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Abstract

Predators can affect prey in many ways both through direct predation and by altering their prey's behavior and spatial distribution. Habitat selection for prey animals is therefore a trade-off between resource availability and predation risk. This trade-off differs from species depending on for example body size, digestive system and escape tactics. In this study I looked at the effect of perceived predation risk (visibility) and forage quality (fertilization) on the selection of micro habitat for eight African herbivores. Grey duiker *(Sylvicapra grimmia)* and warthog *(Phacochoerus africanus)* both preferred plots with low visibility while impala *(Aepyceros melampus)* and zebra *(Equus quagga)* showed the opposite relationship. Elephant *(Loxodonta africana)*, buffalo *(Syncerus caffer)*, giraffe *(Giraffa giraffe)* and white rhino *(Ceratotherium simum)* did not respond to perceived predation risk. No species reacted to forage quality except for elephant which preferred fertilized plots. My results show that the role of perceived predation risk for micro habitat selection varies between species as well as the direction of the effect.

Introduction

Predators can affect prey in several ways, directly by killing them but also indirectly by altering the behavior of their prey through the fear of being killed (Lima, 1998; Lima & Dill, 1990). One way in which the latter manifests itself is through the concept of a "landscape of fear" where prey avoids certain more risky types of habitats where they are more likely to be killed by predators (Laundre et al., 2001; Laundré et al., 2010). However, prey has to account for more factors than predation risk when selecting habitats. Habitat selection usually means a trade-off between avoiding predation risk and selecting areas with enough resources high quality forage. The benefit of decreased the risk of being killed is weighed against the cost of lower energy and vice versa (Lima, 1998). Risk avoidance may lead to reduced energy intake which in turn can lead to a reduction in both reproduction and survival (Creel & Christianson, 2008; Creel et al., 2007; Creel et al., 2013; Hik, 1995). In addition, according to the predation-sensitive foraging hypothesis, reduced energy intake because of risk avoidance may force prey to spend more time foraging in more risky habitats which could lead to a higher mortality rate through predation (Sinclair & Arcese, 1995; Wittmer, et al., 2005). These so-called risk-mediated effects are suggested to not only affect the individual but also the dynamics of the population (Hik, 1995; Lima, 1998).

By altering the behavior of their prey, predators can also influence other parts of the ecosystem through trait-mediated indirect interactions (TMIIs) (Abrams, 1995). Together with density-mediated indirect interactions (DMIIs), TMIIs have been shown to cause trophic cascades in aquatic and terrestrial ecosystems (Gelwick, 2000; Peckarsky & McIntosh, 1998; Trussell et al., 2002). In some cases the TMIIs apparently had a stronger effect than the DMIIs and even existed when direct effects of predation were negligible (Creel & Christianson, 2008; Werner & Peacor, 2003). When it comes to large terrestrial carnivores a well-known example is what happened when wolves *(Canis lupus)* were re-introduced into Yellowstone National Park. Several studies indicated that wolves caused a tropic cascade, especially through TMIIs (Beschta et al., 2016; Fortin et al., 2005; Ripple & Beschta, 2012; Ripple et al., 2015), even though the extent and cause of these effects are debated (Kauffman et al., 2010; Kimble et al., 2011). Examples of trophic cascades in African large mammal systems are rare but Ford et al. (2014) showed that predation risk from leopard *(Panthera pardus)* and wild dog *(Lycaon pictus)* affected habitat selection of impala *(Aepyceros melampus)* which in turn affected the distribution of *Acacia* tree species.

Trade-offs between predation risk avoidance and selection for resources differ between type of prey and type of predator. One factor driving these differences is herbivore body mass. Herbivores with larger body mass suffer a lower predation pressure since only the largest predators can hunt them and predation should, therefore, have a smaller effect on such species than resources. Herbivores with small body sizes are being predated upon by more carnivore species thus suffering from a higher predation pressure resulting in stronger top-down control (Radloff & Du Toit, 2004; Sinclair et al., 2003). Body size also affects resource requirements. According to the Jarman-Bell Principle; small species of herbivores require a higher amount of energy and protein per kg of body weight compared to larger species. Therefore small herbivores depend on highly digestible forage with a high nutritional value and little fiber, large herbivores can compensate for poor quality forage by consuming more (Geist, 1974). A similar relationship is seen between digestion systems. Non-ruminants can compensate for poor forage quality by spending more time feeding which means that they tolerate food with higher fiber content than

ruminants which are more sensitive to forage quality (Demment & Vansoest, 1985; Duncan et al., 1990; Geist, 1974).

Studies have shown that ambush predators have a stronger effect on antipredator behavior than coursing predators in multipredator systems (Preisser et al., 2007; Thaker et al., 2011). The coursing predators' less predictable movements are believed to play a role in this (Thaker et al., 2011; Wikenros et al., 2015). Studies have shown that Lion *(Panthera leo)* can be a strong driver on the distribution of herbivores (Thaker et al., 2011; Valeix et al., 2009), Thaker et al. (2011) also showed that prey animals avoided areas used by lion and leopard but not by the coursing predators cheetah *(Acinonyx jubatus)* and African wild dog. Lion and leopard both have greater success in habitats with high vegetation cover where they can stalk close to their prey without being detected (Balme et al., 2007; Davies et al., 2016; Hopcraft et al., 2005). Elliott et al. (1977) showed that the attack success rate of lion decreased rapidly with an increased predator-prey distance at the start of the attack. At 50 feet (15.24m) less than 50 % of the attacks on zebra *(Equus burchelli)* and 0% of the attacks on Thompson's gazelle *(Eudorcas thomsonii)* were successful. Moreover, for both species prey catchability has been shown to be more important than prey abundance when it comes to selection of hunting habitat (Balme et al., 2007; Davies et al., 2016; Hopcraft et al., 2005) and many African herbivores prefer open habitats due to predation risk (Abu Baker & Brown, 2014; Burkepile et al., 2013; Riginos & Grace, 2008). In contrast to lion and leopard, wild dog have a similar capture success in closed woodland and open habitats (Creel & Creel, 1995; Kruger et al., 1999) although in some systems wild dogs were observed moving and hunting more in closed compared to open woodland (Kruger et al., 1999). This suggests that closed habitats might represent a high predation risk from wild dog as well, at least for small and medium herbivores. Both predation risk and resources may also vary over time and so should a prey animals habitat selection (Lima & Dill, 1990), Riginos (2015) showed that several African herbivores reacted more to predation risk during times with high abundance of food but during drought, patches with more resources were preferred even though they meant a higher predation risk.

In this study I investigated the effects of (represented by visibility) and forage quality (represented by fertilization) on the selection of micro habitat for; elephant *(Loxodonta africana)*, buffalo *(Syncerus caffer)*, giraffe *(Giraffa giraffe)*, grey duiker *(Sylvicapra grimmia)*, impala, warthog *(Phacochoerus africanus)*, white rhino *(Ceratotherium simum)* and zebra *(Equus quagga)*. I hypothesized that the mega herbivores; elephant, and white rhino would not be affected by either predation risk or forage quality due to their large body size and the fact that they are non-ruminants (Demment & Vansoest, 1985; Owen-Smith, 1988). Although buffalo has a large body size they are a preferred prey species for lion (Hayward & Kerley, 2005) and Burkepile et al. (2013) showed that they selected open habitats in order to avoid predation so I expected the same results in this study. Buffalo are ruminants which would mean that they are sensitive to forage quality (Geist, 1974) but due to their large body size, I expected them not to be affected by the fertilization treatment. (Riginos & Grace, 2008) showed that giraffe selected for open habitats due to predation risk and I expected the same relationship. I used the hypothesis that they would not respond to the fertilization treatment due to their large body size (Geist, 1974) and the fact that they are strict browsers since the fertilization was mainly focused on grass. Impala and grey duiker are both small ruminants and I therefore expected them to prefer fertilized and open plots due to their sensitivity to forage quality and high predation pressure (Cromsigt et al., 2009; Kingdon, 1997; Radloff & Du Toit, 2004; Sinclair et al., 2003). Abu

Baker & Brown (2014) showed that grey duiker selected for more open areas and spent little time in forest patches. I used the hypothesis that warthog would have a higher visitation rate in plots with high visibility due to their small body size (Radloff & Du Toit, 2004; Sinclair et al., 2003). Studies have shown that warthog selects habitats that contain grass with high nutritional value (Rodgers, 1984; Treydte et al., 2006), therefore I expected warthog to have a higher visitation rate on fertilized plots. Zebra is a non-ruminant and I therefore used the hypothesis that they would not be affected by fertilization (Geist, 1974). They have been shown to be heavily predated on by lion (Hayward & Kerley, 2005) and I expected them to select for habitat with high rather than low visibility. I also hypothesized that there would be an interaction between both visibility and season and the fertilization treatment and season. During the wet season I expected the perceived predation risk to have a stronger effect and that during the dry season there would be a stronger selection for fertilized plots (Riginos, 2015). I also expected these effects to vary between the years since 2013 had much higher rainfall than the others.

Methods

Study area

The study was conducted in the Hluhluwe part of Hluhluwe-iMfolozi Park (HiP), a 900 km^2 fenced game reserve in central Zululand (see Figure 1). It's a heterogeneous reserve with habitats like grassland, thicket and woodland (Whateley & Porter, 1983). Since 2014 there has been a severe drought with very low rainfall (see Figure 2). The total large herbivore biomass is greater than 10 000 kg/km^2, which is twice as high as in Kruger National Park. This is mostly due to the high biomass of white rhino and elephant. The populations of some small and medium antelopes have suffered heavy declines during the 1900s, for example there are only an estimated 120 waterbucks *(Kobus ellipsiprymnus)* in the whole park and only 25 bushbucks *(Tragelaphus sylvaticus)*. Although not as severe, zebra, wildebeest *(Connochaetes taurinus)* and impala populations have declined since the early 2000s. The reason to these recent declines is thought to be the growth of predator populations during the 2000s. This effect has been greatest in the Hluhuwe section which may indicate that the woody plant encroachment happening there could enhance predation effect (le Roux et al., 2017). The park has a rich predator community although densities of some large predators are low. The population of lion was estimated to 62 individuals in 2004 but has since increased and in 2015 was estimated at approximately 120 individuals. During the study period the estimated number of leopards has ranged from 46 to 72 individuals. The wild dog population increased during the 2000s with a peak of approximately 110 individuals in 2011 but has then declined and there was an estimated 69 wild dogs in 2015. The hyena *(Crocuta crocuta)* population was estimated to 321 in 2003 and 2004 but recent estimates are much lower. However the decrease is thought to be caused by the hyenas being accustomed to the census method used; capture-recapture with call-ups. Cheetah numbers are thought to be less than 15 individuals (Somers et al., 2017).
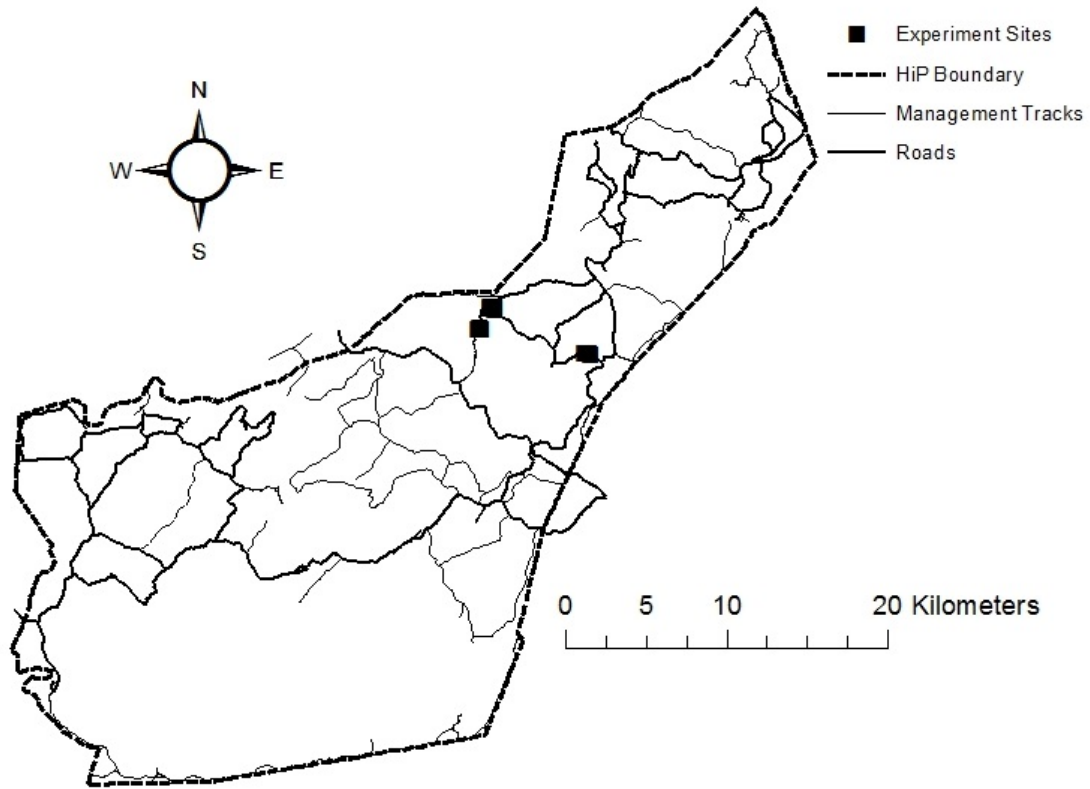
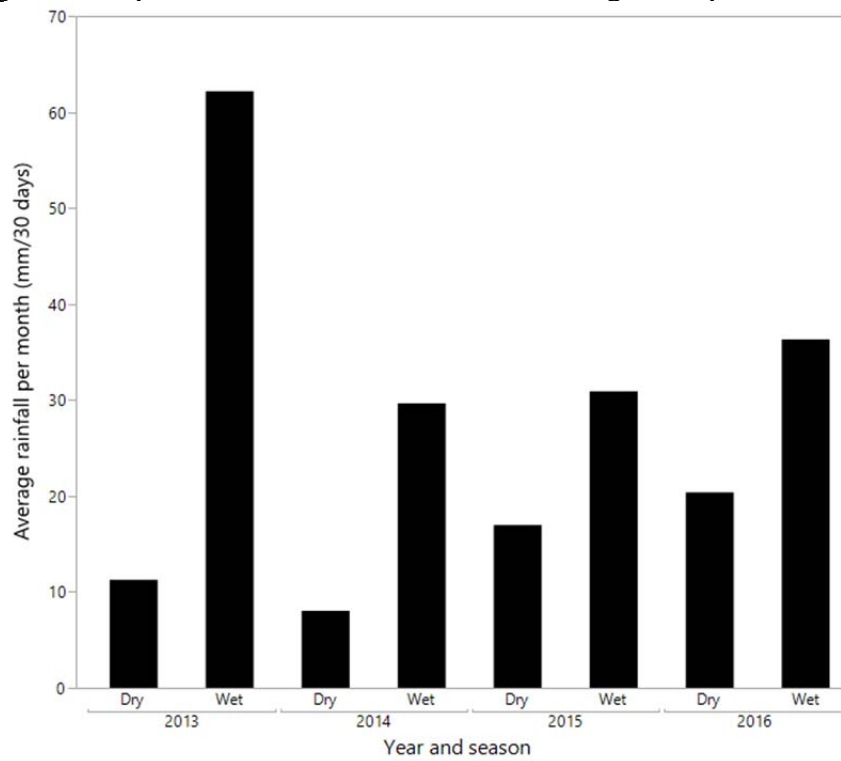Figure 1. Map of Hluhluwe iMfolozi Park showing the experiment sites.

Figure 2. Average rainfall per month at the study site divided by
year and season.

Study design

I used data from an experiment that has been in place since April 2013 and is a part the program "HOTSPOT: Apex predators and their effect on savanna functioning through influencing the behavior of their ungulate prey". The experiment consisted of three different sites with a distance of 1.4 to 5.7km between them (see Figure 1). At each site there were four plots with different treatments: closed, closed fertilized, open and open fertilized (see Figure 3). These treatments represent perceived predation risk through visibility and forage quality through fertilization in order to investigate their role on herbivores micro habitat selection.

All the study sites were initially dominated by woodland encroached savanna. In the open treatments all woody vegetation was cleared in 40*40m squares surrounding central sampling plots of 10*10m. To ensure equal probability of detection between the treatments the central 10*10m plots were also cleared of woody vegetation in closed treatments. In addition to the woody plants, the tall grass in all plots was cut in April and November 2013 as well as in November 2014, in order to simulate animal disturbance and attract grazers. The sites were burned with cool fires in April and July 2013 to prevent intense late-season fires from removing the woody vegetation around the plots. In August 2013 and 2014 the surroundings of two of the three sites were also burned. The fertilizing treatment was performed by adding nitrogen, phosphorus and potassium inside the 10*10m squares at three occasions in the concentrations shown in Table 1.
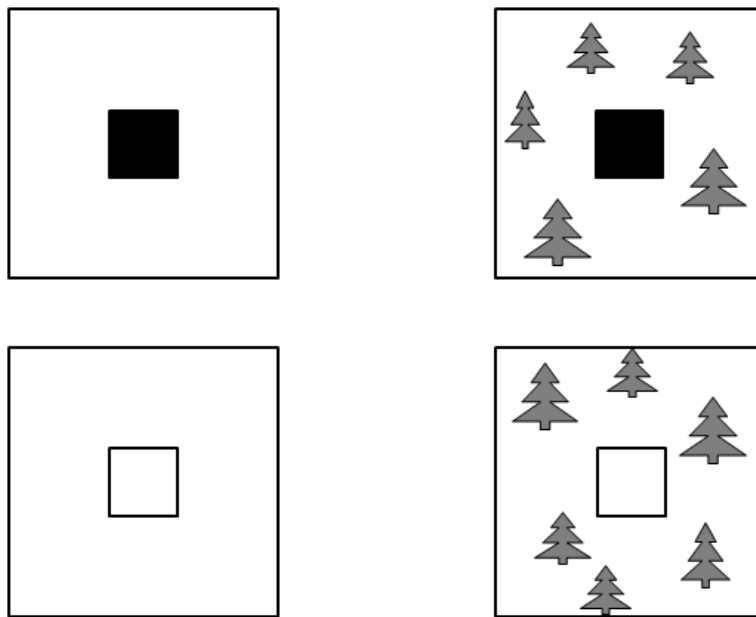

Figure 3. Example of one of the experiment sites, the black plots are fertilized.

Table 1. Overview of how the fertilization treatment was conducted, which substances, in what concentrations and when they were added to the fertilized plots.

	April 2013	November 2013	April 2014
Nitrogen	1.5g/m²	1.5g/m²	3g/m²
Phosphorus	1g/m²	1g/m²	2g/m²
Potassium	1g/m²	1g/m²	2g/m²

Data collection

Camera data

The plots were documented by camera traps from 2013-04-05 to 2016-11-09. At each plot a camera trap (Bushnell trophy cam) was attached to a wooden post at roughly 50cm above the ground in one of the corners of the 10*10m sampling plot (see Figure 4). The cameras were set to record 30s of video when triggered and to take 1 video at 12.00 every day to allow checking of camera functioning. The plots were visited approximately every two weeks to replace camera sd-cards and batteries and to clear woody plants in the open plots. To correct for any variation in performance among individual cameras they were rotated at each visit and broken cameras were replaced.

Figure 4. View of one of the open plots seen from the corner where the camera trap is placed.

Visibility

Visibility was measured for each plot several times a year except for 2015 where no measurements were made. Visibility was measured for three different height classes; 60cm, 90cm and 140cm to represent the eye level of warthog, impala and wildebeest. The measurements were performed by two people with one person (Person A) standing in the center of each plot recording the measurements on a data sheet. The other person (Person B) was equipped with a board consisting of 8 sections each 20 cm high (0-20, 20-40, 40-60, 60-80, 80-100, 100-120, 120-140 and 140-160cm), started at the center of the plot and then walked away from it in a straight line. At each meter, person B stopped and person A checked if half the area of any of the sections was obscured by vegetation for any of the eye levels (60, 90 or 140cm) and if so recorded the distance. This procedure was conducted in eight directions (N, NE, E, SE, S, SW, W and NW) on each plot up to the distance of 20m. Distances further than that were recorded as >20m.

Data processing

Microsoft Excel 2010 was used for organizing and processing of data prior to the analyses. JMP® 12.0.1 was used for all analyzes.

Perceived predation risk

Two factors were used to represent perceived predation risk; whether the plot was closed or open (C/O) and measured visibility (from here on called visibility). The visibility measurements were calculated into three different averages for each plot and height class. The first one was overall visibility (OV) where a mean was calculated from the distance where half the area of each section was covered for each direction which was then averaged into a mean of all directions. The second was visibility at stalking height (SH) where the same procedure as above was performed but only for the three bottom sections of the board (0-60cm). Finally the approach distance (AD) was calculated i.e. the closest distance that a stalking predator could approach the center of the plot while still being hidden by vegetation. To get this measurement the distance at where the three lowest sections were covered by 50% or more for each direction were selected and the shortest distance was used as the measurement. All these measurements were performed for each eye level; 60, 90 and 140cm. A principal component analysis was then performed to turn OV, SH and AD into one measurement for each height class. The distribution of the visibility measurements resembled a binary distribution for all height classes so the factor was transformed from continuous to nominal by defining all values above the median as "high" visibility and all below as "low" visibility. All these calculations were done for each measuring occasion and in the analysis the visibility nearest in time to the date of each video was used, sometimes an average of two measurements was used if the video was recorded in the middle of two measurements.

Visitation rate in response to visibility and forage quality

All videos were watched and the date, time, plot code, camera ID, the number of animals and the species was recorded both inside and outside the 10*10m plots. Only animals that were at some point during the 30 second video inside the plot were included in the study. In order to get a visitation rate, The numbers of animals (Not individuals, the same individual can have appeared several times in the study) per species caught by the camera traps per plot were summarized for longer time periods and then divided by the number of days for the current period. For buffalo, impala and white rhino which had relatively high visitation rates 28 day periods were used and for the other species 56 day periods where used.

To avoid pseudo replication, a mean of the visitation rate and the visibility was calculated for each year, season (dry or wet) and plot. The effect of year, season, visibility, C/O and fertilization on these mean visitation rates of all herbivores was analyzed with two way-ANOVA where all factors were treated as fixed. First an initial model was created for every species, containing all main factors and two-way interactions. Then a final model was constructed by removing all non-significant interactions, all main factors were kept even when no significant effect was shown. Species that showed no significant results were also excluded in the final model.

Results

A total of 59,196 animals were recorded within the 10m*10m plots from April 2013 to November 2016. Species that had small sample sizes or where the number of recordings was unevenly recorded between the sites were excluded from the study. This left me with recordings of 52,809 buffalo, elephant, giraffe, grey duiker, impala, warthog, white rhino and zebra which are shown in Table 2 (for a complete table of all animals recorded and the distribution between sites see Appendix 1). Table 3 and 4 shows the the F-ratios and p-values from the final ANOVA models (for the initial models see Appendix 2).

Table 2. Number of animals of different species recorded inside the plots from 2013-04-05 to 2016-11-09.

Buffalo	6239	Warthog	2225
Elephant	1235	White rhino	6300
Giraffe	1063	Zebra	2317
Grey duiker	1295	Others	6387
Impala	32135	Total	59196

Table 3. F-ratios and p-values from the final model using visibility to represent perceived predation risk.

Species	Year		Season		Fertilization		Visibility		Year* Season	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Elephant	7.6077	**0.0002***	1.6607	0.2014	4.4164	**0.0389***	0.0333	0.8556	8.5549	**<0.0001***
Grey duiker	3.1619	**0.0293***	4.3056	**0.0413***	0.1686	0.6825	6.1712	**0.0152***	3.1870	**0.0284***
Impala	19.2146	**<0.0001***	31.1922	**<0.0001***	0.0369	0.8481	12.7359	**0.0006***	26.2673	**<0.0001***
Warthog	4.4825	**0.0059***	3.2859	0.0738	0.0466	0.8297	6.3012	**0.0142***	4.7363	**0.0044***
White rhino	5.3186	**0.0020***	3.1721	0.0783	1.3053	0.2563	0.8482	0.3595	-	-
Zebra	1.4163	0.2441	3.895	0.0519	0.4078	0.5249	6.6921	**0.0115***	-	-

Table 4. F-ratios and p-values from the initial model using closed/open to represent perceived predation risk.

Species	Year		Season		Fertilization		Open or closed		Year* Season	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Elephant	7.6092	**0.0002***	1.6674	0.2005	4.3972	**0.0393***	0.0797	0.7785	8.5322	**<0.0001***
Grey duiker	3.3096	**0.0244***	4.3478	**0.0404***	0.0898	0.7653	7.7036	**0.0069***	3.1398	**0.0301***
Impala	19.0781	**<0.0001***	32.1658	**<0.0001***	0.0008	0.9780	12.6785	**0.0006***	26.2033	**<0.0001***
Warthog	4.1437	**0.0089***	2.9962	0.0875	0.0836	0.7733	3.9933	**0.0492***	4.0532	**0.0099***
White rhino	5.8414	**0.0011***	3.2728	0.0738	1.4563	0.2307	1.5544	0.2157	-	-
Zebra	1.6412	0.1864	4.0559	**0.0474***	0.1999	0.6560	5.7711	**0.0186***	-	-

Perceived predation risk

The principal component analyses showed that principle component 1 (P1) explained 95.073% of the variation for the impala height class, 92.727% for warthog and 95.896% for wildebeest. The eigenvalue for P2 in all height classes was far below 1 (0.0943 for impala, 0.1344 for warthog and 0.0820 for wildebeest). For further analyses I therefore only used P1 as a measurement of visibility. The effect of perceived predation risk was very similar regardless if visibility or C/O was used (see Table 3 and 4).

Grey duiker, impala, warthog and zebra all showed significant responses to both visibility and closed/open (see Table 3 and 4). Grey duiker visitation rate was higher in plots with low compared to plots with high visibility (see Figure 5) and they also preferred closed over open plots. The same relationship was seen for warthog with higher visitation rate in closed plots and plots with low visibility (see Table 5 and Figure 5). Impala instead preferred plots with high visibility (see Table 5 and Figure 5) and the visitation rate was also higher in open compared to closed plots. Zebra reacted similarly to impala with a higher visitation rate in open plots and plots with high visibility (see Table 5 and Figure 5). For the other species there were no significant responses to either high/low visibility or open/closed (see Table 6) and there were also no significant interactions between perceived predation risk and year, season or forage quality (see Appendix 2).

Table 5. Parameter estimates for the effect of visibility and closed/open a positive estimate means that plots with low visibility or closed plots were preferred

| Effect of visibility					Effect of closed/open				
Species	Estimate	Std Error	t Ratio	p-value	Species	Estimate	Std Error	t Ratio	p-value
Buffalo	-0.0246	0.0714	-0.3400	0.7318	Buffalo	-0.2825	0.0710	-0.4000	0.6918
Elephant	-0.0028	0.0154	-0.1800	0.8556	Elephant	-0.0043	0.0152	-0.2800	0.7785
Giraffe	0.0178	0.0117	1.5300	0.1303	Giraffe	0.0187	0.0115	1.6200	0.1095
Grey duiker	0.0395	0.0159	2.4800	**0.0152**	Grey duiker	0.0430	0.0155	2.7800	**0.0069**
Impala	-0.6830	0.1914	-3.5700	**0.0006**	Impala	-0.6642	0.1865	-3.5600	**0.0006**
Warthog	0.0549	0.0219	2.5100	**0.0142**	Warthog	0.0430	0.0215	2.0000	**0.0492**
White rhino	0.0565	0.0613	0.9200	0.3595	White rhino	0.0747	0.0599	1.2500	0.2157
Zebra	-0.0611	0.0236	-2.5900	**0.0115**	Zebra	-0.0565	0.0235	-2.4000	**0.0186**
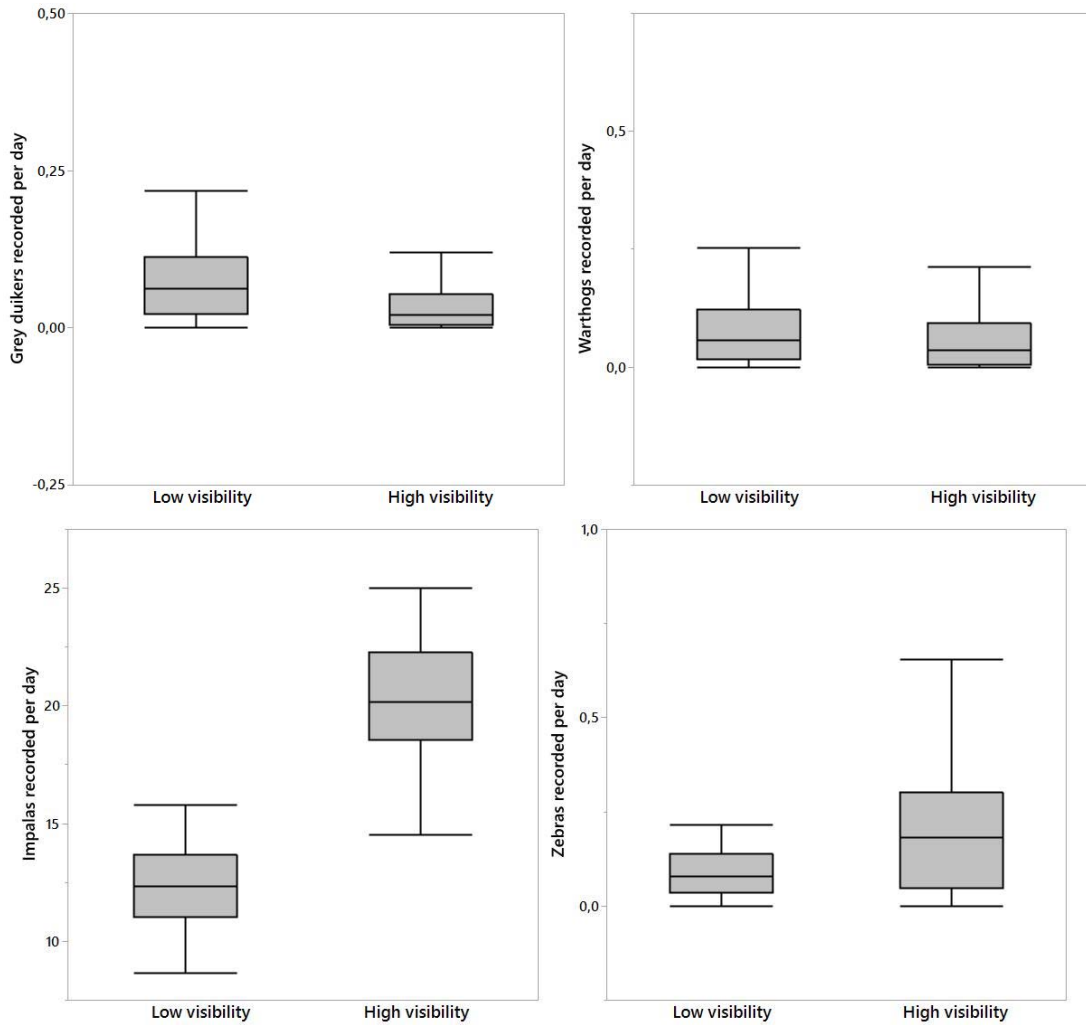
Figure 5. Boxplots showing the response in visitation rate to visibility for grey duiker, warthog, impala and zebra.

Forage quality

Elephant was the only species which showed a significant response to the fertilization treatment (see Table 3 and 4). The visitation rate of elephant was on average 0.0322 (elephants recorded per day) higher in fertilized plots (see Figure 6) with a SE of 0.0153 and a p-value of 0.0389. No other species showed any significant responses (see Table 3 and 4) the parameter estimates are shown in Table 6. There were no significant interactions between forage quality and year, season or perceived predation risk.

Table 6. The estimated effect of fertilization treatment on visitation rate (Animals recorded per day) for all species that showed no significant response.

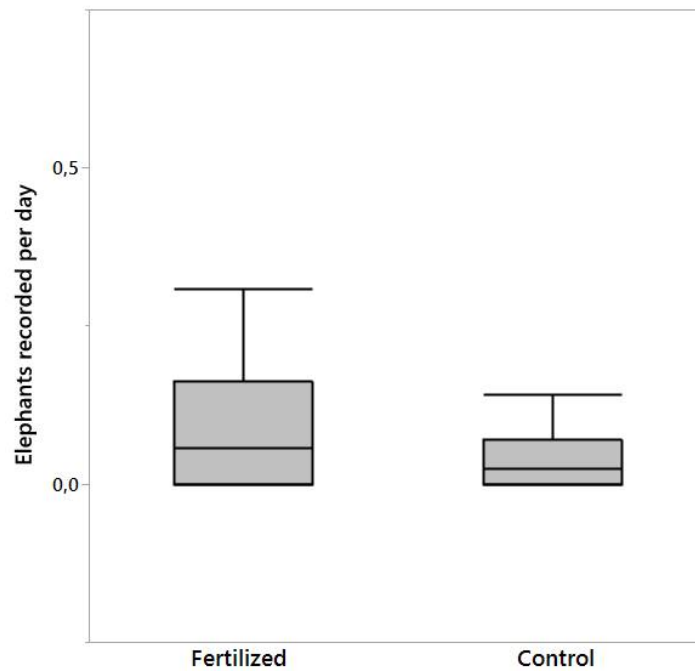| Parameter estimate for fertilization (Fertilized)			
Species	**Estimate**	**SE**	**P-value**
Buffalo	0,0870	0,0710	0,2239
Giraffe	-0,0099	0,0116	0,3972
Grey duiker	-0,0065	0,0157	0,6825
Impala	0,0359	0,1867	0,8481
Warthog	0,0046	0,0213	0,8297
White rhino	0,0688	0,0602	0,2563
Zebra	0,0150	0,0235	0,5249

Figure 6. Boxplot showing the visitation rate of elephant in response to the fertilization treatment.

Discussion

In this study I tested the effect of perceived predation risk manifested as visibility and forage quality represented by a fertilization treatment, on eight African herbivores. As hypothesized, impala and zebra preferred plots with high visibility, probably to avoid predation from e.g. lion and wild dog which prefer dense habitats (Elliott et al., 1977) (Kruger et al., 1999; Riginos & Grace, 2008). Despite their low body size, which usually means a high predation pressure (Radloff & Du Toit, 2004; Sinclair et al., 2003) grey duiker and warthog chose plots with low visibility instead of high which contradicts the results of (Abu Baker & Brown, 2014) where grey duiker selected for habitat with high visibility. My results might be explained for grey duiker by their diet choice since they are browsers and generally prefer forest with dense under vegetation (Skinner & Chimimba, 2005). Another possible explanation might be that the effect of predation risk can vary with escape mode; even though the probability of encountering a predator in a certain habitat other characteristics can increase the prey's chance of escape (Lima, 1992; Wirsing et al., 2010). Grey duiker is a small fast and very agile antelope that moves easily through thick vegetation (Skinner & Chimimba, 2005). So even though dense areas might seem riskier, they probably give the duiker a good chance of escaping their larger and not as agile predators. Duikers often avoid being detected by predators by hiding in dense vegetation (Croes et al., 2007; Estes, 1992); therefore open habitats might pose a higher predation risk through a higher probability of being detected. When it comes to warthog these results can probably not be explained by feeding preferences since they are grazers and should prefer the open habitats with more grass (Rodgers, 1984; Treydte et al., 2006). Warthog is preyed upon by several of the large carnivores (Foley et al., 2014) and predation risk should therefore be an important driver in habitat selection. They are also relatively slow runners (Estes, 1999) so they should not be as efficient at escaping as grey duiker. During night time when most predators are the most active, warthog are residing in burrows (Foley et al., 2014) which might lower the predation risk. The results for elephant and white rhino supported the hypothesis that they would not be affected by visibility. Due to their large body size; the availability of resources should have a larger effect than predation risk (Kinahan et al., 2007; Owen-Smith, 1988; Sinclair et al., 2003). Giraffe showed no significant difference in visitation rate between high and low visibility in contrast to (Riginos & Grace, 2008) who found giraffe to prefer open areas and the same result was seen for buffalo which is not in line with (Burkepile et al., 2013). One reason might be the drought; during times with low food availability prey often increase their search for food while predation risk plays a smaller role for their habitat selection (Lima & Dill, 1990; Riginos, 2015).

I found no significant effects from the fertilization treatment for any of the species other than elephant. Although elephants are mega herbivores that can sustain itself on low quality food (Dutoit & Owensmith, 1989) there is no reason for them not to use high quality forage if it is available. What is more surprising is that none of the herbivores that I hypothesized to react to the fertilization treatment did. Grey duiker is a browser (Skinner & Chimimba, 2005) so if the fertilization had been more focused on woody plants instead of grass it might have had an effect. Habitat selection can vary over spatial scales (Guyot et al., 2017; Orians & Wittenberger, 1991); Ryan et al. (2006) found that buffalo indeed showed significant preference for certain habitats at a large but not at a low spatial scale. In this study I looked at a very small spatial scale with patches of only 10m*10m. The drought might have decreased the effect of the fertilization, with very little rainfall nutrients are probably not the limiting factor for plants but water. If the grass dies due to lack of water then fertilization does not increase the forage quality. The results

supported the hypothesis that giraffe, warthog, white rhino and zebra would not respond to the fertilization treatment. Since giraffe is a mega herbivore, warthog and zebra are non-ruminants and white rhino is both, they can compensate for forage with poor nutritional value and high fiber content by digesting large amounts (Demment & Vansoest, 1985; Dutoit & Owensmith, 1989).

Temporal scale can also play a big role in habitat selection, in this study I did include season and year but I did not compare the effect of time of day for either perceived predation risk or forage quality. Burkepile et al. (2013) showed that herbivores differed in their habitat use between night and day, for example zebra more often selected open areas at night, probably due to increased predation risk from lion (Funston et al., 2001).

The results from this study show the variation in habitat selection among herbivores with different body sizes, diets and anti-predator tactics. Except for elephant, none of the large bodied herbivores reacted to either perceived predation risk or forage quality. Medium- and small-sized herbivores were affected by perceived predation risk but in different ways. This further highlights that habitat heterogeneity is very important in the conservation of many species, especially in fenced game reserves where migration to more suitable habitats is not possible. It also shows that predators can have big effects on prey population which could then translate into trophic cascades. I've found relatively few studies of this phenomenon in African systems in the literature and I think that further research should be focused in this area.

Acknowledgments

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Appendix 1

Table showing the total number of animals recorded inside the 10m*10m plots per species from 2013-04-05 to 2016-11-09.

Site	Aardvark *Orycteropus afer*	Baboon *Papio ursinus*	Banded mongoose *Mungos mungo*	Birds	Black rhino *Diceros bicornis*	Buffalo *Syncerus caffer*	Bushbuck *Tragelaphus sylvaticus*	Bushpig *Potamochoerus larvatus*
1	24	104	2	364	58	1693	0	18
2	6	400	0	62	55	2648	22	10
3	55	164	0	366	49	1898	0	21
Total	85	668	2	792	162	6239	22	49

Site	Kudu *Tragelaphus strepsiceros*	Large spotted genet *Genetta tigrina*	Leopard *Panthera pardus*	Lion *Panthera leo*	Mongoose *Galerella pulverulenta*	Nyala *Tragelaphus angasii*	Porcupine *Hystrix africaeaustralis*	Slender mongoose *Galerella sanguinea*
1	201	19	6	4	81	854	0	5
2	32	10	3	10	10	740	13	0
3	24	8	9	15	39	34	1	1
Total	257	37	18	29	130	1628	14	6

Site	Cheetah *Acinonyx jubatus*	Elephant *Loxodonta africana*	Genet *Genetta genetta*	Giraffe *Giraffa giraffe*	Grey duiker *Sylvicapra grimmia*	Hares/ rabbits	Hyena *Crocuta crocuta*	Impala *Aepyceros melampus*
1	0	402	43	623	760	303	53	11106
2	2	721	19	268	310	83	46	9511
3	0	112	22	172	225	505	46	11518
Total	2	1235	84	1063	1295	891	145	32135

	Warthog *Phacochoerus africanus*	Vervet monkey *Chlorocebus pygerythrus*	White rhino *Ceratotherium simum*	White tailed mongoose *Ichneumia albicauda*	Wild Dog *Lycaon pictus*	Wildebeest *Connochaetes taurinus*	Zebra *Equus quagga*
1	758	8	2456	11	1	66	1177
2	800	51	2341	12	11	128	355
3	667	0	1503	10	12	1012	785
Total	2225	59	6300	33	24	1206	2317

Appendix 2

F-ratios and p-values from the initial ANOVA-models using visibility to represent perceived predation risk.

Species	Year		Season		Fertilization		Visibility		Year* Season	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Buffalo	0.6136	0.6082	0.0183	0.8927	1.2893	0.2597	0.1183	0.7318	0.9037	0.4433
Elephant	8.2501	<0.0001*	1.8709	0.1759	5.9984	0.0169*	0.0947	0.7592	9.1585	<0.0001*
Giraffe	0.566	0.6393	1.6275	0.2064	0.7258	0.3972	2.345	0.1303	2.3607	0.079
Grey duiker	2.9246	0.0400*	3.7069	0.0584	0.3613	0.5498	6.3402	0.0142*	3.0789	0.0332*
Impala	19.9171	<0.0001*	27.1344	<0.0001*	0.2410	0.6248	14.9337	0.0002*	26.7860	<0.0001*
Warthog	5.4693	0.0020*	3.9902	0.0498*	0.0521	0.8202	6.7153	0.0117*	5.4442	0.0021*
White rhino	5.8445	0.0012*	4.2709	0.0421*	2.1107	0.1503	1.0766	0.3027	1.2547	0.2958
Zebra	1.6552	0.1849	3.8851	0.0528	0.2418	0.6245	6.5693	0.0126*	2.0835	0.1105

Species	Year* Fertilization		Year* Visibility		Season* Fertilization		Season* Visibility		Fertilization* Visibility	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Buffalo	0.9107	0.4398	1.4828	0.2257	0.0734	0.7872	0.9865	0.3237	0.0144	0.9048
Elephant	2.4712	0.0692	0.1636	0.9205	1.8598	0.1771	0.2238	0.6377	0.7076	0.4032
Giraffe	0.376	0.7705	1.598	0.1979	0.0385	0.845	0.3767	0.5414	0.0563	0.8132
Grey duiker	0.3971	0.7555	0.9806	0.4072	0.2494	0.6191	0.0215	0.8839	0.5791	0.4493
Impala	0.6052	0.6136	0.8853	0.4526	0.9415	0.3349	2.0332	0.1579	3.2152	0.0768
Warthog	0.1908	0.9024	2.1621	0.1005	2.9104	0.0926	1.4293	0.2360	0.0669	0.7967
White rhino	1.4186	0.2437	2.0750	0.1103	0.9803	0.3252	1.5525	0.2165	0.4570	0.5010
Zebra	0.9395	0.4265	1.0630	0.3707	0.1444	0.7051	0.0040	0.9496	0.4312	0.5136

F-ratios and p-values from the initial ANOVA-models using closed/open to represent perceived predation risk.

Species	Year		Season		Fertilization		Closed or open		Year* Season	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Buffalo	0.6820	0.5657	0.0184	0.8925	1.5029	0.2239	0.1583	0.6918	0.8945	0.4479
Elephant	8.3522	**<0.0001***	2.0038	0.1615	6.1232	**0.0158***	0.3003	0.5855	9.283	**<0.0001***
Giraffe	0.5477	0.6514	1.5621	0.2156	0.7241	0.3978	2.6295	0.1095	2.4439	0.0715
Grey duiker	2.9414	**0.0392***	4.2293	**0.0436***	0.2958	0.5883	7.9870	**0.0062***	2.9786	**0.0375***
Impala	18.9472	<0.0001*	31.8515	<0.0001*	0.0013	0.9711	12.5313	**0.0007***	26.0651	<0.0001*
Warthog	3.8226	**0.0136***	3.1825	0.0789	0.0032	0.9553	3.9557	**0.0507***	3.7740	**0.0144***
White rhino	6.2661	**0.0007***	3.6163	0.0609	1.5365	0.2189	1.7316	0.1921	1.3335	0.2696
Zebra	1.9311	0.1328	3.6568	0.0601	0.1384	0.7111	5.6413	**0.0204***	1.7543	0.1642

Species	Year* Fertilization		Year* Closed or open		Season* Fertilization		Season* Closed or open		Fertilization* Closed or open	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Buffalo	0.8342	0.4791	1.4233	0.2423	0.0354	0.8513	0.3064	0.5815	0.0321	0.8584
Elephant	2.4403	0.0718	0.0789	0.9712	1.7607	0.1890	0.0515	0.8212	0.9845	0.3246
Giraffe	0.3771	0.7698	1.5428	0.2114	0.0442	0.8341	0.3215	0.5726	0	0.9972
Grey duiker	0.3953	0.7568	0.8184	0.4881	0.2695	0.6053	0.1957	0.6596	0.3168	0.5754
Impala	0.3479	0.7908	1.1582	0.3311	0.2450	0.6220	1.4907	0.2258	2.2983	0.1336
Warthog	0.1268	0.9439	0.9756	0.4095	2.7412	0.1024	0.7938	0.3761	0.2599	0.6118
White rhino	1.5981	0.1966	2.6082	0.0575	1.1037	0.2967	1.6302	0.2055	0.4283	0.5148
Zebra	0.8497	0.4716	0.8645	0.4639	0.3051	0.5825	0.0934	0.7609	0.6065	0.4388

SENASTE UTGIVNA NUMMER

2016:11   Artificial gap creation and the saproxylic beetle community: The effect of substrate properties on abundance and species richness
Författare: Nils Bodin

2016:12   Extended phenotypes in the canopies of Norway spruce
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