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Adaptive space use by baboons (*Papio ursinus*) in response to management interventions in a human-changed landscape

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Abstract

Growing human populations are increasingly competing with wildlife for limited resources and this can result in chronic human–wildlife conflict. In the Cape Peninsula, South Africa, chacma baboons *Papio ursinus* are habitual raiders of urban and rural areas, foraging on a variety of human-derived foods. Raiding behaviour is considered a threat to human health and safety, may result in damage to property, and has adverse welfare and conservation impacts on baboons. To mitigate this conflict, Cape Town municipality employs field rangers with paintball markers that 'herd' baboons away from the urban edge. While this strategy is successful in reducing the time baboons spend in urban spaces, baboons still raid successfully. Here, we use direct observation and GPS data to investigate how one troop uses the peri-urban space and exploits human-derived foods in urban areas and on farmland. We contrast this behaviour with the individual management strategies adopted by field rangers which we assessed in individual interviews. We find that baboons utilize space (1) where inter-individual variation in field ranger management strategy is highest, (2) that is close to refuges in forested habitat and (3) that is close to the urban edge. Overall, this suggests adaptive space use by the baboons, whereby they minimize distances to refuges and potential food rewards, while exploiting uncertainty in risk variability that arises due to inter-individual differences in ranger management strategy. Together these results highlight the need for ranger consensus to reinforce management efficiency when dealing with a highly adaptive primate.

Introduction

With the growth of the human population, transition zones between small protected natural areas and human landscapes are eroding (Woodroffe & Ginsberg, 1998). This often results in more frequent human–wildlife interactions (Creachbaum, Johnson & Schmidt, 1998; Seiler, 2005; Gurung *et al.*, 2008) which can have negative consequences for both people and wildlife and manifest in chronic human–wildlife conflict (HWC; Marker, Mills & Macdonald, 2003; Nijman & Nekaris, 2010; Redpath *et al.*, 2013; Takahata *et al.*, 2014). Raiding behaviour – where animals venture into human-changed landscapes to exploit high energy food resources – is one of the most frequent drivers of HWC, and its occurrence is dependent upon the relative costs and benefits associated with raiding (Palmeira *et al.*, 2008; Webber *et al.*, 2011; Beamish & O'Riain, 2014; Fourie *et al.*, 2015). Where the benefits of acquiring resources in human-changed landscapes outweigh potential costs, wildlife populations alter their home range to increase their spatial overlap with human-dominated landscapes to exploit these new food sources (Barnagaud *et al.*, 2011; Sih, 2013).

Among raiding species, primates are exceptionally difficult to manage because of their diverse modes of locomotion, dexterity and problem solving (Naughton Treves, 1998; Nijman & Nekaris, 2010). For instance, deterrents have to be regularly interchanged because of rapid habituation (Hill & Wallace, 2012) and standard fences do not act as barriers because of climbing abilities (Hoffman & O'Riain, 2010). Some of the most high profile and severe cases of HWC involving primates occur with baboons (*Papio* spp.) which are viewed as pests throughout the African continent (Webber & Hill, 2014). Indeed, crop-raiding baboons may damage up to 2774 m^2 of crops per raiding event (Naughton Treves, 1998), and human resources may comprise as much as 58% of their diet in some Southern African populations (Strum, 2010). As such, baboons and their raiding behaviour often lead to severe losses for local economies.

In the Cape Peninsula, South Africa, the lack of a buffer area between the Table Mountain National Park (TMNP) and the city of Cape Town results in high levels of spatial overlap between people and baboons (Hoffman & O'Riain, 2012*a*). A lack of by-laws to enable the efficient policing of resident behaviour and properties adjacent to TMNP translates into baboons exploiting urban areas to access waste bins, fruiting trees, residential houses, shops and even people carrying food (van Doorn, O'Riain & Swedell, 2010; Kaplan *et al.*, 2011; Hoffman & O'Riain, 2012*b*). As a result, the Cape Peninsula baboon population is gaining international notoriety as a major pest species.

Baboons in the Cape Peninsula became protected in 1998, supported by a programme aiming to mitigate baboon raiding (Beamish & O'Riain, 2014). Today, around 60 field rangers are employed to manage 10 baboon troops away from urban spaces. At first, rangers were permitted only to shout and chase the baboons to herd them away from urban spaces, but in 2012, rangers were allowed to use paintball marker guns as an active deterrent (Cape Nature, 2012), increasing the efficiency of rangers (Richardson, 2012). In addition to the activities of the municipality, some crop farmers have developed their own management strategies and hire private rangers to keep baboons away from their property. While these activities do reduce the time baboons spend in the urban space and consequently the frequency of raiding events (van Doorn *et al.*, 2010), baboon–human conflict is still prevalent, and in July 2014 (the time of this study), 331 baboon-raiding events were observed by field rangers and 147 phone calls were received from the public reporting the presence of a raiding baboon(s) in residential areas (Richardson, 2014).

The purpose of this study was to provide an independent assessment of current management strategies. In doing so, we explore the potential trade-offs that baboons make between foraging returns and risk of human–baboon conflict in their patterns of habitat use. To do this, we first use direct observation and GPS data to track baboon space use, categorizing areas used by the baboons according to the level of anthropogenic activities (both vineyards and dense residential areas occur within their home range). We then relate baboon space use to the management strategies adopted by field rangers tasked with managing the troop, assessed via individual interviews. Given that the baboons are continuing to raid the urban space despite ranger activities, we tested the extent to which baboons (1) use habitats to maximize foraging rewards and/or (2) balance their foraging rewards with risk of ranger encounter. The former would indicate poor efficacy of the ranger management strategy, while the latter may inform management on how to improve current practices and so reduce human–baboon conflicts.

Materials and methods

Study site and subjects

We studied a single troop, the 'Constantia troop' that comprised 10 adult males, 20 adult females, 3 sub adult males and approximately 30 juveniles of both sexes. The troop ranged in a varied landscape (S −34.0349, E 18.4156; Fig. 1) that included two wine farms (Farms A and B), commercial

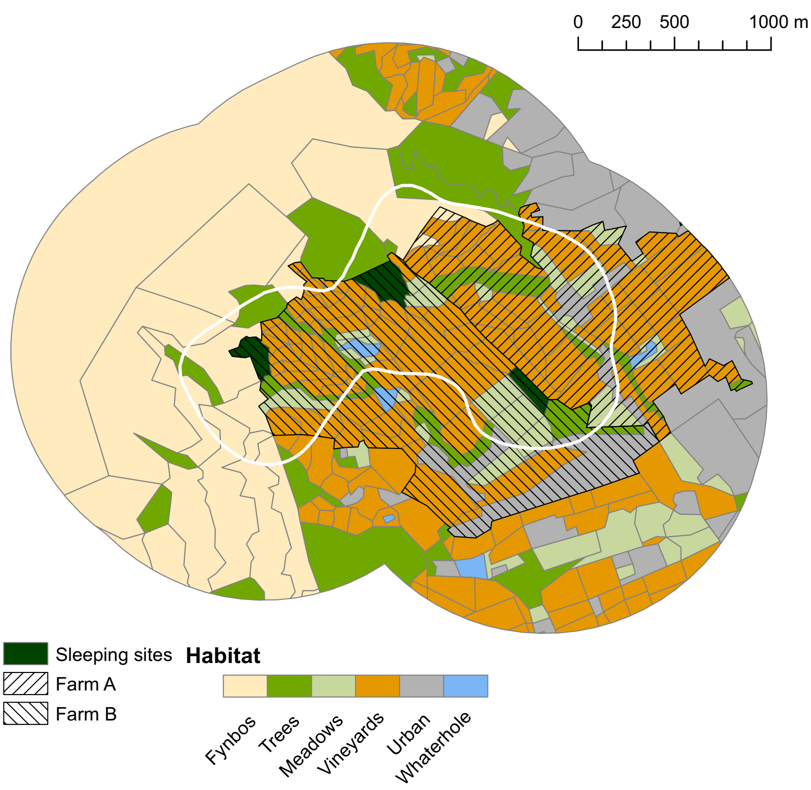

Figure 1 Study area (−34.0349, 18.4156) showing the baboon troop home range (solid white line) estimated by a 95% kernel density, major habitat types and location of baboon sleeping areas used over the study period.

and residential buildings, a restaurant, and commercial pine and eucalyptus plantations, all of which the baboons are known to access and/or raid (Richardson, 2012). The entire western part of their home range was bordered by TMNP which includes indigenous fynbos vegetation that extends over a mountain and down to the Atlantic Ocean. We studied the troop from mid-April to mid-July 2014, which is after the harvest of the grapes, when the vineyards are no longer providing rich energetic food. Baboons tend to urban raid more in these months (van Doorn *et al.*, 2010).

To reduce the frequency and impact of baboon raiding, field rangers actively move baboons out of high-risk raiding areas using shouts and whistles, movements and paintball guns (Cape Nature, 2012). Two alternating teams of five field rangers managed the baboons on a daily basis from approximately 7 am to 5 pm, with each team working 4 days on, 4 days off. Ranger teams were comprised of employees from two different organizations: (1) the City of Cape Town's service provider (Human Wildlife Solutions) whose primary goal is to protect residential properties and (2) the employees of Farm B whose goal is to protect the vineyards. One ranger team would be comprised of individuals from both organizations working together over the whole area.

Baboon troop ranging

The baboons were habituated to close (≤10 m) human observation and could thus be followed on foot by one or two observers. Baboons were observed daily in accordance with the guidelines for the treatment of animals in behavioural research and teaching (Guidelines for the use of Animals, 2012). The troop was followed up for 17 ± 0.8 (mean ± SE) days per month and their position was recorded every 30 min using a handheld GPS device (eTrex 10; Garmin Ltd., Olathe, KS, USA) with the observer positioned at the middle of the troop (*sensu* Hoffman & O'Riain, 2010). This resulted in 51 days of observations, and 13 ± 5 (mean ± SE) GPS fixes per day (total GPS fixes = 685). We estimated troop home range by fixed kernel densities using an *ad hoc* method for selecting the smoothing parameter (Worton, 1989) with the package 'adehabitat', function 'getvolumeUD' (Calenge, 2006) in R.

Habitat type

Based on researcher knowledge of the site and images from Google Earth (accessed 6 June 2014), we categorized the study region into one of the five major habitat types (fynbos, trees, meadows, vineyards and urban areas). We created an index of anthropogenic activities for each habitat ranging from 0 for areas with no human activity during the study period, to 4 for areas with daily human activities based on personal observations. Fynbos habitat is comprised of natural vegetation, vehicle access is restricted and walkers are infrequent (score 0); tree habitat comprises alien pine and eucalyptus plantations where vehicle access is restricted and walkers sometimes pass through to the areas of the TMNP (score 1); meadow habitat comprised open areas dominated by exotic grasses and a variety of annuals including wheat and barley under maintenance by farm workers (score 2); vineyard habitat consisted of planted vines, which had been harvested but kept under maintenance by farm workers (score 3); urban habitat included residential and commercial property with people using the space daily (score 4). We classified all habitats within the baboon home range, and additionally for a radius of half of the mean distance covered by the troop in 1 day (which is akin to an outward and return path from the sleeping sites). We compared habitat composition within and outside of the home range using a chi-squared test.

Management strategies

We assessed ranger 'strategy' as rangers' likelihood of herding baboons from a specific area. Each field ranger's strategy (n = 11) was assessed in an interview with GF and CK. Interviews were anonymous and conducted with the consent of both employers and the field rangers. Field rangers were provided with a map of the study area (Supporting Information Fig. S1) and asked to colour in areas where, in their opinion, the baboons were allowed to be: at any time (green; score 2), allowed some of the time (orange; score 1) or never allowed (red; score 0). Rangers were asked to colour the map according of their plan of action (chase or leave) in the different scenarios regardless of their motivation. This provided us with 11 different maps representing individual field ranger management strategies, and a composite map created by summing cell scores across all field rangers. Low scores indicate that a baboon would be highly likely to be chased or herded away from a given area, while high scores (maximum 22 in the composite map), indicated no conflict with the baboon rangers and baboons would not be chased or herded. In addition, to assess the level of agreement (A) across the field rangers, we calculated the Simpson's diversity index (Simpson, 1949) to express the probability of two field rangers selected by random giving the same score for a specific cell:

$$A = \frac{\sum_0^2 n_i(n_i - 1)}{N(N-1)},$$

where A is computed for each cell, N is the total number of field rangers and n_i is the number of field rangers scoring a given cell with the score i (0, 1 or 2; chased all of the time, sometimes or never).

Spatial and statistical analyses

We divided the study area into 150 × 150 m grid cells (total = 22 500 m^2 cells). This grid cell size was larger than the average spread of baboon troops within the Cape Peninsula (Hoffman & O'Riain, 2012*a*) and elsewhere in South Africa (Henzi, Byrne & Whiten, 1992). We then created raster layers quantifying every grid cell's Euclidian distance to all habitat types (see above) using the 'Spatial Analyst' toolbox of ArcGIS 9.3 (Environmental Systems Research

Institute, Redlands, CA, USA). Each grid cell was also assigned an intensity of baboon use scaled between 0 and 100, where 100 represents the core area of the home range, based upon the utilities for home-range size estimation (see Baboon troop ranging above).

To investigate whether any key landscape or habitat details predicted field ranger strategy, we used partial Mantel tests to test for a correlation between two matrices' grid cell scores (R environment, package 'vegan', Spearman correlation, 10 000 permutations), while controlling for the spatial effect (details of spatial autocorrelation are provided in Supporting Information Fig. S2). Specifically, we tested whether the collective ranger strategy (derived from the composite map, details above) was correlated with (1) habitat type, (2) distance to specific raiding opportunities (i.e. measured as the distance to urban space, or vineyards) or (3) distance to key baboon refuges (measured as the distance to trees).

To test what factors predicted baboon space use (i.e. grid cell use), we used a spatial simultaneous autoregressive lag model (SAR lag). This model based on a classical linear model, control for spatial autocorrelation by building a spatial weight matrix based on nearest neighbours (R environment, package 'spdep'). We adopted this approach because subsampling was impractical due to the degree of spatial autocorrelation (Supporting Information Fig. S2). In all models, we applied a logit transformation to the intensity of baboon cell use, our response variable given as a percentage, to normalize model residuals. We entered a combination of: overall field ranger strategy (summed scores), field ranger agreement (Simpson's diversity index), distances to fynbos, trees, vineyards and residential areas space (in metres) as fixed effects, where they were correlated with a coefficient <0.5 (Supporting Information Table S1). We then used Akaike information criteria to select the best fitting model. All analyses were conducted in R [version 3.1.1; R Core Team (2014)].

Results

Baboon troop ranging and habitat type

The mean (μ) ± standard deviation (SD) troop day path length was 2261 ± 657 m and home range (kernel density, 95%) was 1.97 km^2 (Fig. 1). The home range comprised 16.4% of fynbos, 17.8% of trees, 11.6% of meadows, 50.5% of vineyards and 3.0% of urban areas (Fig. 1). The habitat composition within the troops home range was significantly different to that in the surrounding region which comprised 36.6% of fynbos, 13.5% of trees, 6.4% of meadows, 29.9% of vineyards and 12.9% of urban areas (chi-squared test: $\chi^2 = 756\,611.7$, d.f. = 5, $P < 0.001$).

Management strategies

Individual field ranger strategy scores for urban space were low indicating that baboons are generally prohibited from entering this habitat (μ ± SD = 0.5 ± 0.8; Figs 2 and 3), while scores for fynbos were high (μ ± SD = 20.9 ± 2.3; Figs 2 and 3) suggesting that the baboons are generally permitted. This meant that the sum of field ranger scores was strongly correlated with the habitat type (scored according to level of anthropogenic influence) when controlling for spatial autocorrelation (Partial Mantel test: $R = 0.698$, $P < 0.001$; Figs 2 and 3; Supporting Information Table S2).

Ranger agreement scores were from 27.3 to 100%, with more than half of all the grid cells showing low level of agreement, that is, <50% agreement among rangers. For these cells with a low agreement scores, 75% of these occurred within vineyard habitats, with almost all the remaining low agreement cells (24%) occurring within a 300 m range of a vineyard cell (Figs 2 and 3). Overall, we found that the level of field ranger agreement was most strongly correlated with the distance of cells from vineyards; the further the distance from the vineyards, the more the rangers agreed on a strategy (Partial Mantel test: $R = 0.401$, $P < 0.001$; Figs 2 and 3; Supporting Information Table S2).

Baboon space use

Of all models considered (Supporting Information Table S3), intensity of baboon space use was best predicted by distance from urban space (SAR: estimate: 0.0003; SE: 0.000; $Z = 1.988$, $P = 0.047$; Supporting Information Table S4; Fig. 4a), distance from trees (estimate: −0.0018; SE: 0.000; $Z = 5.738$, $P < 0.001$; Supporting Information Table S4; Fig. 4b), and by the level of field rangers' agreement (SAR: estimate: −1.4187; SE: 0.269; $Z = -5.290$, $P < 0.001$; Supporting Information Table S3; Fig. 4c). All candidate models and details of the selected model predictions are provided in Supporting Information Table S3 and Fig. S3.

Discussion

Our results show that baboons in this study utilized space near to trees and far from the urban edge. We expect that this space use reflects the importance of refuges (trees) and the risk of negative interaction with field rangers that baboons are likely to experience in human-modified landscapes. Perhaps, most importantly, our findings also show that baboons intensively use spaces where rangers show a low agreement score, suggesting that baboons are sensitive to, and exploit risk variability that arises due to inter-individual differences in ranger management strategies.

To prevent HWC and urban raids, the City of Cape Town employs baboon field rangers who are responsible for minimizing the time that troops spend in urban areas (van Doorn *et al.*, 2010; Hoffman & O'Riain, 2012*a*). Our data suggest that the City's objectives are being met, with the proximity of cells to the urban edge showing an overall negative relationship with intensity of baboon cell use. However, baboons frequently use spaces where rangers disagree on how to manage them (whether to herd them away, or not; Fig 4c) and are often found at a distance of 400–600 m from the urban edge (Fig. 4a) consistent with a trade-off between risks and rewards available in the urban environment (Fraser & Huntingford, 1986; Lima & Dill, 1990; Cowlishaw,

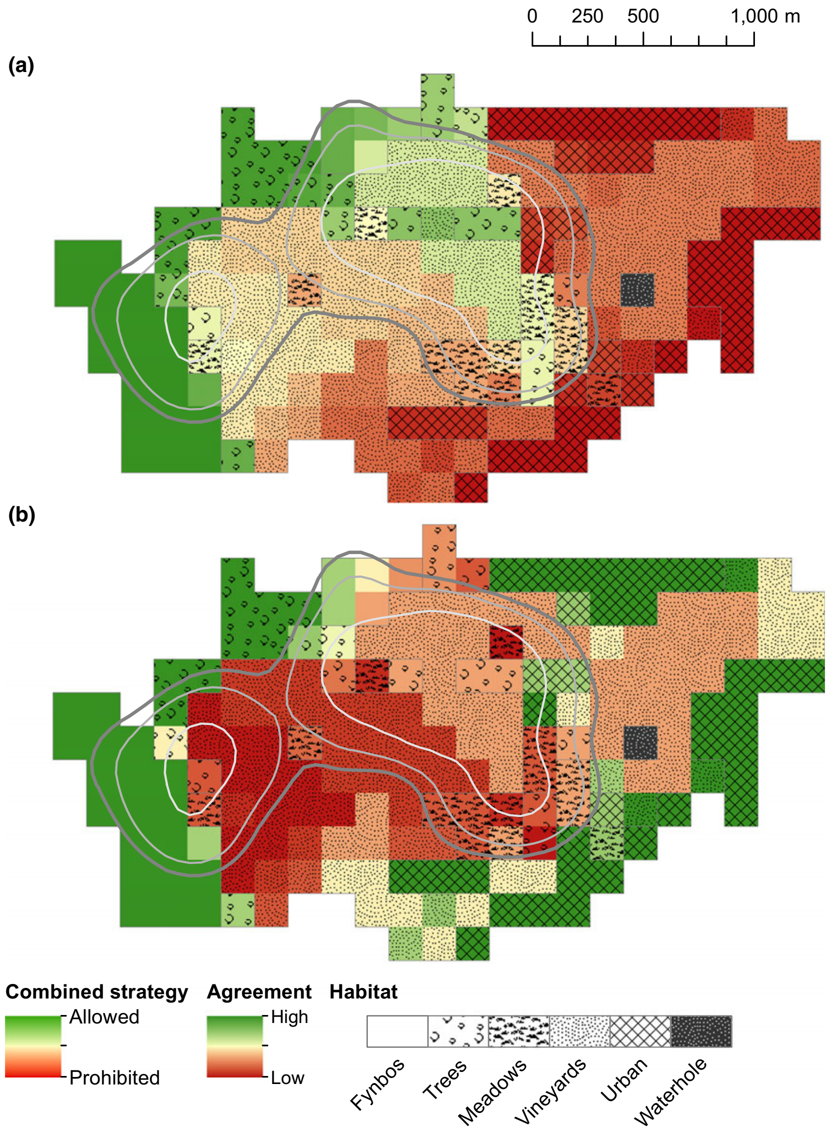

Figure 2 Management strategies and baboon space use. A map of study area divided up into 150 × 150 m grid cells. Baboon home range, defined by kernel densities are represented by the contour lines from light to dark grey that represent 70, 90 95% contours, respectively, in both (a) and (b). (a) Overall field ranger strategy with cells coloured according to whether baboons were 'allowed' or 'prohibited' based on field ranger interviews. (b) Overall ranger agreement across the 11 individuals interviewed, with cells coloured according to the level of field ranger agreement; from 'low agreement' to 'full agreement'.

1997). Although it is difficult to tease apart the effects of habitat and rangers' disagreement (because they are correlated), our models suggest that rangers' disagreement, rather than distance to certain habitats (e.g. the vineyards), explains more of the variance in baboon cell use (Supporting Information Table S4).

In line with our interpretation that baboons are mitigating risks, the most important habitat factor determining baboon space use was the proximity to trees. We expect that the importance of the tree habitat is twofold. Among cells classified as trees in baboons' home range, 42% were used as sleeping sites (n = 3) by the troop. Sleeping sites are among primary resources for baboons, giving protection against nocturnal predation (Cowlishaw, 1994) and influencing baboon ranging behaviour and ultimately home-range size (Hamilton, 1982; Hoffman & O'Riain, 2012*a*). Even in the absence of predators across the Cape Peninsula, sleeping sites remain an important feature of baboon spatial ecology and they have been documented sleeping on cliffs, in pine and eucalyptus plantations and even apartment buildings and factory roofs (Hoffman & O'Riain, 2012*a*). The remaining 52% of tree habitat within the home range were not used as sleeping sites, but rather as cover and refugia when being chased by rangers (G. Fehlmann and C. Kerr-Smith, pers. observ.). Recent theoretical models support these empirical data (Taylor *et al.*, 2016), predicting that buffer zones between refuges and raiding areas can limit raiding behaviour in baboons in the absence of apex predators.

Threat avoidance via refuge use represents a principal survival strategy and its importance in HWC has been highlighted in several species such as bears (Takahata *et al.*, 2014), tigers (Gurung *et al.*, 2008) and langurs, macaques and chimpanzees (Naughton Treves, 1998; Nijman & Nekaris, 2010). Thus, in line with the findings of Hoffman

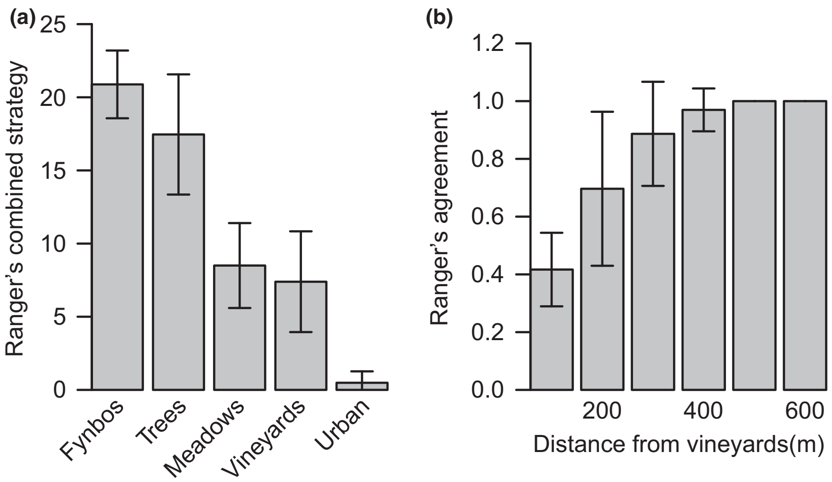

Figure 3 Field ranger's combined strategy according to habitat type and distance to vineyards. (a) The mean ± SE sum of baboons ranger overall strategy scores (0 = prohibited; 22 = always allowed) for grid cells within each of the five major habitat types. (b) The mean ± SE of agreement in field ranger scores (Simpson's diversity index) for grid cells as a function of the distance from vineyard habitat. Cell scores for agreement in ranger scores are significantly positively correlated with the distance from vineyards (Partial Mantel test, $R = 0.401$, $P < 0.001$).

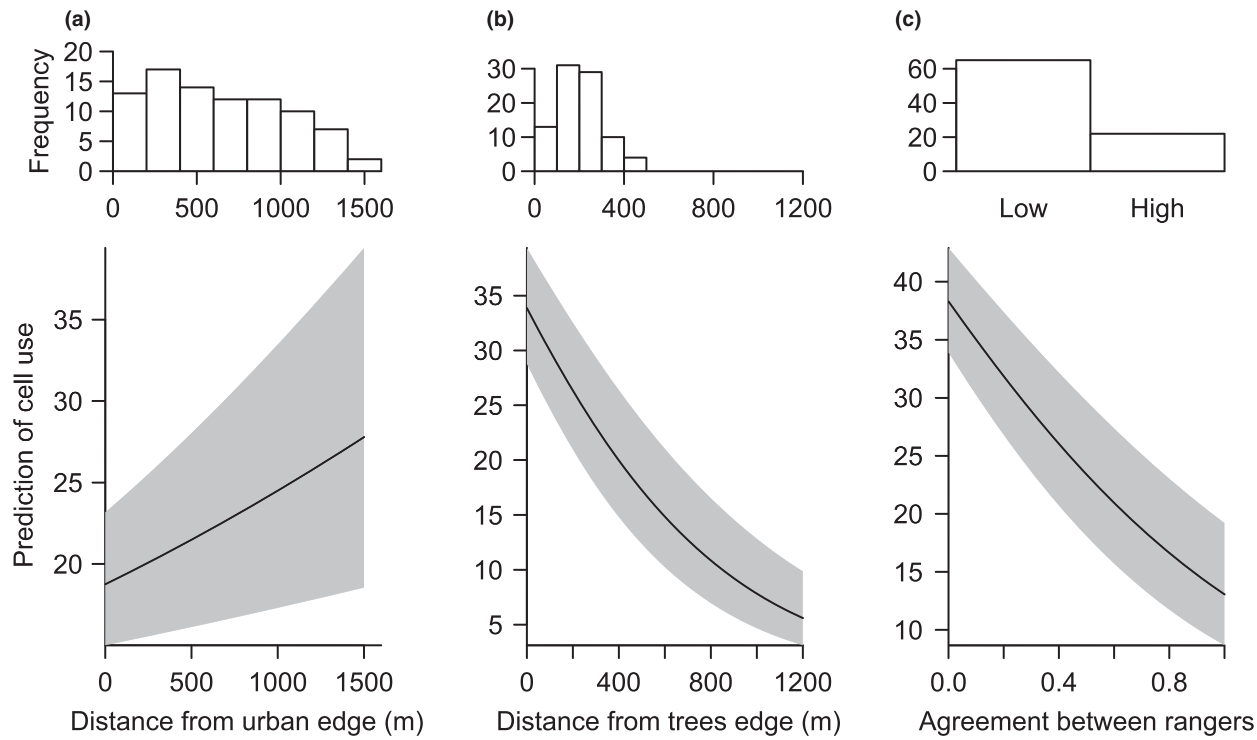

Figure 4 Predictors of baboon space use. The frequency of cells in the home range (95% kernel density) (histograms; upper row), and estimated values of the intensity of baboon grid cell use with their standard errors (grey area) (lower row) as a function of (a) distance from the urban edge, (b) distance from the trees and (c) field ranger strategy agreement. 'Low' agreement refers to a score of less than 50%, and 'high' agreement refers to a score higher than 50%. Baboon space use was predicted by all three of the factors shown in the best fitting (Akaike information criteria: 596.9); Spatial simultaneous autoregressive lag model explaining the intensity of cell use by baboons.

& O'Riain (2012*a*), our results suggest that the removal of large exotic trees in close proximity to either vineyards or urban areas would greatly reduce the intensity of cell use in these areas and ultimately the frequency of raids in nearby residential and commercial areas. However, such management actions would necessitate extra care since habitat engineering can play an important functional role (Vitousek *et al.*, 1997; Foley *et al.*, 2005; Ramesh, Kalle & Downs, 2016). Moreover, it is certainly possible that if we were to conduct this study during a different time of year (e.g. before the harvest of the vineyards), baboon space use and management strategies would likely be different, thus potentially shifting the location of conflict and refuge locations.

Crop or livestock guarding is common and often seen as one of the most effective ways to reduce raiding for a wide diversity of species (Ogada *et al.*, 2003; Sitati & Walpole, 2006; Hill & Wallace, 2012; Hsiao *et al.*, 2013). However, the baboons appear to be sensitive to risk variability that arises due to inter-individual differences in ranger management strategy. This poses an additional, overlooked dimension to our understanding of how wildlife evaluate and adjust their response to human disturbance (Sol, Lapiedra & González-Lagos, 2013). It also highlights the adaptability and cognitive skills of baboons (Naughton Treves, 1998; Hill, 2000), and supports findings of other studies in which baboons are observed to assess risk before raiding (Hill, 2000; Warren, 2009). Being a group-living species with complex social interactions (King *et al.*, 2008; King, Clark & Cowlishaw, 2011), the sampling of intraspecific public information is a common feature of the daily life of baboons and may explain their apparent ability to integrate field rangers' activity and adapt their own strategies in accordance with this information (Dall *et al.*, 2005). Such behaviour reinforces their adaptability, enabling them to mitigate risks associated with raiding behaviours and make the most of the high energetic resources available in the urban areas (Snell-Rood, 2013). As such, management strategies based on guarding should make their spatial strategy clear especially when working with species with high cognitive skills or complex social systems such as other raiding primates, for example, as chimpanzees or macaques (Yeo & Neo, 2010; Krief *et al.*, 2014), or elephants (Sitati & Walpole, 2006; Webber *et al.*, 2011).

One potential cause for inter-individual differences in ranger management strategies may be because rangers are working for two different organizations – local farms and the municipality of Cape Town. Each has a different primary objective: to keep the baboons away from the vineyard, or to keep the baboons from entering the urban edge respectively. However, we found that the majority of cells across the study site had low agreement scores, and this is greater than would be expected by simple disagreement between the six (municipality) versus four (farm) employees. Similar results have been found in other studies where, even if a community or specific group share the same objectives, perceptions and reactions can differ. For example, farmer reaction towards crop raiding by primates in Sri Lanka (Nijman & Nekaris, 2010), and citizen preference for bear zoning management in Japan, consistently differed (Kubo & Shoji, 2014).

Overall, our results suggest that baboon troops in Cape Town balance the foraging rewards gained from raiding against the risk of field ranger (or other human) conflict. This suggests that current management strategies do impact baboons' behaviour and successfully prevent them from frequenting urban spaces. However, baboons also appear sensitive to risk variability that arises due to inter-individual differences in ranger management strategies, and thus, for management to be more effective, a consensus is needed on actions taken with respect to baboon movement close to the urban edge. Forested areas close to raiding spots should also be considered carefully, since these offer refuges that are likely to decrease the efficiency of field rangers' activity. Showing similarities with other studied systems, such as the importance of refuges (Nijman & Nekaris, 2010; Takahata *et al.*, 2014) or risk assessment by wildlife (Hill, 2000; Warren, 2009), we believe our recommendations could be considered in the development of better management strategies throughout the Cape Peninsula or for raiding species more generally, in comparable cases where refuges around raiding spots and/or a management strategy based on guarding exist. Our findings suggest that effective management strategies will be those that increase the attractiveness of natural resources, decrease the attractiveness of human-modified areas and increase the costs in terms of energy or risks associated with these areas (Strum, 2010; Kaplan *et al.*, 2011).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. A map of the study site, subdivided by habitat type areas boundaries (solid lines), that was presented to the field rangers during interviews.
Figure S2. Semivariogram for each factor studied: U. Dist, V. Dist, T. Dist, F. Dist being respectively; Distance from urban areas, vineyards, trees and fynbos, and Comb. Strat. being combined rangers' strategy.
Figure S3. Observed against predicted baboon cell use.
Table S1. Correlation matrix (Spearman) of all fixed effects (U. Dist, V. Dist, T. Dist, F. Dist being respectively; Distance from urban areas, vineyards, trees and fynbos, and Comb. Strat. referring to combined rangers' strategy) considered to explain baboon space use.
Table S2. Results from Partial Mantel Tests (10 000 permutations) for the rangers strategy according to the environmental fixed effects.
Table S3. Spatial Simultaneous Auto Regressive lag models (SAR lag) predicting baboon space use; U. Dist, V. Dist, T. Dist, F. Dist being, respectively, distance from urban areas, vineyards, trees and fynbos, and Comb. Strat. being combined rangers' strategy.
Table S4. Factors explaining baboons' space use.