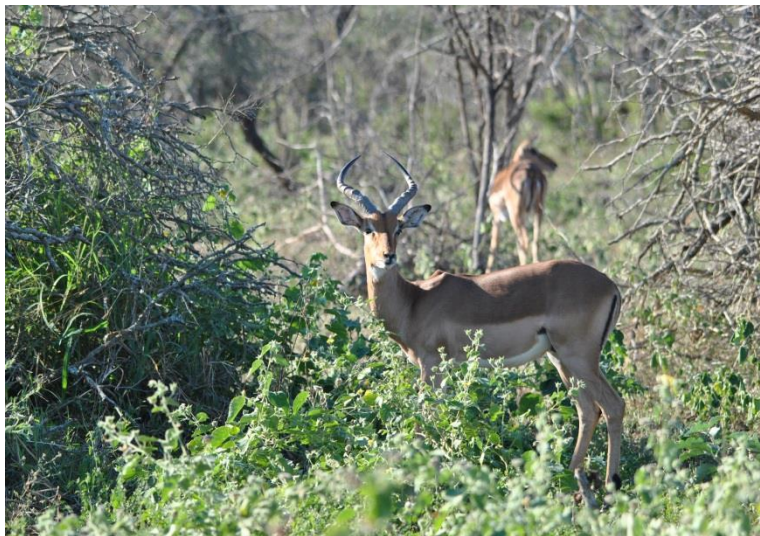# Influence of temperature and predation risk on herbivore micro habitat choice in a South African savanna

Hur temperatur och upplevd predationsrisk påverkar mikrohabitatval hos herbivorer på den sydafrikanska savannen

Hanna Rogers

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Abstract

The challenging conditions animals face on the African savanna influence their time budget. To accomplish the activities needed for survival they have to trade-off the amount of time they can invest in each activity. One well studied example is the trade-off between foraging and avoiding predators. Another trade-off is between avoiding predation and heat stress. In the face of climate change escaping high temperatures is an important behavioural response in animals. Between March and June of 2016 the trade-off between perceived predation risk (with visibility as a proxy) and heat stress was examined for mammalian herbivores (with a focus on ungulates) in Hluhluwe-Imfolozi Park, South Africa. The woody vegetation was manipulated in experimental plots to create a difference in visibility, and animal visitation was recorded through camera traps. The difference in woody vegetation was also predicted to affect temperature which was measured in all plots via Thermochron iButtons. Four species; impala (*Aepyceros melampus*), white rhino (*Ceratotherium simun)*, plains zebra (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*) had enough visitation data for analysis. Impala visitation increased with increasing visibility, and impala showed a temporal avoidance of high temeratures. White rhino visitiation on the other hand was not influenced by visibiliy, but was positively related to average maximum temperature. The results show that perceived predation risk affect micro habitat choice in animals, and that they respond to high temperatures. These findings are important for managing animal populations on the African savanna, especially when concidering the future ramifications of climate change.

Introduction

The savanna is a challenging environment for herbivores. The extreme climate conditions coupled with a high number of predator species constitutes a living environment that requires specific adaptations to survive. These adaptations are reflected in the animals' time budget (Dunbar *et al.*, 2009). An animal's time budget consists of several important activities, such as foraging, socializing, resting, and moving (Dunbar *et al.*, 2009). Due to the fact that animals do not have unlimited time to accomplish these activities they face trade-offs in terms of the amount of time they can invest in each activity (Dunbar *et al.*, 2009). A classical trade-off example is the landscape of fear (Laundré *et al.*, 2010, 2014), where animals may alter their habitat use to avoid predation risk but have to balance this behaviour with their resource needs. In other words animals experience a trade-off between minimizing the risk of being predated upon and performing other activities such as foraging (Lima, 1998). Large African herbivores, for example, show a preference for areas with less woody cover and hence higher visibility where they more easily can detect and avoid predators (Riginos, 2015). They prefer these areas even when it negatively influences their foraging (Riginos, 2015). However, when conditions are poor with little food available, for example during the dry season, the trade-off changes and they show a preference for areas with higher food abundance regardless of the increase in predation risk (Riginos, 2015). This shows that the outcome of trade-offs is not constant but adapts to the conditions and challenges that an animal is subjected to.

One of those conditions, which animals have to consider when facing trade-offs between predation and food acquisition, is temperature. In the face of climate change this factor could become increasingly important, especially since it may be a major cause of extinction (Thomas *et al.*, 2004). Climate change is predicted to have a major impact on plants and animals geographical distribution by, for example, shifting them north or to higher altitudes (Parmesan & Yohe, 2003; Monzón *et al.*, 2011). The home range size of roe deer (*Capreolus* capreolus) closely related to local weather (Morellet *et al.*, 2013), and Martin (2001) observed that precipitation had an influence on bird distribution and habitat choice, resulting in increased predation risk. With the predicted change in the climate system, with increasing and longer lasting heat waves and extreme precipitation events (Pachauri *et al.*, 2014), the change in weather will most likely affect the entire ecosystem.

The predicted impact of climate change for South Africa is that the average, maximum and minimum temperatures will increase, especially over the inland (DEA, 2013). Rainfall may both increase and decrease, depending on where you are in South Africa, with a general pattern of dryer conditions in the west and south, and wetter conditions in the east (DEA, 2013). Climate effects have been predicted to be a major influence on the performance of large herbivore populations in South Africa, by altering the quality and quantity of forage plants (Seydack *et al.*, 2012). With increasing temperatures animals might shift their geographical ranges which could have a major impact on the trade-offs they face. Animals are thus challenged by both the landscape of fear and increasing temperatures. These factors may influence species in different ways. The effect of climate conditions on mammals are different based on size, diet and habitat (Andrews & O'Brien, 2000), where annual temperature has a strong influence on species richness for large mammals (Andrews & O'Brien, 2000). Therefore it may be expected that animals of different size will respond differently to the trade-offs and climate conditions they face.

Body size is an important factor in explaining differences among species in terms of their response to external drivers (Peters, 1986), including responses to risk of predation. Body size is important since smaller herbivores are prey to more predator species than large herbivores (Sinclair *et al.*, 2003). Small herbivore populations are hence more controlled by predation, whereas large herbivore populations are more limited by food availability (Sinclair *et al.*, 2003). The largest herbivores, like elephant, rhino and hippo, almost never suffer from predation and are therefore almost exclusively restricted by food availability (Sinclair *et al.*, 2003). This group of species has also been termed megaherbivores (Owen-Smith, 1988). This implies that body size affects how animals perceive predation risk and therefore how they allocate their time and resources thereafter.

Body size is also important when considering adaptations to extreme temperatures. Larger animals have less surface area in relation to volume, which means they have less area to dissipate heat (Bradley & Deavers, 1980; Phillips & Heath, 1995). Small animals on the other hand are more sensitive to cold since they lose heat faster (Bradley & Deavers, 1980). This suggest that the response to temperature is different between animals of different size. For example, large antelopes are less active than small antelopes during periods of high temperature (Shrestha *et al.*, 2014), and male alpine ibex (*Capra ibex*) with larger body mass show a higher reduction in foraging during high temperatures compared to smaller males (Aublet *et al.*, 2009). Animals can also respond to thermal stress by changes in spatial behaviour. For example, black-tailed deer *(Odocoileus hemionus columbianus*) select habitat depending on thermal conditions (Bowyer & Kie, 2009), male alpine ibex make daily changes in altitudinal position in response to temperature (Aublet *et al.*, 2009), and moose (*Alces alces*) select microhabitats in response to ambient temperature with negative consequences for their foraging (van Beest *et al.*, 2012). There are very few examples of how African herbivores use microhabitats to adjust their thermal load. However, African elephants (*Loxodonta africana*) have been recorded to choose habitat based on temperature fluctuations to help with their thermoregulation (Kinahan *et al.*, 2007), and chacma baboon (*Papio hamadryas ursinus*) spent more time in shaded areas at high temperatures (Hill, 2006). Concluding, body mass thus seem to influence an animal's response to both predation risk and temperature in predictable ways.

Landscape structure, and particularly woody cover, also influence both predation risk and temperature. Visibility has been used frequently as a measurement of perceived predation risk, especially for prey with an escape tactic of outrunning its predators (Valeix *et al.*, 2009; Pays *et al.*, 2012; Riginos, 2015). Lima (1992) stated that prey should show a preference for habitats where their escape tactic is most successful. Distance between predator and prey is important for a successful escape (Elliott *et al.*, 1977), and one can therefore assume that spotting predators at a greater distance is important for survival. Hence, woody cover and its influence on visibility have an important influence on preys' habitat choice. Woody cover may also affect the microclimates of an area. Studies have recorded lower temperatures under woody vegetation (Bader *et al.*, 2007; van Beest *et al.*, 2012), and several species has been seen to use shade as an escape from high temperatures (Hill, 2006; Giotto *et al.*, 2013). This indicates that woody vegetation facilitates cooler microclimates that could be of vital importance for many species. Therefore it is reasonable to assume that both visibility and temperature affect micro habitat choice.

This study investigated how variation in woody cover influenced perceived predation risk and ambient temperature, and if this affected herbivore micro habitat choice in a South African savanna. With the help of an existing experiment, that has manipulated woody cover to create an experimental landscape of fear, the aim was to see: 1. if visitation rates were affected by ambient temperature in micro habitats of different vegetation structure, 2. if temperature had an effect on temporal activity patterns, 3. if visibility, as a proxy for perceived predation risk, affected visitation rates and, 4. which of the two, ambient temperature or predation risk, had the strongest effect on visitation rates of differently-sized mammalian herbivores. The study focused on ungulates since this group was common in the study area and has been extensively researched for many years. The prediction was that species with a larger body mass would be more affected by high temperatures than predation risk, in comparison with smaller species which were predicted to be more affected by predation risk.

Method
Study area
Hluhluwe-iMfolozi Park (HIP) is located in the northern part of KwaZulu-Natal Province, South Africa. It is comprised of two parts, the northern Hluhluwe section and southern iMfolozi section, totalling 900km² of fenced area (Boundja & Midgley, 2010). The area is hilly with a difference in altitude of between 60m to 750m (Whateley & Porter, 1983; Boundja & Midgley, 2010) and includes several large rivers (Whateley & Porter, 1983; Boundja & Midgley, 2010). Mean annual precipitation varies from 650mm in the lower regions to 1000mm in regions with higher altitude, and most of the rain falls in summer (Cromsigt & Olff, 2006; Jolles *et al.*, 2006; Boundja & Midgley, 2010).

The vegetation in the reserve is characterized by a high heterogeneity and includes forest, woodland, thicket, savanna and grassland (Whateley & Porter, 1983; Boundja & Midgley, 2010). The park is home to over a 1000 plant species (Cromsigt & Olff, 2006; Boundja & Midgley, 2010), and a rich fauna. The mammalian fauna consists of a wide range of herbivores and several large carnivores. The larger herbivore species include African elephant, giraffe (*Giraffa camelopardalis*), white rhino (*Ceratotherium simun*), black rhino (*Diceros bicornis*), buffalo (*Syncerus caffer*), and plains zebra (*Equus quagga*) (Jolles, 2007). There are also several different antelope species including impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), and blue wildebeest (*Connochaetes taurinus*) (Jolles, 2007). The large predator species in the park include lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), wilddog (*Lycaon pictus*), leopard (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*) (Jolles, 2007).

Study design
This study was conducted as part of an ongoing experiment within the program "HOTSPOT: apex predators and their effect on savanna functioning through influencing the behaviour of their ungulate prey". This experiment consists of three sites (Site 1: Mnqabatheki, Site 2: Shooting Range and Site 3: Seme) located in the central part of the park (figure 1). Each site consists of 4 experimental plots created in 2013 to investigate, with the help of camera traps, the effect of woody cover (as proxy for predation risk) and forage quality on herbivore habitat choice. The plots are 40x40m squares with a 10x10m square at their centre (figure 2). The size of the plots was determined based on the distance lions need to successfully hunt prey.

According to (Elliott *et al.*, 1977), at 20m between lion and prey the probability of escape was as high as 75% for wildebeest and zebra and 100% for Thomson's gazelle. Each 40x40m plot was given one out of two treatments: open or closed. In the open treatment all woody vegetation was cleared within the 40 x40m plot, leaving an open space consisting of grasses, forbs and sedges. In the closed treatment only the 10x10m plot was cleared of woody vegetation, leaving a small open space surrounded by shrubs and trees. The clearing treatment created strong contrasts in visibility, which was assumed to influence perceived predation risk. The inner squares in the closed plots were cleared to avoid any difference in detection rate of animals on the camera traps. To maintain the two treatments all woody vegetation in the open plots and the 10x10m square in the closed plots was cleared every time the experiment was visited (2 times a month).
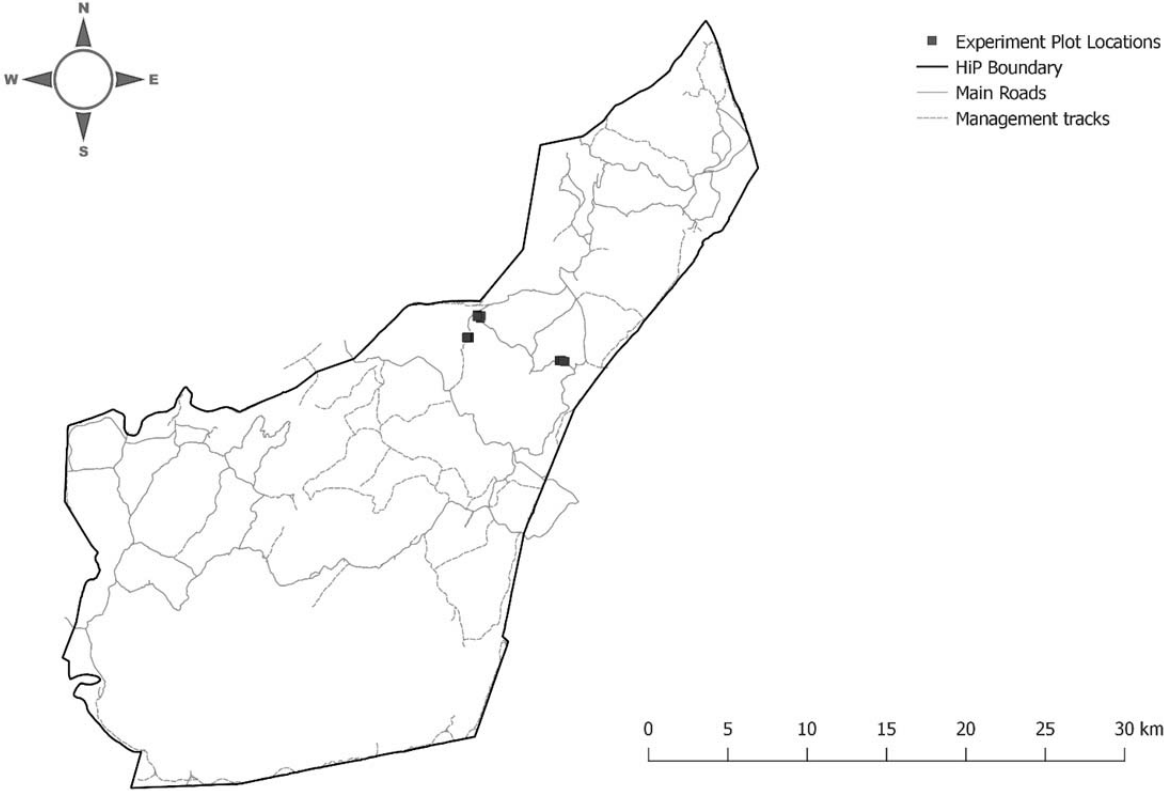

Figure 1: Map of Hluhluwe-Imfolozi Park outlining the three sites used in this study. Site 1 (Mnqabatheki) was located to the right, Site 2 (Shooting range) was the lower site to the left and the top left was Site 3 (Seme).
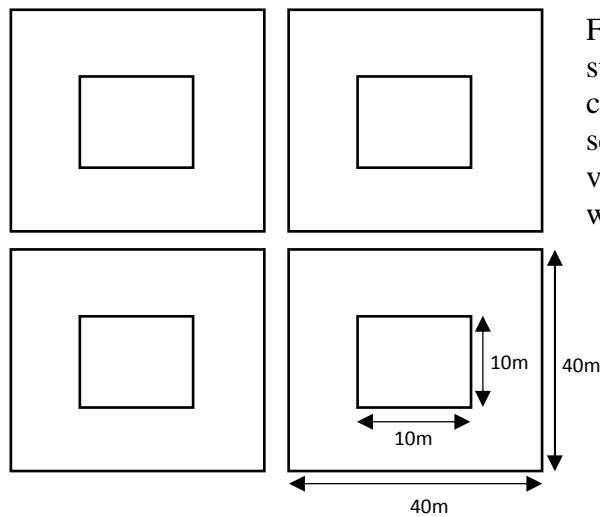
Figure 2: Schematic figure of site and plot structure where dotted squares represent closed plots with woody vegetation and white squares represent open plots cleared of woody vegetation. All inner squares were cleared of woody vegetation.

The plots were burned in April and July of 2013, and the surroundings were burned in August 2013 (except for the Shooting Range site), and August 2014. The plots were subjected to brushcuts (April and November 2013, and April 2014) to simulate animal disturbance to the bunch grass layer.

Data Collection
Monitoring animal visitation
Each plot was equipped with a camera trap (Bushnell trophy cam) attached to wooden poles located in the corner of the 10x10m central plot to capture all animals visiting the inner plot. The camera traps were set to record a 30s video with each trigger. Data collection has been conducted continuously since April 2013, with a gap in data processing between October 2014 and March 2015. For the purpose of this thesis each plot was visited on a 2 week cycle for maintenance and camera trap data collection between March 2016 and June 2016 and only data of this period was used. The batteries and SD-cards in the camera traps were changed and the iButtons replaced. The camera traps were rotated among plots to compensate for differences between individual camera trap detection rates.

Monitoring temperature
In the beginning of March 2016, each plot was equipped with a Thermochron iButton (DS1921G) to log the ambient temperature at every hour until the end of June 2016. The iButtons were attached to the same pole as used for the camera traps to minimize the risk of interference from wildlife. The camera trap poles had been in place for several years making them a familiar sight for the local wildlife, minimizing the risk of interference that occurs when novel items are added to their habitat. The iButtons were attached with a metal hook at a height of approximately 0.5m above the ground. All iButtons were set up in a southward direction with sensors facing the wooden pole to avoid heating of the sensor from direct sunlight. A total of 24 iButtons, divided into two sets of 12, were used. Each of the 12 iButtons in one set were randomly assigned to a plot and positioned in the field for two weeks. After two weeks the first 12 iButtons were collected and replaced with the second set which was deployed for two week.

This resulted in a biweekly pattern where one set replaced the other for the entire period.

Visibility measurements
In March and June 2016 visibility measurements were conducted on each plot. Visibility was measured with the help of a visibility board consisting of a rectangular board divided into 20cm sections up to 160cm. The observer stood in the centre of the plot while another person moved the board outwards in a straight line one meter at a time. At every meter the observer checked to see which sections of the board were obscured from view for three different heights (60cm, 90cm, and 140cm) mimicking the view of three common prey species (warthog, impala and wildebeest respectively). If more than half of a section were obscured by vegetation it counted as "not visible" and the distance from the centre were noted for that section and height. The board was moved outwards until all sections were obstructed from view or the board reached 20m. For every plot this was done in 8 directions (N, NW, W, SW, S, SE, E, and NE).

Data processing
At several instances the camera traps had been knocked over by wildlife, mainly white rhino and elephant, resulting in a loss of video data due to malfunction of the camera trap. In other instances the camera traps malfunctioned due to technical issues resulting in loss of data, or videos with the wrong time settings. All data with the wrong time settings were excluded. Interference with the iButtons happened several times during the study period, resulting in the iButton ending up on the ground. All temperature data from iButtons collected on the ground were checked for deviating temperature cycles. At the instance of deviating temperature cycles all data after the first sign of disturbance was excluded. When possible data from the camera traps were used to confirm the time of disturbance, which in all cases coincided with the start of the deviating temperature cycles.

Camera trap data was processed by, for every video, recording the date, time, plot code, camera trap ID and the number of all species that was identifiable on the videos. Animals within the 10x10m plot were recorded as inside, and all other animals were recorded as outside. If an animal at some point during the 30s video stepped inside the inner plot it was considered to be inside. For this study only data on herbivores were used, and all data on animals outside the 10x10m plot was excluded to avoid differences in detection rate due to variation in woody cover and issues with species identification.

To link animal visitation to the hourly temperature recordings, the number of camera trap triggers half an hour before and after logged temperature was summarized, resulting in a per hour database for each species. This database was used to calculate selection indices for specific temperature ranges for the different species (see data analyses below). To link average daily visitation rates to average daily temperature, trigger rates for each species was calculated by dividing the number of triggers for each species with the number of working camera trap days.

Visibility was calculated by averaging all distances under 120cm for a height of 90 cm for impala and 140cm for white rhino, zebra and wildebeest. This was done in all eight directions, then all the direction values were averaged to create a single visibility value for each plot. All distances under 120cm was used to include most scenarios of perceived predation risk.

Data analyses

All data analyses were conducted in R (version: 3.3.1) with the help of RStudio (version: 0.99.903, RStudio, Inc.), and Microsoft Excel (2013). To get an overview of how the temperature changed over the day for the entire study period and how it differed among plots three temperature measurements were used; the average hourly temperature, the average daily maximum temperature and the average temperature for the hottest period of the day (08-14). These three temperature measurements were used for the rest of the analyses as well and represented the averages for the entire study period (March – June 2016). To study the effect of temperature on temporal behaviour, Jacob's selection index was calculated for impala. Impala was the only species with enough visitation to all plots to calculate any variation, the other species had too many plots with zero visitation to get a reliable selection index and was therefore excluded. Jacob's selection index is based on the formula $D = (r-p)/(r+p-2rp)$ (Jacobs, 1974), where in this case r would be the proportion of temperature ranges available and p is the proportion of temperature ranges used by impala. The index ranges from -1 (total selection against a temperature range) and 1 (total selection for a temperature range). Jacob's selection index was calculated for the full 24 hours, only daylight hours (06-18), and only night time hours (19-05), using the 12 plots as replicates. Two plots were excluded in the calculation for the full 24 hour index, 3 plot were excluded for the daylight hours and 6 for the nighttime hours. This due to low visitation numbers at these plots.

A linear regression model was used with visibility versus average daily temperature values per plot to test if visibility influenced temperature. A linear regression model was also used to test if visibility influenced trigger rates. A multiple linear regression was finally used to test if visibility and temperature influenced trigger rates. This was done to test how temperature and visibility affected the use of the microhabitats available i.e. the 12 plots.

Results

Camera trap data

All ungulate species, plus scrub hare, caught on the camera traps between March and June 2016 are presented in table 1. Impala, white rhino, zebra and wildebeest were the only species with sufficient visitation numbers to all sites to be included in the analysis. Some species, like buffalo, were excluded from analysis because their high visitation numbers came from a single event.

Table 1: Visitation numbers of all ungulates, plus scrub hare, from each site between March and June 2016. The number in the parentheses represents the number used in the analyses after trigger data was matched with temperature data. This because when matched with the temperature data some triggers coincide with removed temperature periods, e.g. due to iButton failure, and was therefore excluded.

Species	Number of triggers			Number of animals			Total # triggers	Total # animals
	Mnqabatheki	Seme	ShootingRange	Mnqabatheki	Seme	ShootingRange		
Black Rhino	4	2	5	5	2	5	11	12
Buffalo	22	5	87	40	14	259	114	313
Bushpig	0	0	4	0	0	5	4	5
Elephant	19	1	45	37	1	69	65	107
Giraffe	40	18	2	41	20	2	60	63
Grey Duiker	16	7	67	16	8	68	90	92
Scrub Hare	29	23	13	30	25	13	65	68
Impala	592 (588)	458	196	1443	923	562	1246	2928
Kudu	3	0	4	3	0	4	7	7
Nyala	19	2	90	32	3	123	111	158
White Rhino	27 (25)	11	62 (60)	30	16	74	100	120
Warthog	19	6	14	34	10	26	39	70
Wildebeest	7	88	28	32	136	44	123	212
Zebra	35	43	46	58	97	80	124	235

Temperature

Overall temperature varied from a minimum of 4.5C° to a maximum of 47.5C° with an overall average of 22.2C° [± 0.04 SE] between March and June 2016. The overall average temperature dropped from 25.2C° [± 0.09 SE] for the first two weeks to 19.4C° [± 0.08 SE] for the last two weeks. Average hourly temperatures were very similar among plots during late afternoon and night. The greatest variation occured during the day when temperatures peaked between 08-14 (figure 3). During this period the difference between the hottest and coolest plot was about 4 degrees on average (see figure 3). There was no clear connection between the visibility treatment and temperature. At site 1 (Mnqabatheki) the open plots had a higher average hourly temperature than the closed plots, but in site 2 (Shooting Range) the closed plots had a higher average hourly temperature. In site 3 (Seme) however, only one open plot showed a higher average hourly temperature. Linear regressions showed that visibility did not influence average temperature (Linear regression: Estimate = -0.014, t = 0.033, P = 0.687; figure 4a), average maximum temperature (Linear regression: Estimate = -0.002, t = 0.111, P = 0.983; figure 4b) or the average temperature during the hottest time of the day (Linear regression: Estimate = 0.03, t = 0.089, P = 0.744; figure 4c).

Trigger rate vs. temperature
Impala clearly avoided high temperatures of 30C° and over, and selected against temperatures between 15-20C° (figure 5a), and this pattern was the same for both daylight and nightime hours (figure 5b & c).

Trigger rate vs. temperature & visibility
For impala, visitation increased with increased visibility (Linear regression: Estimate= 0.227, t= 2.95, P= 0.0145; figure 6a), but for white rhino, zebra and wildebeest visibility had no significant effect on trigger rate (White rhino: Estimate: 0.005, t= 0.837, P= 0.422; Zebra: Estimate: 0.005, t= 0.634, P= 0.540; Wildebeest: Estimate: 0.021, t= 0.012, P= 0.125; figure 6 b-d). For impala, multiple linear regression of visibility and temperature for each plot, on trigger rate for each plot showed that visibility positively influenced trigger rate when run with average temperature (Estimate= 0.239, t= 3.133, P= 0.012) and average maximum temperature (Estimate= 0.227, t= 2.836, P= 0.0195). The average temperature and average maximum temperature, however, did not influence trigger rate (Estimate= 0.852, t= 1.170, P= 0.272; Estimate= 0.105, t= 0.460, P= 0.656). Multiple linear regression with data restricted to the hottest period of the day (08-14) indicated that visibility had a positive effect on trigger rate (Estimate= 0.03, t= 2.095, P= 0.0657).

For white rhino average maximum temperature had a positive effect on trigger rate (Estimate: 0.043, t= 2.921, P= 0.0170; figure 7b), but visibility had no effect (Estimate= 0.005, t= 1.021, P= 0.334). Overall average temperature and average temperature for the hottest period of the day had no effect on trigger rate for white rhino (figure 7a,c). For zebra on the other hand the average temperature for the hottest period of the day had a positive effect on trigger rate (Estimate= 0.0267, t= 2.775, P= 0.0216). For wildebeest neither visibility nor temperature had any effect on visitation.
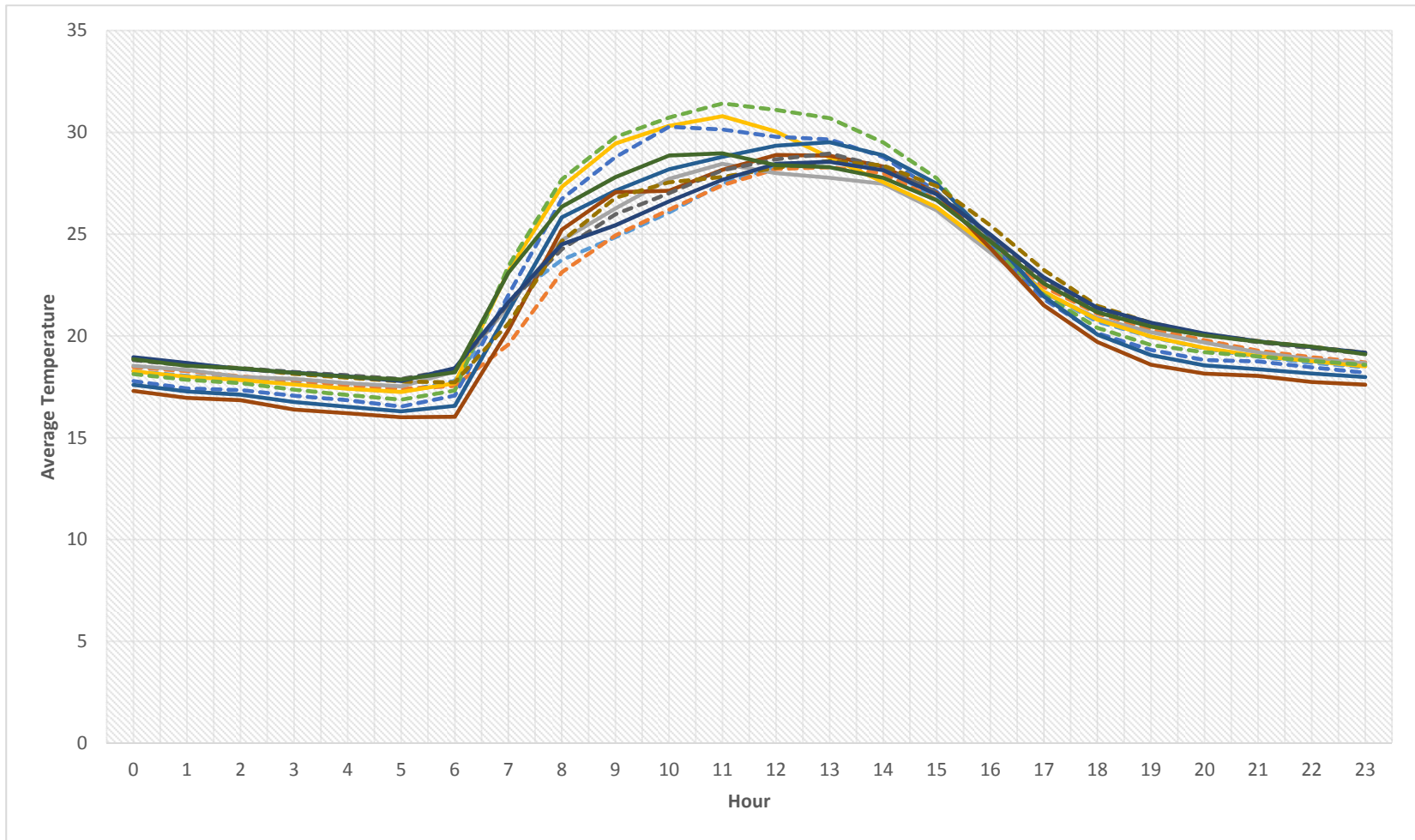
Figure 3: Average hourly temperature for all 12 plots. Dotted lines represent closed plots and solid lines represent open plots.
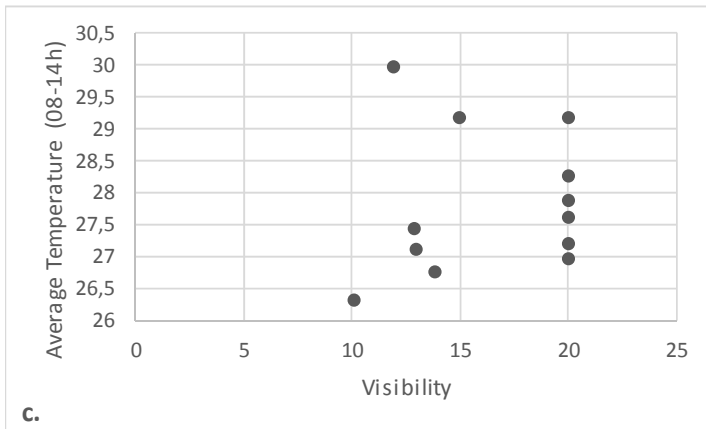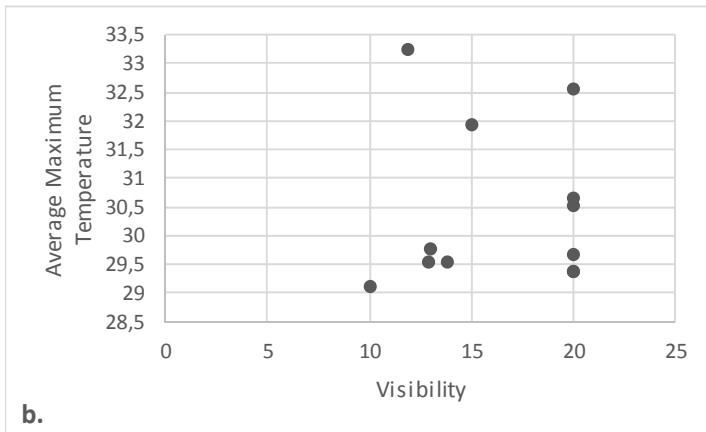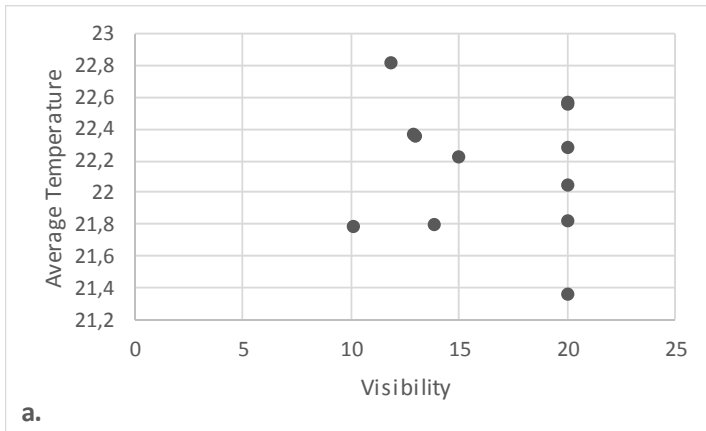
a.

b.

c.

Figure 4: Relationship between visibility and a: average temperature, b: average maximum temperature and c: average temperature during the hottest part of the day.
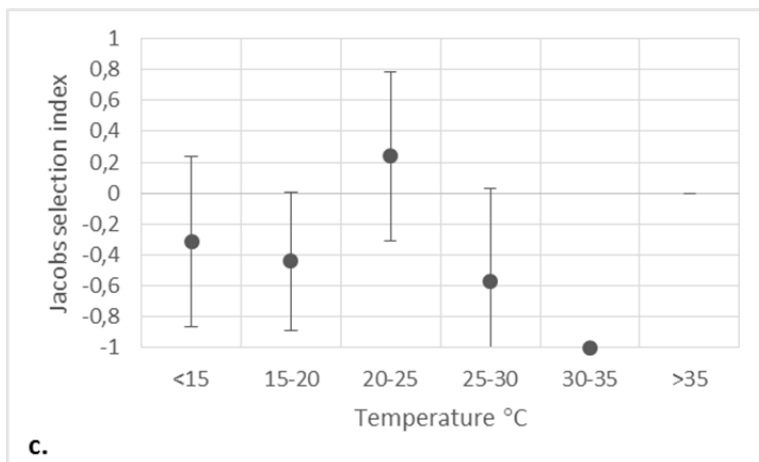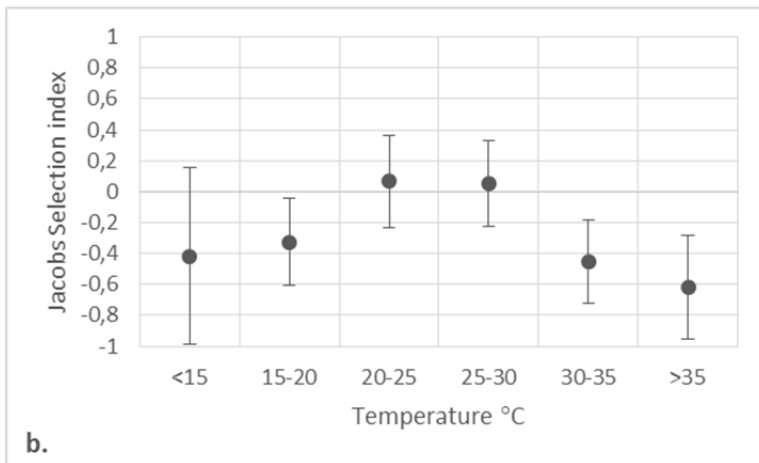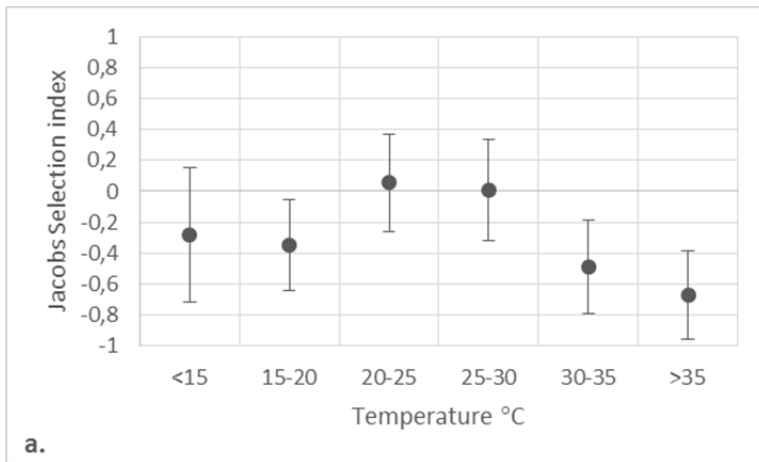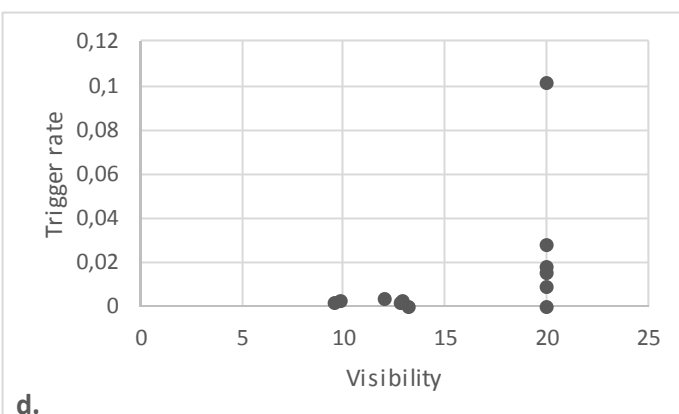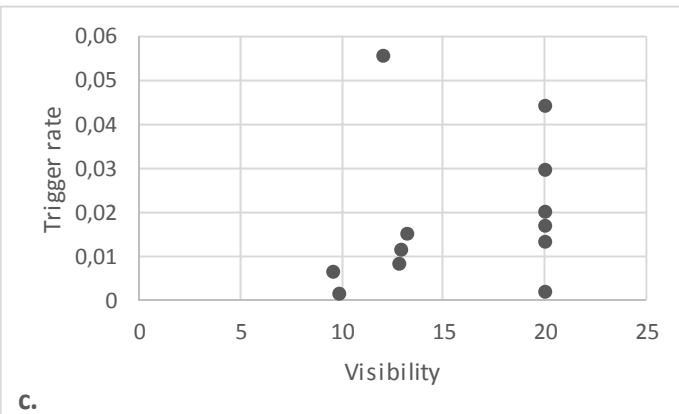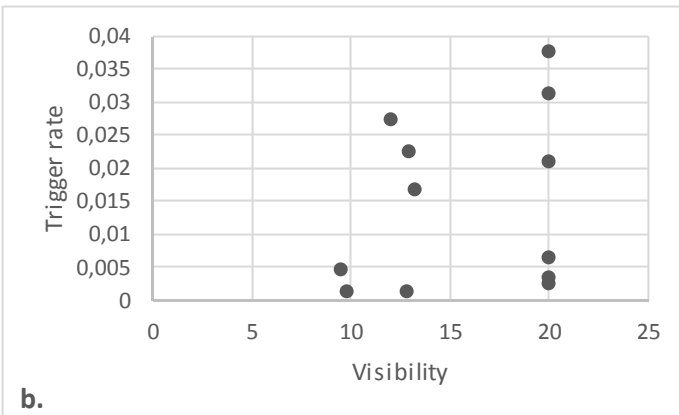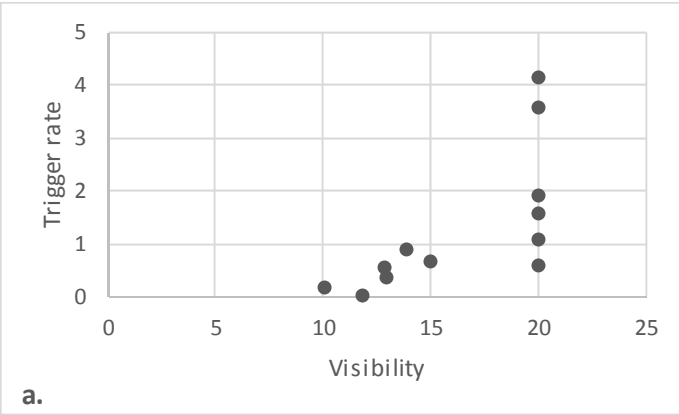
Figure 5: Jacob's selection index for impala with a 95% confidence interval. a: full 24-hours (n=10 plots), b: daytime 06-18h (n=9 plots), and c: nighttime 19-05h (n=6 plots).

Figure 6: Relationship between visibility and trigger rate for a: Impala, b: white rhino, c: zebra, and d: wildebeest.
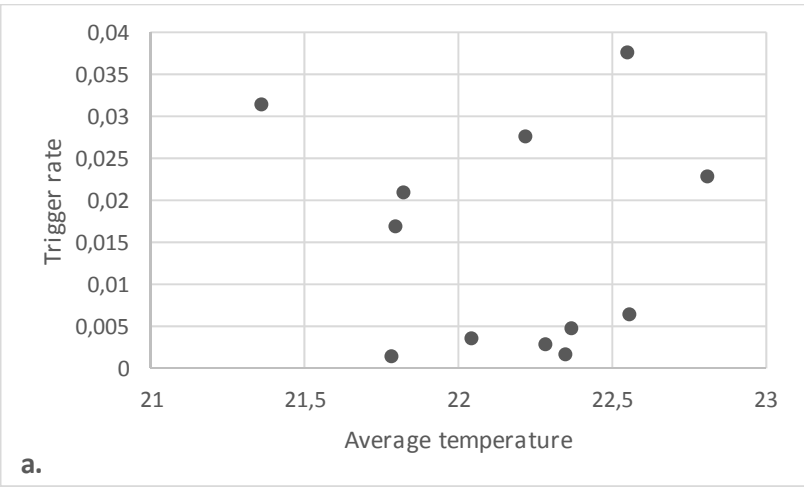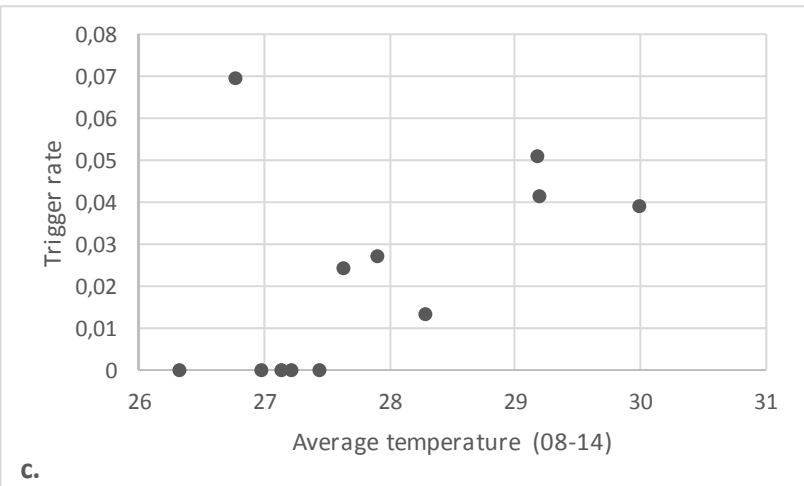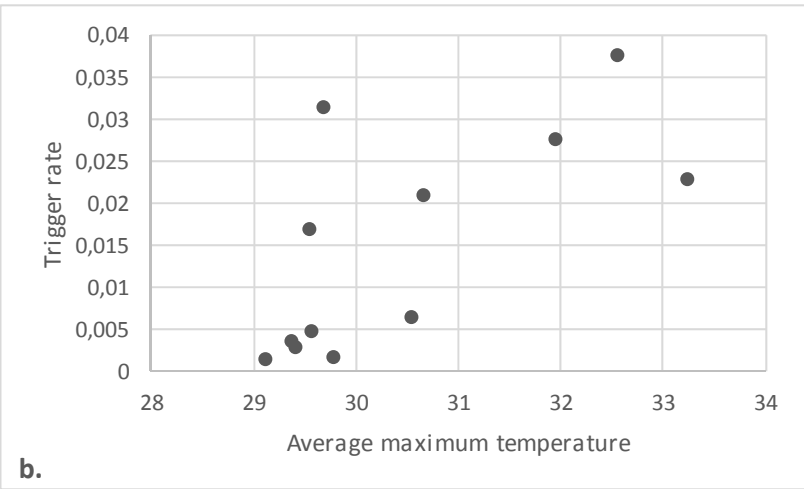
a.

b.

c.

d.

Figure 7: Relationship between temperature and trigger rate for white rhino.

a.

b.

c.

Discussion

Impala visitation increased with increasing visibility in plots. Visibility is linked with percieved predation risk since a lower visibility decreases the chance of spotting predators (Elliott *et al.*, 1977; Lima, 1992; Valeix *et al.*, 2009; Riginos, 2015). Lions prefer areas where the probability of catching prey is higher, such as areas with more woody vegetation (Hopcraft *et al.*, 2005). Several studies have noted that African herbivores show a preference for areas with higher visibility (Riginos & Grace, 2008; Valeix *et al.*, 2009; Thaker *et al.*, 2011; Riginos, 2015). Impalas select habitats with less woody vegetation (Thaker *et al.*, 2011) and display a higher frequency of vigilance behaviour in areas where visibility is low (Pays *et al.*, 2012). Visibility did not, however, influence visitation of white rhino which could be due to the rhinos large body mass. White rhino almost never suffer from predation (Sinclair *et al.*, 2003), except from humans, and would therefore not have to consider predation risk when choosing habitat. The results in this study and the literature clearly show that visibility and perceived predation risk are important factors in habitat selection for a smaller animal like impala but not for a larger animal like white rhino.

Even though the multiple linear regression for impala did not show any influence of temperature on visitation, the Jacob's selection index clearly showed that temperatures over 30°C had a temporal effect. Impala have been noted to reduce activity in response to high temperatures (Klein & Fairall, 1986; du Toit & Yetman, 2005), and black-faced impala prefer sites with high shade availability during feeding (Matson *et al.*, 2005). The selection against temperatures between 15-20 for impala for the full 24-hour period may have been due to perceived predation risk since lower temperatures occur at night when predators are most active (Funston *et al.*, 2001; Crosmary *et al.*, 2012). However, the selection index for only daylight hours still showed the same pattern and it was indicated for nightime hours as well. This may be due to that lower temperatures occur at dawn and dusk when predators are still active, so the avoidance of these temperatures might still be due to perceived predation risk. For the nightime hours the dataset was very small which affects the accuracy of the result. Still, the avoidance of lower temperatures might be due to unconsidered factors and therefore needs further examination. It would be appropriate to divide the day into more sections, like dawn, day, dusk and night to get a clear picture if impala is avoiding this temperature range or if it is connected to other factors.

Higher temperatures had a positive effect on visitation for white rhino. This is contradictory to the hypothesis that white rhino should be more sensitive to high temperatures due to its larger body mass. In previous research white rhino have been observed to be less active when temperatures are high and that activity increased on cloudy days compared to sunny days (Owen-Smith, 1988). There was a severe drought in the park at the time of the study which may partly explain why activity of white rhino did not decrease with higher temperatures. White rhino have been observed to roam out of their home ranges during dry periods in apparent search of forage, and also to show a higher activity during the cool months of early dry season (April-June) (Owen-Smith, 1988). Since the drought decreased the amount of forage and water available, rhinos might not have a choice but to forage during higher temperatures to meet their nutritional needs. Also, the majority of the study was conducted during the relatively cool months so it may be possible that the maximum temperature during the study period was still within the rhinos thermal range and that they therefore could stay

active even when temperatures peaked during midday. Thermal stress might only have a considerable effect on animals micro habitat choice during certain seasons (van Beest *et al.*, 2012). This however does not explain the increase in white rhino visitation with increasing temperatures. This could be due to the small dataset, since only 120 animals and 100 triggers were registerd. However, the increasing visitation with maximum temperature could be influenced by unconsidered factors and require futher investigation.

High temperature was also positively influencing visitation of zebra. Even though zebra have been observed to decrease activity during midday when temperatures are the highest they did not seem to be as constricted by high temperatues as for example buffalo (Owen-Smith & Goodall, 2014). In dry season zebra show an increase in daily foraging time, especially in the end of the dry season (Owen-Smith & Goodall, 2014). The dry conditions in HIP may have affected the activity of zebra during hot hours giving the impression that they are not constraint by high temperatures. It may also be as described for white rhino that the maximum temperatures were so low that they did not result in thermal stress. The data for zebra was also relatively small and may have affected the results. To further investigate how white rhino and zebra are influenced by high temperatures it would be of interest to compare the data of this study with data from the summer months when temperatures are higher, both for a drought period and a normal period.

An inital hypothesis was that the closed plots would provide more shade and therefore lower temperatures which should be favoured by animals with larger body mass. Seeking shade is an important behavioural response to high temperatures and has been observed in several species: baboons utilized shade when temperatures were high (Hill, 2006), Arabian oryx (*Oryx leucoryx*) and Arabian sand gazelle (*Gazella subgutturosa marica*) used cool shaded microhabitats when temperature rose (Hetem *et al.*, 2012), and the beira (*Dorcatragus megalotis*) foraged and rested in shaded areas during the hot season of May-Sep when midday temperatures climbed to 40°C (Giotto *et al.*, 2013). However, in this study temperatures in the closed plots were not consistently lower than in open plots. One reason for this was perhaps because the study was done during a severe drought. Due to this drought, the woody vegetation in the closed plots was leafless and provided little shading. iButtons were in most cases subjected to very similar conditions in respect to sunlight. Only in one site, Mnqabatheki, the iButtons were placed under vegetation that provided some kind of shade. At this site the average temperature was cooler in the closed plots, indicating that the closed plots may have provided cooler microclimates. It would be of interest to compare temperature measurements between this study and data from a non drought period to see how shade affects temperature.

In this study only ambient temperature was used which might not give a accurate representation of the experienced temperature. Radiation, wind and humidity also strongly affect an animals thermoregulation (Porter & Gates, 1969), and should therefore be considered in future studies when examining the effect of temperature on animal habitat choice.

The results in this study clearly show that visibility have a strong influence on animals micro habitat choice. Visibility influenced the habitat choice of the smaller impala but not of the larger white rhino, as predicted. Even though temperature was not shown to have a direct effect on impala habitat choice, the Jacob's selection index showed that high temperatures affected

impala on a temporal scale. Understanding of the trade-off between predation risk and the risk of heat stress is becoming incresingly important, especially in the face of climate change. With rising temperatures the importance of escaping heat might become essential, forcing animals to shift to riskier habitats. In riskier habitats the the animals survival rate might decrease to a point where the population is no longer viable. If a suitable habitat is not available, due to human disturbance for example, animals might face extinction. For larger animals the increasing temperature could have severe consequences since there might not be a suitable habitat cool enough for them to survive. This is especially important for large threatened species like the white rhino, and recently giraffe, who already face the threath of extinction. Therefore, understanding of the trade-offs animals face is becoming increasingly important in managing todays and future animal populations.

Acknowledgments

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