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Hyraxes and humans in Serengeti National Park - flight initiation distance and demography

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Abstract

Human activity acts as a source of disturbance for most animals which display a variety of behavioural responses e.g. increased antipredator behaviour or relocating to a new area, often with costs affecting the animals' fitness. Other animals seemingly thrive in human premises benefiting from human-induced resources. The flight initiation distance (FID; i.e. the distance between predator and prey when prey starts to flee) is a commonly used tool to measure animals' tolerance to humans. In this study I tested how FID changed in relation to human premises, starting distance and other ecological factors such as habitat, presence of young, species, behaviour, time of day and group size in two species of hyrax in Serengeti National Park. I also looked at population size and recruitment rate to assess demographic responses to human activity.

FID was significantly shorter inside human premises possibly due to habituation or risk allocation, while presence of young had no significant effect on FID but can have been affected by a small sample size. Starting distance had a strong positive correlation with FID, and had the most explanatory value for the variation in FID. Habitat did not prove to be a significant factor. Feeding individuals had the shortest FID of the behaviours likely due to a high cost to flee. Late morning was the time of day with the shortest FID which coincides with the time the hyraxes feed. Group size had a positive correlation with FID likely due to increased detection of predators. There were a difference in FID between the species, where the smaller bush hyrax (*Heterohyrax brucei*) had a longer FID possible due to that they are preferred prey by many raptors. The demographic data showed that hyrax populations are significantly higher inside human premises, but with no significant difference in recruitment rates, suggesting a higher survival rate possibly due to less predation. Habitat type was not a significant factor explaining the variance in population densities. There were a positive correlation in group size between the two species.

The variation in FID in this study is affected by the variables starting distance, human activity, group size and behaviour and suggest that antipredator behaviour is a plastic adaptive trait. Starting distance was the variable with the most explanatory value for the variation in FID, and shows how important it is to include starting distance in FID studies. From the results it seems like the hyrax are not negatively affected by the current number of visitors in Serengeti National Park.

Sammendrag

Menneskelig aktivitet er en kilde til forstyrrelser for de fleste dyr, som reagerer med en rekke atferdsmessige responser e.g. økt antipredator atferd eller relokalisering til et nytt område, ofte med kostnader som påvirker dyrets form. Andre dyr tilsynelatende trives i menneskelige områder og nyttiggjør seg menneskeskapte ressurser. Fluktstart avstand (FID; i.e. distansen mellom rovdyr og bytte når byttet begynner å flykte) er ofte brukt som et verktøy for å måle et dyrs toleranse til mennesker. I denne studien testet jeg hvordan FID endret seg i relasjon til menneskelige områder, start distanse og andre økologiske faktorer som habitat, tilstedeværelse av unger, art, atferd, tid på dagen og gruppestørrelse i to arter av hyrax i Serengeti Nasjonalpark. Jeg så også på populasjonsstørrelse og rekrutteringsrate for å vurdere demografiske responser på menneskelig aktivitet.

FID var signifikant kortere i menneskelige områder muligens på grunn av habituering eller risiko allokering, mens tilstedeværelse av unger hadde ingen signifikant effekt på FID men kan ha blitt påvirket av få data med unger. Start distanse hadde en sterk positiv korrelasjon med FID, og hadde høyest forklarende verdi på variasjonen i FID. Habitat viste seg å ikke være en signifikant faktor. Individer som spiste hadde kortest FID av atferdene trolig grunnet høy kostnad ved flukt. Sen morgen var tiden på dagen med kortest FID som sammenfaller med tiden hyraxene spiser. Gruppestørrelse hadde en positiv korrelasjon med FID trolig grunnet økt deteksjon av rovdyr. Det var en forskjell i FID mellom artene, der den mindre bush hyraxen (*Heterohyrax brucei*) hadde en lenger FID muligens på grunn av at de er et foretrukket bytte av flere rovfugler. De demografiske dataene viser at hyrax populasjonene er signifikant høyere i menneskelige områder, men med ingen signifikant forskjell i rekrutterings rate, som tyder på en høyere overlevelsesrate muligens grunnet mindre predasjon. Habitat var ikke en signifikant faktor som forklarte variasjonen i populasjonsstørrelse Det var en positiv korrelasjon i gruppestørrelse mellom de to artene.

Variasjonen i FID i denne studien er påvirket av variablene start distanse, menneskelig aktivitet, gruppestørrelse og atferd og tyder på at antipredator atferd er et plastisk adaptivt trekk. Startdistanse hadde høyest forklarende verdi på variasjonen i FID, og viser hvor viktig det er å inkludere startdistanse i FID studier. Fra resultatene ser det ut som at hyraxen ikke er negativt påvirket av nåværende besøksnivå i Serengeti Nasjonalpark.

Introduction

Nature-based tourism is the fastest growing sector of tourism, with developing countries having the highest increase in numbers of visitors (Balmford et al. 2009; Kuenzi & McNeely 2008). The increase of this type of tourism might be due to factors as e.g. more developed infrastructure making it easier to reach such places. Also, a growing number of people live in cities and urban areas feeling disconnected from nature, and feeling connected with nature is found to be related to happiness (Zelenski & Nisbet 2014). Thus, a demand for outdoor activities is growing and through media channels people will learn about the beauty of nature from all perspectives. Such experiences encourage people to visit such areas by themselves through a holiday experience different from everyday life (Kuenzi & McNeely 2008). National parks and wilderness areas with high biodiversity are popular to visit. In Tanzania, East Africa, tourism has grown from 153 000 visiting tourists in 1990 to 800 000 in 2008, where the majority are visiting Serengeti National Park (SNP) (Gereta 2010). The tourism industry gives many benefits to locals like jobs, education on environmental protection, developed infrastructure and water catchments. Because most of the tourism industry is nature based, biodiversity conservation is a key. The revenues from nature based tourism is used to maintain and develop conservation (Gereta 2010).

The increased human activity resulting from tourism, even though it aims to help conservation efforts, might on the other hand have negative effects on biodiversity. Several studies have demonstrated that many species avoid areas with human activities, pushing such species into less suitable habitats, or they might be interrupted from activities such as parental care, foraging, resting and mating displays (Burger 1981; Gander & Ingold 1997; Klein et al. 1995; Manor et al. 2005). It has been reported that human disturbance can affect reproductive success negatively in several bird species (Beale & Monaghan 2004; Carney & Sydeman 1999; Reijnen et al. 1995; Verhulst et al. 2001), as well as mammals (Kerley et al. 2002; Phillips & Alldredge 2000). In areas with human activity animals use more time on antipredator behaviour and less time foraging compared to areas without human activities (Burger 1994; Carney & Sydeman 1999). Some animals might seem unaffected by human presence including several species of penguins, but stress hormones (Fowler 1999) and body temperature (Regel & Pütz 1997) have been reported to increase when approached by humans. As a result such animals might experience an energy cost due to human induced

stress being up to 10% of the daily energy demand, ultimately resulting in a population decline. Why do animals react this way to nonlethal human activity? Human-caused disturbance is perceived as a form of predation risk, and animals therefore react in the same way as they would to an actual predation risk, with both types of disturbances being costly in time and energy (Beale & Monaghan 2004; Frid & Dill 2002). This effect is called the risk-disturbance hypothesis (Frid & Dill 2002) and predicts that animals react according to the degree of threat perceived with the same economic principles as when facing predators. Various factors can influence the degree of risk perceived by prey, such as distance to refuge and number of predators (Beale & Monaghan 2004; Engelhardt & Weladji 2011).

There are animals that seemingly thrive in human premises, and can adapt to survive in urban environments by directly or indirectly increase their fitness by exploiting human-induced resources and benefits like cultivated plants or garbage, decreased predation pressure, and shelter (Kark et al. 2007; McKinney 2002). Urban adapters are found in less urbanized areas and are not as specialized on human-subsidised resources as the urban exploiters which are well adapted to urban environments and may be specialized to the degree that they are dependent upon human-subsidised resources (Blair 2001; McKinney 2002).

Animals constantly make behavioural decisions based on costs and benefits in different situations. Activities such as foraging, mating displays, parental care and resting increases fitness, while escaping predators or being vigilant are costly through time and energetic loss. Since antipredator behaviour are costly it should be adjusted based on the perceived level of threat (Lima & Dill 1990), and one way to evaluate this is to measure the distance between predator and prey when prey start to flee, called the flight initiation distance (FID) (Bonenfant & Kramer 1996; McGowan et al. 2014). Fleeing as soon as a predator is detected seems to be the safest decision since if caught there will be no future fitness gain (Cooper Jr & Frederick 2007), but it is not necessarily the most beneficial. This is because of the lost opportunity cost: if the animal flees early it has lost time and energy that could be spent on fitness increasing 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 is bigger than the benefits. Various factors are found to influence FID, like 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 i.e. the distance between predator and prey when approach begins (Bateman & Fleming 2014b; Bonenfant & Kramer 1996; Gotanda et al. 2009; Lima & Dill 1990; Sreekar & Quader 2013; Ydenberg & Dill 1986).

Repeated low risk exposure to a potential predator can facilitate change in risk assessment toward the predator in question. This is a process where the animal reduces the response over time as it learns that there is no advantage or disadvantage to the occurrence of the stimulus (Bejder et al. 2009; Thompson 2009). This process is called habituation and is a plastic behavioural response found in many animals (Thompson 2009). This kind of behaviour is often developed towards humans in animals inhabiting areas with human activity (McGowan et al. 2014; Rodriguez-Prieto et al. 2009; Samuni et al. 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. It is then predicted to be a negative relationship between FID and density of predators. In both cases of habituation and risk allocation, FID is expected to decrease with increased non-lethal human activity. In a study on blackbirds (*Turdus merula*) Rodriguez-Prieto et al. (2009) tested FID in parks with different levels of human activity, and approached the birds with both a test person and a radio-controlled vehicle to see if the decreased FID was due to habituation towards humans or risk allocation. The results suggested that both habituation and risk allocation was acting to reduce FID.

Minimal levels of human activity can have effect on wildlife, even a temporary tented camp, a small research station or a popular hiking area can be a source of disturbance that could influence risk assessment (McGowan et al. 2014). Settlements, livestock keeping or hunting is not allowed within SNP, but there are several hotels and lodges with staff villages, tented camps, balloon safari centres as well as a visitor centre and a research centre. They are often built on or around rock outcrops called kopjes, where two species of hyraxes are commonly found. Frequent non-lethal exposure to humans in these areas may reduce FID in hyrax populations compared to populations in kopjes outside of human premises. The life history of hyraxes in human premises might therefore differ from populations outside of human premises due to less predation pressure, higher population densities and human-induced stress disrupting their energy budget (Ditchkoff et al. 2006). In an experiment with artificial bird nests along a gradient from natural habitats to urban areas, there was a decline in predation with increased urbanization (Gering & Blair 1999). Also the woodchuck (*Marmota monax*) had higher survival rates with increasing urban-agricultural development (Lehrer et al. 2011). In previous studies on FID in relation to varying levels of non-lethal human disturbance, the FID decreased with increased human activity (Engelhardt & Weladji 2011; Malo et al. 2011; McGowan et al. 2014; Mikula 2014).

The starting distance is found to influence the FID significantly and should be taken into consideration when doing FID experiments (Blumstein 2003; Engelhardt & Weladji 2011). When a prey become aware of a predator it must allocate attention to monitor the approaching predator. As the duration of the approach increases the cost of not fleeing increases due to the cost of monitoring and assessed risk increases as the predator move closer. The prey should flee early to avoid monitoring cost and decrease the risk of capture (Cooper Jr 2005; Cooper Jr & Blumstein 2014).

To my knowledge there has so far not been conducted any FID experiments on hyraxes. Hence, the objective of this study was to test how FID changes in relation to human premises and other ecological factors such as habitat, presence of young, species, behaviour of hyraxes before the onset of the experiment, time of day and group size. I also looked at population size and recruitment rate to assess demographic responses to human disturbance. I tested the following predictions: 1) FID is shorter within human premises than outside of human premises due to changes in tolerance towards humans; 2) FID is shorter in wooded grassland than in grassland due to more vegetation coverage and hiding places resulting in a decreased risk assessment; 3) FID is shorter when feeding due to high costs of fleeing. FID increases when resting or basking due to small costs of fleeing, and are longer when vigilant due to earlier detection of the risk; 4) FID is shorter in late morning due to feeding activity and high costs of fleeing; 5) FID is longer in larger groups due to earlier detection of predators; 6) FID is longer when young are present due to their vulnerability and inexperience with various predators; 7) FID increases with increased starting distance due to monitoring costs; 8) population densities are higher in human premises due to human induces resources; 9) recruitment rates are higher in human premises due to human induced resources; 10) population densities are higher in wooded grassland due to more browse and coverage from predators; 11) recruitment rates are higher in wooded grassland due to more browse and coverage from predators.

Methods

Study area

The Serengeti-Mara ecosystem lies on the border between Tanzania and Kenya in east Africa, situated on a plateau covering 25,000 km². The Rift Valley and the Crater Highlands lies in the east, and dry, rocky woodland in the southern and south-western area forms a natural boundary. The Western corridor stretches west almost to Lake Victoria and are surrounded by dense cultivation. The Isuria escarpment and the Loita plains in Kenya forms the northern boundary (Sinclair & Arcese 1995). These boundaries prevent emigration or immigration of large mammals (Sinclair & Norton-Griffiths 1979) and the wildebeest (*Connochaetes taurinus*) migration coincides with the boundaries, moving through the ecosystem with the rainfall pattern (Boone et al. 2006; Holdo et al. 2009). The ecosystem includes several different conservation administrations; Serengeti National Park, Ngorongoro Conservation Area, Maswa Game Reserve, and Grumeti, Ikorongo, and Lolindo Game Controlled Areas in Tanzania, and Masai Mara National Reserve in Kenya (Sinclair & Arcese 1995).

The field work was conducted in the Serengeti National Park (SNP) in the central area around Seronera, Lobo in the north, and Moru, Simba, Gol and Barafu in the south of the park (*figure 1*). Temperature varies with elevation, being at a mean maximum of 15°C on the Crater Highlands to 30°C at Lake Victoria. In Seronera the mean maximum is around 28°C year round and at a minimum of 16°C in hot months (October – Mars) to 13°C in cold months (May – August) (Sinclair et al. 2009). The short rain season is in November and December, and the long rain season is from March to May, ranging from 500 mm/year in the southern plains to 1,200 mm/year in the northwest (Sinclair et al. 2009). Grassland is the dominant vegetation type and covers 61% of the park. The southern plains consist of large homogenous grasslands, whereas around Seronera there is a transition to wooded grasslands with varying densities of trees and bushes (Reed et al. 2009).
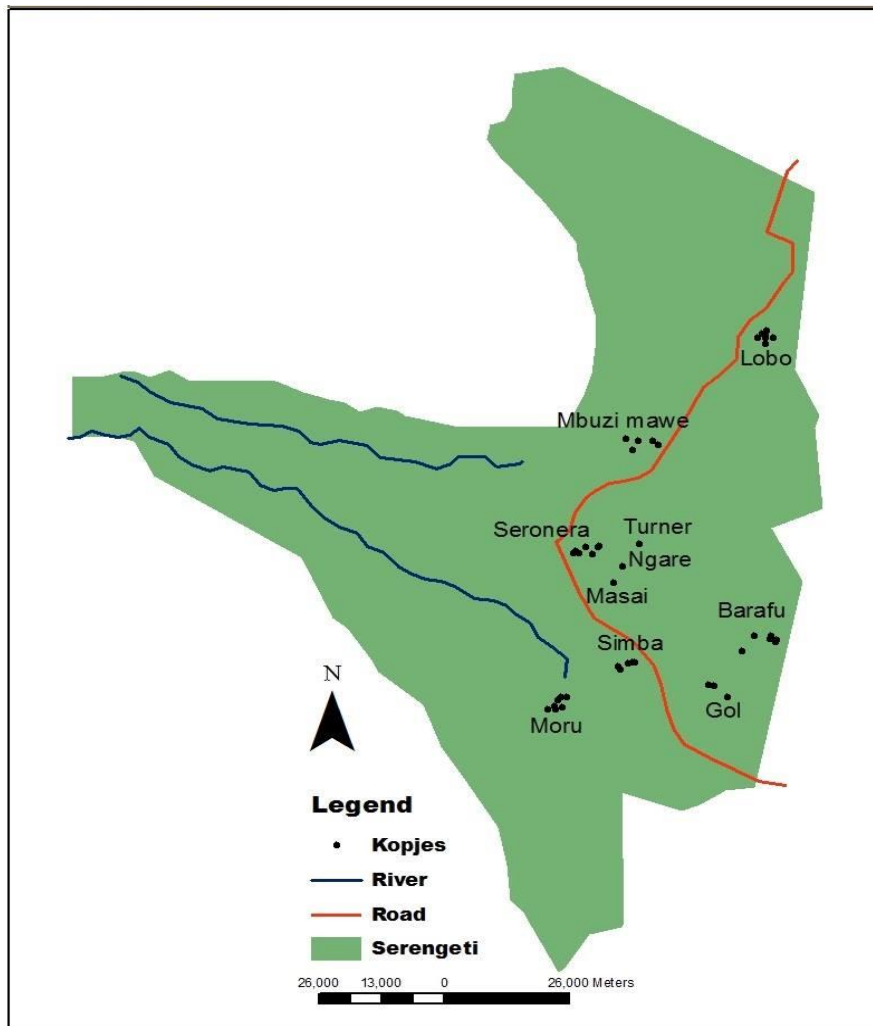
Figure 1. A map of the Serengeti National Park with the 43 kopjes we visited; Research center, Visitor center, Seronera wildlife lodge , Seronera, Staff villages in Seronera, Sero1, Maasai kopjes, Ngarinanyuki, Turner spring, Lobo, Lobo wildlife lodge, Moru ranger post, Moru, Moru 6, Four seasons lodge, Mbuzi Mawe tented camp, Mbuzi Mawe, Barafu, Gol, and Simba kopjes. Map is made by Franco Mbise.

Kopjes are rock outcrops that act as habitat islands surrounded by vast plains (Gerlach & Hoeck 2001; Hoeck et al. 1982) (*figure 2*). They were formed during a late Precambrian orogenic event and consist of granitic gneisses and quartzite (Sinclair et al. 2009). Erosion by rainwater and wind have formed many caves, crevices, fissures and holes on the kopjes (Hoeck 1975; Turner & Watson 1965), and these formations can retain water and have mild temperature changes. The vegetation differs strikingly from the surrounding plains consisting of trees, bushes, herbs and forbs (Hoeck 1975). Poelchau and Mistry (2006) looked at forb diversity on kopjes in SNP and found that kopjes support very different communities than the surrounding grassland, and 78% of all forb species found were exclusive to a habitat type. Wooded vegetation, small mammal and bird communities are also reported to differ between

kopjes and grassland (Sinclair 1975; Trager & Mistry 2003), suggesting kopjes to be distinct habitats with more diverse communities. Most of the kopjes in SNP consists of several small and large rock formations, forming separate kopje groups. The kopjes we visited varied in size from 746 m² to 282733 m².

Figure 2. A part of the Maasai kopje (73289 m²) surrounded by grassland. The kopje vegetation differs drastically from the surrounding grassland. Both species of hyrax were observed on this kopje.

Study species

The rock hyrax (*Procavia capensis*) and the bush hyrax (*Heterohyrax brucei*) are diurnal and occur sympatric or allopatric on kopjes throughout the 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* (Rose & Archibald 2005). The rock hyrax is the bigger of the two and has a mean body weight of 3.2 kg, and the bush hyrax has a mean body weight of 1.8 kg (Hoeck 1982). The bush hyrax is also referred to as the yellow-spotted rock hyrax, and colours range from grey to reddish brown, while the stomach and chest are creamy in colour. They have distinct creamy eyebrows, and have a narrower muzzle than the rock hyrax (Barry & Shoshani 2000). The rock hyrax coloration is brownish grey on the back,

while stomach and chest is light brown, and eyebrows are not as distinct as the bush hyrax (Olds & Shoshani 1982). Gestation last for about 7.5 months for both species, and the young are well developed at birth (Barry & Shoshani 2000; Olds & Shoshani 1982). In SNP the birth event last from April to June and vary between kopje groups, with all young being born within a three week period. The bush hyrax is observed to have a second birth event in January after the short rain season. Litter size for bush hyrax varies from 1 – 3, and for rock hyrax from 1 – 4 (Hoeck 1982).

The hyrax has labile body temperatures and use huddling and basking behaviour to maintain body temperature during the day, especially in the morning (Bartholomew & Rainy 1971; McNairn & Fairall 1984). They depend on crevices, caves and vegetation crown cover to avoid temperature stress (Brown & Downs 2005, 2007) as well as shelter from predators (Hoeck 1975). Suitable sleeping holes and hiding places are found to be the limiting factor for rock hyrax population growth (Fairall et al. 1986). The two species in SNP are the main prey for the black eagle (*Aquila verreauxii*) (Barry & Barry 1996; Gargett 1990), also several other raptors, snakes and leopards (>30% of *Panthera pardus* diet in Western Cape) are common predators (Fröhlich et al. 2012; Grobler & Wilson 1972; Hoeck 1982; Martins et al. 2011). Other mortality factors are parasites, especially the "sarcoptic mite" which is lethal in the rock hyrax, and intra- and interspecific competition (Hoeck 1982). Both species live in colonies with a territorial male, several adult females and subadults and juveniles of both sexes (Hoeck et al. 1982). Males disperse shortly after reaching sexual maturity (at around 16 months, but some late dispersers as late as 28 months) while most females stay in the group (Hoeck 1982). Subordinate males occupy the peripheral area around the core area of the colony if the kopje is big enough to provide suitable hiding places outside the core area. A dominance hierarchy apply among the peripheral males, each defending a small area around their individual sleeping hole. When the dominant male disappears the dominant peripheral male displace him. Kopjes bigger than 4000 m² can have two or more family groups (Hoeck et al. 1982). When both species occupy the same kopje they can live in close association; sharing the same dens, huddle together, play and feed together. Furthermore communal nurseries are formed which are watched by a subadult or adult with juveniles of both species (Hoeck 1989). Barry and Mundy (2002) reported that heterospecific groups are bigger than homospecific groups, and there were more heterospecific groups after birth than before the birth event, and heterospecific groups had more young per adult. Further on, they suggested that predation pressure favoured cooperative behaviour to increase predator detection and avoidance, thus increasing survival of young. The hyrax feed in groups with a sentinel on a high point keeping

watch (Hoeck 1975). In the wet season with plenty of green vegetation the rock hyrax is mainly a grazer while the bush hyrax is a browser, but as the grass dries and have less nutrients the rock hyrax shift between grazing and browsing (DeNiro & Epstein 1978; Hoeck 1975; Zimman 2003).

Fieldwork

Fieldwork was carried out from June 2nd to August 12th 2014 on dry and sunny days, during this time 43 kopjes were visited (*figure 1*). Kopjes were grouped as either in human premises i.e. an establishment with permanent human activity as lodges etc., or outside of human premises. Habitat type were categorized as grassland or wooden grassland, the latter being defined by grassland with occurrence of varying degrees of trees and bushes.

Demography and behaviour

Group sizes were recorded by monitoring kopjes three times during three consecutive days for about two hours, as recommended by MacKenzie and Royle (2005) for occupancy studies. Each visit was at different times; morning (07.00 – 09.00), late morning (09.30 – 11.30) and evening (16.30 – 18.30). During these times the hyraxes come out from their dens to bask in the sun, feed and play which make them easier to see and count. The two species look very similar, and it can be hard to differentiate between them when looking at young and sub-adults. Therefore, we used a couple of days to practice in the field before we recorded any data. At kopjes away from human premises observations were done from inside the car, driving around the kopje once, and if possible in between the kopjes. At kopjes in human premises observations were done by walking inside and around the area once if it was safe. In this way double counting was avoided as much as possible, and the numbers are minimum estimates. Mean observer distance was 59.2 m outside human premises and 21.7 m inside human premises. At each kopje we used binoculars and recorded number of individuals and species. We were at all times two observers, but only one that identified species and did the final counting at each spot to avoid double counting. We classified individuals by body size in three age groups; adult (>16 months, $n = 1925$), sub-adult (6 – 15 months, $n = 752$), and young (<6 months, $n = 650$). Finally we recorded behaviour when first sighted as 1) resting, 2) feeding, 3) vigilant 4) playing, 5) moving, and 6) 50/50 resting and feeding, logging up to two behaviours most seen from maximum count at that visit.

Flight distance

FID experiments were done between 7 am to 6 pm, and only once in every kopje to avoid using the same animals twice. General methods were done in accordance with Setsaas et al. (2007). When we sighted a suitable test animal or group of animals we stopped the car or stood still and recorded number of individuals, species, age and behaviour. There were always the same observer and same test person in all experiments. The observer used a laser rangefinder to measure the SD, then the test person walked toward the animal or group in a straight line and at a constant speed and immediately stopped when the animal fled, then the observer measured the distance to the test person and recorded it as the first flight distance. If not all the animals in the group fled at first flight, the test person continued to walk when signalled from the observer until the last animal fled and immediately stopped, and the observer recorded the second flight distance. The species and age of the first and last individual to flee were recorded. The flight distance is the difference between the starting distance and the test person. In some human premises the flight distance was less than 10 meters, and the rangefinder we used could measure from 10 – 1000 meters. In those cases we did a visual estimate (*figure 3*).
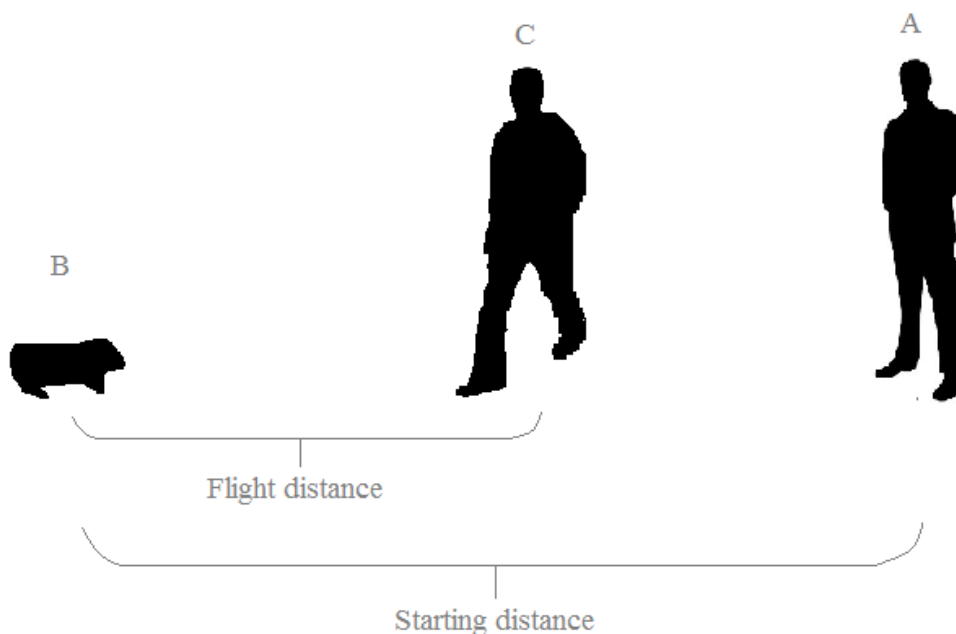

Figure 3. If observer A measure 15 meters to test animal B, and the test animal flees when test person C is approximately halfway between A and B we estimate that the FID is around 7 or 8 meters. If the test animal flees when the test person is 1/3 length between A and B we estimate that the FID is 10 meters.

Statistical analyses

All tests were conducted in SPSS Statistics 21 for windows, and a 95% confidence interval was used. Before the population analyses were conducted, the average of the counts from the three visits on each kopje were calculated. The demographic data was not normal distributed so it was log-transformed before the analyses. One-way analysis of variance (ANOVA) was used to compare means between groups with different variables. Also bivariate correlation tests, paired sample t-tests, and linear regression were used. Significance level was set to $p = 0.05$.

Results

Flight distance

Mean FID for both species was statistically significantly shorter for kopjes in human premises than in kopjes outside of human premises ($F = 83.3$; $p < 0.0001$) (*figure 4*).
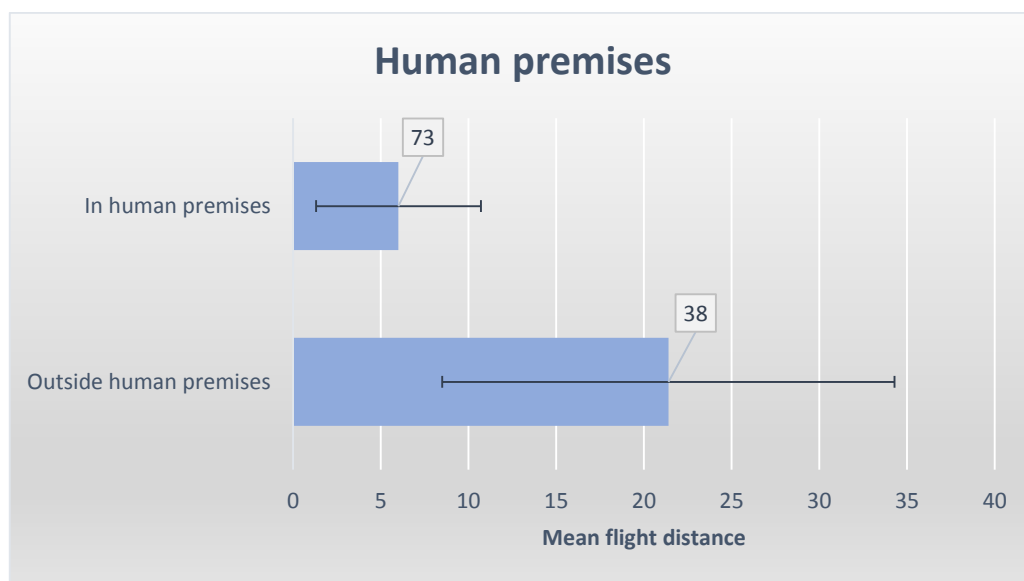

Figure 4. Mean FID measured in meters in human premises (upper column) and outside of human premises (bottom column). Above the columns are numbers in sample. Error bars show standard deviation.

Mean FID for both species was statistically significantly shorter for kopjes in wooded grassland than for kopjes in grassland ($F = 22.9$; $p < 0.0001$) (*figure 5*).
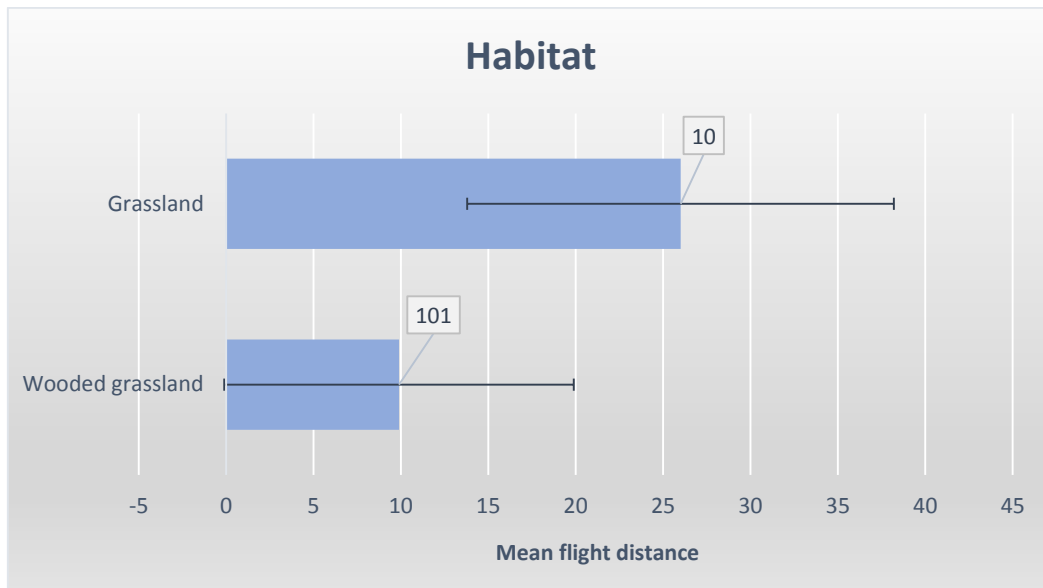
Figure 5. Mean FID measured in meters in grassland (upper column) and wooded grassland (bottom column). Above the columns are numbers in sample. Error bars show standard deviation.

There was a statistically significant difference in mean FID between behaviours ($F = 8.0$; $p = 0.001$), where feeding individuals had a shorter FID than vigilant and resting individuals (*figure 6*).

Figure 6. Mean FID measured in meters when individuals were resting (upper column), vigilant (middle column), and feeding (bottom column). Above the columns are numbers in sample. Error bars show standard deviation.

There was a statistically significant difference in mean FID between different times of the day ($F = 7.9$; $p = 0.001$). Mean FID was longest in the morning while mean FID was shortest in late morning (*figure 7*).
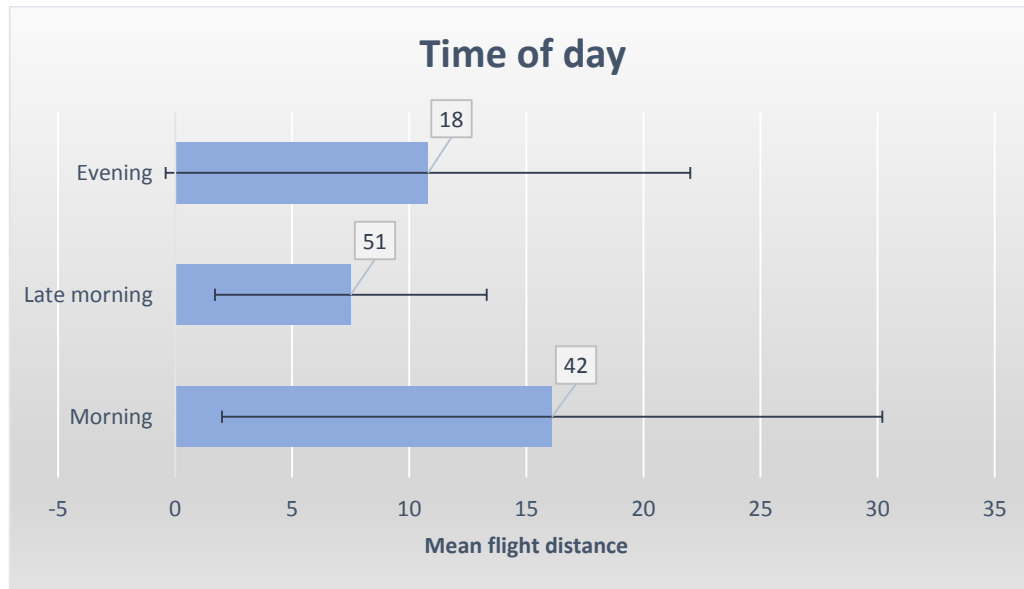

Figure 7. Mean FID measured in meters in the evening (upper column), late morning (middle column), and morning (bottom column). Above the columns are numbers in sample. Error bars show standard deviation.

There was a statistically significant difference in mean FID between species group compositions ($F = 4.6$; $p = 0.012$). The rock hyrax had a shorter mean FID than the bush hyrax. When both species were seen together the mean FID was longer (*figure 8*).
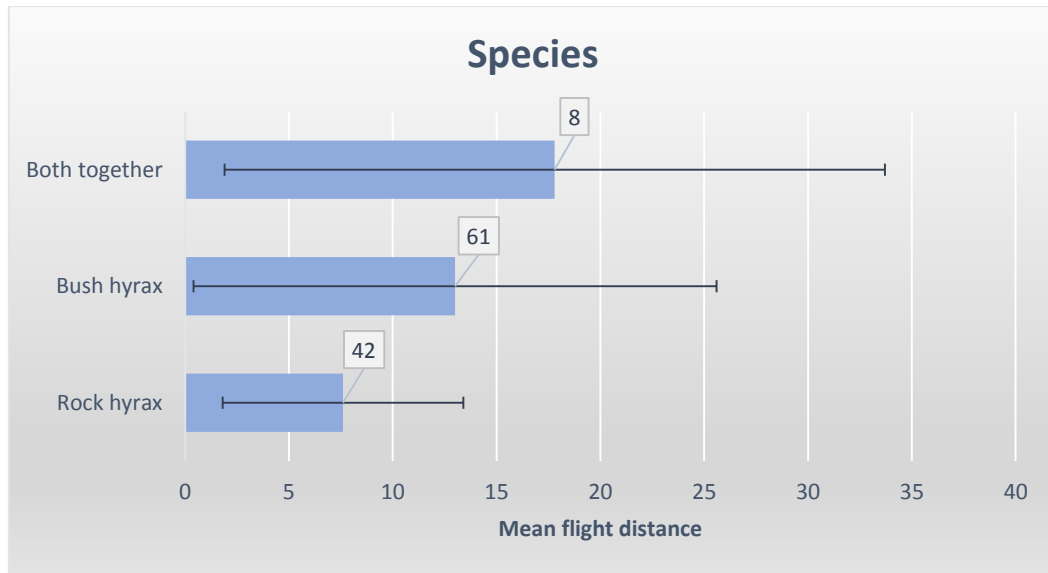
Figure 8. Mean FID measured in meters when both species were in a group together (upper column), only bush hyrax (middle column), and only rock hyrax (bottom column). Above the columns are numbers in sample. Error bars show standard deviation.

A correlation test showed a weak but statistically significant positive correlation between group size and FID ($n = 111$; *Pearson r* $= 0.189$; $p = 0.047$). Young presence in the group had no significant effect on FID. Starting distance ($n = 112$) and FID ($n = 109$) proved to have a statistically significant strong positive correlation (*Pearson r* $= 0.719$; $p < 0.0001$). A linear regression using FID as the dependent variable and seven independent variables proved to be statistically significant ($F = 42.8$; $p < 0.0001$). These variables explained 72.7% of the variation in FID ($r^2 = 0.727$). Two of the variables were significant contributors to the variation, and two were almost significant. The variable with the most statistically significant explanatory value was starting distance, then human premises, followed by the almost significant group size, and behaviour was also close to significant (Table 1).

Table 1. A linear regression with FID as dependent variable and starting distance, human premises, group size, behaviour, habitat type, time of day and species as independent variables.

Independent variables	Rank	t	P
Starting distance	1	9.119	0.0001
Human premises	2	2.787	0.006
Group size	3	1.970	0.052
Behaviour	4	1.797	0.075
Habitat type	5	-1.585	0.116
Time of day	6	1.325	0.188
Species	7	0.808	0.421
Constant		-0.890	0.375

Demographic analysis

Population size of both the rock hyrax ($F = 14.7$; $p = 0.001$) and bush hyrax ($F = 25.0$; $p < 0.0001$) was statistically significantly higher in kopjes in human premises compared to kopjes away from human premises. Proportion of bush hyrax and rock hyrax young was not statistically significantly higher in human premises. Total population size with both species combined was statistically significantly higher in human premises (mean = 85.6; $n = 11$; SD 47.9) compared to kopjes outside of human premises (mean = 8.7; $n = 32$; SD 14.3; $p < 0.0001$) (*figure 9*).
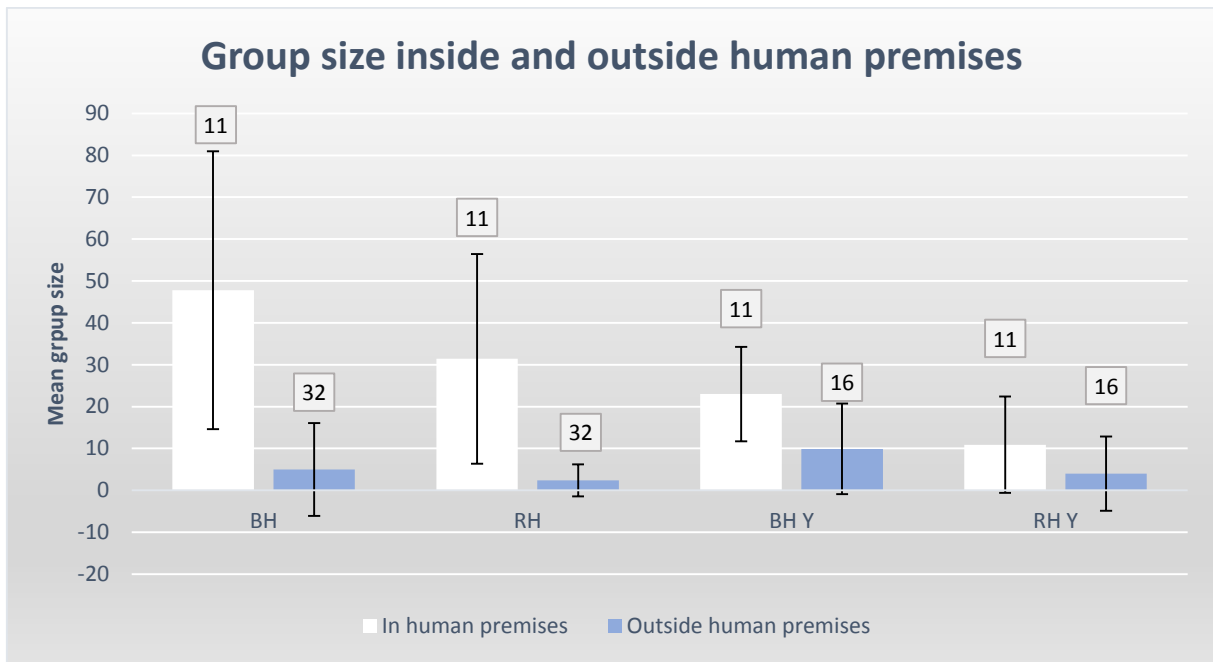
Figure 9. Mean group size inside (white) and outside (blue) of human premises for bush hyrax (BH) and rock hyrax (RH), and proportion of bush hyrax young (BH Y) in the group, and proportion of rock hyrax young (RH Y) in the group. Above the columns are numbers in sample. Error bars show standard deviation.

Total mean population size for both species combined was statistically significantly higher in kopjes in wooded grassland compared to kopjes in grassland ($F = 6.2$; $p = 0.020$). Population size for the rock hyrax was almost statistically significantly higher in kopjes in wooded grassland compared to kopjes in grassland ($F = 4.1$; $p = 0.054$), while it was not statistically significantly higher for the bush hyrax. Proportion of young was not statistically significantly higher in either habitat for both species (*figure 10*).
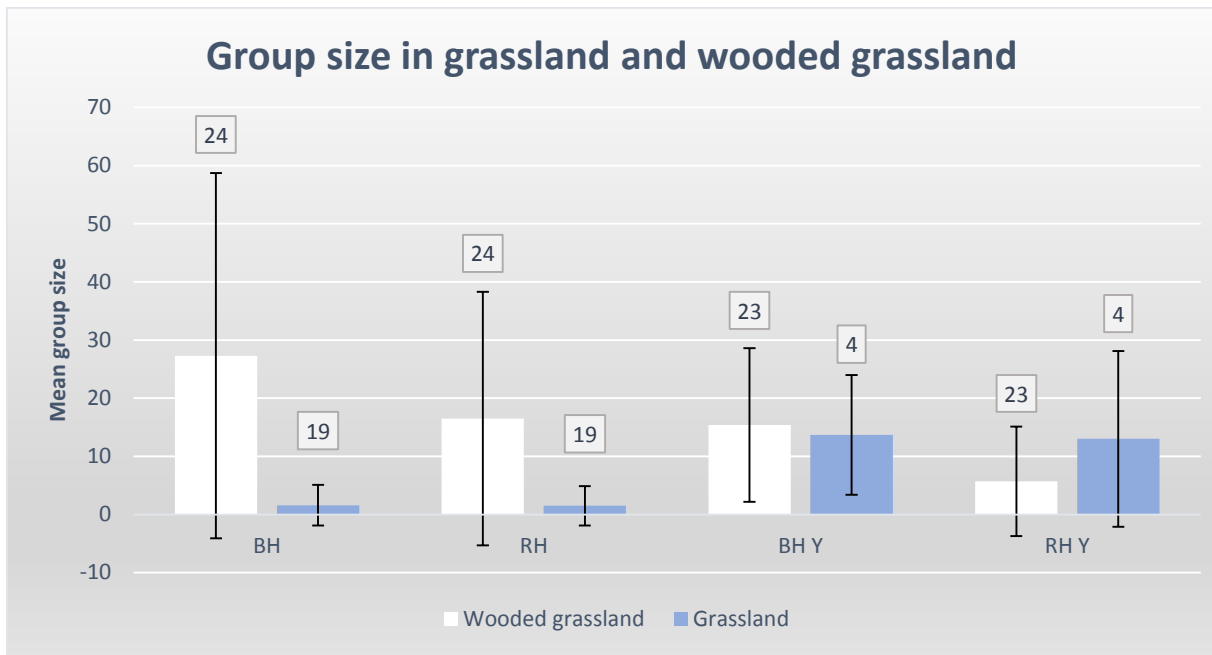
Figure 10. Mean group size in wooded grassland (white) and grassland (blue) for bush hyrax (BH) and rock hyrax (RH), and proportion of bush hyrax young (BH Y) in the group, and proportion of rock hyrax young (RH Y) in the group. Above the columns are numbers in sample. Error bars show standard deviation.

A paired sample t-test comparing the difference between the total rock hyrax group size (mean = 9.8; n = 43; SD 18.0) and total bush hyrax group size (mean = 15.9; n = 43; SD 26.7; t = -1.8; p = 0.081) was almost statistically significant. There was almost a statistically significant difference between total group size of rock hyrax young (mean = 1.4; n = 43; SD 3.2) and bush hyrax young (mean = 3.6; n = 43; SD 7.1; t = 2.1; p = 0.064). A correlation test showed a statistically significantly strong positive relationship between bush hyrax group size and rock hyrax group size (*Pearson r* = 0.600; n = 23; p = 0.001). Proportion rock hyrax young and proportion bush hyrax young had no correlation. There were no correlation between bush hyrax group size and number of bush hyrax young, as well as no statistically significant correlation between rock hyrax group size and number of rock hyrax young. A linear regression analysis with rock hyrax group size as dependent variable and habitat type and human activity as independent variables proved to be statistically significant, explaining 41.4% of the variation in rock hyrax group size (r^2 = 0.414). Human activity was the only statistically significant factor (t = -3.028; p = 0.006) explaining this variation. The same analysis were done for the bush hyrax and proved to be statistically significant, explaining 50.3% of the variation in bush hyrax group size (r^2 = 0.503). Human activity was the only statistically significant factor explaining this variation (t = -4.731; p < 0.0001).

Discussion

If human disturbance causes behavioural changes in animals which negatively affect a population we would essentially see a reduced demographic performance in that population (Gill et al. 2001). Hyraxes in human premises showed a decreased sensitivity towards human approach with a significantly shorter FID, which is consistent with my first prediction. Furthermore, the demographic analyses indicate that human disturbance does not negatively affect demographic performance in either species. On the contrary both species had higher population levels in human premises compared to kopjes outside of human premises in accordance with prediction number 8, suggesting a higher survival rate, but with no significant difference in recruitment rates, which do not support prediction 9. There are several possible explanations for why FID is shorter in human premises. Animals can learn through experience with local predators and adjust antipredator behaviour thereafter (Bateman & Fleming 2014a; Deecke et al. 2002). The hyraxes frequently exposed to humans may have learned from experience that humans do not pose a threat and thus by lowering FID decreases cost of escape and have more time to do fitness increasing activities. According to optimal escape theory (Cooper Jr & Frederick 2007; Ydenberg & Dill 1986) it is advantageous to adjust antipredator behaviour like FID according to the degree of risk posed to optimize fitness.

Reduction in FID due to habituation towards humans have been found in several other species (Engelhardt & Weladji 2011; McGowan et al. 2014; Rodriguez-Prieto et al. 2009; Runyan & Blumstein 2004; Stankowich & Blumstein 2005). Habituation towards humans in the hyrax is likely since there is year round human activity in all human premises we visited. But due to the short duration of the study I can only confirm that hyraxes in human premises had a higher tolerance (i.e. the amount of disturbance tolerated before reacting) toward human disturbance than hyraxes outside of human premises (Nisbet 2000). To confirm habituation, which is defined as a process of a decrease in response toward a non-harmful stimulus over time, in this case the stimulus being human activity, repeated test on tolerance levels in an individual must be done over time (Bejder et al. 2009). If tolerance levels are increasing over time it can be termed habituation (Bejder et al. 2009; Thompson 2009).

Another possible explanation to the shorter FID in human premises could be the risk allocation hypothesis (Lima & Bednekoff 1999). The constant high level of disturbance

causes the hyraxes to make a trade-off between antipredator behaviour and fitness increasing activity, lowering the FID to meet their needs. To further test this hypothesis one could test the FID by approaching the hyraxes separately with a novel object like a flying drone and a test person in accordance to Rodriguez-Prieto et al. (2009). Rodriguez-Prieto et al. (2009) suggest from their results in an experiment on blackbirds that both risk allocation and habituation was acting on the birds reduction in FID, and there is a possibility that both systems are acting on the hyraxes' reduction in FID too. Also worth considering is that predators are found to have a longer FID than prey (Moller 2012) and so human premises can act as refuge from predators for the hyrax. Thus a reduction in FID can be a response from reduced predation pressure.

Yet another explanation, which do not exclude habituation and risk allocation, could be that at the onset of the disturbance the less tolerant individuals moved out of the disturbed area due to the high cost of psychological stress whereas only tolerant individuals remained, lowering tolerance levels outside human premises as a function of avoidance (Fowler 1999). The FID measured would thus be a measurement between personality traits of more and less tolerant individuals, or possibly a combination of more tolerant individuals and habituation towards humans. In a FID experiment on birds by Carrete and Tella (2010) they found that individual FID was highly constant and might be heritable as a personality trait, and hypothesised that birds distributed themselves based in their tolerance to human disturbance. Rodríguez-Prieto et al. (2011) found that differences in personality traits like ability to assess risk affected how fast individuals habituated. Thus it seems that tolerance can vary on an individual level and be a heritable component within a species, over time possibly resulting in genetic differences in tolerance between populations (Møller 2008). If or not the hyrax distribute themselves upon individual susceptibility to disturbance could be tested by opening a new tourist visitation area and measuring tolerance levels in tagged individuals before and after start of tourist activity, and also see if individuals assigned as least tolerant relocates. But in a study on Marmots (*Marmota flaviventris*) by Runyan and Blumstein (2004), which is a good comparative species to hyraxes, they found that individual differences in FID was too small to have a significant effect on the variation in FID.

Many studies find differences in FID between species (Blumstein et al. 2003; Mikula 2014) and suggest that it is a species specific trait. Rock hyraxes had a shorter FID than bush hyraxes, which may be due to differences between the two species. There have been found in previous studies that risk taking decreased with decreasing body size (Helfman 1989), smaller litter size (Ghalambor & Martin 2001; Møller & Liang 2013), predation pressure (Díaz et al.

2013; Møller & Ibáñez-Álamo 2012; Riechert & Hedrick 1990) and adult survival (Ghalambor & Martin 2001). The hyraxes are predated by several raptors, and both the black eagle (Barry & Barry 1996) and verreaux's eagle (*Aquila verreauxii*) are reported to prefer the smaller bush hyrax which may apply to other raptors as well, additionally the bush hyrax have fewer offspring (Hoeck 1982), at which both factors might cause the bush hyrax to decrease risk-taking by increasing FID.

Habitat type do not appear to be an important factor for the variance in FID with several other variables being significant contributors explaining the variance, which do not support the second prediction. Although there was a significant difference between habitat types this could have been biased by the fact that all human premises were in wooded grassland and FID were much shorter in human premises. Even so wooded grassland is probably perceived as lower-risk habitat than grassland because of more cover from predators, thus expected to be preferred. Druce et al. (2006) found that the hyrax had a lower giving up density when feeding close to cover due to a higher perceived risk away from cover.

Vigilance was predicted to be the behaviour with the longest FID since predators would likely be detected sooner, but when comparing behaviours resting proved to have the longest FID. There is a possibility that vigilance was misinterpreted as resting if the animals were lying down. The difference in FID between the two behaviours was small. Feeding was the behaviour with shortest FID as expected due to a higher cost of fleeing from the activity in accordance to optimal escape theory (Cooper Jr & Frederick 2007; Ydenberg & Dill 1986), thus the 3rd prediction is partially supported by the results. For the time of day, late morning was the time with the shortest FID, which coincides with when the hyraxes feed and supports the 4th prediction.

When both species were together in a group, mean FID were longer compared to homospecific groups, likely due to a larger group size when both species occur together as there were a strong positive correlation between the two species. Furthermore, there was a significant positive correlation between group size and FID, as well as group size being close to significant in explaining the variance in FID, and this supports the 5th prediction. Fanson et al. (2011) found that the rock hyrax altered vigilance behaviour according to changes in group size, where a decrease in group size increased time spent vigilant and how often they interrupted feeding to scan for predators. Also after controlling for factors such as distance from shelter, distance from kopje, vegetation cover and time spent feeding there was a negative relationship between group size and vigilance behaviour. Their results could be explained by both the many eyes hypothesis i.e. a larger group will detect predators sooner,

and the dilution hypothesis i.e. risk of capture for an individual decreases as group size increases (Dill & Ydenberg 1987; Lagos et al. 2014; Lima 1995; Roberts 1996). The FID results in this study supports the many eyes hypothesis; that a larger group detects danger sooner and thus flees at longer distances. While vigilance behaviour is predicted to decrease with increased group size for both hypothesis, FID is expected to decrease for the dilution hypothesis, while for the many eyes hypothesis FID is predicted to increase. Similar results have been found in primates (*Macaca fascicularis*) (Van Schaik et al. 1983), house sparrows (*Passer domesticus*) (Barnard 1980), and geese (*Branta bernicla*) (Owens 1977).

Surprisingly, young presence in the group had no significant effect on FID, thus the 6th prediction had no support. The results can have been affected by a small number of experiments with juveniles ($n = 13$). Also a large portion of the experiments were done with lone adults, while all experiments involving juveniles were in groups with adults or sub-adults which possibly affected the FID. Females with young are found to have a longer FID possibly due to juveniles underdeveloped escape tactics (Stankowich & Blumstein 2005). Juvenile robins (*Turdus migratorius*) also had longer FID than adults (Eason et al. 2006), likely due to little experience with humans. Based on the factor that experience with predators is found to influence perception of risk (Stankowich & Blumstein 2005), as well as underdeveloped escape tactics make juveniles easy targets for predators, we might have seen significant results if we had more experiments involving juveniles.

The starting distance proved to have a significant effect on the FID with a strong positive correlation as expected in prediction number 7, and was the most significant variable explaining differences in FID. Many studies have found a positive correlation between starting distance and FID (Blumstein 2003; Cooper Jr 2005; Cooper Jr & Blumstein 2014; Williams et al. 2014) due to the preys increased monitoring cost as predator approach time increases. There have been argued that alert distance i.e. the distance between animal and human when an animal becomes alert of the approaching human, should be used rather than FID to measure an animal's tolerance to humans (Fernández-Juricic et al. 2001) because it can be influenced by many other factors as seen here with the starting distance. The FID was the most convenient to use since we used a car to look for hyraxes outside of human premises, and the hyraxes was probably aware and alert of us before we started the experiment or even before we had spotted them. Also inside human premises 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) (Blumstein 2003).

Ydenberg and Dill (1986) model predicts that FID increase with increasing distance to

refuge and have been supported in several studies (Bonenfant & Kramer 1996; Cooper Jr 1997; Gotanda et al. 2009; Kramer & Bonenfant 1997), but we did not control for distance to refuge. Other disruptive variables that could be affecting the FID which we did not take into consideration 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 et al. 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 2014a), 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.

Demographic responses

A high survival rate in human premises may be due to utilization of human-induced resources and less predation pressure. Predators have a longer FID than prey, and so human premises can act as a refuge from predators for prey (Moller 2012). We did observe hyraxes using a partition and the underside of a porch as a hiding place on all three visits and were told by the people living there the hyrax commonly used it. Also, by the entrance to the research centre there were a latrine in the shade of the roof commonly used when feeding away from the kopje. Furthermore, food utilisation were observed at a ranger post where they ate peanuts that was dropped from rangers sorting out bad ones. It is likely that the tourists give the hyraxes food at lodges and at the visitor centre.

A less likely explanation (based on no observed difference in recruitment rates), but still worth mentioning is that the presence of hyraxes on kopjes in human premises might not be due to human-induced resource utilisation, but that the kopjes in human premises is of high quality or with no sufficient alternative kopjes to relocate to, forcing hyraxes to stay despite the disturbance (Gill et al. 2001). The high population density could be caused by the lack of predators despite a stressful environment. Moving out of an area is of high risk when moving through open unfamiliar land without cover in between kopjes, and have costs in the form of time, locomotion and lost investments like territories, status, and information (Gill et al. 2001). If this is the case, then the hyraxes would probably be experiencing some degree of stress caused by human-induced disturbance, consequently having a disrupted energy budget

(Frid & Dill 2002). Further tests that could be conducted to measure the effect human activity has on the hyraxes stress level is by comparing time spent vigilant and time spent feeding inside and outside of human premises. Disturbed animals have been found to increase time spent vigilant and decrease time spent feeding, consequently resulting in decreased fitness and lowered reproductive rate (Frid & Dill 2002; Verhulst et al. 2001). Additionally, the more intrusive method of monitoring heart rate and body condition (e.g. weight) would show a clearer picture of possible stress in the animals (Frid & Dill 2002; Regel & Pütz 1997). Based on the demographic data it seems like the hyraxes are not negatively affected by human activity. There was no significant difference in proportion of young between inside and outside of human premises, suggesting there is no lowered reproductive rate in the populations experiencing constant human disturbance. Thus it seems there is no long term negative effects on the hyraxes' reproductive rate in human premises.

All over the bush hyrax was close to being significantly more abundant than the rock hyrax, as well as bush hyrax young was close to being significantly more abundant than rock hyrax young. Barry et al. (2015) reported that the bush hyrax was more affected by fluctuations in annual rainfall with a positive relationship between population densities and rainfall, but the rock hyrax had no such correlation. The same trend was reported by Hoeck (1989) where the rock hyrax increased in numbers after nearly a decade with low rainfall. Top-down processes could also be a factor in regulating hyrax densities due to their importance as prey for many predators (Barry et al. 2015). There was a strong positive correlation between bush hyrax group size and rock hyrax group size suggesting a higher population density when both species occur together. Barry and Mundy (2002) reported similar results for hyraxes in Zimbabwe where they too found that the groups were bigger when both species occurred together. They also found that homospecific groups had fewer offspring than heterospecific groups. I did not find a correlation between group size and number of offspring, nor a correlation between bush hyrax young and rock hyrax young suggesting no significant difference in recruitment rates between heterospecific and homospecific groups. Further, Barry and Mundy (2002) saw an increase of heterospecific groups after a birth event, and the association lasted for about two months until the offspring were weaned. For hyraxes in SNP the birth event are found to occur from April to June (Hoeck 1982), and since the offspring were observed in nursery groups we can be quite sure they were less than two months of age. Therefore, the occurrence of both species in groups together can have been higher during the study period than rest of the year in some places.

The hyrax was significantly more abundant in wooded grassland when looking at total

population size for both species combined, but when taking human activity into account it was the only significant contributor of the two explaining the variance in population size between habitat types. All human premises we visited ($n = 10$) were located in wooded grassland which may have influenced the results due to higher population densities in human premises. Thus the results do not seem to support the 10th prediction. Recruitment rates was not statistically significantly higher in either habitat type and do not support the last prediction. The bush hyrax is a year round browser, while the rock hyrax is more general and can switch to browse when the grass has lost its nutritional value, consequently creating interspecific competition for food (Hoeck 1975, 1989). Thus wooded grassland are expected to decrease competition between species and support a higher population density compared to kopjes in grassland by providing more food as well as shelter. If we had data from more kopjes and more exact estimates of vegetation surrounding the kopjes there might be a significant differences between hyrax populations in grassland and wooded grassland. In the Simba, Barafu and Gol kopjes located in the south-eastern grasslands we did not observe any populations of hyraxes, which might be due to inadequate vegetation cover not supporting hyrax populations, or that the lack of trees makes the grassland difficult to cross for migrating hyraxes.

There is a possibility that the population estimates are far below what they really were for some large kopjes outside of human premises. When driving around a large kopje one only sees a small area, and many hyraxes might be out of sight in between vegetation or located in the centre of the kopje. Hyraxes in kopjes away from roads might be less tolerant to cars and hide when cars come close making them difficult to see.

To summarize there were found a significant difference in FID inside and outside human premises in accordance with the first prediction, but the second prediction are not confirmed with no significant difference between habitat types. The third prediction is partially supported with the shortest FID when feeding and with little difference in FID between resting and vigilance, with a possibility that sometimes vigilance have been misinterpreted as resting. The fourth prediction is confirmed with shortest FID in the late morning, which coincides with the time the hyraxes are feeding (Hoeck 1975). FID was longer in large groups in accordance with the fifth prediction, but there were no significant difference in FID when young were present and do not support the 6th prediction. There were a positive correlation between starting distance and FID in accordance to the 7th prediction. Prediction number 8 were supported with significantly higher population densities in human premises likely due to decreased predation pressure, but there were no difference in

recruitment rates inside and outside human premises nor between habitats which do not support prediction number 9 and 11. Even though hyraxes were significantly more abundant in wooded grassland the 10th prediction is not supported with human activity being the only variable of the two explaining the variation.

The variation in FID in this study is affected by variables as starting distance, human activity, group size and behaviour and suggest that antipredator behaviour is a plastic adaptive trait. Whether the difference in FID inside and outside human premises is caused by habituation, risk allocation, individual differences in tolerance or some other factor needs further study. Starting distance was the variable with the most explanatory value for the variation in FID, and shows how important it is to include starting distance in FID studies. Further on for future FID experiments on hyraxes or other animals hiding in burrows I would include distance to refuge as it is possibly an important variable affecting FID, as well as collect more FID data with young. From the results it seems like the hyrax are not negatively affected by the current number of visitors in SNP.

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