The effect of human presence on the routine and induced vigilance behaviour of impala (*Aepyceros melampus*) in the Kruger National Park, South Africa

<u>Category</u> : <u>Participants</u> :	Independent Project Cecilia Cerrilla, Jessica Coulter, Deanna Ineson, Caroline Schechinger, and Donovan Tye (resource person)
<u>Site</u> : <u>Key words</u> :	Skukuza, Kruger National Park, Mpumalanga Province, South Africa anti-predator behaviour, energy costs, habituation, human-wildlife conflict, impala, vigilance

Abstract

Human presence can impact the behaviour of wildlife, which can ultimately influence the survival and fitness of populations. Specifically, studies have shown that human presence changes the vigilance patterns of many ungulate species, which can alter an individual's energy budget due to the high cost of vigilance. However, recent studies have found conflicting results regarding the effect of human presence on vigilance patterns, signifying that this relationship needs to be studied at the population level. Our study focused on determining the effect of longterm human presence on the vigilance behaviour of impala (Aepyceros melampus) populations in the Kruger National Park (KNP), South Africa through continuous observation of impala in sites with high and low human presence. Behaviour was monitored without stimuli to compare routine vigilance between high and low human presence levels. To compare induced vigilance levels of different perceived threats, two sound stimuli-human voices and a leopard growl-were played at both site types. In addition, flight initiation distances were measured in both site types to determine the effect of long-term human presence on an impala's response to the approach of a human. Although the level of human presence did not have significant effects on routine vigilance behaviour, impalas tended to spend a greater proportion of time being vigilant in high human presence localities (16% in high human presence, 6% in low human presence). Moreover, high human presence resulted in a decrease in induced vigilance in response to human voices and shorter flight initiation distances. However, there was no difference in response to the leopard growl between sites. These results suggest that impala become habituated to human presence, thus lowering their vigilance levels to minimize their energy costs. However, this did not hinder their ability to perceive threats of predators, which implies that this habituation may not necessarily have a negative impact on impala survival. As the human population and popularity of ecotourism increase, an understanding of this relationship within protected areas is crucial to preserving and maintaining healthy wildlife populations.

Introduction

In the field of conservation biology, concern about strained human-wildlife interactions is growing as an increasing human population encroaches on both protected and unprotected areas. In particular, human presence has been shown to adversely impact habitat selection, foraging patterns, and overall energy expenditures of wildlife, ultimately affecting reproduction and mortality patterns (Reimers *et al.* 2010, Ciuti *et al.* 2012). Despite these far-reaching implications, the extent of the effects of human presence on wildlife behaviour, life history, and fitness are still poorly documented, especially considering that impacts have been shown to display considerable inter-specific and intra-specific variation (Stankowich *et al.* 2008, Ciuti *et al.* 2012). Consequently, scientists have acknowledged the need to quantify these impacts on specific wildlife populations across gradients of human presence (Setsaas *et al.* 2007).

Changes in vigilance behaviours (the visual scanning of the environment to detect predators) are widely utilized as a measure of human presence impacts on wildlife because they can detract time from essential activities like foraging and reproduction (Ciuti *et al.* 2012). Human presence may alter patterns of routine vigilance, or periodic monitoring of surroundings, as well as induced vigilance, or response to a particular stimulus (Blanchard and Fritz 2007).

Various studies have proposed explanations for how human presence may affect vigilance patterns. The risk-disturbance hypothesis predicts that human presence will lead to an increase in vigilance since prey species have evolved anti-predator responses to generalized threats, such as loud noises (Frid and Dill 2002). Several studies support this hypothesis; for instance, Ciuti *et al.* (2012) detected increased vigilance in Canadian elk (*Cervus elaphus*) in sites with higher human presence. The risk allocation hypothesis, however, proposes an opposing outcome, predicting that animals will become less sensitive to long-term stimuli as human presence increases. In particular, it posits that wildlife will be more vigilant when periods of risk are brief and infrequent, whereas animals will exhibit reduced response when risk periods are lengthy and frequent to avoid the high cost of lost foraging time (Manor and Saltz 2003, Brown *et al.* 2012). Past research on both elk in Grand Teton National Park and impala (*Aepyceros melampus*) in Serengeti National Park found decreased vigilance responses to simulated visual and auditory human presence in support of risk allocation (Setsaas *et al.* 2007, Brown *et al.* 2012).

Determining if human presence affects vigilance behaviour may be confounded by several factors including group size, position in the group, and vegetation cover. However, there is no consensus in the literature as to whether or not these variables significantly influence vigilance. For example, Setsaas et al. (2007) concluded that impala in Serengeti National Park displayed increased vigilance in open vegetation due to higher exposure to predators. Conversely, Shorrocks and Cokayne (2005) found no effect of vegetation on impala vigilance in Nairobi National Park. Effects of group size and position in the herd display similar discrepancies in the literature (Burger and Gochfeld 1994, Roberts 1996, Hunter and Skinner 1998, Manor and Saltz 2003, Matson et al. 2005, Smith and Cain 2008). In particular, several studies reported decreased vigilance with increasing group size (Roberts 1996, Hunter and Skinner 1998). They suggest that individuals can afford to reduce their own vigilance by taking advantage of the vigilance of other herd members, dubbed the 'many-eyes' hypothesis (Roberts 1996, Manor and Saltz 2003). Much research, however, has found no effect of group size on vigilance both within and between species. This lack of consensus over inter-specific and intra-specific impacts of potential confounding factors suggests that research on vigilance responses to human presence should be conducted at the population level.

The impact of human presence on vigilance responses can still be detected if the effect of a confounding factor is known. For example, Manor and Saltz (2003) propose four potential outcomes of the relationship between vigilance and group size under different human presence levels. If ungulates become paranoid or habituated to human presence, individual vigilance may increase (Type I) or decrease (Type II), respectively, but will change proportionally with group size. In contrast, paranoia or habituation may weaken or discount the relationship between vigilance and herd size due to disproportional impacts on herds of varying sizes. Paranoia may

have a smaller impact on small herds that already allot a maximum proportion of their energy budget to vigilance (Type III), while habituation may have less of an impact on large herds that already utilize a minimum threshold vigilance level (Type IV).

The Kruger National Park (KNP) in South Africa provides an ideal location for investigating the role of human presence on wildlife vigilance. Tourism has increased dramatically in the park since 1926 with peak estimates of one million visitors per year, resulting in management strategies to minimize visitor dissatisfaction with traffic congestion and facility overuse (Freitag-Ronaldson and Foxcroft 2003). Little has been done, however, to investigate adverse consequences of human presence on wildlife rather than on visitor enjoyment. There is therefore a need to quantify the impacts of human presence on vigilance behaviour in KNP wildlife to facilitate effective management and conservation.

In this study, we examined the potential changes in vigilance behaviour of impala populations in the KNP in relation to the level of human presence, which we defined as longterm human influence in the form of roads, vehicles, pedestrians, and other anthropogenic disturbances. We first compared the proportion of time spent on routine vigilance between individuals in low and high human presence localities across a range of herd sizes. Furthermore, we aimed to determine if risk disturbance or risk allocation could explain the potential differences in vigilance behaviours. In order to address this question, we exposed impala to experimental threat stimuli (auditory and visual) and compared anti-predator behaviours, (induced vigilance and flight response) between LHP and HHP sites.

Methods

Study area

The study was conducted within a 50 km radius of Skukuza Rest Camp in the KNP, Mpumalanga Province, South Africa (24°59'S, 31°46'E). The KNP is part of the northeastern South African lowveld, which makes up the landscape between the Drakensburg Great Escarpment and the Mozambique coastal plain. The Skukuza area consists of moderately undulating plains with granitic rock soils (Venter *et al.* 2003). Receiving over 500 mm of mean annual precipitation, the Skukuza region is a mesic savanna characterized by dense, broad-leaved bushveld in the sandy uplands and open, small-leaved shrubveld with thorny woody plants along footslopes of duplex soils. The grasses are nutritious bulk growers, attracting many herbivores to the area (Venter *et al.* 2003).

Study species

Impala are a medium-sized antelope species distributed widely across southern Africa (Matson *et al.* 2005). They inhabit small home ranges in open woodland landscapes. Although selective mixed feeders, they prefer a diet primarily consisting of grass (Apps 2012). They are ruminants, digesting food through repeated swallowing and regurgitation; they thus must spend much of their day foraging. As a key component of many predator diets – including those of lions, leopards, cheetahs, wild dogs, and spotted hyenas – impala are highly vulnerable to predation under natural conditions (Matson *et al.* 2005, Apps 2012). Herd vigilance is crucial for predator detection, and sudden alarm may cause herds to flee. They typically live in herds of 6 to 20, but occasionally can be found in groups of 50 to 100 individuals (Apps 2012).

Classification of human presence sites

In our study, two different site classifications were utilized—high human presence (HHP) and low human presence (LHP). Sites that are frequently visited by people and/or cars, such as the Skukuza staff village and high-traffic tourist roads, were considered HHP locations. LHP sites consisted of management roads or infrequently used tourist roads. Vegetation density varied between sites from dense shrubveld to open grazing lawns.

Experimental design and protocol

The influence of human presence on routine vigilance levels

This study was carried out from November 12 to 15, 2014, and observations were conducted between the hours of 6:00-9:00 and 15:00-18:00 each day. To study the effect of human presence on the proportion of time impala dedicate to routine vigilance, we searched for herds of impala in HHP and LHP locations in the Skukuza area. Herds, as defined by Matson et al. (2005), were considered aggregations of impala within 100 m of each other among which information about potential threats could be exchanged. A minimum herd size of four individuals was the threshold for observation. When a suitable herd was spotted, the vehicle was parked as far from the herd as possible, and individuals were observed through binoculars. In order to discount responses caused by the vehicle's approach, the herd was allowed to settle for a oneminute period before observations began (Mooring and Hart 1995, Kitchen et al. 2010). Immediately following this period, two observers each chose a focal impala for observation. Only impala that were foraging were chosen, as the trade-off between foraging and vigilance has the greatest fitness cost (Creel et al. 2014). Continuous observations of behaviour were recorded for a maximum of five minutes. If the impala moved out of sight prior to that time, the observation was terminated. Only observations lasting at least two minutes were analysed, as excessively short intervals may misrepresent the proportions of time spent on particular behaviours. Whenever possible, a total of four impala per herd were observed.

Eight behaviours were defined and recorded during observations: vigilance, vigilancechewing, foraging, moving, avoidance movement, grooming, resting, and defecating. As defined by Matson *et al.* (2005), vigilance was considered an interruption in other activities to scan the environment with a raised head, rigid posture, and erect ears. Vigilance-chewing was defined as simultaneously being vigilant while ruminating. As explained by Favreau *et al.* (2013), it is necessary to distinguish between the two since ruminants' short-term food intake is limited by chewing and swallowing rates rather than the rate at which food is encountered. Vigilancechewing can thus be considered low-cost vigilance. Foraging was defined as grazing or browsing. Impala were considered to be moving if they took more than two steps in an unhurried manner without feeding (Smith and Cain 2008). Avoidance movement, on the other hand, was defined as directional movement away from a stimulus. Grooming involved using the mouth or tongue to self-groom or allogroom. Resting was defined as lying down, and defecating encompassed both urination and defecation.

Potential confounding factors of herd size, position of the focal impala in the herd, and vegetation density were also recorded. The position of the impala was either classified as periphery, having no neighbors in one direction at an arc of 180°, or center, having neighbors on all sides (Matson *et al.* 2005). Vegetation density was measured with an ordinal ranking system: 1 for open savanna, 2 for intermediate density of shrubs and trees, and 3 for thick bush that restricted an impala's field of vision.

The influence of human presence on induced vigilance levels

This portion of the study was carried out during the same dates and times as the routine vigilance study; the same behavioural definitions and methods for searching for impala and recording data were used. If a herd was still visible after observing routine vigilance, the same herd could again be utilized. New herds were used as well, and the same one-minute adjustment period occurred before recording observations. The behaviour of one focal individual, initially foraging, was then continuously recorded for a two-minute pre-stimulus period. At two minutes, an auditory stimulus, either the sound of humans talking or a leopard growl, was played from a Samson XP 40I speaker. In accordance with the methods of Favreau *et al.* (2013), playbacks were calibrated to volumes perceived as "natural" in order to appear realistic to the impala, and recordings of the same duration (six seconds) were utilized for each observation. Behaviour was continuously recorded for two minutes post-stimulus. Both sound stimuli would be played to the same focal individual if it did not flee after the first sound. Another two-minute pre-stimulus observation period was conducted before playing the second sound, resulting in a total of four minutes between stimuli.

The influence of human presence on flight initiation distances

This portion of the study was conducted on November 16 and 17, 2014 between 7:00-9:00 and 17:00-19:00 each day. Using different herds and focal individuals than the previous portions of the study, we recorded flight initiation distances (FIDs) in the Skukuza staff village (HHP site) and along management roads and infrequently used tourist roads (LHP sites). FID was defined as the distance between the focal impala and an approaching human at the time the impala began to move away (Setsaas et al. 2007). In HHP sites, herds were located while searching on foot, whereas for the LHP condition, they were located while driving along management roads and lightly-traveled dirt roads. Upon sighting a herd on an LHP road, the car was turned off and two researchers exited the vehicle with a game guard. In accordance with the methods of Setsaas et al. (2007), impala in herds of any size, including singletons, were chosen for approach. When a herd was spotted, the walker (researcher approaching the impala) selected a starting distance as far away as possible from a focal impala while still allowing for a direct approach. The walker and game guard then approached the impala directly at a standard walking pace until the impala responded. Response was defined as either walking away or fleeing. The initial distance between the walker and impala as well as the distance the walker travelled were measured using a Nikon Forestry 550 rangefinder. FID was then calculated as the difference between these measurements.

Data analyses

All analyses excluded vigilance-chewing so as to only consider high-cost vigilance. Prior to analysis of vigilance behaviour between HHP and LHP sites, we explored potential factors confounding the relationship between human presence and impala vigilance. We tested for a relationship between vigilance level and group size using linear regression analysis. We also sought to determine if vigilance levels were influenced by either a focal individual's position in the herd or by the level of vegetation cover with a Wilcoxon rank sum test and a Kruskal-Wallis rank sum test, respectively.

In order to compare the average proportions of time spent on routine vigilance in the HHP condition with that in the LHP condition we ran a Wilcoxon rank sum test. The same test was used in order to see if there was a relationship between frequencies of vigilance displays and the level of human presence.

We tested for a difference between proportion of time spent on vigilance two minutes before and after an auditory stimulus was played using a non-parametric paired-samples Wilcoxon test. This test was run separately for the HHP condition and the LHP condition in both call treatments (human and leopard). We thereafter used a Wilcoxon rank sum test to evaluate whether the changes in vigilance levels after each call was played were significantly different between human presence conditions.

We explored whether or not the focal impala exhibited an immediate response to the stimuli by analysing their behaviour for 10 seconds after each call was played. A binary response/non-response classification was used, with response defined as the impala either exhibiting high-cost vigilance or fleeing (Brown *et al.* 2012).

Differences in FID between the HHP and the LHP conditions were analysed by using a Wilcoxon rank sum test. All tests were run in the Roommander function of Rstudio (2013).

Results

The influence of human presence on routine vigilance levels

For the routine vigilance portion of the study, a total of 97 impala at 17 HHP sites and 16 LHP sites were observed over a five-day period. Herds ranged from 4 to 33 individuals, with a mean of 10.9 (\pm 1.3 SE) impala per herd.

The proportion of time spent on vigilance was not related to herd size at HHP sites ($t_{(96)} = 1.036$, p > 0.05) or at LHP sites ($t_{(90)} = 0.813$, p > 0.05), nor was it affected by position in the herd ($W_s = 1071.5$, p = 0.262). Vegetation cover was also found to be unrelated to vigilance levels ($H_{(2)} = 1.623$, p = 0.444).

Although there was no significant effect of the level of human presence on the proportion of time spent on vigilance between human presence conditions ($W_s = 927$, p = 0.072) or on the frequency of vigilance displays between human presence conditions ($W_s = 995.5$, p = 0.192), impala in low human presence areas tended to allocate more time to vigilance (16%) than those in areas of high human presence (6%; Figure 1). Increased vigilance in LHP areas came primarily at the cost of foraging time more so than of any other behaviour, indicating a foraging-vigilance trade-off.

It is worth noting that the relationship between vigilance and human presence levels is nearly significant with 95% confidence intervals. The statistical insignificance of this relationship is thus most likely due to a combination of small sample size and high levels of variation around the mean for both foraging (± 0.049 SE in HHP and ± 0.084 SE in LHP) and vigilance (± 0.017 SE in HHP and ± 0.042 SE in LHP) behaviours.



Figure 1. Average proportion of time spent on each behaviour by focal impala averaged across sites around Skukuza, KNP for each human presence condition (n=97). Error bars denote SE.

The influence of human presence on induced vigilance levels

Auditory stimuli were played at 10 HHP and 11 LHP sites for 24 focal impala over the same five-day period. The average herd size for this portion of the study was $13.7 (\pm 1.8 \text{ SE})$ with a minimum of 6 and a maximum of 33.

There was no significant difference between the proportion of time spent on vigilance two minutes before and after the human recording was played in either the HHP condition (T = 19, p = 0.447) or the LHP condition (T = 5, p = 0.590; Figure 2). Vigilance levels did, however, change significantly from before to after the leopard call was played both in the HHP condition (T = 0, p = 0.031) and in the LHP condition (T = 0, p = 0.016).

Comparing between human presence levels, there was no significant difference in the change in vigilance after either the human call ($W_s = 42.5$, p = 0.856) or the leopard call was played ($W_s = 16$, p = 0.534). The insignificance of these results is again most likely due to the high variation of the data around the mean, illustrated by the large error bars in Figure 2. We therefore analysed response to each auditory stimulus as a binary (response or no response) in order to discern whether the stimuli had produced an immediate change in the threat-avoidance behaviour of focal impala.



Figure 2. Average proportion of time spent on vigilance before and after the (a) human and (b) leopard recordings were played (n=20 and n=14, respectively). Observations were conducted around Skukuza, KNP for two minutes before and for two minutes after the auditory stimulus was introduced. Error bars denote SE.

When we analysed the binary response of impala during the first 10 seconds following each stimulus, we found that 100% of focal impala responded to the leopard recordings in both human presence conditions. However, only 20% and 60% of impala responded to the human recording in the HHP and LHP conditions, respectively (Figure 3).



Figure 3. Proportion of impala that responded to auditory stimuli around Skukuza, KNP (n=24). Only observations from the first 10 seconds after the calls were played were considered when determining whether or not a focal impala had responded to the stimulus (defined as either fleeing or exhibiting vigilance).

It should be noted that in the sites with the lowest human presence (located on a management road at 25°0'S, 31°34'E) we were unable to conduct more than one auditory stimulus trial because fourteen out of the fifteen herds we encountered fled from sight before our vehicle came within a few hundred meters of the herd.

The influence of human presence on flight initiation distances

Focal individuals from nine herds were observed in each of the human presence conditions (high and low) during the FID portion of the study. One individual was observed per herd.

We found that there was a significant difference in FID between the HHP and LHP conditions ($W_s = 5.5$, p = 0.002; Figure 4). Impala in HHP sites fled at a shorter distance (23.5 m, ± 4.1 SE) than those in LHP sites (58.8 m, ± 5.5 SE). The minimum FID between the focal impala and the walker was also shorter in the HHP sites (10.5 m) than in the LHP sites (23.0 m). Additionally, initial flight response differed between conditions, with eight of nine impala walking away in HHP sites and all impala running away in LHP sites.





Discussion

The influence of human presence on routine vigilance levels

The trend in our data suggests that the proportion of time impala dedicate to routine vigilance is lower in areas of high human presence. Factors commonly thought to influence individual vigilance behaviour in impala, such as position in the herd, group size, and vegetation cover, did not appear to play a role in the vigilance levels of impala populations around Skukuza. Previous studies have not agreed upon the actual effects of these factors between and within species (Underwood 1982, Burger and Gochfeld 1994, Setsass *et al.* 2007). We suggest that the

lack of consensus may be caused by seasonal variation between studies, the length and location of studies, or variation in dominant predators in the area. Most notably, the insignificance of group size found in our study contrasts with the 'many-eyes' hypothesis, as anti-predator behaviour did not decrease in bigger groups (Hunter and Skinner 1998). As such, our results did not align with any of the vigilance response types proposed by Manor and Saltz (2003), and we therefore did not consider a relationship between herd size and vigilance in our analysis. It should be noted that potential interactions between confounding factors were not considered in our analysis.

The trend of lower vigilance levels at HHP sites refutes the risk disturbance hypothesis that suggests anthropogenic factors elicit increased anti-predator behaviour (Brown et al. 2012). On the contrary, our data, which depicts lower vigilance in areas of high human presence, supports the risk allocation hypothesis. Previous studies have identified three explanations for the trend proposed by this hypothesis. First, a difference in resource availability between human presence levels could explain a difference in vigilance patterns. If LHP areas consisted of closed habitats due to dense vegetation, giving predators better cover, individuals would need to be more vigilant to detect danger and may only be willing to incur this cost if there was a benefit to be gained in the form of high quality forage. However, since vegetation cover was found to have no effect on the proportion of time spent being vigilant among our study populations, this explanation is not plausible. Two more likely theories relate to the concept of human presence. The trend could be a result of animals perceiving HHP areas as safe and therefore being drawn to human settlements as a refuge from predators. The refuge effect would thus result in individuals exhibiting lower levels of vigilance at HHP sites (Brown et al. 2012). A final hypothesis suggests the trend could be the result of habituation to human presence in HHP areas. As impala in HHP areas are constantly exposed to anthropogenic disturbances, it is to their benefit to adapt by decreasing vigilance, consequently allowing more time for behaviours that benefit fitness (Brown et al. 2012).

The influence of human presence on induced anti-predator responses

The use of auditory and visual stimuli on focal impala allowed us to further investigate the disparity in vigilance between HHP and LHP sites. Our study found no change in the proportion of time spent being vigilant in the two-minute intervals before and after impala were exposed to human auditory stimuli at both levels of human presence. It is possible that the impala were able to identify the vehicle as the source of the sound and were therefore able to assess the threat and return to their previous activity when they saw the vehicle was not advancing. Unlike the human stimulus, however, there was a change in vigilance behaviour in response to the leopard auditory stimulus in both LHP and HHP sites. This indicates a greater fear of leopards than humans regardless of exposure to human presence. Nonetheless, there was no difference in the change in vigilance between LHP and HHP sites for either the human or leopard recording, suggesting that human presence did not have an impact on impala's vigilance response to either stimulus.

However, Kitchen *et al.* (2010) found that animals returned to baseline behaviours within a few seconds to a minute after exposure to a predator call. As such, we focused on the immediate reaction to the auditory stimuli to more clearly illustrate the effects of human presence on threat perception. Immediately following a leopard auditory stimulus, every focal impala responded regardless of the human presence level. This undercuts the refuge effect explanation for the trend in time spent being vigilant across human presence levels. Since impala always responded to the leopard call, the impala at HHP sites may not have felt more protected in their habitat than did impala at LHP sites. However, more impala immediately responded to the human auditory stimulus at sites of low human presence, which suggests that habituation to human presence in HHP areas is a more likely explanation of impala behaviour. This follows from the notion that impala at LHP sites were less likely to have encountered human noise and would perceive more risk from the stimulus than would impala that had encountered the stimulus before without being negatively affected (Reimers *et al.* 2010). A lack of habituation may thus explain why the impala at sites of low human presence responded more often to the human stimulus.

Our FID results provide further support for habituation in explaining decreased threat avoidance behaviour in HHP sites. Notably, the mean FID of impala was two and a half times shorter at HHP sites than at LHP sites. This indicates a lower risk perception of humans at HHP sites, as FID can be used as a proxy to measure fearfulness (Reimers *et al.* 2010). These results agree with those of the auditory experiment, suggesting impala in HHP areas are habituated to human disturbances and therefore do not have as strong of a fear reaction to human "threats." However, we were unable to obtain FID measurements for a predator approach, leaving us unable to compare the FID from humans to that of predators within and between human presence levels.

The higher incidence of immediate induced response to both human auditory and visual stimuli in LHP locations could correlate with lower fitness of impala in relation to those at HHP locations. Being vigilant while chewing does not necessarily impede impala foraging rate. Conversely, induced vigilance can disrupt the ingestion process, thus incurring an opportunity cost and reducing fitness (Blanchard and Fritz 2007). Consequently, the immediate induced response of impala may have the highest fitness cost of all vigilance behaviours. Impala more prone to induced vigilance responses, those in LHP areas, would thus be expected to incur lower fitness as human encroachment continues. That being said, increased vigilance can also increase predator detection rates, possibly increasing survival. There could therefore be both positive and negative consequences for impala fitness, especially within HHP sites. Since impala inhabiting HHP sites are habituated to human presence and its associated anthropogenic noise as our results suggest, they do not respond to human presence as frequently and so do not sacrifice time from fitness-enhancing activities, such as foraging, in order to be vigilant (Brown et al. 2012). However, if impala are missing predator noises due to anthropogenic noise and are not being vigilant, they may miss cues of the predator's presence and thereby decrease survival rate (Brown et al. 2012).

Conclusions and future implications

Our study suggests that human presence is influencing impala behaviour. The habituation of impala within the KNP is likely to continue as the ecotourism of the park increases. In an area with an ecotourism-based economy, it is to the benefit of impala to reduce their vigilance towards humans so as not to lose time foraging or engaging in other important fitness activities, such as mating or caring for young. However, since impala's fear of human presence decreases with habituation, future studies should investigate if habituation corresponds to higher rates of vehicular collisions. Additionally, habituation to humans should be studied in other species within the park, as interspecific variation in vigilance response has been reported across studies. If the habituation seen in impala also occurs in other species in the park that are rare or prone to human conflict, the effects of human presence through tourism could have much wider-ranging consequences.

Acknowledgements

We would like to thank Donovan Tye for his guidance throughout the research and analysis process as well as Jordan Calder for her involvement and advice during the project. We would also like to thank SANparks for allowing us to conduct our research in the Kruger National Park and our game guard, Moffat, for his assistance during our fieldwork.

References

- Apps, Peter. 2012. *Smithers' Mammals of South Africa: A Field Guide*. Stuik Nature, Cape Town, South Africa.
- Blanchard, P. and H. Fritz. 2007. Induced or routine vigilance while foraging. *Oikos* 116: 1603-1608.
- Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. *PLoS ONE* 7(7): e40505.
- Burger, J. and M. Gochfeld. 1994. Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour* 131(3/4): 153-169.
- Ciuti, S., J.M. Northrup, T.B. Muhly, S. Simi, M. Musiani, J.A. Pitt, and M.S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE* 7(11): e50611.
- Creel, S., P. Schuette, and D. Christianson. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*: 1-12.
- Favreau, F., O. Pays, A.W. Goldizen, and H. Fritz. 2013. Short-term behavioural responses of impalas in simulated antipredator and social contexts. *PLoS ONE* 8(12): 1-11.
- Freitag-Ronaldson, S. and L.C. Foxcroft. 2003. Anthropogenic influences at the ecosystem level. Pp 391-421 in J.T. Du Toit, K.H. Rogers, and H.C. Biggs, editors. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, D.C., USA.
- Frid, A. and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1): 11.
- Hunter, L. T. B. and J. D. Skinner. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135(2): 195-211.
- Kitchen, D. M., T. J. Bergman, D. L. Cheney, J. R. Nicholson, and R. M. Seyfarth. 2010. Comparing responses of four ungulate species to playbacks of baboon alarm calls. *Animal Cognition* 13: 861-870.
- Manor, R. and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications* 13(6): 1830-1834.
- Matson, T.K., A.W. Goldizen, and D.A. Putland. 2005. Factors affecting the vigilance and flight behavior of impalas. *South African Journal of Wildlife Research* 35(1): 1-11.

- Mooring, M.S. and B.L. Hart. 1995. Costs of allogrooming in impala: distraction from vigilance. *Behavioral Ecology* 49: 1414-1416.
- Reimers, E., K. H. Røed, Ø. Flaget, and E. Lurås. 2010. Habituation responses in wild reindeer exposed to recreational activities. *Rangifer* 30(1): 45-59.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behavior* 51: 1077-1086.
- Setsaas, T.H., T. Holmern, G. Mwakalebe, S. Stokke, and E. Røskaft. 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: 563-570.
- Shorrocks, B. and A. Cokayne. 2005. Vigilance and group size in impala (*Aepyceros melampus* Lichtenstein): a study in Nairobi National Park, Kenya. *African Journal of Ecology* 43: 91-96.
- Smith, S.M. and J.W. Cain. 2008. Foraging efficiency in vigilance behavior of impala: the influence of herd size and neighbour density. *African Journal of Ecology* 47: 109-118.
- Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and metaanalysis. *Biological Conservation* 141: 2159-2173.
- Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* 79(2/4): 81-107.
- Venter, F.J. R.J. Scholes, and H.C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern. Pp 83-129 in J.T. Du Toit, K.H. Rogers, and H.C. Biggs, editors. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington D.C., USA.