

Anthropogenic effects on the physiology and behaviour of chacma baboons in the Cape Peninsula of South Africa

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As animals increasingly occupy habitats in proximity to humans, with home ranges a mosaic of natural and anthropogenic landscapes, it becomes imperative from a conservation perspective to understand the impacts of human activities on wildlife. Many non-human primates share habitats with humans, an ability stemming largely from shared ecological needs due to our close evolutionary relationship. Such proximity, however, is often accompanied by direct conflict between humans and wildlife, leading to higher stress levels, injuries, mortality and behavioural changes, with detrimental effects on long-term health and fitness. Glucocorticoid (GC) hormones, which are released in response to ecological and social challenges, are increasingly employed to understand responses to anthropogenic disturbance. Here we investigate physiological and behavioural responses of female chacma baboons (*Papio ursinus*) to variation in spatial overlap and conflict with humans in their natural home range. The baboons resided in the Tokai Section of Table Mountain National Park in the Cape Peninsula of South Africa, where their home range included four types of habitats: protected, suburban, agricultural and mosaic areas. We studied the largest group of baboons in Tokai (70 individuals) and examined the effects of ranging in these different habitats on the faecal GCs and behaviour of all adult females in the troop ($N = 16$). We found time spent ranging in more anthropogenic habitats to be associated with higher levels of GCs, more aggression, less time socializing and shorter grooming bouts. Self-directed behaviour, however, varied and did not necessarily reflect physiological measures of stress. Taken together, the results of this study highlight the risks associated with ranging in anthropogenic environments and point to the need for a multifaceted approach to studying the negative impacts of human activities on animals so as to better inform conservation practices.

Key words: anthropogenic disturbance, glucocorticoids, self-directed behavior, stress, baboon

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Introduction

Human domination of the earth's ecosystems is a major driver of wildlife extinctions (Vitousek *et al.*, 1997; Estrada *et al.*, 2017; Tilman *et al.*, 2017). In addition to habitat loss and modification for anthropogenic use, many animals now live in close proximity to humans as we extend our ranges and encroach further and wider into their habitats. Some animals derive benefits from their proximity to humans due to their ability to share resources with them (Hulme-Beaman *et al.*, 2016). However, this proximity can also lead to interspecific conflict and can impact animals in negative ways, causing injuries, mortality and even extinction of species (Nyhus, 2016). Thus, it has become increasingly important to understand these negative consequences if we are to maintain healthy wildlife populations and manage our own behaviours so as to sustain wildlife.

Non-human primates (hereafter referred to simply as primates), unlike many other animals, often thrive in human-modified environments due to shared biological features and adaptations resulting from their close evolutionary relationship with humans. Examples of commensal primates are abundant among both catarrhines and platyrrhines in most of their ranges and in many cases appear to be the result of shared generalist strategies such as those found in macaques and baboons (Fuentes and Wolfe, 2002; Strum, 2010; Leite *et al.*, 2011; McKinney, 2011; Swedell, 2011; Radhakrishna, *et al.*, 2013). Although non-human primates typically inhabit tropical forests, these habitats are becoming increasingly fragmented and degraded. Many primates now live in human-modified or -impacted habitats, with the number of species and populations found in proximity to humans continuing to increase (McLennan *et al.*, 2017). It is thus becoming vitally important to learn more about the effects of these changes on primate populations (Almeida-Rocha *et al.*, 2017).

Predictably, competition for shared resources often results in conflict between commensal primates and humans (Woodroffe *et al.*, 2005; Hill *et al.*, 2017). Direct conflict as well as other indirect effects of human activities can have negative consequences on the behaviour, ecology, activity patterns and health of these primates (Tarlow and Blumstein, 2007; Abondano and Link, 2012). Primates living in anthropogenic habitats may experience constraints on their activity budgets (macaques: Priston *et al.* 2012; chimpanzees: Bryson-Morrison *et al.* 2017), spend less time socializing (howlers: Aguilar-Melo *et al.* 2013), suffer increased parasitism (indris: Junge *et al.* 2011) and be affected in other negative ways.

In particular, anthropogenic activities in the form of agriculture, urban development and transient human presence, e.g. pastoralists and tourists, are known to have a negative impact on wild primates. Non-human primate exploitation of agricultural crops, which are available year-round and have a higher and faster energetic yield than natural foods, has been an immense problem in many parts of the world (Africa:

Naughton-Treves, 1998, Hill, 2000, Strum, 2010, Schweitzer *et al.*, 2017; Asia: Riley, 2007, Marchal and Hill, 2009, Priston *et al.*, 2012), with farmers frequently employing deterrent tactics that are harmful or fatal for animals (Hulme and Hill, 2016). Many primates also live in more urban and suburban areas and directly share space and resources with humans, again leading to conflict between them (Kaplan *et al.*, 2011; Hoffman and O'Riain, 2012; Radhakrishna *et al.*, 2013). Interactions between humans and non-human primates in these and other contexts are frequently of an aggressive nature, e.g. stone throwing and catapults, leading to high rates of injury and mortality for the primates involved (Hockings and Hulme, 2009; Yihune *et al.*, 2009; Beamish, 2010; Strum, 2010; Mtoka *et al.*, 2014; Zisadza-Gandiwa *et al.*, 2016).

An important tool to help us understand the impact of potentially negative environmental factors on animals is measurement of their physiological stress response. Animals respond to stressors by activating the hypothalamic–pituitary–adrenal (HPA) axis, which mediates the stress response by initiating a cascade of physiological changes, including the release of glucocorticoid (GC) hormones (Sapolsky *et al.*, 2000; Nelson, 2005). GCs can thus be an important tool in assessing the effects of exposure to chronic stressors such as habitat disturbance. An association between habitat disturbance and GC levels has been demonstrated in a wide array of taxa (tigers: Bhattacharjee *et al.*, 2015; greater rheas: Leche *et al.*, 2014; owls: Wasser *et al.*, 1997). Similarly, higher GC levels have been associated with human activities related to tourism, human settlements or urban environments (spotted hyenas: Van Meter *et al.*, 2009; grouse: Arlettaz *et al.*, 2007; wolves and elk: Creel *et al.*, 2002; elk: Millspaugh *et al.*, 2001; capercaillie: Thiel *et al.*, 2008; blackbirds and mockingbirds: Fokidis *et al.*, 2009; European pine martens: Barja *et al.*, 2007), as well as human–wildlife conflict related to crop-foraging (elephants: Ahlering *et al.*, 2011).

The negative effects of anthropogenic disturbance on physiology also extend to primates. Many studies have revealed that, unsurprisingly, primates living in disturbed, fragmented or unprotected forests experience higher GC levels compared to those living in undisturbed, unfragmented or protected habitats (red colobus: Chapman *et al.*, 2006; black howlers: Martinez-Mota *et al.*, 2007, Gomez-Espinosa *et al.*, 2014, Rangel-Negrin *et al.*, 2014; mangabeys: Jaimez *et al.*, 2012; spider monkeys: Rangel-Negrin *et al.*, 2009, Rimbach *et al.* 2013). The level of tourism that primates are exposed to has been linked to higher GC levels as well (black howlers: Behie *et al.*, 2010; orangutans: Muehlenbein *et al.*, 2012; Barbary macaques: Marechal *et al.*, 2011; gorillas: Shutt *et al.*, 2014). Elevation of GCs has also been found in crop-foraging primates (chimpanzees: Carlitz *et al.* 2016) as well as primates living in human-impacted or urban areas (vervets: Fourie *et al.*, 2015; bushbabies: Scheun *et al.*, 2015, howlers: Vanlangendonck *et al.*, 2015).

The negative impacts of living in anthropogenic environments are manifested in both the behaviour and physiology

of non-human primates, and, correspondingly, both physiological and behavioural indicators can be used to measure responses to these hypothesized stressors. In addition to physiological stress as measured by higher GC levels, another measure that can be used to study stress responses in primates is self-directed behaviour (SDB), such as scratching, yawning, self-touching and body-shaking. SDB has been used in a wide array of primate studies as a measure of anxiety and stress (Castles and Whiten, 1998; Castles *et al.*, 1999; Troisi, 2002; Kutsukake, 2003; Anselme 2008) and often occurs in situations of psychosocial stress (Schino *et al.*, 1988; Pavani *et al.*, 1991; Troisi *et al.*, 1991; Maestripieri *et al.*, 1992; Manson and Perry, 2003). In the wild, higher rates of SDB have been associated with environmental stressors such as high predation events (Palagi and Norsci, 2011). Many studies have shown that being in captive conditions is associated with higher rates of SDB and harmful self-injurious behaviours (Lutz *et al.*, 2003), including in baboons (Lutz *et al.*, 2014). As with captive conditions, living in disturbed habitats or in proximity to humans can lead to behavioural adjustments by primates that help them to cope, adapt and ultimately survive. Behaviours such as SDBs, therefore, could reflect coping mechanisms used by primates to mitigate the negative effects of anthropogenic stress.

Here we focus on the effects of anthropogenic environments on the behaviour and physiology of baboons, which are among the most generalist non-human primates. Baboons are behaviourally, ecologically and socially flexible monkeys that breed throughout the year and occupy diverse habitats throughout sub-Saharan Africa (DeVore and Washburn, 1963; Strum and Mitchell, 1987; Jolly, 2001; Alberts and Altmann, 2006; Swedell, 2011). Chacma baboons, *Papio ursinus*, are found in a wide range of habitats throughout southern Africa and show substantial flexibility in behaviour and ecology (Whiten *et al.*, 1987, Henzi and Barrett, 2005). In the Cape Peninsula of South Africa, as in much of their distribution, baboons live in a mosaic of natural and anthropogenic landscapes (Kansky and Gaynor, 2000). Within this mosaic, there are 16 troops of chacma baboons scattered throughout the Peninsula (Drewe *et al.*, 2012). We studied a troop of baboons residing in the northern peninsula, encompassing an area that includes parts of Table Mountain National Park, suburban areas, agricultural land and natural and forested areas interspersed within the suburban areas. This mosaic landscape constituted the home range of the largest troop of baboons in this northern region, the MT1 troop. Because of the mosaic nature of both its habitat and its contact with humans, this troop serves as an excellent model for testing the effects of anthropogenic disturbance on the behaviour and physiology of the baboons.

A previous study in the Cape Peninsula showed that urbanization increases baboon–human conflict and found that the best predictor of conflict levels is the percentage of a troop’s home range that is urbanized (Hoffman and O’Riain 2012). Another study found that rates of injury and mortality increase with time spent by the baboons in residential areas

(Beamish and O’Riain 2014). Given this previously documented straightforward relationship between urbanization and baboon–human conflict, we sought with this study to assess the physiological consequences of this conflict on the baboons. To do so, we quantified the amount of time our study troop spent ranging in each of the following four habitat types and used this measure as a proxy for the degree of human impact and conflict. (i) *National park* (low impact): ranging within the boundaries of the national park, which is a protected area, is, by definition, associated with the least amount of conflict because human presence is lower within the park. Also, due to the protected status of the baboons, people tend to be more affiliative and less aversive to the baboons in their more natural environment. (ii) *Suburban* (high impact): the highest level of conflict occurs within the suburban areas because the baboons are considered invasive in these spaces and humans react with aggression to the baboons’ raiding and destructive behaviours. (iii) *Mixed areas* (medium impact): these areas encompass patches of forest within suburban areas and are characterized by an intermediate level of human interaction due to a reduced presence of humans and the more naturalistic environment, where baboons are not seen as out of place. (iv) *Agricultural land* (medium to high impact): These are vineyards, which are defended by humans from the baboons during grape harvesting season and are thus characterized by high degrees of conflict on a seasonal basis (see below for further details on the four habitats).

Here we examine the relationship between the amount of time spent by the baboons in each of these habitats, which vary in their degree of human conflict as described above, and two measures of the baboons’ stress levels, faecal GC concentrations and self-directed behaviour. We also assess variation in activity patterns and social behaviour across habitats to determine whether the baboons modify their behaviour in relation to the amount of anthropogenic disturbance they experience. We hypothesized at the outset of the study that the degree of baboon–human conflict would be reflected in the behaviour and physiology of the baboons, with increased GC levels as well as behavioural indicators of anxiety in areas characterized by greater conflict with humans. We believe that our approach complements, and may be more informative than, the usual approach that focuses on comparisons of groups of animals in disturbed or urban environments versus those in less disturbed environments. By contrast, here we are able to compare the same individuals in the same social group across habitats via an examination of changes in patterns of behaviour and GC levels within the same individuals over time.

Methods

Study site and subjects

This study was conducted in the Tokai section of Table Mountain National Park (TMNP), under the jurisdiction of

South African National Parks, located at 34°03' S, 18°24' E in the Cape Peninsula, Western Cape Province, South Africa. The Cape Peninsula covers an area that is ~470 km², more than half of which is undeveloped and which currently has protected conservation status under the TMNP. The remaining half of the Peninsula is highly modified and urbanized with a rapidly growing human population. The Western Cape is characterized by a Mediterranean climate, with hot, dry summers and cool, wet winters and higher primary productivity in winter compared to summer (Cowling *et al.*, 1996). During the time of this study, the Tokai section of the park, Tokai Forest, was a mosaic of pine and eucalyptus forest with patches of fynbos. The forest was being increasingly cleared during this time so that the land could revert to the indigenous and endemic fynbos. Surrounding the national park in Tokai are both suburban and agricultural (vineyard) areas.

The study subjects were wild chacma baboons (*Papio ursinus*) living in the 'MT1' troop, the largest of four troops residing in Tokai. The MT1 troop, one of two fission products of the 'Main Tokai' troop, has been studied intermittently since 2006 and is fully habituated to humans (Hoffman and O'Riain, 2011). During the study, there were approximately 70 individuals in the troop, with 16 adult females and 3–7 adult males. All 16 adult females were subjects of this study. We collected data from December 2009 through September 2011, with a 1-month break in data collection in July 2011, totalling 21 months.

The baboon population in Tokai is managed due to its proximity to and conflict with humans. During the study period, the population was managed by Nature Conservation Corporation (NCC), which employed individual people known as 'monitors' to follow the baboons on foot daily and herd them as necessary to keep them away from specific human-inhabited areas (including houses on the suburban edge and administrative offices within the park) to both minimize conflict with humans and ensure safety for the baboons (e.g. by keeping them away from busy commercial roads to prevent injuries and death). The monitors would typically follow the troop closely only when they were outside of the national park, as the mandate of NCC applied only to City of Cape Town land and not national park land. When inside the park, the monitors would track the troop at a much greater distance and would not usually herd them. During the time of this study, the monitors were not allowed to use aggressive herding methods such as paint balling, which was implemented for this population later, ca. 2013.

Data collection

Behavioural data

With the help of a field assistant, SC conducted 15-min focal animal sampling (as per Altmann 1974) on the 16 female subjects, rotating randomly among focal females. During focal samples, we continuously recorded the focal female's activity states, behavioural elements and social interactions.

We also recorded all instances of self-directed behaviours, including scratching, body-shaking, nose touching, self hair pulling, self-touching and yawning that occurred during focal samples. We recorded all observations of aggression, both during focal samples and as *ad libitum* data outside of focal samples.

On each observation day, we noted the reproductive state of all adult females. Females were categorized into four reproductive states: cycling (recognized from the cyclical swelling of their perineal skin (Bielert and Busse, 1983)), pregnant (identified by reddening of the paracallosal skin accompanied by slight bulging of the perineal skin (Altmann, 1973), followed by weight gain later in pregnancy), lactating (females with suckling infants, from the day of birth until the female started developing sexual swellings again) and 'other', which included females who could not be identified as being in any of the other three states, including an older female who had stopped cycling.

Ranging data

We obtained ranging data from three sources. First, we recorded the location of the troop *ad libitum* at the beginning of the day and then throughout the day every time they travelled and changed locations. Second, we recorded the location of the focal animal at the beginning of every focal sample. Third, whenever a faecal sample was collected for hormone data, we recorded the location and time of collection. Thus, we were able to integrate the location records from the *ad lib* data, focal samples and faecal sample data to track the daily ranging of each troop.

We categorized ranging data into four types of habitats:

(i) *National park* (low impact): this included most areas within the boundaries of Table Mountain National Park (with some exceptions as described below). The park was open for recreational use, and thus the baboons sometimes encountered humans when ranging within the park, but this contact was less frequent than in any other parts of their range and usually the interactions were not of an aggressive nature. The Cape Peninsula population of chacma baboons has protected conservation status due to its demographic and genetic isolation from other baboon populations, which ostensibly prevents people from injuring baboons, and this is especially true within the confines of the national park. Moreover, monitors did not typically follow the baboons into the national park; as this was the baboons' natural home range, it was not usually a context for baboon–human conflict, and the mandate of NCC did not extend to national park land.

(ii) *Suburban* (high impact): outside of the boundaries of the park is situated the Tokai suburb, an affluent part of Cape Town. This was the most developed part of the baboon home range and included residential houses, roads, commercial developments, horse farms, a country club and

offices belonging to the national park service. The baboons interacted with humans the most frequently when in these areas. Many of the interactions were of a conflict nature because baboons often raided private property and garbage at public access sites to obtain human-derived foods. The baboons were frequently chased by humans (both on foot and from vehicles) and their dogs in these areas. The residents used deterrents to try to keep the baboons away, including slingshots, paintball guns, shotguns, snares and noise deterrents such as firecrackers and bangers. The intensity of use of these deterrents varied throughout the months of the study. Most houses had high walls with either electric fencing or cut wire fences, both of which could injure the baboons. The baboons also used commercial roads with relatively heavy traffic, the crossing of which was associated with mortality among the baboons. Monitors followed the baboons on a regular basis when they ranged in these areas and were an additional source of conflict as they would usually attempt to herd the baboons back into the national park by chasing and shouting at them. Thus, overall, there were many potential sources of anthropogenic stress in these areas. It is important to note in this context that troops in the Cape Peninsula that spend more time on urban edges incur greater mortality and human-induced injuries, and this was the case in Tokai as well (Beamish, 2010; Beamish and O’Riain, 2014; Beamish, pers. comm.).

(iii) *Mixed areas* (medium impact): this category includes areas of natural vegetation, mostly outside of the boundaries of the national park, forming a mosaic of forested and human-frequented areas within the suburban areas. It also includes some parts of the national park that were located on the edges of the park, bordering suburban areas or vineyards. As an example, inside the forested area of the park was a small restaurant that the baboons were attracted to because of the food served there. Another example is a small patch of forest that lay between a road and a few houses, which was eventually partially cleared, but which was frequently used by the baboons. Mixed areas were therefore areas where contact with humans was greater than inside the national park but not as regular as in the suburban areas. Depending on which type of mixed area they were in, the baboons were sometimes followed and chased by monitors. These are therefore considered to be medium-impact areas, i.e. areas that may or may not be potential sources of stress for the baboons.

(iv) *Vineyards* (medium to high impact): to the northeast of and bordering the Tokai section of the national park are several agricultural farms that grow grapes for wine production. These vineyards were used by the baboons for several foods, including grapes, barley planted between vine rows, fruits in the residential gardens of farm workers and other resources naturally available (pine cones, weeds and water). The vineyards were variably protected from the baboons, but most intensely so during grape harvest season, between February and April. Vineyard workers often used aggressive methods to chase baboons, including shotguns, paintball guns, slingshots and firecrackers. Thus, the vineyards can represent relatively

high human impact areas, depending on the time of the year—at certain times such as during harvest season, the amount of conflict with humans is on par with the conflict experienced in the suburbs, whereas at other times it could be considered to be more similar to the lower levels of conflict experienced in the mixed areas.

Glucocorticoid data

We collected and analyzed a total of 695 faecal hormone samples. We collected faecal samples opportunistically in the field, as and when we saw females defecating, throughout observation hours. As diurnal variation in faecal GC metabolites is not significant in baboons (Beehner and Whitten, 2004), we did not control for variation in collection time. We pooled data for each month for each female because our aim was to assess chronic rather than acute stress. We collected the faecal samples in airtight plastic bags in the field and dried the samples at the end of each day at 90–100°C in a portable oven. We stored the dried samples in a –20°C freezer until they were transported back to the US for extraction and analysis.

Labwork was conducted by S.C. at the Smithsonian Conservation Biology Institute (SCBI) in Front Royal, VA. At the SCBI, we extracted GC hormones from 0.20 g of crushed individual faecal samples using the following method. We extracted the steroids in 90% ethanol, by adding 5 ml ethanol twice to the samples. The first addition of 5 ml ethanol was followed by 30 min of mixing on a rack shaker and 20 min of centrifugation at 2000 rpm. We collected the supernatant in a fresh tube and washed the pellet again in another 5 ml ethanol. This time, we hand-vortexed for 30 s and centrifuged at 2000 rpm for 15 min, then added the supernatant to the previously collected ethanol supernatant. Double washing of the faecal samples ensured removal of as much steroid as possible from the faecal matrix. The total 10 ml of liquid supernatant collected from each sample was then dried in an air hood under compressed air. We reconstituted the supernatant in 2.5–3 ml 100% ethanol, pulsed in a sonicator for a few seconds, then dried again with compressed air. We reconstituted it in 1 ml of PBS dilution buffer via sonication and stored all samples in a –20°C freezer until radioimmunoassay. The mean extraction efficiency was 78%.

We analyzed GC concentrations using a corticosterone I-125 radioimmunoassay kit (MP Biomedicals, Catalog No. 07-120102), following the methods of Wasser *et al.* (2000). This assay has previously been validated for use in baboons (Beehner and Whitten, 2004). We ran all assays in duplicates. The mean inter-assay coefficient of variation was 17.5% for the high control and 10.3% for the low control. The intra-assay coefficient of variation averaged 10.3%. We calculated mean monthly GC levels for each female (2.1 ± 1.5 samples/female) and used these monthly GC measures to determine associations with the mean percentage of time the baboons spent ranging in each habitat.

Data analysis

Ranging data

With the ranging data described above, we calculated the total amount of time spent in each location on each day and converted it to a percentage of total observation time. We used these ranging data to analyze how the monthly percentage of time spent in each location was associated with monthly GC levels. Because the troop used all types of habitats on any given day, we could not separate ranging data by time blocks within a day to determine the effects on GCs, but rather investigated the proportion of time spent ranging in each type of habitat on each day that we followed them. Unlike other studies that characterize entire groups as being located in disturbed or undisturbed habitats, we focused on variation within one troop over time in the amount of time spent in more versus less disturbed habitats.

Behavioural data

Our behavioural data derived from our focal samples, representing 604 h of focal observation data ($N = 2498$ total focal samples, mean of 7.4 ± 4.4 focal samples/female/month). We used the location that was recorded at the beginning of every focal sample as the habitat for that entire sample. Our data from the vineyards are not comparable to the data from the other habitats given the difficulty of conducting focal samples inside the vineyards. Visibility was poor in the vine fields, which often had dense foliage, and we frequently had to conduct observations from great distances due to our inability to access the baboons from closer proximity. Thus, the behavioural data from the vineyards may not be as reliable as the other data and may underestimate frequencies of behaviour, but we still include these data here for comparative purposes.

Activities: To determine overall activity budgets, or the amount of time spent in different activities at different locations, we calculated the amount of time spent in each of four activities—feeding, moving, socializing and passive—within each 15-min sample, to obtain the percentage of total focal observation time spent in the four activities. For each of the 16 focal females, we calculated the overall average amount of time she spent in each activity in each location based on all her focal samples.

Grooming bout: We calculated the length of each grooming bout within each focal sample. We defined a grooming bout as a continuous (without a break) period of grooming between two individuals (Silk *et al.* 1999, Barrett *et al.* 2000). If there was a break of 10 s, we would record a new bout of grooming. If the partners switched roles such that the groomee started grooming the groomer (even without a break), we coded this as a different bout. We calculated the average length of all grooming bouts within each sample and then compared average grooming bout lengths of the females across locations.

SDB rates: We calculated total SDB rates for each female by calculating the frequency with which the females exhibited

all self-directed behaviours (scratching, body-shaking, nose-touching, self-touching and yawning) in each focal sample. Even though some SDBs occur much more frequently than others, we lumped all the SDBs together to get rates of total SDBs.

Aggression: We calculated aggression rates in two ways. First, we tallied the frequency during focal samples of overt forms of aggression or threats, including lunging, eyebrow raising, chasing, fighting, physical attacks such as biting and other forms of aggressive contact. We divided this by the total sample time to obtain hourly rates of aggression for each focal sample. We used these data to compare the aggression rates experienced by individual females across habitats. Secondly, we calculated the total number of aggressive interactions that females were involved in with other adult females and males each day, using data from both focal samples and *ad libitum* data, and divided this by the total observation time for each day to yield estimates of daily aggression rates. From daily aggression rates, we calculated average aggression rates for each month.

Submission: To determine rates of submission, we used the more commonly observed submissive behaviours used by baboons. These included screaming and kecking, grimacing, fleeing and avoiding other individuals. We calculated the rate of submission within each focal sample in order to compare average submission rates of females by location.

We used matched-pair *t* tests and Wilcoxon signed-rank tests to compare each female's amount of time spent in a behaviour in one location to that in another location.

Dominance ranks: We determined dominance relationships for females based on all observations of agonism from focal samples and *ad libitum* observations. A winner was assigned only when it could be definitively determined based on the outcome of the interaction, i.e. when just one individual displayed submissive behaviour. Using the I&SI (Inconsistencies and Strength of Inconsistencies) method, implemented in the Excel package DomiCalc (Schmid and deVries, 2013), we calculated hierarchies for the females in each troop by combining agonism data in 3-month blocks. Dominance ranks in female baboons are known to be stable, and as such, we felt that combining data from 3 months gave an accurate representation of their rank. We calculated standardized ranks for each female by dividing that female's rank by the total number of adult females in the troop, then used these standardized ranks to assign females to one of three dominance rank categories in each month: high, medium and low. In the mixed models, we controlled for both rank and reproductive state as these are known to affect female GC levels.

Glucocorticoid data

We used log-transformed GC values for all analyses because the raw GC values were not normally distributed. However, we used raw (untransformed) GC levels for graphical repre-

Table 1: Correlation table for ranging in the four habitats

| | | National park | Suburb | Mixed | Vineyard |
|---------------|---------|---------------|--------|--------|----------|
| National park | r | 1 | | | |
| | P | | | | |
| Suburb | r_s | -0.853 | 1 | | |
| | P | 0.000* | | | |
| Mixed | r/r_s | 0.099 | -0.355 | 1 | |
| | P | 0.671 | 0.114 | | |
| Vineyard | r/r_s | 0.272 | -0.446 | -0.014 | 1 |
| | P | 0.234 | 0.043* | 0.951 | |
| | N | 21 | 21 | 21 | 21 |

sentation for ease of viewing. For each female, we obtained a mean monthly value for her GC concentration by averaging all samples obtained from her in that month. We used these monthly measures of GCs to construct our linear mixed models (LMM).

LMM construction to predict effects of ranging on GC levels

To determine the effects of habitat on GC levels, we used linear mixed models (LMMs). Because there may be effects of individual differences in females on GC levels, we included female identity as a random factor in the LMMs. The predictor variables were the monthly proportions of time spent ranging in each of the four categories of habitats: national parks, suburbs, mixed areas and vineyards. We used monthly measures for several reasons. First, because of the time lag between hormone secretion and metabolite excretion in faeces (known to peak at ~26 h in baboons (Wasser *et al.*, 2000)), we would have to use ranging data from one to two days prior to the day of faecal collection and we did not always have such data. Secondly, as we are not determining the effects of smaller-scale stressors of an acute nature, which can occur randomly on a given day to cause GC elevation, the more informative method is to determine baseline or average levels of GC hormones over a longer period of time so as to enable us to understand the longer-term impacts of ranging in anthropogenic versus natural habitats on chronic stress levels. A similar approach of using monthly aggregate GC data to determine its variation with ecological stressors has been taken in other studies (Strier *et al.* 1999; Engh *et al.* 2006; Gesquiere *et al.* 2008). Although temporally matched GC data can be useful for assessing the impact of behaviours such as aggression, long-term average GC data have been found to be more useful and robust for assessing impacts of general behavioural patterns in macaques (Edwards *et al.* 2013). If the baboons in general spent a larger proportion of time during a certain period in a specific area and during that time

they experienced higher overall levels of GCs, then this might suggest negative impacts of ranging in that habitat on health.

We tested for correlation between all ranging variables (Table 1) before determining the combination of predictor variables to use for each model, as highly correlated variables cannot be used in the same model. We used the cut-off suggested by Tabachnick and Fidell (2001) and did not incorporate two predictors in the same model if their absolute correlation was above 0.6. We thus built two separate models: one with ranging in each of national park, mixed areas and vineyards as predictor variables and another with only ranging in the suburbs as a predictor. Because rank and reproductive state are both known to influence GC levels in female baboons, we controlled for both these factors by including them as fixed factors in both models. We used the maximum likelihood method of estimation to evaluate the parameters in each model.

All data analyses were conducted in IBM SPSS 25.0. We report descriptive statistics as mean \pm SE.

Ethical note

This research complied with protocols approved by the Institutional Animal Care and Use Committee of Queens College of the City University of New York (Protocol #132, L. Swedell). This research was conducted with the permission of and following the guidelines of South African National Parks and adhered to the legal requirements of South Africa.

Results

Ranging

Overall, the MT1 troop spent the majority of its time in suburban areas (50.6%, Fig. 1). The next most frequently used areas were mixed areas (25.7%) and national park (16.6%), followed by ~7% of time spent in the vineyards.

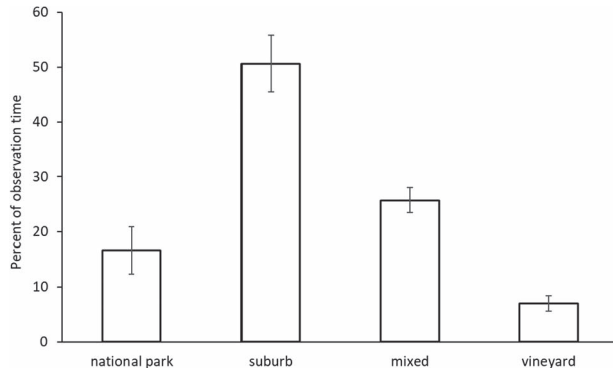


Figure 1: Percentage of total observation time spent in each habitat, Dec 2009–Sep 2011

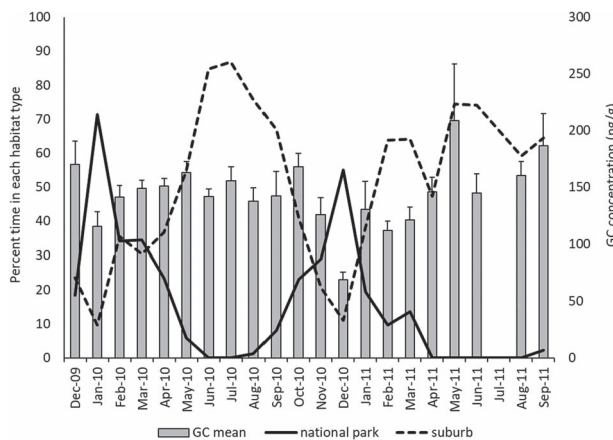


Figure 2: Monthly variation in proportion of time spent in national park (solid line) and suburb (dashed line) and in GC levels (filled-in bars; ng/g dry faeces) for all females ($N = 695$ samples), Dec 2009–Sep 2011

The ranging patterns of the MT1 troop underwent significant monthly variation (Figs 2 and 3). Suburban ranging was relatively high throughout all months of the study, with the greatest proportion of time spent there from May through September 2010, and again from February through September 2011. Mixed areas were used at relatively high frequencies throughout each month, with their use falling below 15% in only 4 out of 21 months. Use of areas within the national park was higher from January through March 2010, with almost three-quarters of their time spent there in January 2010, and again from October through December 2010, with more than half of their time spent there in December 2010. Ranging in the suburban areas was significantly and strongly negatively correlated with ranging in the national park ($r_s = -0.847$, $P < 0.001$; Table 1), i.e. in months when the troop spent more time ranging in the suburbs, they correspondingly spent much less time ranging in the national park. Vineyard use was typically below 20%, with no use of vineyards recorded at all during observation hours in certain months, including

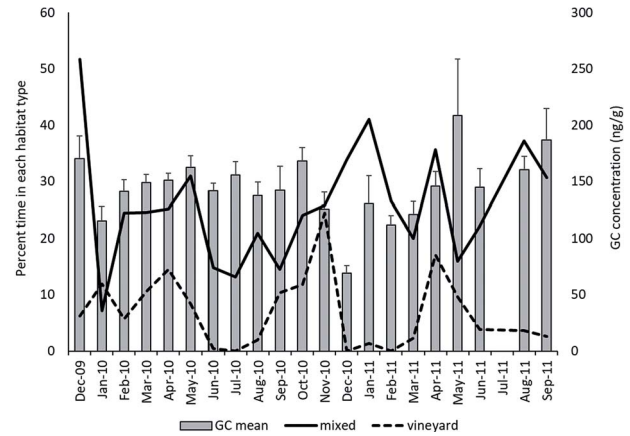


Figure 3: Monthly variation in proportion of time spent in mixed areas (solid line) and vineyards (dashed line) and in GC levels (filled-in bars; ng/g dry faeces) for all females ($N = 695$ samples), Dec 2009–Sep 2011

December 2010 and February 2011. Ranging in the vineyards was significantly negatively correlated with ranging in the suburbs ($r_s = -0.446$, $P = 0.043$; Table 1).

Activity budgets

The time spent by focal subjects in different activities varied by ranging location (Fig. 4). They spent significantly more time *feeding* when ranging in the suburbs (paired $t(15) = -7.413$, $P < 0.001$), mixed areas (paired $t(15) = -7.152$, $P < 0.001$) and vineyards (paired $t(15) = -8.825$, $P < 0.001$) compared to national park ranging. On the other hand, compared to ranging in national park, females spent significantly less time being *social* when ranging in all other habitats: suburbs (paired $t(15) = 5.862$, $P < 0.001$), mixed areas (paired $t(15) = 8.288$, $P < 0.001$) and vineyards (paired $t(15) = 12.073$, $P < 0.001$). Compared to when ranging in the national park, the females spent significantly less time being *inactive (passive)* when ranging in the suburbs (paired $t(15) = 3.972$, $P = 0.001$), mixed areas (paired $t(15) = 2.677$, $P = 0.017$) and vineyards (paired $t(15) = 4.632$, $P < 0.001$). Time spent *moving* did not differ significantly by location of ranging.

Grooming bouts

Grooming bout lengths differed between some habitats. Females had significantly shorter grooming bouts when ranging in mixed areas (158 ± 11 s) than when in the national park (179.1 ± 14.7 s; Wilcoxon $Z = -2.158$, $P = 0.031$). Grooming bouts were shorter in the suburbs (164 ± 8.4 s) than in the national park, but not significantly so. Grooming bouts were significantly shorter in the vineyards (116.8 ± 23 s) when compared to both the suburbs (paired $t(15) = 2.180$, $P = 0.046$) and national park (Wilcoxon $Z = -2.017$, $P = 0.044$). When we analyzed bouts of grooming with only other adult members of the group, we found signifi-

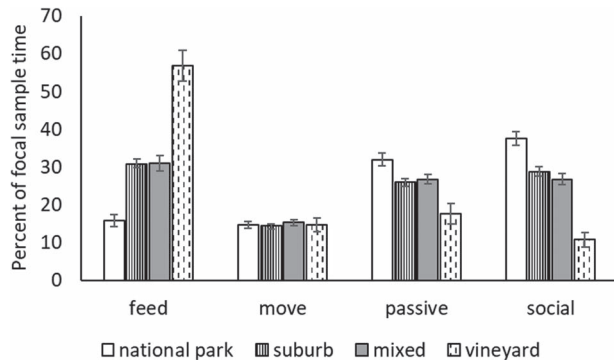


Figure 4: Mean (\pm SE) percent of focal sample time spent by females ($N = 16$) in each activity in each of national park, suburb, mixed areas and vineyard

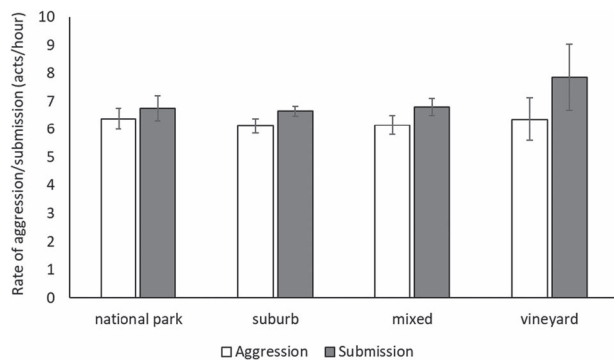


Figure 5: Mean (\pm SE) rates of aggression (open bars) and submission (shaded bars) experienced by females ($N = 16$) in each habitat (from focal data)

cant differences in the length of these bouts between vineyards and all other locations, with grooming bouts with adults being shorter in vineyards (100.1 ± 29.3 s) compared to national park (179.3 ± 16.6 s; Wilcoxon $Z = -2.327$, $P = 0.020$), suburb (179.9 ± 13.6 s; Wilcoxon $Z = -2.585$, $P = 0.010$) and mixed areas (180 ± 12 s; Wilcoxon $Z = -2.482$, $P = 0.013$).

Self-directed behaviour

The rate at which the female baboons performed self-directed behaviours differed by location. On average, females performed SDBs at a higher rate of $0.44 (\pm 0.02)$ SDBs/minute while ranging in the national park, compared to a rate of $0.38 (\pm 0.01)$ SDBs/minute when ranging in the suburbs, and this was a significant difference (paired $t(15) = 5.240$, $P < 0.001$). Similarly, they performed SDBs at a lower rate when ranging in the mixed areas (0.42 ± 0.02 SDBs/min) compared to ranging in national park, though this was not a significant difference. The rate at which they performed SDBs in mixed areas was significantly higher than in the suburbs (paired $t(15) = -2.956$, $P = 0.010$). There were no significant differences in rates of SDB between vineyards and other locations. Overall, therefore, it appears that self-directed

behaviours were performed at higher rates in national park and mixed areas, and at lower rates in the suburbs.

Aggression

Based on agonism data from focal samples only, agonism did not vary significantly between the four locations of the focal samples. Females experienced similar rates of aggression as well as similar rates of submission in all four types of habitats (Fig. 5).

However, analysis of variation in total monthly aggression rates, from both focal and *ad lib* data, did reveal some monthly differences across habitats. Total aggression rates within the troop were significantly positively correlated with time spent in suburban areas ($r = 0.564$, $P = 0.008$) and negatively correlated with time spent in mixed areas ($r = -0.436$, $P = 0.048$); total aggression, however, was not correlated with time spent in either national park or vineyard.

Glucocorticoids

Because ranging in the suburbs was correlated with ranging in both national park and vineyards, we built two different LMMs, one using time spent ranging in each of national park, mixed areas and vineyard, and the second using only ranging in suburbs. In both models we controlled for rank and reproductive state of the female. In the first model, reproductive state had a significant effect on GC levels. In addition, time spent ranging in the national park was a significant negative predictor of GC levels while time spent in the vineyards was a significant positive predictor of GC levels (Table 2; Figs 2 and 3). In the second model using only ranging in suburbs along with rank and reproductive state as predictor variables, we found an effect of reproductive state but not of rank. We also found that ranging in the suburbs was a significant positive predictor of GC levels (Table 2; Fig. 2).

Discussion

The baboons in this study ranged in a mosaic environment and spent varying amounts of time throughout the year in each of four habitat types, including protected areas within the national park, suburbs, vineyards and mixed areas with both natural and anthropogenic elements. Overall, the troop spent much more time in human-occupied or -influenced areas—~83% of their time in suburbs, mixed areas and vineyards combined—than they did within the boundaries of the national park (17%). As the amount of time spent in each of these areas changed, the baboons exhibited habitat-specific changes in two aspects of their biology: their glucocorticoid (GC) levels and their behaviour.

Firstly, our results demonstrate an association between habitat use and variation in the GC levels of the females in this troop. Ranging in areas where the baboons encountered more humans and experienced conflict with humans—suburbs and vineyards—was associated with higher concentrations of GC

Table 2: Results of linear mixed models examining whether ranging in the different habitats significantly predicted females' GC levels, while controlling for rank and reproductive state (we do not provide the estimates for each level of rank and reproductive state as they are not the focus of this study and instead provide only the significance values). Bolded text indicates statistical significance ($P < 0.05$)

| Predictor variables | Estimate | SE | t | P |
|---------------------------------------------------|----------|-------|--------|------------------|
| (Model also included rank and reproductive state) | | | | |
| Intercept | 2.218 | 0.037 | 59.152 | <0.001 |
| National park ranging | -0.0026 | 0.000 | -5.153 | <0.001 |
| Mixed areas ranging | -0.001 | 0.001 | -0.871 | 0.385 |
| Vineyard ranging | 0.004 | 0.001 | 2.927 | 0.004 |
| Rank | | | | 0.643 |
| Reproductive state | | | | 0.007 |
| (Model also included rank and reproductive state) | | | | |
| Intercept | 2.118 | 0.033 | 64.106 | <0.001 |
| Suburb ranging | 0.001 | 0.000 | 3.223 | 0.001 |
| Rank | | | | 0.712 |
| Reproductive state | | | | 0.005 |

metabolites, whereas ranging in national park was associated with lower GC levels. This troop is highly urban, spending about half its time in suburban areas, largely during the winter months. It increased its time spent in the suburbs in 2011 compared to 2010, and this can be largely or at least partially attributed to the loss of foraging ground and sleeping sites resulting from the clearing of the forest.

Many of the human encounters that the troop experienced outside of the national park were of an aggressive nature, with the baboons frequently coming into conflict with humans and receiving mild to intense forms of aggression. The baboon population in Tokai, in fact, experiences among the highest levels of human-induced mortality and injuries of the troops in the Cape Peninsula (Beamish, 2010). As an example of conflict levels, in March 2010, paintball gun and air gun use by residents and farm owners was recorded on 10 out of 19 observation days with this troop, and on many of those days, shots were recorded on multiple occasions within a day. While we cannot assess the acute effects of short timescale disturbances such as these on GC levels because we did not collect faecal samples from individual females every day, it is likely that these types of human disturbance were chronic stressors for the baboons. Supporting this notion is a study on vervet monkeys by Fourie *et al.* (2015), who found that males from suburban groups that received aggression from humans exhibited higher chronic GC levels compared to those from groups that did not. The results of our study support the hypothesis that proximity to humans—and in particular conflict with humans—may be associated with increases in the GC levels of animals, potentially reflecting the stressful nature of these human-wildlife interactions (Behie *et al.*, 2010; Marechal *et al.*, 2011; Jaimez *et al.*, 2012; Shutt *et al.*, 2014).

Secondly, our results demonstrate an association between habitat use and variation in behaviour. In human-modified landscapes, primates may make behavioural adjustments either to take advantage of a new resource or to cope with the costs of lower-quality habitats. In this study, time spent in more anthropogenic environments, including suburbs, mixed areas and vineyards, was associated with more feeding, less resting and less socializing, whereas time spent in the national park was associated with less feeding, more resting and more socializing. Despite differences among primate species and in study design, the greater time spent feeding in anthropogenic environments in our study does interestingly contrast with the findings of other studies reporting that primates spend less time feeding when in such habitats (e.g. Jaman and Huffman, 2013; Thatcher *et al.*, 2019). The fact that the baboons in this study spent more time feeding when in anthropogenic environments may be due to lower feeding efficiency in these areas due to the necessity of vigilance for human aggression (or baboon aggression; see below). Alternatively, the baboons may simply consume beyond their caloric requirements when in energy-rich environments. The Tokai baboons do appear to be larger in body mass compared to baboons from some other troops in the Cape Peninsula, especially compared to a troop in the southern Peninsula (Kanonkop) that ranges exclusively within protected areas (pers. obs.), suggesting a higher caloric intake in Tokai.

In contrast to the greater time spent feeding in anthropogenic environments, the baboons in this study spent less time socializing and resting when in these areas. A reduction in social time can have negative consequences for a species such as chacma baboons for which social bonds are extremely important and have adaptive benefits (Silk *et al.*, 2010a,b).

Other studies have also found that primates in disturbed habitats have less time to socialize because other activities take up more time (Aguilar-Melo *et al.*, 2013; Marty *et al.*, 2019), and this may be one cost of ranging in anthropogenic habitats. It also appears that the baboons in this study had less time to rest in human-influenced habitats, which could reduce their ability to conduct self-maintenance activities such as self-grooming. It is possible that the baboons' increase in feeding time in these areas imposed time constraints on social interactions. Additionally, the baboons may have had to spend more time being vigilant and monitoring human activities and may thus have been unable to maintain similar levels of social behaviour compared to when they were in protected areas. Kaburu *et al.* (2018) found that macaques have shorter grooming bouts when they interact more with humans, when they also spend more time being vigilant. We also see evidence of negative impacts on baboon sociality in the shorter length of grooming bouts in one type of anthropogenic environment, the mixed areas in Tokai. Despite being natural areas to some extent, these mixed areas lie in close proximity to humans, are used by people to a large extent and are also frequented by monitors, who chase the baboons. The unpredictable nature of human interactions in these areas may have resulted in more interruption of grooming bouts, leading to shorter grooming bout lengths overall.

Our data on self-directed or displacement behaviours (SDBs), which previous studies have suggested are useful behavioural measures of stress (Maestripieri *et al.*, 1992; Castles and Whiten, 1998; Troisi, 2002; Manson and Perry, 2003), contrasted with our expectations. We had predicted that females would experience higher SDB rates, reflecting higher levels of anxiety and psychosocial stress, when ranging in more anthropogenic environments, due not only to the aggressive interactions that occur with people but also as a result of heightened aggression among baboons within the group, as occurred in this study when the baboons ranged in some anthropogenic environments. Contrary to our expectations, we found higher rates of SDBs when females ranged in the national park than when they were in the suburbs.

Self-directed behaviours, however, do not always vary in similar ways across studies and conditions and in the manners predicted (e.g. Ellis *et al.*, 2011; Pearson *et al.*, 2015). A study on Barbary macaques found that scratching was related to some but not all measures of tourist pressure examined and did not necessarily follow similar patterns of GC response (Marechal *et al.*, 2011). In this study also, the relationship between SDB rates and habitat as a measure of anthropogenic effects was not straightforward. Females exhibited higher rates of SDB when they ranged in the national parks, i.e. when they in fact had lower GC levels, and lower rates of SDB in the suburbs when females experienced both higher GC levels and higher levels of intraspecific aggression. This counters the argument that SDBs function as straightforward correlates of stress. This is not surprising, however, as the relationship between behavioural factors (such as aggression,

psychosocial stress and SDB) and physiology (GC levels) is complex and frequently contradictory (Honest and Marin, 2006). Despite the positive association found between SDB rates and stress in many studies (Castles *et al.*, 1999; Troisi, 2002; Brand *et al.*, 2016), others have failed to find such an association (Higham *et al.*, 2009; Ellis *et al.*, 2011). There is variation among different self-directed behaviours, however, and it is likely that some SDBs may be used more than others in situations of stress and perhaps even depending on the type of stressor experienced. A study on Barbary macaques found that different types of SDB were used in different situations to cope with stress associated with tourism (Marechal *et al.*, 2016). In our study, we grouped all self-directed behaviours together, which may have concealed variation in the use of individual SDB types across habitats.

While we did not find any effect of ranging location on aggression levels when we analyzed aggression rates on an individual female basis, our results did reveal that total monthly aggression rates, using both focal and *ad libitum* data, were associated with anthropogenic environments: positively so with suburban areas and negatively so with mixed areas. These results are consistent with those of other studies, which have found that primates living in anthropogenic habitats with access to human sources of food experience higher levels of aggression than those in more naturalistic environments (Hill, 1999; Ram *et al.*, 2003; Hsu *et al.*, 2009; Scheun *et al.*, 2015). Provisioning and access to smaller packages of dense nutritious foods often lead to greater degrees of contest competition among group members, with associated increases in aggression levels (hamadryas baboons: Kamal *et al.*, 1997; Formosan macaques: Hsu *et al.*, 2009; bonnet macaques: Ram *et al.*, 2003; vervet monkeys: Brennan *et al.*, 1985). MT1 is the largest group in the area, and larger groups typically experience greater feeding competition (Sterck *et al.*, 1997); thus, it is possible that the concentrated sources of human foods in the suburbs increased contest competition and associated aggression among MT1 individuals. Higher aggression rates and associated vigilance may also explain the larger amount of time spent feeding in the suburbs. Aggression in rhesus macaques, for example, was found to be influenced both by aggressive behaviour from humans as well as from conspecifics (Beisner *et al.*, 2015).

A second explanation for increased aggression in suburban habitats in this study may lie in the underlying relatively high levels of aggression in the chacma baboon social system. Similar to other cercopithecine primates, chacma females maintain dominance hierarchies and experience contest competition over food (Barrett *et al.*, 2002). Additionally, chacma males are highly aggressive to females and frequently direct high levels of aggression towards them, which often include instances of redirected aggression whereby a male may attack a female even though unprovoked by her (Kitchen *et al.*, 2009). In the Cape Peninsula, where male baboons are frequently the target of aggression from humans and their domestic animals, there may be a greater likelihood of increased aggression among males as well as situations in which the males relieve their

stress by redirecting aggression towards females, as is known to occur in chacma baboons elsewhere (Kitchen *et al.*, 2009).

Our results revealed an increase in both aggression and GCs when the baboons spent more time in the suburbs compared to the national park. While these two measures were both independently associated with time spent in the suburbs, there may also be a causal link between them. When ranging in the suburbs, the baboons frequently received aggression of many types and levels from humans—from physical aggression (shooting with paintball and other guns, stone throwing) to being chased to loud vocalizations, all of which could exacerbate aggression among the baboons themselves. It is not uncommon to find positive feedback between human aggression and non-human primate aggression (e.g. in macaques, Beisner *et al.*, 2015). Supporting this notion, a study on howler monkeys found that even though agonism was only slightly higher in unprotected versus protected areas, GC levels were significantly higher in individuals that participated in agonism in unprotected areas (Rangel-Negrin *et al.*, 2014).

A unique feature of this study is that, unlike other studies that have compared groups in disturbed or urban habitats with groups in undisturbed or rural habitats, we are able to demonstrate here how variation in home range use over time within a single group can affect the behaviour and glucocorticoid levels of its members. Such variation may be more prevalent in more seasonal environments such as the one inhabited by the baboons in this study, where time spent in the national park versus the suburban areas varied on a seasonal basis, with corresponding implications for contact with humans. As the world becomes increasingly heterogeneous over space and time due to both climate change and a reduction in clear-cut distinctions between natural and urban habitats (Ellis and Ramankutty, 2008), studies such as this can contribute greatly towards understanding the biological consequences of living in these mosaic anthropogenic environments. The results of this study also demonstrate the importance of determining the effects of different types of anthropogenic environments on animals. Not all anthropogenic environments are the same, and there may be significant qualitative differences between these habitats that may differentially affect animal behaviour and physiology, as we found in Tokai among suburbs, mixed areas and vineyards.

Changes in GC levels are often used as a proxy for negative fitness consequences (Bonier *et al.* 2010). Elevated GCs, however, may in fact be a signal of effective adaptive responses that enable individuals to survive challenge and achieve higher fitness (Beehner and Bergman, 2017). Although the relationship between GC levels and fitness is not straightforward, fluctuations in GCs are informative and often do indicate important consequences of stressors. As with all studies of the relationship between physiology and behaviour, therefore, this study should be interpreted with caution for several reasons. First, GC responses may differ across species and among populations of the same species. GC concentrations

do not always change in predictable directions in response to stressors. There may be multiple confounding factors in the natural environments of animals that affect GC levels in different ways and thus may or may not cause measurable changes in GCs over time (Dantzer *et al.*, 2014). In Tokai, for example, the baboons spent more time near human-frequented areas during the winter months and more time in the national park during the summer. Thus, seasonal differences in temperature and rainfall may play a role in their stress response. Additionally, animals may acclimate over time to chronic stressors and not exhibit the expected stress response because they may no longer perceive the stressor as such (Romero, 2004). It is also possible that animals exposed to chronic stressors may become incapable of mounting an appropriate stress response due to diminished functioning of the HPA axis, which in itself can be maladaptive. Thus, a reduction in GC levels does not necessarily imply beneficial adaptation to the conditions and may instead reflect dysregulation of the HPA axis (Romero, 2004). Even in cases of assumed habituation due to lack of any evidence of elevated GCs, the results should be interpreted carefully as presumed habituation may simply reflect differences in tolerance levels of animals to anthropogenic disturbance (Bejder *et al.*, 2009). Finally, although some researchers have pointed out that the relationship between disturbance and GCs is not straightforward (Busch and Hayward, 2009), others have argued that GC levels may in fact be among the most important of measures of responses to anthropogenic stressors, emphasizing the need to study GC responses across taxa because individual species vary in their responses to anthropogenic stressors (Tarlow and Blumstein, 2007).

Most primate populations live in habitats that have been impacted by humans in some way, and it is vital to study and understand the effects of these anthropogenic factors if we are to foster the sustainability of primate populations (Fuentes, 2012; Dore *et al.*, 2017; Riley, 2018). Generalist taxa such as baboons are the types of species that are expected to be able to cope the best with anthropogenic change because of their ability to adapt, in contrast to more specialized taxa. Already, there has been a worldwide decline in the number of specialist species (Clavel *et al.*, 2010). Therefore, any evidence suggesting that generalist species such as baboons are being negatively impacted by anthropogenic changes, such that their physiology and behaviour are affected in negative ways, may be an indicator of far worse effects on less generalist species. The baboons in Tokai are clearly habituated to human presence, but it appears that their stress response has not been correspondingly attenuated. It is likely that, despite being habituated to the presence of humans overall, the baboons are not habituated to the types of conflict interactions that they experience in this area. The situation of the Cape Peninsula baboons is not a unique one, yet their dire status from a conservation perspective has been noted (Strum, 2012). The results of this study suggest that successful management of baboon populations in the Cape Peninsula requires inclusion of conflict mitigation strategies to minimize anthropogenic

interactions, particularly of an aggressive nature. Even though baboons are not yet a threatened taxon, as we close the gap between human and wildlife habitats, baboons may stop thriving in human-modified environments and the negative consequences of anthropogenic interactions, such as elevated GCs, may outweigh any benefits obtained from living in proximity to humans, potentially threatening their long-term survival.

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References

- Abondano LA, Link A (2012) The social behavior of brown spider monkeys (*Ateles hybridus*) in a fragmented forest in Colombia. *Int J Primatol* 33: 769–783.
- Aguilar-Melo AR, Andresen E, Cristobal-Azkarate J, Arroyo-Rodriguez V, Chavira R, Schondube J, Serio-Silva JC, Cuarón AD (2013) Behavioral and physiological responses to subgroup size and number of people in howler monkeys inhabiting a forest fragment used for tourism. *Am J Primatol* 75: 1108–1116.
- Ahlering MA, Millsbaugh JJ, Woods RJ, Western D, Eggert LS (2011) Elevated levels of stress hormones in crop-raiding male elephants. *Anim Conserv* 14: 124–130.
- Alberts SC, Altmann J (2006) The evolutionary past and the research future: environmental variation and life history flexibility in a primate lineage. In L Swedell, S Leigh, eds, *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*. Springer, New York, pp. 277–303.
- Almeida-Rocha JM, Peres CA, Oliveira LC (2017) Primate responses to anthropogenic habitat disturbance: a pantropical meta-analysis. *Biol Conserv* 215: 30–38.
- Altmann SA (1973) The pregnancy sign in savannah baboons. *J Zoo Anim Med* 4: 8–12.
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.
- Anselme P (2008) Abnormal patterns of displacement activities: a review and reinterpretation. *Behav Process* 79: 48–58.
- Arlettaz R, Patthey P, Baltic M, Leu T, Schaub M, Palme R, Jenni-Eiermann S (2007) Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proc R Soc B* 274: 1219–1224.
- Barja I, Silvan G, Rosellini S, Pineiro A, Gonzalez-Gil A, Camachob L, Illera JC (2007) Stress physiological responses to tourist pressure in a wild population of European pine marten. *Journal Steroid Biochem & Mol Biol* 104: 136–142.
- Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (2000) Female baboons do not raise stakes but they give as good as they get. *Anim Behav* 59: 763–770.
- Barrett L, Gaynor D, Henzi SP (2002) A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Anim Behav* 63: 1047–1053.
- Beamish EK (2010) Causes and consequences of mortality and mutilation in the Cape Peninsula baboon population, South Africa. M.Sc. thesis, University of Cape Town, Cape Town, South Africa.
- Beamish EK, O'Riain MJ (2014) The effects of permanent injury on the behavior and diet of commensal chacma baboons (*Papio ursinus*) in the Cape Peninsula, South Africa. *Int J Primatol* 35: 1004–1020.
- Beehner JC, Whitten PL (2004) Modifications of a field method for fecal steroid analysis in baboons. *Physiol Behav* 82: 269–277.
- Beehner JC, Bergman TJ (2017) The next step for stress research in primates: to identify relationships between glucocorticoid secretion and fitness. *Horm Behav* 91: 68–83.
- Behie AM, Pavelka MSM, Chapman CA (2010) Sources of variation in fecal cortisol levels in howler monkeys in Belize. *Am J Primatol* 72: 600–606.
- Beisner BA et al. (2015) Human-wildlife conflict: proximate predictors of aggression between humans and rhesus macaques in India. *Am J Phys Anthropol* 156: 286–294.
- Bejder L, Samuels A, Whitehead H, Finn H, Allen S (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar Ecol Prog Ser* 395: 177–185.
- Bhattacharjee S, Kumar V, Chandrasekhar M, Malviya M, Ganswindt A, Ramesh K, Sankar K, Umopathy G (2015) Glucocorticoid stress responses of reintroduced tigers in relation to anthropogenic disturbance in Sariska Tiger Reserve in India. *PLoS One* 10: e0127626. doi: 10.1371/journal.pone.0127626.
- Bielert C, Busse C (1983) Influences of ovarian hormones on the food intake and feeding of captive and wild female chacma baboons (*Papio ursinus*). *Physiol Behav* 30: 103–111.

- Bonier F, Martin PR, Moore IT, Wingfield JC (2010) Clarifying the Cort-Fitness Hypothesis: a response to Dingemanse *et al.* *Trends Ecol Evol* 25: 262–263.
- Brand CM, Boose KJ, Squires EC, Marchant LF, White FJ, Meinelt A, Snodgrass JJ, (2016) Hair plucking, stress, and urinary cortisol among captive bonobos (*Pan paniscus*). *Zoo Biol* 35: 415–422.
- Brennan EJ, Else JG, Altmann J (1985) Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. *Afr J Ecol* 23: 35–44.
- Bryson-Morrison N, Tzanopoulos J, Matsuzawa T, Humle T (2017) Activity and habitat use of chimpanzees in the anthropogenic landscape of Bossou, Guinea, West Africa. *Int J Primatol* 38: 282–302.
- Busch DS, Hayward LS (2009) Stress in a conservation context: a discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biol Conserv* 142: 2844–2853.
- Carlitz EHD, Miller R, Kirschbaum C, Gao W, Hanni DC, van Schaik CP (2016) Measuring hair cortisol concentrations to assess the effect of anthropogenic impacts on wild chimpanzees (*Pan troglodytes*). *PLoS One* 11: e0151870.
- Castles DL, Whiten A (1998) Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology* 104: 148–160.
- Castles DL, Whiten A, Aureli F (1999) Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Anim Behav* 58: 1207–1215.
- Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006) Do food availability, parasitism, and stress have synergistic effects on red Colobus populations living in forest fragments? *Am J Phys Anthropol* 131: 525–534.
- Clavel J, Julliard R, Devictor V (2010) Worldwide decline of specialist species: toward a global functional homogenization? *Front Ecol Environ* 9: 222–228.
- Cowling RM, MacDonald IAW, Simmons MT (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodivers Conserv* 5: 527–550.
- Creel S, Fox JE, Hardy A, Sands J, Garrott B, Peterson RO (2002) Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conserv Biol* 16: 809–814.
- Dantzer B, Fletcher QE, Boonstra R, Sheriff MJ (2014) Measures of physiological stress: a transparent or opaque window into the status, management and conservation of species? *Conserv Physiol* 2: 1–18.
- DeVore I, Washburn SL (1963) Baboon ecology and human evolution. In FC Howell, F Bourliere, eds, *African Ecology and Human Evolution*. Aldine, Chicago, pp. 335–367.
- Dore KM, Riley EP, Fuentes A (eds) (2017) *Ethnoprimatology: A Practical Guide to Research on the Human-Nonhuman Primate Interface*. Cambridge University Press, Cambridge.
- Drewe JA, O’Riain MJ, Beamish E, Currie H, Parsons S (2012) Survey of infections transmissible between baboons and humans, Cape Town, South Africa. *Emerg Infect Dis* 18: 298–301.
- Ellis, Ramankutty N (2008) Putting people in the map: anthropogenic biomes of the world. *Front Ecol Environ* 6: 439–447.
- Ellis JJ, MacLarnon AM, Heistermann M, Semple S (2011) The social correlates of self-directed behavior and faecal glucocorticoid levels among adult male olive baboons (*Papio hamadryas anubis*) in Gashaka-Gumti National Park, Nigeria. *Afr Zool* 46: 302–308.
- Engl AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006) Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc R Soc B* 273: 707–712.
- Estrada A *et al.* (2017) Impending extinction crisis of the world’s primates: why primates matter. *Sci Adv* 3: e1600946. doi: 10.1126/sciadv.1600946.
- Edwards KL, Walker SL, Bodenham RF, Ritchie H, Shultz S (2013) Associations between social behavior and adrenal activity in female Barbary macaques: consequences of study design. *Gen Comp Endocr* 186: 72–79.
- Fokidis HB, Orchinik M, Deviche P (2009) Corticosterone and corticosteroid binding globulin in birds: relation to urbanization in a desert city. *Gen Comp Endocr* 160: 259–270.
- Fourie NH, Turner TR, Brown JL, Pampush JD, Lorenz JG, Bernstein RM (2015) Variation in vervet (*Chlorocebus aethiops*) hair cortisol concentrations reflects ecological disturbance by humans. *Primates* 56: 365–373.
- Fuentes A (2012) Ethnoprimatology and the anthropology of the human-primate interface. *Annu Rev Anthropol* 41: 101–117.
- Fuentes A, Wolfe LD (eds) (2002) *Primates Face to Face: The Conservation Implications of Human-Nonhuman Primate Interconnections*. Cambridge University Press, Cambridge.
- Gesquiere LR, Khan M, Shek L, Wango TL, Wango EO, Alberts SC, Altmann J (2008) Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). *Horm Behav* 54: 410–416.
- Gomez-Espinosa E, Rangel-Negrin A, Chavira R, Canales-Espinosa D, Dias PAD (2014) The effect of energetic and psychosocial stressors on glucocorticoids in mantled howler monkeys (*Alouatta palliata*). *Am J Primatol* 76: 362–373.
- Henzi SP, Barrett L (2005) The historical socio-ecology of savannah baboons. *J Zool* 265: 215–226.
- Higham JP, MacLarnon AM, Heistermann M, Ross C, Semple S (2009) Rates of self-directed behavior and faecal glucocorticoid levels are not correlated in wild female olive baboons (*Papio hamadryas anubis*). *Stress* 12: 526–532.

- Hill DA (1999) Effects of provisioning on the social behavior of Japanese and rhesus macaques: implications for socioecology. *Primates* 40: 187–198.
- Hill CM (2000) Conflict of interest between people and baboons: crop raiding in Uganda. *Int J Primatol* 21: 299–315.
- Hill CM, Webber AD, Priston NEC (eds) (2017) *Understanding Conflicts about Wildlife: A Biosocial Approach*. Berghahn Books, New York.
- Hockings KJ, Humle T (2009) *Best Practice Guidelines for the Prevention and Mitigation of Conflict Between Humans and Great Apes*. IUCN/SSC Primate Specialist Group (PSG), Gland.
- Hoffman TS, O'Riain MJ (2011) The spatial ecology of chacma baboons (*Papio ursinus*) in a human-modified environment. *Int J Primatol* 32: 308–328.
- Hoffman TS, O'Riain MJ (2012) Monkey management: using spatial ecology to understand the extent and severity of human–baboon conflict in the Cape Peninsula, South Africa. *Ecol Soc* 17: 13.
- Honess PE, Marin CM (2006) Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neurosci Biobehav R* 30: 390–412.
- Hsu MJ, Kao C, Agoramoorthy G (2009) Interactions between visitors and Formosan macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. *Am J Primatol* 71: 214–222.
- Hulme-Beaman A, Dobney K, Cucchi T, Searle JB (2016) An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends Ecol Evol* 31: 633–645.
- Humle T, Hill C (2016) People–primate interactions: implications for primate conservation. In SA Wich, AJ Marshall, eds, *An Introduction to Primate Conservation*. Oxford University Press, Oxford, pp. 219–240.
- Jaimez NA, Bribiescas RG, Aronsen GP, Anestis SA, Watts DP (2012) Urinary cortisol levels of gray-cheeked mangabeys are higher in disturbed compared to undisturbed forest areas in Kibale National Park, Uganda. *Anim Conserv* 15: 242–247.
- Jaman MF, Huffman MA (2013) The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques in Bangladesh. *Primates* 54: 49–59.
- Jolly CJ (2001) A proper study for mankind: analogies from the Papionin monkeys and their implications for human evolution. *Am J Phys Anthropol* 116: 177–204.
- Junge RE, Barrett MA, Yoder AD (2011) Effects of anthropogenic disturbance on indri health in Madagascar. *Am J Primatol* 73: 632–642.
- Kaburu SSK, Marty PR, Beisner B, Balasubramaniam K, Bliss-Moreau E, Kaur K, Mohan L, McCowan B (2018) Rates of human–macaque interactions affect grooming behavior among urban-dwelling rhesus macaques (*Macaca mulatta*). *Am J Phys Anthropol* 168: 92–103.
- Kamal KB, Boug A, Brain PF (1997) Effects of food provisioning on the behavior of commensal hamadryas baboons, *Papio hamadryas*, at Al Hada Mountain in western Saudi Arabia. *Zool Middle East* 14: 11–22.
- Kansky R, Gaynor D (2000) Baboon management strategy for the Cape Peninsula. *Final report, Table Mountain Fund Project number ZA 568, World Wide Fund for Nature, Cape Town, South Africa*.
- Kaplan BS, O'Riain MJ, van Eeden R, King AJ (2011) A low-cost manipulation of food resources reduces spatial overlap between baboons (*Papio ursinus*) and humans in conflict. *Int J Primatol* 32: 1397–1412.
- Kitchen DM, Beehner JC, Bergman TJ, Cheney DL, Crockford C, Engh AL, Fischer J, Seyfarth RM, Wittig RM (2009) The causes and consequences of male aggression directed at female chacma baboons. In MN Muller, RW Wrangham, eds, *Sexual Coercion in Primates and Humans: an Evolutionary Perspective on Male Aggression Against Females*. Harvard University Press, Cambridge, pp. 128–156.
- Kutsukake N (2003) Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behaviour. *Behaviour* 140: 1153–1171.
- Leche A, Bazzano G, Hansen C, Navarro JL, Marin RH, Martella MB (2014) Stress in wild Greater Rhea populations *Rhea americana*: effects of agricultural activities on seasonal excreted glucocorticoid metabolite levels. *J Ornithol* 155: 919–926.
- Leite GC, Duarte MHL, Young RJ (2011) Human–marmoset interactions in a city park. *Appl Anim Behav Sci* 132: 187–192.
- Lutz C, Well A, Novak M (2003) Stereotypic and self-injurious behavior in rhesus macaques: a survey and retrospective analysis of environment and early experience. *Am J Primatol* 60: 1–15.
- Lutz CK, Williams PC, Sharp RM (2014) Abnormal behavior and associated risk factors in captive baboons (*Papio hamadryas* spp.). *Am J Primatol* 76: 355–361.
- Maestripieri D, Schino G, Aureli F, Troisi A (1992) A modest proposal: displacement activities as an indicator of emotions in primates. *Anim Behav* 44: 967–979.
- Manson JH, Perry S (2003) Correlates of self-directed behaviour in wild white-faced capuchins. *Ethology* 106: 301–317.
- Marchal V, Hill C (2009) Primate crop-raiding: a study of local perceptions in four villages in North Sumatra, Indonesia. *Primate Conserv* 24: 107–116.
- Marechal L, Semple S, Majolo B, Qarro M, Heistermann M, MacLarnon A (2011) Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. *Biol Conserv* 144: 2188–2193.
- Marechal L, MacLarnon A, Majolo B, Semple S (2016) Primates' behavioural responses to tourists: evidence for a trade-off between potential risks and benefits. *Sci Rep - UK* 6: 32465.
- Martinez-Mota R, Valdespino C, Sanchez-Ramos MA, Serio-Silva JC (2007) Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Anim Conserv* 10: 374–379.

- Marty PR *et al.* (2019) Time constraints imposed by anthropogenic environments alter social behaviour in longtailed macaques. *Anim Behav* 150: 157–165.
- McKinney T (2011) The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 73: 439–448.
- McLennan MR, Spagnoletti N, Hockings KJ (2017) The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *Int J Primatol* 38: 105–121.
- Millsaugh JJ, Woods RJ, Hunt KE, Raedeke KJ, Brundige GC, Washburn BE, Wasser SK (2001) Fecal glucocorticoid assays and the physiological stress response in elk. *Wildlife Soc B* 29: 899–907.
- Mtoka S, Ngongolo K, Mahulu A (2014) Human-baboon conflicts inside protected areas, some glance from Kingupira Camp, Selous Game Reserve, Tanzania. *J Zool Biosci Res* 1: 32–36.
- Muehlenbein MP, Ancrenaz M, Sakong R, Ambu L, Prall S, Fuller G, Raghanti MA (2012) Ape conservation physiology: fecal glucocorticoid responses in wild *Pongo pygmaeus morio* following human visitation. *PLoS One* 7: e33357. doi: 10.1371/journal.pone.0033357.
- Naughton-Treves L (1998) Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conserv Biol* 12: 156–168.
- Nelson RJ, ed. (2005) *An Introduction to Behavioral Endocrinology*, Third Edition. Sinauer Associates, Inc. Sunderland, Massachusetts.
- Nyhus PJ (2016) Human-wildlife conflict and coexistence. *Annu Rev Env Resour* 41: 143–171.
- Palagi E, Norsci I (2011) Scratching around stress: hierarchy and reconciliation make the difference in wild brown lemurs (*Eulemur fulvus*). *Stress* 141: 93–97.
- Pavani S, Maestripiéri D, Schino G, Turillazzi PG, Scucchi S (1991) Factors influencing scratching behaviour in long-tailed macaques (*Macaca fascicularis*). *Folia Primatol* 57: 34–38.
- Pearson BL, Reeder DM, Judge PG (2015) Crowding increases salivary cortisol but not self-directed behavior in captive baboons. *Am J Primatol* 77: 462–467.
- Priston NEC, Wyper RM, Lee PC (2012) Buton macaques (*Macaca ochreata brunnescens*): crops, conflict, and behavior on farms. *Am J Primatol* 74: 29–36.
- Radhakrishna S, Huffman MA, Sinha A (eds) (2013) *The Macaque Connection: Cooperation and Conflict between Humans and Macaques*. Springer, New York.
- Ram S, Venkatachalam S, Sinha A (2003) Changing social strategies of wild female bonnet macaques during natural foraging and on provisioning. *Curr Sci* 84: 780–790.
- Rangel-Negrin A, Alfaro JL, Valdez RA, Romano MC, Serio-Silva JC (2009) Stress in Yucatan spider monkeys: effects of environmental conditions on fecal cortisol levels in wild and captive populations. *Anim Conserv* 12: 496–502.
- Rangel-Negrin A, Coyohua-Fuentes A, Chavira R, Canales-Espinosa D, Dias PAD (2014) Primates living outside protected habitats are more stressed: the case of black howler monkeys in the Yucatan Peninsula. *PLoS One* 9: e112329. doi: 10.1371/journal.pone.0112329.
- Riley EP (2007) The human–macaque interface: conservation implications of current and future overlap and conflict in Lore Lindu National Park, Sulawesi, Indonesia. *Am Anthropol* 109: 473–484.
- Riley EP (2018) The maturation of ethnoprimateology: theoretical and methodological pluralism. *Int J Primatol* 39: 705–729.
- Rimbach R, Link A, Heistermann M, Gómez-Posada C, Galvis N, Heymann EW (2013) Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. *Conserv Physiol* 1: 1–11.
- Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. *Trends Ecol Evol* 19: 249–255.
- Sapolsky RM, Romero LM, Munck AU (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev* 21: 55–89.
- Scheun J, Bennett NC, Ganswindt A, Nowack J (2015) The hustle and bustle of city life: monitoring the effects of urbanisation in the African lesser bushbaby. *Naturwissenschaften*. 102: 57.
- Schino G, Scucchi S, Maestripiéri D, Turillazzi PG (1988) Allogrooming as a tension-reduction mechanism: a behavioral approach. *Am J Primatol* 16: 43–50.
- Schmid VS, de Vries H (2013) Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. *Anim Behav* 86: 1097–1105.
- Schweitzer C, Gaillard T, Guerbois C, Fritz H, Petit O (2017) Participant profiling and pattern of crop-foraging in chacma baboons (*Papio hamadryas ursinus*) in Zimbabwe: why does investigating age–sex classes matter? *Int J Primatol* 38: 207–223.
- Shutt K *et al.* (2014) Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biol Conserv* 172: 72–79.
- Silk JB, Seyfarth RM, Cheney DL (1999) The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour* 136: 679–703.
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010a) Female chacma baboons form strong, equitable, and enduring social bonds. *Behav Ecol Sociobiol* 64: 1733–1747.
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010b) Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* 20: 1359–1361.
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41: 291–309.
- Strier KB, Ziegler TE, Wittwer DJ (1999) Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Horm Behav* 35: 125–134.

- Strum SC (2010) The development of primate raiding: implications for management and conservation. *Int J Primatol* 31: 133–156.
- Strum SC (2012) Darwin's monkey: why baboons can't become human. *Am J Phys Anthropol* 149: 3–23.
- Strum SC, Mitchell W (1987) Baboon models and muddles. In WG Kinzey, ed, *The Evolution of Human Behavior: Primate Models*. State University of New York Press, New York, pp. 87–104
- Swedell L (2011) African Papionins: diversity of social organization and ecological flexibility. In C Campbell, A Fuentes, K MacKinnon, S Bearder, R Stumpf, eds, *Primates in Perspective*, EdEd 2. Oxford University Press, New York, pp. 241–277.
- Tabachnick BG, Fidell LS (2001) *Using Multivariate Statistics*, Ed 4. Harper-Collins, New York.
- Tarlow EM, Blumstein DT (2007) Evaluating methods to quantify anthropogenic stressors on wild animals. *Appl Anim Behav Sci* 102: 429–451.
- Thatcher HR, Downs CT, Koyama NF (2019) Anthropogenic influences on the time budgets of urban vervet monkeys. *Landscape Urban Plan* 181: 38–44.
- Thiel D, Jenni-Eiermann S, Braunisch V, Palme R, Jenni L (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *J Appl Ecol* 45: 845–853.
- Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C (2017) Future threats to biodiversity and pathways to their prevention. *Nature* 546: 73–81.
- Troisi A (2002) Displacement activities as a behavioral measure of stress in nonhuman primates and human subjects. *Stress* 5: 47–54.
- Troisi A, Schino G, Dantoni M, Pandolfi N, Aureli F, Damato FR (1991) Scratching as a behavioral index of anxiety in macaque mothers. *Behav Neural Biol* 56: 307–313.
- Vanlangendonck N, Nuñez G, Chaves A, Gutiérrez-Espeleta GA (2015) New route of investigation for understanding the impact of human activities on the physiology of non-human primates. *J Primatol* 4: 2.
- Van Meter PE, French JA, Dloniak SM, Watts HE, Kolowski JM, Holekamp KE (2009) Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Horm Behav* 55: 329–337.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science* 277: 494–499.
- Wasser SK, Bevis K, King G, Hanson E (1997) Noninvasive physiological measures of disturbance in the northern spotted owl. *Conserv Biol* 11: 1019–1022.
- Wasser S, Hunt K, Brown J, Cooper K, Crockett C, Bechert U, Millspaugh J, Larson S, Monfort S (2000) A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocr* 120: 260–275.
- Whiten A, Byrne RW, Henzi SP (1987) The behavioral ecology of mountain baboons. *Int J Primatol* 8: 367–388.
- Woodroffe R, Thirgood S, Rabinowitz A (eds) (2005) *People and Wildlife: Conflict or Coexistence?* Cambridge University Press, Cambridge.
- Yihune M, Bekele A, Tefera Z (2009) Human–gelada baboon conflict in and around the Simien Mountains National Park, Ethiopia. *Afr J Ecol* 47: 276–282.
- Zisadza-Gandiwa P, Gandiwa E, Muboko N (2016) Preliminary assessment of human–wildlife conflicts in Maramani Communal Area, Zimbabwe. *Afr J Ecol* 54: 500–503.