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Human habituation reduces hyrax flight initiation distance in Serengeti

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Abstract
Many animal populations are exposed to disturbance originating from human activities. In response to human disturbance, certain animals display a variety of potentially costly behavioural responses, such as increased antipredator behaviour or relocation to new areas. In contrast, other animals seemingly thrive in the presence of humans and benefit from human-derived resources. Flight initiation distance (FID: the distance between predator and prey when prey starts to flee) is a measure commonly used to assess animals' tolerance to humans. In this study, we tested how FID changes in relation to human presence in two hyrax species in Serengeti National Park. Hyraxes living on kopjes (rock outcrops) among human settlements showed a significantly shorter FID than hyraxes living on kopjes without human settlements. In addition, we found that hyraxes feeding before the experiment had shorter FID than hyraxes resting or being vigilant, and hyraxes disturbed during the early morning had shorter FID than hyraxes disturbed during late morning. We did not find any significant effects of group size or species composition on FID. Our results suggest that hyraxes living in the presence of humans are habituated and are not adversely affected by human settlements.

KEYWORDS
antipredatory behaviour, flight initiation distance, kopje, Tanzania

1 | INTRODUCTION

Protected areas aim to conserve ecosystems and the wildlife they support from threatening anthropogenic processes (Sinclair & Dobson, 2015). While tourism provides important economic revenue for conservation efforts, increased human disturbance might on the other hand have negative impacts on wildlife populations. Nature-based tourism is the fastest growing sector in the tourism industry, with developing countries having the highest increase in visitor numbers (Balmford et al., 2009). National parks and wilderness areas with high levels of biodiversity are popular areas for tourists. In Tanzania for example, tourism has grown from 783,000 tourists in 2010 to 1.14 million in 2014 (Turner, 2015), of which ca. 25% visit Serengeti National Park (SNP).

Many wildlife species avoid areas with human activities, displacing such species into less suitable habitats, or negatively affecting the amount of time spent on parental care, foraging, resting and mating displays (Brubaker & Coss, 2015, 2016; Burger, 1981; Gander & Ingold, 1997; Klein, Humphrey, & Percival, 1995; Manor, Saltz, & McCorquodale, 2005). However, certain species seemingly thrive within human-altered habitats and can adapt to survive in urban environments by directly or indirectly increasing their fitness through exploiting human-induced resources and benefits such as cultivated plants, garbage, decreased predation pressure and shelter (Kark, Iwaniuk, Schalimtzek, & Banker, 2007; McKinney, 2002). Normally, antipredator behaviour such as vigilance is costly through time and energy loss, and it should thus be adjusted based on the perceived level of threat (Lima & Dill, 1990). One way to evaluate this is to measure the distance between predator and prey when prey start to flee, called flight initiation distance (FID) (Stankowich & Blumstein, 2005; Stankowich & Coss, 2005; Ydenberg & Dill, 1986). Given the potentially fatal consequences, fleeing as soon as a predator is detected is seemingly the safest decision. Such a strategy is, however, not necessarily the most beneficial, as costs are incurred when the animal flees early as it loses time and energy that could be spent on fitness-enhancing activities, such as energy gain through foraging. Optimal escape theory (Cooper Jr. & Frederick, 2007; Ydenberg & Dill, 1986) predicts that animals will flee when the cost of staying exceeds potential benefits.

Various factors influence FID, for example patch forage quality, reproductive state, risk of capture (e.g. distance from hiding place), speed and direction of the approaching predator, number of predators, individual fitness, group size and starting distance (SD: i.e. the distance between predator and prey when approach begins) (Cooper Jr. & Blumstein, 2015). Repeated low-risk exposure to a potential predator can facilitate change in risk assessment towards the specific predator. Through this process, the animal reduces its response over time as it learns that there is no advantage or disadvantage to the stimulus (Rankin et al., 2009; Shulgina, 2005). This process is called habituation and is a plastic behavioural response found in many animals (Blumstein, 2016; Thompson, 2009). Habituation refers to stimulus repetition due to sustained exposure that results in an individual becoming inattentive towards an object or situation that initially conveyed important cues (Rankin et al., 2009; Shulgina, 2005). This kind of behaviour is often developed towards humans for animals inhabiting areas with human activity (McGowan, Patel, Stroh, & Blumstein, 2014; Rodriguez-Prieto, Fernández-Juricic, Martín, & Regis, 2009; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015; Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014). The risk allocation hypothesis (Lima & Bednekoff, 1999) predicts that if animals experience frequent or prolonged high-risk events, they must make a trade-off between antipredator behaviour and fitness-increasing activity and reduce the antipredator behaviour to meet its needs for food and rest. In both cases of habituation and risk allocation, FID is expected to decrease with increased non-threatening human activity. For example, when approached by a human, impalas (*Aepyceros melampus*) exposed to illegal hunting pressure outside SNP fled at greater distances compared to those inside the protected national park (Setsaas, Holmern, Mwakalebe, Stokke, & Røskaft, 2007).

Minimal levels of human activity can have serious effects on wildlife. Even a temporary tented camp, a small research station or a popular hiking area can be a source of disturbance that could increase the risks for different animals (McGowan et al., 2014). Human settlements (villages), livestock keeping and hunting are not allowed within SNP, but there are several hotels, lodges and tented camps with staff villages, as well as a visitor and research centre. They are often built on or around rock outcrops called kopjes, and these natural features are also home to two species of hyraxes (the rock hyrax—*Procavia capensis johnstoni* and the bush hyrax—*Heterohyrax brucei*). We have previously documented that hyraxes in SNP seem to benefit from human presence with human-inhabited kopjes having higher hyrax densities than other kopjes (Mbise et al., 2017). The behaviour and socio-ecology of hyraxes in habitats influenced by human presence might therefore differ from populations without human presence due to lower predation pressure, higher population densities and human-induced stress affecting their energy budget (Ditchkoff, Saalfeld, & Gibson, 2006). Frequent non-threatening exposure to humans in these areas may result in shorter FID compared to hyrax populations in kopjes lacking human presence. Studies on bird FID in relation to varying levels of non-threatening human disturbance found a decrease in FID with increasing exposure rates (Engelhardt & Weladji, 2011; Malo, Acebes, & Traba, 2011; McGowan et al., 2014; Mikula, 2014).

However, previous experiments on different mammals in the Serengeti Ecosystem have shown that some mammals flee at greater distances in areas associated with threatening human activities compared to the well-protected central areas of the national park (Holmern, Setsaas, Melis, Tufto, & Røskaft, 2016; Marealle, 2011; Setsaas et al., 2007). Furthermore, hyraxes living around dwellings are more relaxed because predation rate is very low (Mbise et al., 2017). In animals, when predator encounters prey, the flight initiation distance (FID) is often quantified to examine the perception of security for an individual (or group) (Stankowich & Blumstein, 2005; Williams, Samia, Cooper, & Blumstein, 2014). The FID helps to differentiate between various factors that explain animals' alertness (Blumstein, 2014; Stankowich & Blumstein, 2005). One potential factor is the presence of humans (Williams et al., 2014); hence, we examined various factors in an experimental setup with heterogeneity of human presence. To our knowledge, there have not been any FID experiments conducted on hyraxes. The objective of this study was to test how FID changes in relation to dwellings and other factors such as hyrax species, presence of young, behaviour of hyraxes before the onset of the experiment, time of day and group size. We expected FID to be shorter for hyraxes that were regularly exposed to human activities, as their tolerance towards humans would be greater than for hyraxes unfamiliar with humans.

2 | METHODS

2.1 | Study area, species and data collection

The Serengeti-Mara ecosystem lies on the border between Tanzania and Kenya in east Africa, situated on a plateau covering approximately 30,000 km^2. Fieldwork was conducted in different parts of SNP; around Seronera in the central area, Lobo in the north, and Moru, Simba, Gol and Barafu in the south of the park (Figure 1).

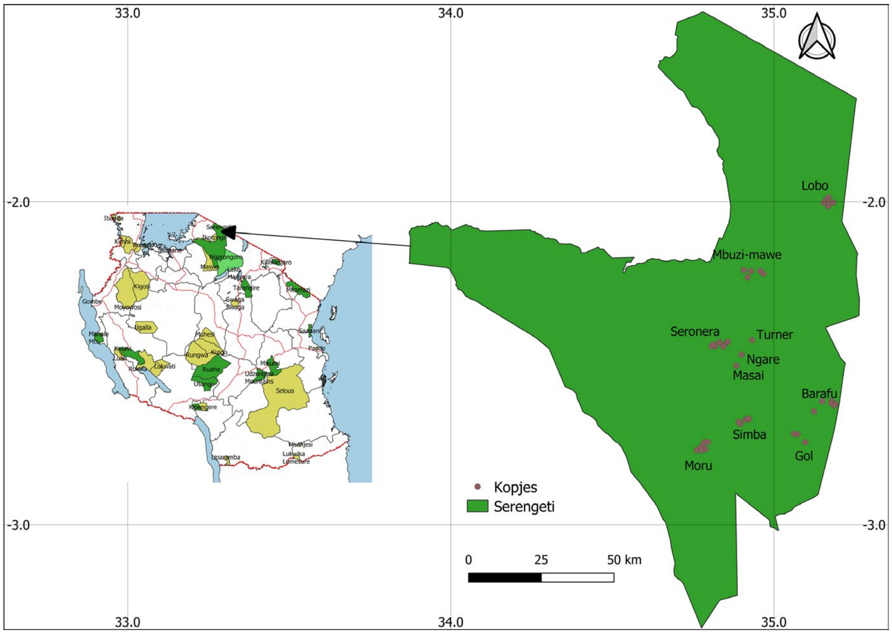

FIGURE 1 A map of the Serengeti National Park with the 43 kopjes we visited

The rock hyrax and the bush hyrax are both diurnal and may occur sympatrically or allopatrically on kopjes throughout SNP (Hoeck, 1975). They belong to the order Hyracoidea and are related to the elephants and sirenians, and include three extant genera: *Dendrohyrax*, *Heterohyrax* and *Procavia* (Hoeck, 1982).

Fieldwork was carried out between June and August 2015 on dry and sunny days, during this time we visited 43 kopjes and FID experiments were done only on the kopjes which are easy to access while approaching focal individuals (20 kopjes) (Figure 1). Kopjes which were surrounded by thick bushes were not included. Kopjes were randomly selected and categorized as either part of dwellings, that is an establishment with permanent human activity as lodges, campsites, workers villages, etc., or kopjes devoid of any form of human dwellings. At each kopje, we used binoculars and recorded number of individuals and species. There were two observers all the time, but only one that identified species and did the final counting at each spot to avoid double counting. Observed individuals had two age groups which were classified according to their body size; adult (n = 211) and young (n = 37) (Hoeck, 1989; Ilany, Lee Koren, & Hoeck, 2013). Before doing experiments, we recorded hyraxes' behaviour as; resting (laying down with no any activity), feeding (focused on browsing, grazing or eating insects) or vigilant (head up and looking around).

2.2 | Flight initiation distance

Flight initiation distance experiments were done between 7 a.m. and 6 p.m. General methods were done in accordance with Setsaas et al., (2007) and Holmern et al., (2016). When we sighted individual hyrax or a group of hyraxes on a kopje, we stopped the car or stood still and recorded the number of individuals, species, age and behaviour. The same observer and test person (person who initiated the flight response) were used in all experiments. The observer used a rangefinder (Phoxx 600M) to measure the starting distance, and then the test person walked towards the animal or group in a straight line and at a constant speed (1.3 metres per second) and immediately stopped when the focal individual fled. The focal individual was picked randomly by observer. Then the observer measured the distance to the test person and recorded it. The species and age of the first and last individual to flee were also recorded. The FID was recorded as the difference between the starting distance and the distance at which the test person stopped his approach in response to the targeted individual taking flight. In some dwellings, the flight distance was less than 10 metres. Because the rangefinder only was able to record distances between 10 and 1,000 metres, we had to estimate distances in such cases.

2.3 | Statistical analyses

Starting distance can influence FID and should be taken into consideration when doing FID experiments (Blumstein, 2003; Engelhardt & Weladji, 2011). Hence, we used the traditional way of controlling for starting distance in our models by including starting distance as a covariate. We used a linear mixed model to analyse our data with FID as response variable and starting distance, human presence, number of individuals, hyrax species and behaviour at start of experiment as predictor variables. FID + 1 was log-transformed to fit a normal distribution, and starting distance + 1 m was also log-transformed to operate on the same scale. Kopje identity was included as a random factor. Statistical analyses were performed in R (R Core Team, 2017), and we used the package "lmerTest" (Kuznetsova, Brockhoff, & Christensen, 2015) to run mixed models and the package "effects" to illustrate the modelled effects (Fox, 2003).

TABLE 1 Output of fixed factors from a linear mixed model with the logarithm of FID + 1 as response variable and kopje-ID as a random factor. In total 112 experiments in 20 different kopjes were conducted

	Estimate	*SE*	*df*	T	*p*
Intercept	−0.47	0.45	100	−1.055	.294
Log(Starting distance + 1)	0.63	0.14	100	4.337	<.001
Number of individuals	0.04	0.03	100	1.191	.236
Resting versus feeding	0.24	0.15	100	1.564	.121
Vigilant versus feeding	0.61	0.21	100	2.874	.005
Late morning versus early morning	0.27	0.15	100	1.785	.077
Midday versus early morning	0.04	0.19	100	0.216	.829
Evening versus early morning	0.14	0.181	100	0.763	.447
Both species versus rock hyrax	−0.18	0.28	100	−0.674	.502
Bush hyrax versus rock hyrax	−0.01	0.13	100	−0.120	.905
No human presence	0.69	0.19	100	3.509	<.001

3 | RESULTS

A total of 112 experiments in 20 different kopjes were conducted. Only bush hyraxes were present in 62 experiments (mean group size = 1.76), only rock hyraxes in 42 experiments (mean group size = 1.88), while both species (mean group size = 7.88) were present in eight experiments. Median starting distance was 23 metres (95% CI: 10.5–61.5), and median FID was 7 metres (95% CI: 1–36). Among the predictors, we found statistically significant effects of human presence, behaviour at the onset of the experiment and time of day for the experiment in addition to the expected effect of starting distance (Table 1). Hyraxes living in kopjes with human presence had shorter FID (mean FID = 5.9 m ± *SE* 0.5) than hyraxes living in other kopjes (mean FID = 22.4 ± *SE* 2.8; Figure 2a). Hyraxes feeding at the onset of the experiment had significantly shorter FID than hyraxes being vigilant and had shorter FID than resting hyraxes (Figure 2b). Hyraxes disturbed during early morning (07:00–09:00) had significantly shorter FID than hyraxes disturbed during late morning (09:30–11:30) (Figure 2c). We also tested the model with the other categories as reference, but none of the other three categories differed significantly from each other. We did not find any significant effects of hyrax species or number of individuals on FID (Table 1).

4 | DISCUSSION

Hyraxes living on human-inhabited kopjes showed decreased sensitivity towards human approach and had significantly shorter FID than hyraxes living on kopjes without human settlements. This is consistent with our prediction of habituation to humans. In addition, we found that hyraxes feeding before the initiation of experiments had shorter FID than hyraxes being vigilant, and hyraxes disturbed during early morning had shorter FID than hyraxes disturbed during late morning.

There are several possible explanations for why FID is shorter around dwellings. One is that animals can learn through experience with human encounters and adjust antipredator behavioural responses (Bateman & Fleming, 2014; Deecke, Slater, & Ford, 2002). Human settlements within SNP are not associated with any direct harvesting or persecution of hyraxes, so encounters with humans constitute low risk. Lowering FID decreases the costs of unnecessary fleeing leaving animals with more time for fitness-increasing activities such as foraging. According to optimal escape theory (Cooper Jr. & Frederick, 2007; Ydenberg & Dill, 1986), it is advantageous to adjust antipredator behaviour according to the degree of risk posed in order to optimize fitness. Reduction in FID due to habituation towards humans has been found in several other species such as zebras (*Equus quagga* and *E. grevyi*), eastern grey squirrels (*Sciurus carolinensis*), skinks (*Eumeces laticeps*), tricoloured blackbirds (*Agelaius tricolor*) and yellow-bellied marmots (*Marmota flaviventris*) (Brubaker & Coss, 2016; Engelhardt & Weladji, 2011; McGowan et al., 2014; Rodriguez-Prieto et al., 2009; Williams et al., 2014). Hyrax habituation towards humans seems likely as there is non-threatening, year-round human activity in all dwellings included in our study. We have also previously shown that hyrax numbers are higher in kopjes with human settlements than in other kopjes (Mbise et al., 2017).

Another possible explanation to the shorter FID around dwellings could be explained by the risk allocation hypothesis (Lima & Bednekoff, 1999). The constant high disturbance level could cause the hyraxes to make a behavioural trade-off between antipredator behaviour and fitness-increasing activities, consequently lowering FID to meet their needs. Rodriguez-Prieto et al. (2009), suggested that both risk allocation and habituation were acting together in reducing FID in an experiment on blackbirds. Possibly, both mechanisms are also acting on the hyraxes. Predators have longer FID than prey around dwellings (Møller & Ibáñez-Álamo, 2012), and hence dwellings could act as refuges from predators for the hyraxes.

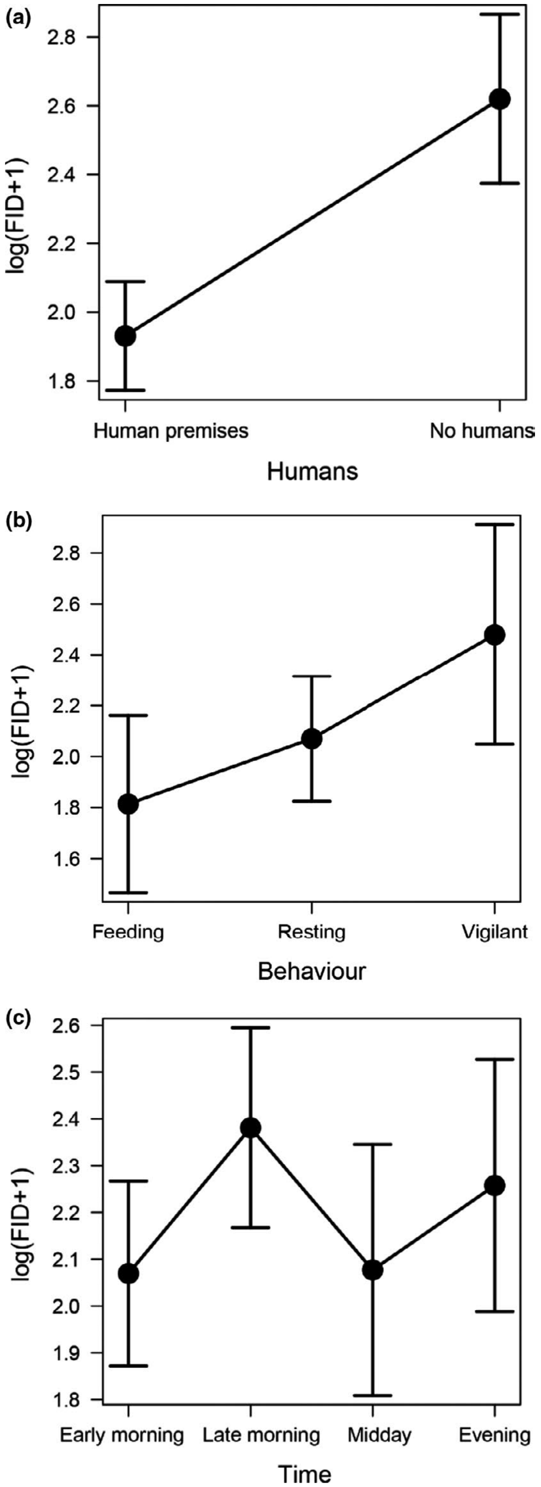

FIGURE 2 Graphical representation of the modelled effects estimated in the linear mixed model in Table 1 between log FID + 1 and (a) human presence, (b) behaviour at the start of the experiment and (c) time of day. Error bars denote 95% confidence intervals

Feeding hyraxes had shorter FID than vigilant hyraxes. This could either stem from feeding hyraxes being less observant or potentially due to a higher cost of fleeing in accordance to optimal escape theory (Cooper Jr. & Frederick, 2007; Ydenberg & Dill, 1986), that is there is likely a higher cost of leaving feeding than leaving a less fitness-related behaviour. We also found that hyraxes had shorter FID in the early morning than during late morning, which also could be associated with most animals feeding during this time, or that the risk of predation is higher during this period. Although not statistically significant, it appears that FID was also shorter during midday (12:00–14:00) and longer during evenings (16:30–18:30) (Figure 1c).

Similarly as in zebras (Brubaker & Coss, 2016), we did not find any significant effect of group size or species composition (Table 1). Hence, whether the two species were found together or in separate groups, or the number of individuals in each group, did not affect FID. Because group sizes were large when both species were present, it was not possible to disentangle the effect of heterospecific presence and group size. However, large group size in general could increase FID via the "many eyes" hypothesis, but also reduce FID via the "dilution" hypothesis, such as found in crab-eating macaques (*Macacafascicularis*) (van Schaik, Noordwijk, Warsono, & Sutriono, 1983), house sparrows (*Passer domesticus*) (Barnard, 1980) and brant geese (*Brantabernicla*) (Owens, 1977). Thus, we encourage specific testing of such an effect.

Starting distance was, as expected, strongly associated with FID, which has also been found in many other studies (Blumstein, 2003; Cooper Jr., 2005; Cooper Jr. & Blumstein, 2014; Williams et al., 2014). Recent studies have suggested alternative ways of assessing FID in order to escape the mathematical dependency between starting distance and FID (Bonnot et al., 2017). However, this methodology requires more information than we recorded during our field experiments. We used a car to look for hyraxes outside dwellings, and the hyraxes were probably aware of us before we started the experiment. Around dwellings, the alert distance could have been misinterpreted since the hyrax may have been aware of our presence and alert without looking directly at us or halt in the ongoing activity (showing an alert response). Ydenberg and Dill (1986) predicted that FID increases with increasing distance to refuges and this model has been supported in several studies (Bonenfant & Kramer, 1996; Cooper Jr., 1997; Gotanda, Turgeon, & Kramer, 2009; Kramer & Bonenfant, 1997). Other variables that could affect FID are position between approaching predator and prey's refuge (Kramer & Bonenfant, 1997), eye contact, patch quality for feeding animals and temperature (Cooper Jr., 1997; Fernández-Juricic, Jimenez, & Lucas, 2002; Sreekar & Quader, 2013). Taking one or more of these variables into consideration would probably help explain more of the variation in FID. Other variables that could be interesting to take into consideration is how far the animal flees (Bateman & Fleming, 2014), if it flees directly into refuge or stops to look back, which is observed in the woodchuck (Bonenfant & Kramer, 1996), and time it takes for the animal to resume to the former activity after flight which could be used to interpret how much human disturbances affect them.

Due to non-detrimental effects posed by human presence on hyraxes in SNP, we conclude that hyraxes show a lower FID around dwellings because they are habituated towards human disturbances. We suggest that future studies should investigate how trade-offs between fitness, predation pressure and access to refuges might interplay.

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REFERENCES

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M., & Manica, A. (2009). A global perspective on trends in nature-based tourism. *PLoS Biology*, *7*, e1000144. https://doi.org/10.1371/journal.pbio.1000144

Barnard, C. J. (1980). Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Animal Behaviour*, *28*(1), 295–309. https://doi.org/10.1016/S0003-3472(80)80032-7

Bateman, P. W., & Fleming, P. A. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Zoology*, *294*(2), 93–98. https://doi.org/10.1111/jzo.12156

Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *Wildlife Management*, *67*(4), 852–857. https://doi.org/10.2307/3802692

Blumstein, D. T. (2014). Attention, habituation, and antipredator behaviour: Implications for urban birds. In D. Gil & H. Brumm (Eds.), *Avian urban ecology* (pp. 41–53). Oxford, UK: Oxford University Press.

Blumstein, D. T. (2016). Habituation and sensitization: New thoughts about old ideas. *Animal Behaviour*, *120*, 255–262. https://doi.org/10.1016/j.anbehav.2016.05.012

Bonenfant, M., & Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, Marmota Monax. *Behavioral Ecology*, *7*(3), 299–303. https://doi.org/10.1093/beheco/7.3.299

Bonnot, N. C., Hewison, A. J. M., Morellet, N., Gaillard, J.-M., Debeffe, L., Couriot, O., … Vanpé, C. (2017). Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Animal Behaviour*, *124*, 35–46. https://doi.org/10.1016/j.anbehav.2016.11.031

Brubaker, A. S., & Coss, R. G. (2015). Evolutionary constraints on equid domestication: Comparison of flight initiation distances of wild horses (*Equus caballus ferus*) and plains zebras (*Equus quagga*). *Comparative Psychology*, *129*(4), 366–376. https://doi.org/10.1037/a0039677

Brubaker, A. S., & Coss, R. G. (2016). Effects of single- and mixed-species group composition on the flight initiation distances of plains and Grevy's zebras. *Ethology*, *122*(7), 531–541. https://doi.org/10.1111/eth.12500

Burger, J. (1981). The effect of human activity on birds at a coastal bay. *Biological Conservation*, *21*(3), 231–241. https://doi.org/10.1016/0006-3207(81)90092-6

Cooper, W. Jr (1997). Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): Predator speed, directness of approach, and female presence. *Herpetologica*, *53*, 464–474. org/stable/3893260

Cooper, W. Jr (2005). When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology*, *83*(8), 1045–1050. https://doi.org/10.1139/z05-104

Cooper, W. Jr, & Blumstein, D. (2014). Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behavioral Ecology*, *25*(1), 44–52. https://doi.org/10.1093/beheco/art083

Cooper, W. Jr, & Blumstein, D. (Eds.) (2015). *Escaping from predators: An integrative view of escape decisions*. Cambridge: Cambridge University Press.

Cooper, W. Jr, & Frederick, W. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, *244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Deecke, V. B., Slater, P. J. B., & Ford, J. K. B. (2002). Selective habituation shapes acoustic predator recognition in harbour seals. *Nature*, *420*(6912), 171–173. https://doi.org/10.1038/nature01030

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems*, *9*(1), 5–12. https://doi.org/10.1007/s11252-006-3262-3

Engelhardt, S. C., & Weladji, R. B. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Canadian Journal of Zoology*, *89*(9), 823–830. https://doi.org/10.1139/z11-054

Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra-and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, *80*(7), 1212–1220. https://doi.org/10.1139/z02-104

Fox, J. (2003). Effect displays in R for generalised linear models. *Statistical Software*, *8*(15), 1–27.

Gander, H., & Ingold, P. (1997). Reactions of male alpine chamois *Rupicapra r. rupicapra* to hikers, joggers and mountainbikers. *Biological Conservation*, *79*(1), 107–109. https://doi.org/10.1016/S0006-3207(96)00102-4

Gotanda, K. M., Turgeon, K., & Kramer, D. L. (2009). Body size and reserve protection affect flight initiation distance in parrotfishes. *Behavioral Ecology*, *63*(11), 1563–1572. https://doi.org/10.1007/s00265-009-0750-5

Hoeck, H. N. (1975). Differential feeding behaviour of the sympatric hyrax *Procavia johnstoni* and *Heterohyrax brucei*. *Oecologia*, *22*(1), 15–47. https://doi.org/10.1007/BF00345256

Hoeck, H. N. (1982). Population dynamics, dispersal and genetic isolation in two species of hyrax (*Heterohyrax brucei* and *Procavia johnstoni*) on habitat islands in the Serengeti. *Zeitschrift Für Tierpsychologie*, *59*(3), 177–210. https://doi.org/10.1111/j.1439-0310.1982.tb00338.x

Hoeck, H. N. (1989). Demography and competition in hyrax: A 17 years study. *Oecologia*, *79*(3), 353–360. https://doi.org/10.1007/BF00384314

Holmern, T., Setsaas, T. H., Melis, C., Tufto, J., & Røskaft, E. (2016). Effects of experimental human approaches on escape behavior in Thomson's gazelle (*Eudorcas thomsonii*). *Behavioral Ecology*, *27*(5), 1432–1440. https://doi.org/10.1093/beheco/arw052

Ilany, A., Lee Koren, L., & Hoeck, H. N. (2013). *Order Hyracoidea and the family Procaviidae*. IUCN - Afrotheria Specialist group. Retrieved from https://thehyrax.wixsite.com/hyrax/

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: Can anyone become an 'urban exploiter'? *Biogeography*, *34*(4), 638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Klein, M. L., Humphrey, S. R., & Percival, H. F. (1995). Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conservation Biology*, *9*(6), 1454–1465. https://doi.org/10.1046/j.1523-1739.1995.09061454.x

Kramer, D. L., & Bonenfant, M. (1997). Direction of predator approach and the decision to flee to a refuge. *Animal Behaviour*, *54*(2), 289–295. https://doi.org/10.1006/anbe.1996.0360

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B.. (2015). *lmerTest: Tests in Linear Mixed Effects Models*. R package version 2.0-29. Retrieved from https://CRAN.R-project.org/package=lmerTest
Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, *153*(6), 649–659. https://doi.org/10.1086/303202
Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092
Malo, J. E., Acebes, P., & Traba, J. (2011). Measuring ungulate tolerance to human with flight distance: A reliable visitor management tool? *Biodiversity and Conservation*, *20*(14), 3477–3488. https://doi.org/10.1007/s10531-011-0136-7
Manor, R., Saltz, D., & McCorquodale. (2005). Effects of human disturbance on use of space and flight distance of mountain gazelles. *Wildlife Management*, *69*(4), 1683–1690. https://doi.org/10.2193/0022-541x(2005)69[1683:eohdou]2.0.co;2
Marealle, W. N. (2011). *Factors affecting group size and vigilance behaviour of Maasai giraffe (Giraffa camelopardalis tippelskirchi) in the Serengeti-Ngorongoro ecosystem, Tanzania*. (MSc), NTNU, Trondheim.
Mbise, F. P., Fredriksen, K.-E., Fyumagwa, R. D., Holmern, T., Jackson, C. R., Fossøy, F., & Røskaft, E. (2017). Do hyraxes benefit from human presence in Serengeti? *African Journal of Ecology*, *55*, 672–678. https://doi.org/10.1111/aje.12405
McGowan, M. M., Patel, P. D., Stroh, J. D., & Blumstein, D. T. (2014). The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology*, *120*(11), 1081–1089. https://doi.org/10.1111/eth.12281
McKinney, M. L. (2002). Urbanization, biodiversity, and conservation - The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, *52*(10), 883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2
Mikula, P. (2014). Pedestrian density influences flight distances of urban birds. *Ardea*, *102*(1), 53–60. https://doi.org/10.5253/078.102.0105
Møller, A. P., & Ibáñez-Álamo, J. D. (2012). Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour*, *84*, 341–348. https://doi.org/10.1016/j.anbehav.2012.04.030
Owens, N. W. (1977). Responses of wintering brent geese to human disturbance. *Wildfowl*, *28*(28), 10.
R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., … Thompson, R. F. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, *92*(2), 135–138. https://doi.org/10.1016/j.nlm.2008.09.012
Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J., & Regis, Y. (2009). Antipredator behavior in blackbirds: Habituation complements risk allocation. *Behavioral Ecology*, *20*(2), 371–377. https://doi.org/10.1093/beheco/arn151
Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, *16*, 8877. https://doi.org/10.1038/ncomms9877
Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, *17*(4), 997–1005. https://doi.org/10.1007/s10071-014-0731-6
Setsaas, T. H., Holmern, T., Mwakalebe, G., Stokke, S., & Røskaft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas? – A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation*, *136*(4), 563–570. https://doi.org/10.1016/j.biocon.2007.01.001
Shulgina, G. I. (2005). The neurophysiological validation of the hyperpolarization theory of internal inhibition. *The Spanish Journal of Psychology*, *8*, 86–99. https://doi.org/10.1017/S1138741600004996
Sinclair, A. R. E., & Dobson, A. (2015). Conservation in human-dominated world. In A. R. E. Sinclair, K. L. Metzger, S. A. R. Mduma & J. M. Fryxell (Eds.), *Serengeti IV: Sustaining biodiversity in a coupled human-natural system* (pp. 1–10). Chicago, London: The University of chicago Press.
Sreekar, R., & Quader, S. (2013). Influence of gaze and directness of approach on the escape responses of the Indian rock lizard, *Psammophilus dorsalis* (Gray, 1831). *Biosciences*, *38*(5), 829–833. https://doi.org/10.1007/s12038-013-9378-8
Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2627–2634. https://doi.org/10.1098/rspb.2005.3251
Stankowich, T., & Coss, R. G. (2005). Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behavioral Ecology*, *17*(2), 246–254. https://doi.org/10.1093/beheco/arj020
Thompson, R. F. (2009). Habituation: A history. *Neurobiology of Learning and Memory*, *92*(2), 127–134. https://doi.org/10.1016/j.nlm.2008.07.011
Turner, R. (2015). *Travel and tourism economic impact 2015 Tanzania* (pp. 16–24). London: Harlequin Building, 65 South Street.
van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in Sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083
Williams, D. M., Samia, D. S. M., Cooper, W. E. Jr, & Blumstein, D. T. (2014). The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. *Behavioral Ecology*, *25*(5), 1136–1147. https://doi.org/10.1093/beheco/aru098
Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, *16*, 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8

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