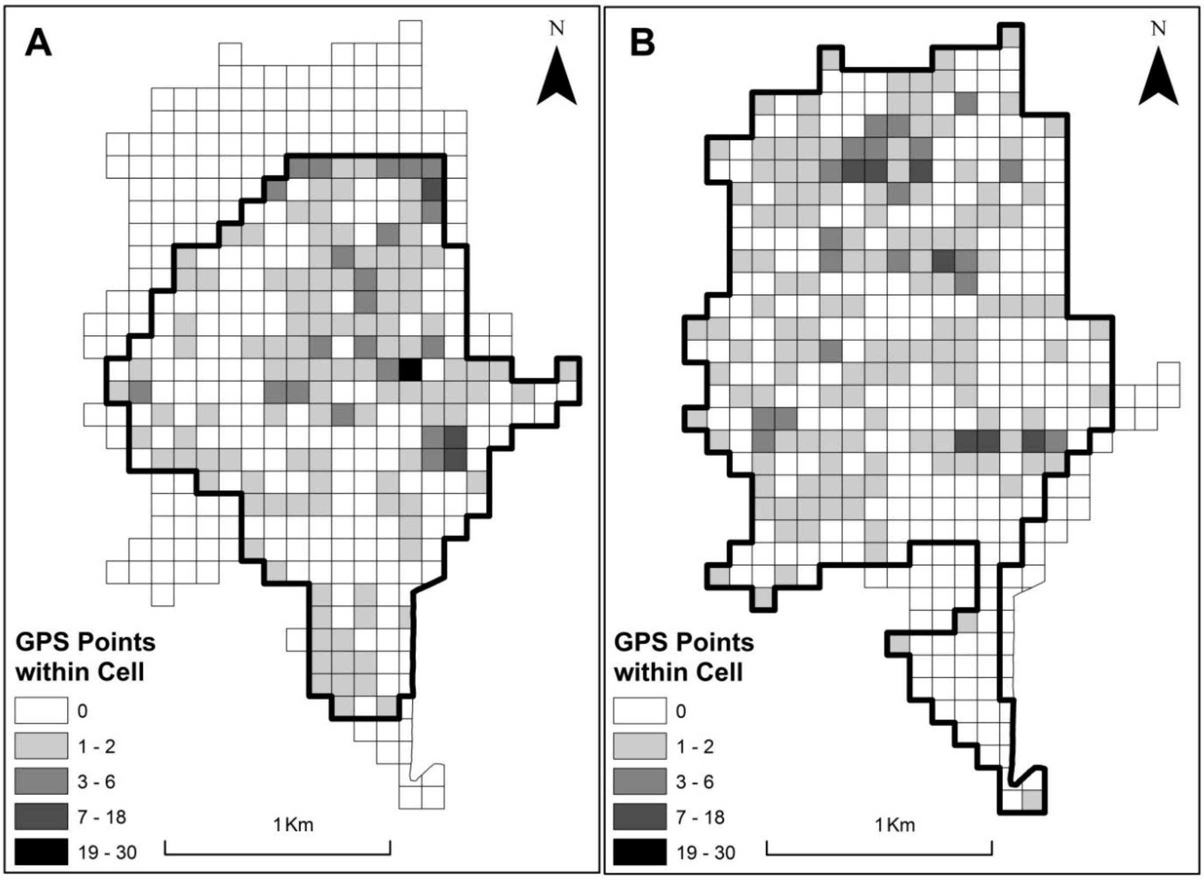

Figure 5. The area used by the Tokai troop the year prior (A) and post-fire (B). Cells represent the combined home range across both sampling periods, while the thick black outline represents the area used in each respective period. Shade of cells indicates frequency of use for that period as denoted in the legend.

Table 1. Correlations between observed cell use and fitted cell use derived from the SGLMMs of home range use post-fire and the year prior (*n* = 459).

Year Prior Sparse SGLMM		**Post-Fire Sparse SGLMM**	
Pearson’s R	0.74	Pearson’s R	0.64
p-value	< 0.001	*p*-value	< 0.001
Spearman’s ρ	0.61	Spearman’s ρ	0.53
p-value	< 0.001	*p*-value	< 0.001

Table 2. Results of the sparse SGLMM fitted to the home range cell use frequency in the year prior to the fire.

		Highest Posterior Density Intervals		
Predictor	**Estimate**	**Lower**	**Upper**	**MCSE**
Intercept (Pine Plantation)	**-2.001**	-2.564	-1.434	0.00357
Distance to Sleeping Site	**-1.369**	-1.821	-0.906	0.00327
PC1*	**0.249**	0.040	0.458	0.00121
Habitat - Clearing	0.341	-0.318	0.997	0.00243
Habitat - Eucalyptus	0.428	-0.190	1.054	0.00316
Habitat - Grassland	**1.741**	0.738	2.751	0.00495
Habitat - Mixed Other	0.784	0.017	1.548	0.00289
Habitat - Shrubland	0.512	-0.265	1.307	0.00489
Habitat - Urban	-0.753	-2.452	0.909	0.00623
Habitat - Vineyard	-1.413	-3.024	0.147	0.00652

*PC1 includes elevation, slope, and distance to the urban edge
MCSE = Monte Carlo Standard Error
Bold estimate values indicate confident significance. Note that Distance to Water variable was not retained.

Table 3. Results of the sparse SGLMM fitted to the home range cell use frequency post fire.

		Highest Posterior Density Intervals		
Predictor	**Estimate**	**Lower**	**Upper**	**MCSE**
Intercept (Pine Plantation)	**-1.165**	-1.553	-0.782	0.00126
Distance to Sleeping Site	**-1.166**	-1.527	-0.795	0.00191
PC1*	**-0.281**	-0.451	-0.114	0.00072
Habitat - Clearing	0.095	-0.347	0.541	0.00112
Habitat - Eucalyptus	0.273	-0.217	0.765	0.00145
Habitat - Grassland	-0.245	-1.496	0.961	0.00289
Habitat - Mixed Other	-0.412	-1.343	0.489	0.00178
Habitat - Shrubland	0.124	-0.432	0.674	0.00163
Habitat - Urban	-1.139	-3.096	0.713	0.00394
Habitat - Vineyard	0.078	-1.093	1.264	0.00317
Percent of Cell Burned	**-0.422**	-0.764	-0.074	0.00097

*PC1 includes elevation, slope, and distance to the urban edge
MCSE = Monte Carlo Standard Error
Bold estimate values indicate confident significance. Note that Distance to Water variable was not retained.

Activity budget

Wilcoxon rank tests revealed that percent of time spent engaged in social activities was the only behaviour category with significant differences between the two years (Table 4; Figure 6). There were no significant differences in percent of time spent moving (*V* = 25, *p* = 0.0999; Figure 6A) or percent of time spent resting (*V* = 48, *p* = 1.0000; Figure 6B) after the fire compared to the year before. A trend can be seen for percent of time spent feeding being higher after the fire compared to the year before (*V* = 23, *p* = 0.0730; Figure 6C). Furthermore, percent of time allocated to social behaviour was significantly lower after the fire than the year before (*V* = 129, *p* = 0.0023; Figure 6D).

Table 4. Percent of time engaged in each behaviour category for the same 16 adult female baboons after the fire and the year prior.

	Year Prior		**Post-Fire**	
Behaviour Category	**Median**	**Range**	**Median**	**Range**
Moving	22.7	15.5 – 31.9	26.9	20.9 – 33.0
Resting	26.0	16.6 – 32.7	28.2	21.8 – 39.4
Feeding	25.1	8.8 – 33.5	29.3	17.3 – 43.9
Social *	27.0	17.7 – 41.8	15.6	7.1 – 27.7

Asterisk indicates significance difference between years.

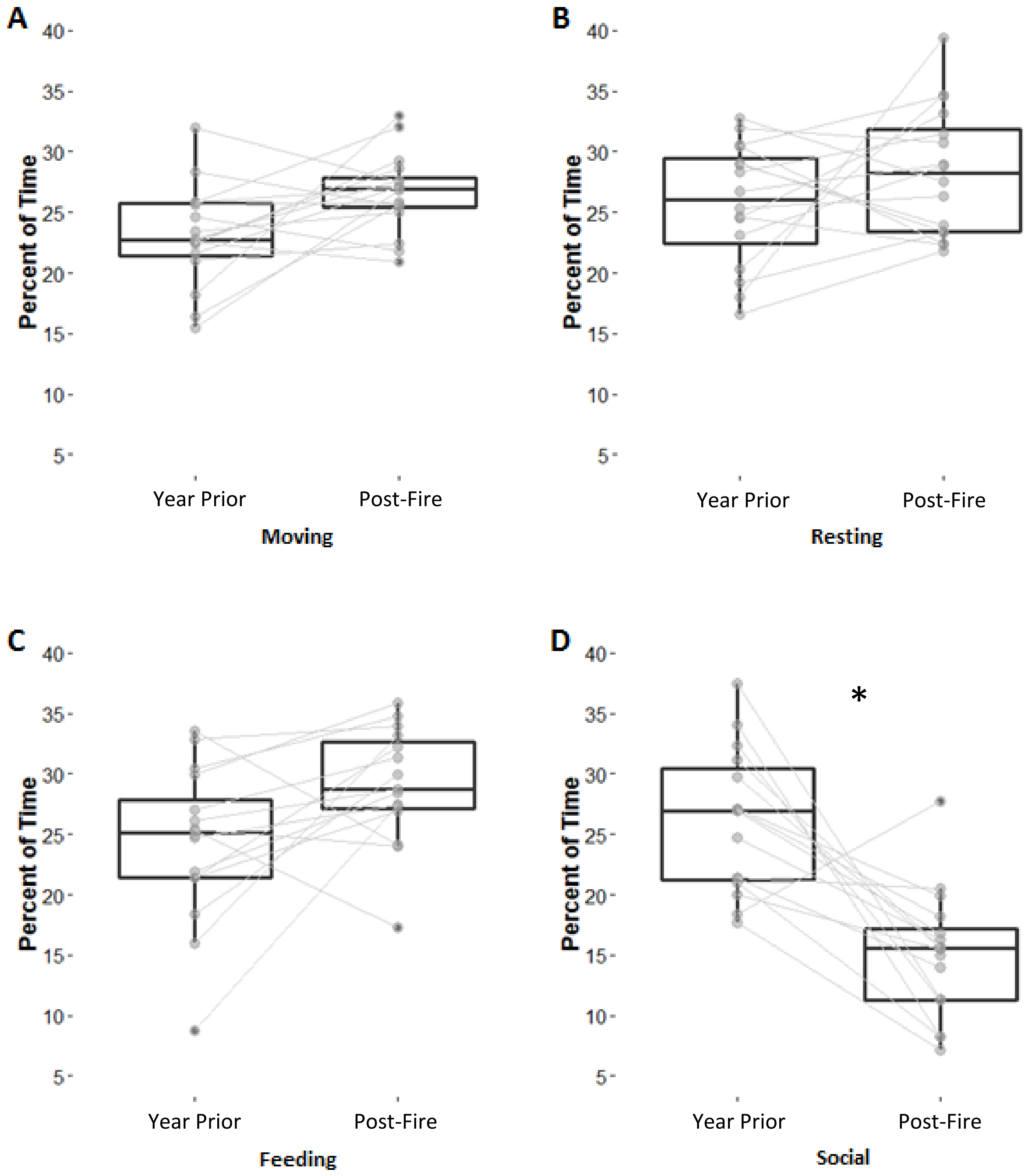

Figure 6. Percent of time engaged in moving (A), resting (B), feeding (C), and social behaviour (D) for the same 16 adult female baboons after the fire and the year prior. Boxes show inter-quartile range (IQR), with the median represented by an interior line and whiskers indicating 95% confidence intervals. Plotted points and associated connecting lines indicate the change in each female's percent of time spent engaged in the behaviour. Asterisk indicates significance differences.

Glucocorticoid concentrations

A paired Wilcoxon rank test revealed that glucocorticoid concentrations were lower for females after the fire (median: 58.0, range: 33.7 – 105.8) than the year before (median: 84.1, range: 72.3 – 100.8) (*V* = 120, *p* = 0.005; Figure 7).

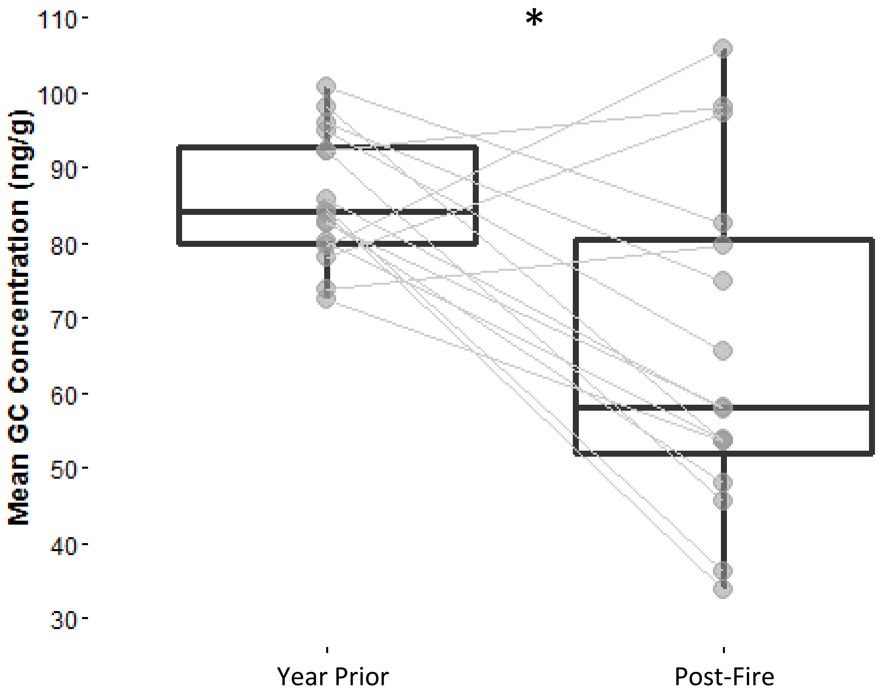

Figure 7. Faecal glucocorticoid concentrations of the same 16 adult female baboons in the year prior to the fire and after the fire. Boxes show inter-quartile range (IQR), with the median represented by an interior line and whiskers indicating 95% confidence intervals. Plotted points and associated connecting lines indicate the change in each female's mean year prior and post-fire glucocorticoid concentration. Asterisk indicates significance differences.

C-peptide concentrations

A paired Wilcoxon rank test revealed that the adult females' C-peptide concentrations after the fire (median: 53.6, range: 2.4 – 90.4) were not significantly different than the year before (median: 30.2, range: 12.0 – 141.5) (*V* = 52, *p* = 0.679; Figure 8).

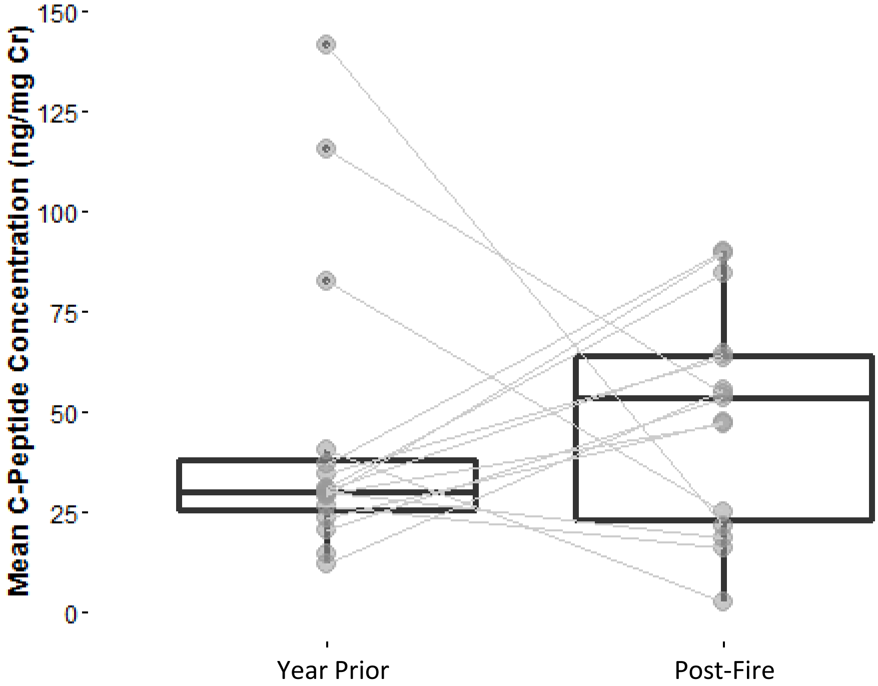

Figure 8. Urinary C-peptide concentrations of the same 16 adult female baboons in the year prior to the fire and after the fire. Boxes show inter-quartile range (IQR), with the median represented by an interior line, and whiskers indicating 95% confidence intervals. Plotted points and associated connecting lines indicate the change in each female's mean year prior and post-fire C-peptide concentration.

Discussion

This study assessed aspects of the behaviour and physiology of 16 adult female baboons in a peri-urban troop after an extensive fire compared to the same months in the year before. In the months following the fire the baboons had a larger spatial range compared to the previous year, and spent notably less time engaging in social behaviours post-fire than in the year prior. Perhaps most surprisingly, physiological indicators did not suggest higher levels of psychological, energetic, or nutritional stress post-fire. In fact, glucocorticoid concentrations were significantly lower post-fire compared to the year before, while C-peptide concentrations did not significantly differ between the two periods. These analyses provide the first insight into the responses of free-ranging baboons to wildfire in a peri-urban human-modified landscape.

Behavioural changes

The Tokai troop preferentially used unburnt areas after the fire. These findings contrast with the limited previous observations of yellow baboons (*Papio cynocephalus*) and vervet monkeys (*Cercopithecus aethiops*) that show preference for freshly burnt areas over unburnt areas (Rasmussen 1983; Jaffe & Isbell 2009). This discrepancy is to be expected, however; in both aforementioned cases the groups were heavily predated by ambush hunting felines and preference for burnt areas was attributed to increased visibility and hence lower perceived predation risk. This is not the case for the Tokai troop as all natural predators of baboons were eradicated from the Cape Peninsula approximately a century ago (Skead 1980; Stuart et al. 1985). This suggests that the absence of predation risk allows primates to be more flexible in their responses to a large scale habitat disturbance.

The spatial range of the troop was larger by approximately 1 km^2 after the fire as they expanded their home range northward to incorporate unburnt areas. Per capita area increased by roughly 0.02 km^2. Range increases of other troops in the peninsula have been attributed to changes in food availability, as food sources that are scarcer, more thinly distributed, or of lower quality may result in an increase in range size so as to increase each individual's intake of food (Hoffman & O'Riain 2011, 2012a; Lewis & O'Riain 2017). The fire undoubtedly impacted the availability of food resources, as most above-ground biomass was burned.

Although the home range of the troop was 36% larger after the fire compared to the year prior, time allocated to traveling remained generally the same. This may be explained by the addition of a new sleeping site in the northern region of their range that borders the unburnt area and hence reduced travel distance from the roosting site to foraging areas. Sleeping sites can be selected by primates to increase foraging efficiency by reducing daily travels (Anderson 2000), and baboons specifically have been shown to adjust sleeping sites when ecological factors have required wider ranging patters (Rasmussen 1979; Hamilton 1982). Unfortunately, having not collected full days of data I could not compare daily distance moved during each period, which may have revealed how selection of a new sleeping site influenced this variable. What is clear from the spatial modelling of this study, however, is that distance to the nearest sleeping site was an influential factor in spatial use for the Tokai troop both after the fire and in the year prior.

The importance of social bonds in female baboons is well known (Silk 2007), hence it is interesting to note that time engaged in social behaviours was the only category of the activity budget that was sacrificed post-fire. Though studies assessing the impacts of fire on activity budgets are lacking, insights can be gained by examining baboons experiencing similar hardships under different ecological pressures. For instance, female baboons in a highly-predated troop of the Okavango Delta allocate more time to social grooming and groom a wider variety of partners directly following the loss of favoured companions (Engh et al. 2006). Similar behaviour occurs in the Amboseli populations, where females who experience the death of a close relative subsequently focus their grooming patterns to strengthen bonds with other females (Silk et al. 2006a, 2006b). This social adjustment is attributed to the importance of strengthening and broadening social networks after they had been altered. Therefore, after losing many adult females to the fire, the remaining females of the Tokai troop could be predicted to increase socialising time in order to repair community ties. Notably, this did not occur. It may be that too much time had elapsed since the loss of the troop members to detect a post-fire effect or that increased foraging requirements curtailed time available for socialising. While there is the potential that the observed differences between years in time spent socialising could be a group size effect, it should be noted that roughly 42% less social time was recorded post-fire despite losing only about 18% of individuals in the fire. It remains a challenge of the broader Tokai Baboon Sociality Project to analyse how social bonds were altered after the fire.

The impact of ecological adversities on baboon social behaviour is heavily debated, with some believing social time is the critical bond that holds a troop together and others arguing that time spent engaging in social behaviour is flexible time that will be sacrificed first under adverse conditions (summarised in Alberts et al. 2005). For example, in times of food scarcity associated with dry seasons in Amboseli, female baboons increased moving and foraging time, while preserving time for socialising at the expense of resting (Alberts et al. 2005). This supports previous claims that female baboons preferentially conserve socialising above other activities (Dunbar & Sharman 1984; Dunbar 1992). However, this same troop did sacrifice social time when faced with dramatic, long-term habitat change more intense than regular seasonal fluctuations (Bronikowski & Altmann 1996), suggesting that baboons "may indeed *attempt* to conserve social time" but are only able to do so "within a fairly narrow range of habitat change" (Alberts et al. 2005). After the fire, the Tokai troop spent insignificantly more time moving, resting, and feeding, and significantly less time socialising, providing support for the hypothesis that social behaviours are sacrificed over other behaviours.

It is important to recognise that comparisons of spatial ranges, per capita area, and absolute activity budget with other studies, both in the peninsula and other regions, are limited by differences in data collection protocols. In this study we did not perform full-day observations and thus important late afternoon and evening behaviour were omitted. This does not preclude comparisons between post-fire and year prior sampling periods, however, given that observation methods remained constant across these two periods.

Physiological shifts

Contrary to my prediction, mean faecal glucocorticoid concentrations of the females in this study were lower after the fire compared to the year before. As glucocorticoids are often used as a measure of physiological stress, I predicted that higher glucocorticoids would be seen post-fire. Elevated glucocorticoid levels, specifically in female baboons, have been attributed to physically stressful situations, such as periods of food and water restrictions (Gesquiere et al. 2008) and decreases in time spent resting (Weingrill et al. 2004), as well as psychological stressors, such as the deaths of close companions (Engh et al. 2006). In the context of these results, it does not appear that the females of the Tokai troop were experiencing high levels of physiological stress in the months following the fire.

In baboons, as well as other primate species, pregnant females consistently have the highest glucocorticoid concentrations (Ziegler et al. 1995; Smith & French 1997; Cavigelli 1999; French et al. 2004), with post-partum levels quickly returning to those of non-pregnant females (Ziegler et al. 1995; Bahr et al. 1998; Bardi et al. 2003; Weingrill et al. 2004; Beehner et al. 2006). In my study, three of the four females that showed slightly higher glucocorticoid levels after the fire were pregnant, which may explain the individual variation seen in glucocorticoid trends. In fact, there were twice as many pregnant females in the post-fire sampling period, which arguably makes the 25% decrease in mean glucocorticoid concentrations post-fire even more surprising.

C-peptide concentrations were also predicted to change in response to the fire, with an assumed depletion of food resources resulting in energetic stress and lower C-peptide values. There was, however, no significant change in the mean C-peptide concentrations of the troop post-fire, suggesting that the overall energy status of the Tokai troop females remained fairly constant. Broadly, C-peptides can be used as an indicator of body condition, nutritional status, and energetic balances in primates (Hoogwerf & Goetz 1983). Decreases in body mass, body mass index, and body fat have all been linked to reductions of urinary C-peptide levels in primates (Thompson & Knott 2008; Thompson et al. 2009; Girard-Buttoz et al. 2011). Not only have periods of food restriction and poor habitat quality produced low C-peptide concentrations in various primate taxa (Deschner et al. 2008; Thompson & Knott 2008; Thompson et al. 2009), including baboons (Lodge 2012), but severely diseased wild chimpanzees showed decreased C-peptide levels too (Thompson et al. 2009). Notably, low C-peptide concentrations of the diseased chimpanzees were still manifested despite excellent foraging conditions and high levels of food consumption, reminding us that although important, energy intake is not the only contributing factor to C-peptide excretion, and energy expenditure of individuals needs to be considered as well. The results of this study would suggest that in the months following the fire, the females of the Tokai troop were not experiencing high levels of energetic stress. This is one of the first studies examining urinary C-peptides of baboons as a result of ecological pressures (see Lodge 2012 also) and adds to the thin base of literature assessing this approach in wild baboon populations.

It is essential to point out that all post-fire faecal and urine samples were collected at least one month after the fire, thus any immediate impacts of the fire on glucocorticoid or C-peptide concentrations have gone unrecorded. Levels of stress biomarkers may have been remarkably different in the four weeks directly following the fire, with the post-fire concentrations analysed here potentially representing a time of newly attained normalcy. In Okavango baboons, increases in glucocorticoid levels due to sudden social disturbances were reported to return to baseline levels within the second month following the destabilising event (Engh et al. 2006). Further, females of this group that contracted their social networks to focus on fewer bonds following the loss of troop members may have exhibited glucocorticoid concentrations that decreased towards baseline levels after only one week (Wittig et al. 2008). While this study cannot attest to stress levels that ensued promptly after the fire, the finding that there were no long-term or chronic physiological indicators of stress is important to wildlife managers, who were resisting public pressure to provision the troops.

Feeding and nutritional impacts of the fire

It might be expected that urban troops under food stress would increase their utilisation of anthropogenic food sources in an attempt to supplement their caloric intake. Crop-raiding baboon troops have been shown to have higher C-peptide and lower glucocorticoid concentrations than troops restricted to natural foods, and therefore appear better equipped to manage environmentally-induced energetic stress (Lodge 2012). In this study, the area to the north that was added to the troops' spatial range post-fire included private vineyards which troops regularly raid to consume grapes left behind from recent harvests (Hoffman and O'Riain 2011; Fehlmann et al. 2017).

A previous study on this troop recorded seeds obtained from pine cones to be the largest component of the Tokai troop's diet (Johnson et al. 2013). It is well established that *Pinus radiata*, the dominant exotic pine trees planted throughout Tokai, open their cones and release pine seeds when subjected to extreme heat, such as fire (Richardson & Brown 1986; Cope 1993). It was apparent to field rangers and researchers that the baboons were primarily feeding on these abruptly abundant and readily available seeds after the fire. Under normal circumstances, obtaining seeds from pine cones requires considerable handling time as the baboons must forcefully pry open the cones using their hands and teeth. By contrast, qualitative observations revealed that the consumption of pine seeds post-fire involved searching through burnt leaf litter on the soil surface for released seeds, and hence considerably less handling time and effort was required per seed consumed. Due to the shift in the manor of foraging, handling, and ingesting of food items including pine seeds after the fire, the impact of the fire on overall diet could not be determined. However, the Tokai troop appears to have experienced a surfeit of preferred food as a result of the fire, which may explain the lack of physiological indicators suggesting the adult females were nutritionally stressed despite the loss of most above ground biomass.

Conclusion

Overall, it appears that behavioural flexibility allowed the adult females of the Tokai troop to successfully adjust to a large scale natural disaster in the form of an extensive fire. The fire clearly exacted a cost to the troop with the death of 12 troop members and injury to a further 12. These losses and injuries resulted from troop members climbing trees in response to the approaching fire; retreat to an arboreal habitat when faced with a terrestrial threat is an evolved response in baboons, but one that proved costly in this instance. Thereafter, behavioural flexibility in ranging behaviour and activity budget allowed the troop to adjust to the post-fire landscape with no physiological indications of either social or nutritional stress, demonstrating the baboons' adaptability to drastic ecological change.

In a highly-managed fire-prone landscape such as the Cape Peninsula, understanding adaptive strategies of local wildlife can lead to more informed management decisions and improved public awareness in the face of natural disasters. After the Muizenberg Fire, there was strong public demand through social media to feed the affected troops out of concern over a lack of available food resources; nonetheless, it appears that management authorities were vindicated in not provisioning the baboons and avoiding the well-established short- and long-term costs associated with such an intervention (Kaplan et al. 2011). Furthermore, while the anticipated removal of exotic trees from the Tokai landscape may be a positive development for the Table Mountain National Park's general ecology, the baboons' loss of access to pine seeds can be predicted to increase pressure on anthropogenic food resources and hence increase human-baboon conflict in this region of the Cape Peninsula.

This study provides rare insights into how baboons may react to expansive and sudden habitat change due to wildfire damage in a peri-urban environment, and suggests that baboons can adjust adequately.

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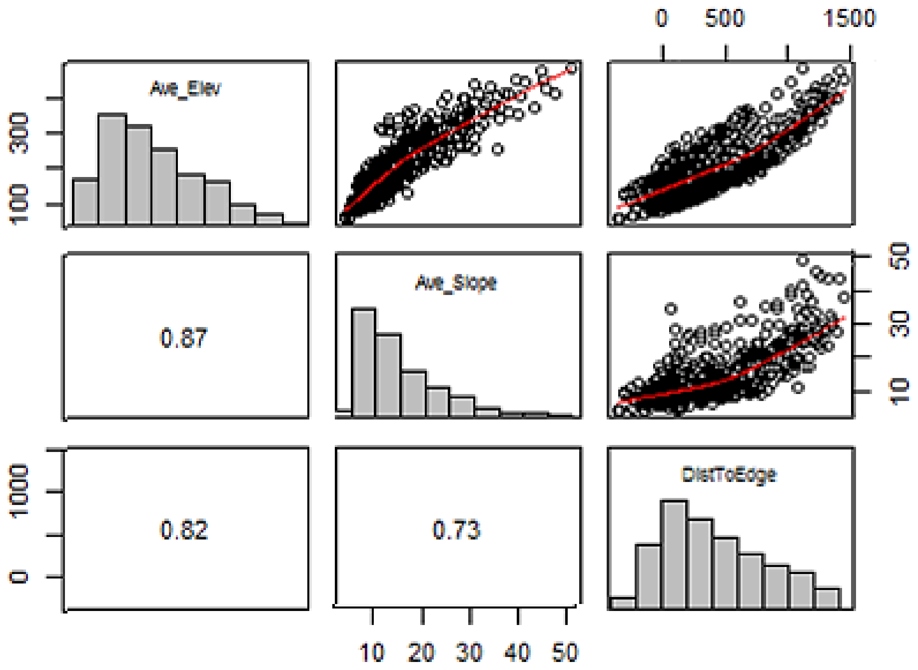
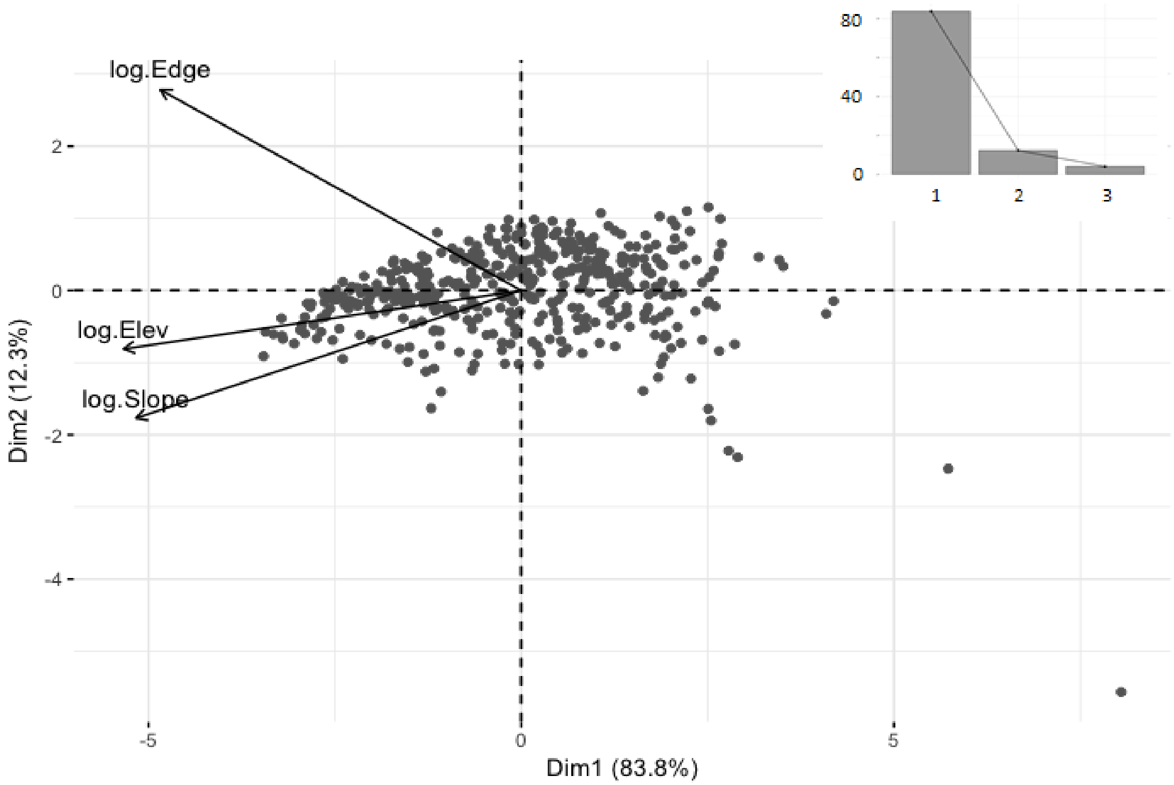
Appendices

Appendix 1. Abridged activity descriptions defined by the Tokai Baboon Sociality Project.

Activity	**Definition**
Moving	Includes: walking; climbing; and running
Stationary	Includes: resting; and standing
Feeding	Putting food items in mouth, or handling food items (i.e., cleaning, breaking apart) not involved in significant search for food, usually applies for feeding in a patch
Foraging	Actively searching for food using hands, by turning over leaves and leaf litter, digging in soil, pulling away bark, trying to open containers, etc.
Resting in Contact	Sitting or standing (being) in skin contact with other adult or (known) subadult males/females.
Grooming Self	Grooming themselves (parting fur with hands; does not include scratching)
Grooming with Other	Includes: active grooming (actively grooming another) and passive grooming (being groomed by another). All grooming with any kind of partner (age/sex) is recorded



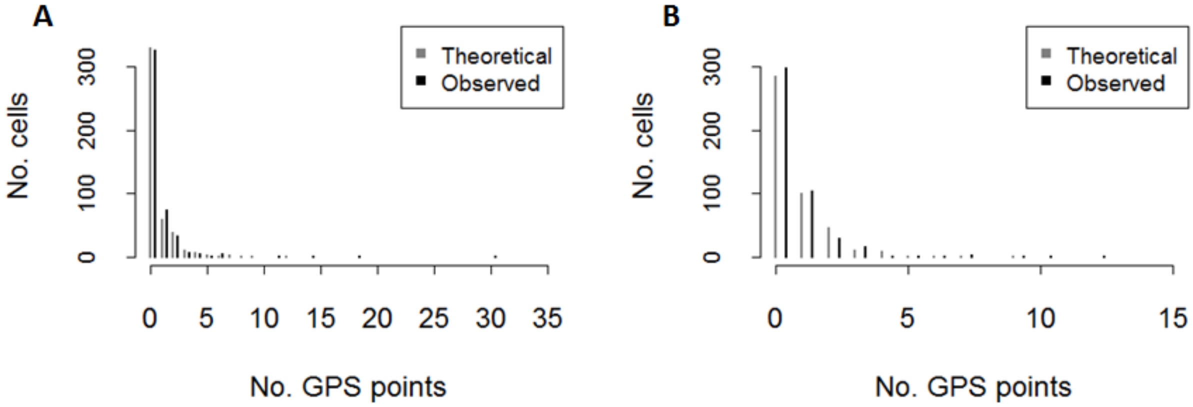
Appendix 2. Correlation matrix showing the collinearity between elevation (Ave_Elev), slope (Ave_Slope), and distance to urban edge (DistToEdge) for the Tokai troop's home range. Numbers shown indicate Pearson's correlation coefficients.



Appendix 3. Two Principal Components (PC1 and PC2) from the PCA on log transformed values of elevation (log.Elev), slope (log.Slope), and distance to urban edge (log.Edge). The x and y axes represent the first and second Principal Components (PC), respectively, and arrows represent the relative contribution of climatic covariates to PCs. Inserted histogram shows eigenvalues for each PC.

Appendix 4. Akaike Information Criterion (AIC) for goodness of fit of theoretical distributions with equal parameters to observed cell use frequencies (corrected), for post-fire and year prior sampling periods.

Year Prior		**Post-Fire**	
Tested Distributions	**AIC**	**Tested Distributions**	**AIC**
Poisson	1368.3	Poisson	1144.7
Zero-Inflated Poisson	1138.3	Zero-Inflated Poisson	1060.3
Negative Binomial	952.2	Negative Binomial	984.8



Appendix 5. Histograms of observed cell use frequencies (corrected) compared to theoretical cell use frequencies with true negative binomial distribution with equal parameters to observed, for the year prior sampling period (A) and the post-fire sampling period (B).

Appendix 6. Deviance Information Criterion (DIC) values produced from post-fire and year prior SGLMMs used for variable selection of three highly correlated predictor variables.

Year Prior		**Post-Fire**	
Tested Variable	**DIC**	**Tested Variable**	**DIC**
Elevation	774.2	Elevation	852.6
Slope	781.5	Slope	854.2
Dist. to Urban Edge	774.7	Dist. to Urban Edge	855.1
PC1	776.6	PC1	851.3