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SOUTHERN AFRICAN
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Environmental predictors for spatial variation in temperature in a South African savanna and their predictive value for distribution of Southern White Rhinoceros (*Ceratotherium simum simum*)

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15-08-2019

<u>MSc thesis Sustainable Development</u>

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Acknowledgements

I would like to thank my supervisors Joris Cromsigt and Cleo Graf for their guidance during the project and their patience. I would also like to sincerely thank Alan Gardiner for his critical viewpoints on my methods (and conservation ecology in general). Special thanks to Peter Hamming, he was not only a great housemate, but also invaluable as a field guard, field guide and source of many interesting conversations in between his already full schedule. For the data concerning waterholes, and for helping me put problems into a more positive perspective and giving the research house a sense of homeliness, I also thank Rosie Wool. Lastly, thanks to everyone at SAWC for providing a fun yet educational place to stay during the study period.

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Summary

High temperature extremes are projected to increase in frequency and severity in southern Africa. This could negatively impact large animals more than smaller animals. The southern white rhinoceros is experiencing population declines across southern Africa, and efficiency of protection efforts are needed. Adverse effects from a warming climate could further decrease the potential for rhino population sizes to grow. If rhino distribution is limited by high peak temperatures, spatial variations of temperature in the landscape could be a predictor for rhino distribution. Certain landscape features are assumed to be potentially influential with regard to local air temperature. This research investigated the effect of canopy cover, vegetation density and dominant slope aspect on local air temperature measured at 160 cm height in the Kempiana reserve in South Africa. Subsequently, rhino distribution based on these and additional landscape features (elevation, waterhole availability and dominant vegetation type) was modelled. Patches with high canopy cover, low vegetation density and south-facing slopes were hypothesized to be cooler than patches with no canopy cover, high vegetation density and north-facing slopes, respectively. During relatively hot days, rhinos were hypothesized to predominantly be in areas with landscape features associated with lower temperatures. 24 iButton thermometers were used to measure temperature in 2 groups of 4 landscape features in separate experiments: dense versus sparse vegetation and closed versus open canopy in the first experiment, south-facing slopes versus north-facing slopes in the second experiment, and east-facing slopes versus west-facing slopes in the last. Distribution patterns of the white rhino in Kempiana were modelled on a scale of 500*500 meters against canopy cover, vegetation density, elevation, dominant aspect, dominant vegetation and waterhole availability using Generalized Linear Mixed Models. 2 GLMMs were used, one with presence-absence data, and another with presence-only data. This was done for hot-season data, comparing rhino location data of cooler days with that of hotter days. The rhino location data was collected by spotter plane in irregular intervals during the years of 2014-2019. Patches under tree canopy were on average 0.5°C cooler than intercanopy patches. Rhino distribution did not show different correlations with any of the landscape features between hot and cold days. In the study area as a whole, rhino density in the cold period was twice as high as in the hot period, suggesting larger scale limitations to rhino distribution as an effect of temperature. This could be a finding to investigate in future research.

1. Introduction

1.1 Changing climate & shifting species demographics

Across the world, human impacts on ecosystems have been the cause of the decline and loss of a wide range of plant and animal species. Environmental change, including anthropogenic global warming, has been shown to force species to local and regional extinction (Barnosky et al., 2011; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; IPCC, 2013). Southern Africa in particular is projected to experience some of the largest increases in temperature extremes (Ove Hoegh-Guldberg et al., 2018). The distribution and abundance of its native flora and fauna could be strongly affected by these changes.

Climate change and its effects on biodiversity on different spatial scales are being researched more and more, and lower latitude areas and South-African ecosystems specifically have been found to be among the areas with the highest vulnerability to climate change (Crossman, Bryan, & Summers, 2012; Visconti et al., 2011). A species' vulnerability is affected by a multitude of factors, like the species rarity, restriction of distribution, the habitats a species is able to use and these habitats' respective accessibility (Fahrig, 2007; Pacifici et al., 2015). However, research concerning vulnerability of specific species has been limited to mainly North America, Europe and Australia, and as such has been relatively understudied in many other regions of the world, including southern Africa (Pacifici et al., 2015). The effect of shifts in (peak) temperatures on species distribution could therefore add to the understanding of habitat suitability in a changing climate.

High temperatures can affect animals in multiple ways. Vegetation composition and therefore food availability for herbivores is partly determined by temperature (Battisti & Naylor, 2009; He, Zheng, Li, & Qian, 2007). High temperatures can also influence animals more directly when their body temperature becomes too high for cells to optimally perform, for example decreasing reproductive success (P. J. Hansen, 2009). Especially large-bodied animals have been suggested to experience problems concerning loss of excess heat during prolonged periods of heat because of their low body surface to mass ratio (Mccain & King, 2014).

Apex consumers are species that are at the top of their food-chain and are generally large animals. Megaherbivores, such as the rhino and elephant (Owen-Smith, 1969) can be considered apex species (Cromsigt & te Beest, 2014). Since environmental change in southern Africa is predicted to lead to an increase of ambient temperatures, it may adversely affect these kinds of large animals especially.

South Africa is home to multiple apex species like the lion (*Panthera leo*), common hippopotamus (*Hippopotamus amphibious*) and the southern white rhinoceros (*Ceratotherium simum simum*) and African bush elephant (*Loxodonta africana*). Due to their high charisma, these animals hold a relatively high economic value for tourism and high intrinsic value in the eyes of the general public (Lubbe, du Preez, Douglas, & Fairer-Wessels, 2017). The southern white rhinoceros in particular (from here on, I will use 'rhino' when referring to the southern white rhinoceros) is regarded as an ecologically impactful species (Asner, Vaughn, Smit, & Levick, 2016; Cromsigt & te Beest, 2014; Waldram, Bond, & Stock, 2008). Through their feeding behaviour and dietary preferences, rhinos do not only directly alter the vegetational composition of the ecosystems they inhabit, but may subsequently also reduce wildfire intensity and continuity by reducing fuel load (Waldram et al., 2008). One of the mechanisms facilitating this large ecological impact is the fact that apex consumers are not controlled top-down by predation but rather controlled bottom-up by food and water resources. Another characteristic that is strongly connected to the rhino is the high value of its horn on the black market, with annual rates of rhino poaching in South-Africa rising to over 1000 individuals over the 2013 to 2015 period (Büscher, 2015; Wittemyer et al., 2014). Alterations to the current wildfire frequency and intensity can have cascading effects on many plant and animal species which have developed to thrive in the current dynamics of the system. The ongoing reduction of the rhino's population size as a consequence of poaching can therefore lead to largescale ecosystem impacts.

Many environmental factors can shape animal distribution patterns, and this is no different for rhinos (Birkett, Vanak, Muggeo, Ferreira, & Slotow, 2012; White, Swaisgood, & Czekala, 2007). Food and water availability both make up part of animal habitat choice, but factors like the presence of other species, fire in recent history (Archibald, Bond, Stock, & Fairbanks, 2005), and ambient temperature (Kinahan, Pimm, & van Aarde, 2007) also play an important role. Since temperature extremes are projected to be relatively severe in southern Africa and this may most severely impact large species, the behavioural response of rhinos in respect to ambient temperatures may provide valuable insights in the animals' response to climate change.

Assessing rhino distribution across the landscape can help construct ecological conservation approaches that are suitable for these animals and their management in protected areas. In addition, having a greater understanding of the animals' distribution patterns and habitat selection choices increases knowledge as to where the animals are most likely to be in certain periods of the year. This can in turn lead conservation managers to use their limited resources more efficiently and protect rhinos more effectively from natural and human threats.

The methods used for this report to assess temperature at a small scale are time consuming. The Moderate Resolution Imaging Spectroradiometer (MODIS) project (Wan, Z.; Hook, S.; Hulley, 2015) provides daily land surface temperatures on a 1x1 km scale. This temperature dataset has been used in many studies assessing large-scale temperature effects (e.g Benali, Carvalho, Nunes, Carvalhais, & Santos, 2012; Mildrexler, Zhao, & Running, 2011; Schwarz, Lautenbach, & Seppelt, 2011). A comparison of MODIS land surface temperature data with temperature data as collected for this report can help gain insights in the usability of this data source in comparable projects.

1.2 Theoretical background

1.2.1 Types of thermoregulation

Thermoregulation in warm-blooded animals is realized in multiple ways: autonomically through morphological and physiological traits, and otherwise through behavioural traits. Thermoregulation of animals through morphological traits (e.g. body covering like hair of fur, shape, size and surface area) has been studied for over 170 years (Bergmann, 1847). An example of thermoregulation through morphology is the increase of surface area through elongated flat extremities (elephant ears, for example) which can increase heat dissipation to the environment. One morphological adaptation that rhinos have is a relatively high vascularity in their skin, which might aid in heat dissipation by increased blood flow near the body surface (Plochocki, Ruiz, Rodriguez-Sosa, & Hall, 2017).

Physiological traits that influence thermoregulation in warm blooded animals can be summarized in traits that influence body heat production (thermogenesis) and body heat dissipation (thermolysis) (Terrien, Perret, & Aujard, 2011). Contrary to morphological traits, physiological traits can generally change rapidly and reversibly (Harrison, 1960). Thermogenesis can be increased mainly through increased muscular activity (shivering) for higher heat production. Body heat dissipation can be increased mainly by an increased blood flow to extremities (vasodilation), panting and sweating, or decreased by the reduction of blood flow to extremities (vasoconstriction) (Terrien et al., 2011) and the erection of hair or feathers to trap warm air (piloerection), like ‘goose bumps’ in humans (Satinoff, 1978).

Behavioural thermoregulatory traits can be divided into multiple behaviour types. One type of response is related to selection of habitats with a temperature that allows the animal to continue activities: for example, during hotter times animals may move to cooler areas such as those with more shade to continue their daily activities (Terrien et al., 2011). Similarly, use of habitats where water is amply available allows animals to wet their body in order to increase heat transfer from their body to the environment via evaporation (Mole, Rodrigues DÁraujo, van Aarde, Mitchell, & Fuller, 2016). These behavioural responses related to landscape use will be called ‘spatial responses’ from here on. Another response type is connected to being inactive during hotter times. This inactivity during hot times has been observed in a wide range of species and can in the most extreme cases result in animals becoming nocturnal, seeking refuge in holes during the heat of day (Terrien et al., 2011). These kinds of behavioural responses related to changing temporal activity patterns will be called ‘temporal responses’ from here on.

1.2.2 Temperature as behavioural predictor

The effect of temperature throughout the day on movement and activity patterns has been studied for a multitude of African ungulates like sable antelopes, zebra and buffalo (N. Owen-Smith & Goodall, 2014) and eland, blue wildebeest and impala (Shrestha et al., 2014). However, less research has looked at the impacts of variation in temperature across a landscape on habitat selection. Such spatial variation in heat across the landscape is called heatscape from here on. Ambient temperature is more usually investigated as an effect between seasons: comparing the winter season with the summer season gives large temperature differences between the two groups. However, looking at differences between seasons in most cases includes variation in food availability and precipitation patterns as well as temperature variations (Laakso et al., 2012). Because of this, the conclusions of these studies are not directly applicable to temperature alone, but to an aggregate of parameters that change with the seasons. The research of Shrestha et al. (2012) did focus on heat stress specifically, following previous studies concerning African ungulate activity as a response to temperature (e.g. Lewis, 1977; Maloney, Moss, Cartmell, & Mitchell, 2005). They found that the animals are less active during times of high temperatures, with larger bodied animals being impacted most during the warm seasons. These results suggest that the very large body size of rhinos may make them particularly susceptible to longer periods of high temperatures. Like most studies to date, this study focused only on the temporal thermoregulatory responses as described above and ignored effects of temperature on habitat selection. In fact, we strongly lack studies on temperature as a driver of habitat use by African ungulates. Studies from the northern hemisphere suggest that temperature may be a very important driver of space use. For example, a study on habitat selection of moose as a response to high temperatures showed moose would retreat to more closed forests, which limited their foraging accessibility, as a response to higher temperatures (van Beest, Van Moorter, & Milner, 2012). The relatively large body size of moose may be an indication of how other large mammals may respond to temperature related habitat selection.

Research on the effect of temperature on behavioural thermoregulation has been conducted to some extent for elephants (Kinahan et al., 2007; Mole et al., 2016; Thaker, Gupte, Prins, Slotow, & Vanak, 2019). Kinahan et al. (2007) found that for elephants, habitat selection is partly affected by ambient temperature. More specifically, the rate of temperature change in the landscape affected elephant movement. Elephants moved to habitats with relatively slowly rising temperatures during hotter times of the day, effectively minimizing warming by their surroundings. During cooler periods, the animals selected for environments with relatively quickly falling temperatures, maximizing heat loss to their surroundings. Similarly, a recent study (Thaker et al., 2019) concluded that temperature is an important predictor for elephant movement, finding that higher temperatures result in fast movement towards and away from water sources. The question is how applicable these results are to other very large bodied animals like rhinos. We do know that rhino wallow often (Vanschoenwinkel et al., 2011), an activity that enhances heat dissipation (Minett, 1947), but few to no studies have looked at the effect of temperature on spatial thermoregulatory responses of rhino.

Elephants and rhinos share a number of traits like high weight, relative hairlessness, low predation (R. N. Owen-Smith, 1989) and being hindgut-fermenters (Parker & Robbins, 2017). However, there are some important differences in their diet. Even though both animals graze during the wet season, elephants are browsers in the dry season as opposed to white rhinos which are purely grazers (Buss, 1961; Waldram et al., 2008). This dietary distinction between the two may result in different habitat choices, especially in the dry season. However, similarities between the species makes it possible to produce testable hypotheses on rhino distribution based on those found for elephant distribution. If rhino distribution can be predicted based on temperature, management efforts can then be more specifically targeted at habitats most likely to be of importance to the animals.

1.2.3 Drivers of local spatial temperature variation

To predict how variation in temperature across landscapes shapes animal distributions, it is useful to know what landscape features shape the heatscape. Previous research showed that regional temperature (average over 32,000x32,000 m) explained about 70-80% of local (average over 30x30 m) temperature variation in California, USA (Dobrowski, Abatzoglou, Greenberg, & Schladow, 2009). The remaining portion of local temperature variation must however be explained by other factors.

Variability of direct solar irradiation (through cloud or vegetation cover and slope) and outgoing radiation (albedo, greenhouse effects) affect local temperature (Swift, 2018). Cloud (Cess et al., 2016) and canopy cover (Hardy et al., 2004) decrease the direct solar energy input, and slopes facing north in the southern hemisphere receive a relatively high radiation per area (Kumar, Skidmore, & Knowles, 1997). Similarly, high albedo, e.g. through soil and vegetation of lighter colour, limits the amount of solar radiation absorbed by the surface, limiting the heating of the environment (Soden et al., 2008). Wind speed also has an effect on the perception of temperature, with higher wind speeds increasing animal heat loss, resulting in a perceived cooling of the environment (Walsberg & Wolf, 1995). Heat entrapment by vegetation cover through decreased wind speeds can elevate perceived heat. The effect of woody vegetation is therefore potentially twofold: it reduces direct irradiation, but in case of dense vegetation also increases heat entrapment, causing a buffering effect with a warming effect in colder months, and a cooling effect in warmer months as compared to intercanopy patches (Breshears, Nyhan, Heil, & Wilcox, 1998). However, local spatial temperature variation has additional drivers. Elevation in subtropical mountainous areas like Bhutan correlates with a decrease in temperature of 0.42 to 0.58 °C per 100 meters increased elevation, on average across all seasons (Dorji et al., 2015). In alpine regions in northern Italy, similar values were found, of 0.54 to 0.58 °C decreases per 100 meter elevation increase (Rolland, 2003). Additionally, proximity to streams has been shown to buffer temperature, with streamside areas being cooler in warmer months, and in several cases warmer in cooler months when compared to the average regional temperature (Fridley, 2009). Similarly, local maximum temperatures are affected by soil moisture content, through evaporative cooling: incoming solar energy first evaporates (part of) the soil moisture before heating up the local environment (Dai, Trenberth, & Karl, 1999).

In summary, several ecological aspects influence temperature. Canopy cover and slope aspect affect temperature through differences in solar irradiation. Dense vegetation can limit wind speeds, increasing warming. Surface water can act as a temperature buffer, and higher elevation correlates with lower temperatures.

2. Objectives and key questions

This study aims to assess how landscape features of a South African savanna landscape shape local temperature and will then investigate if rhino distribution across this landscape is subsequently linked to these same – and additional – landscape features.

Knowledge regarding rhino habitat choices as a response to regional and local temperature fluctuations can increase efficiency of anti-poaching efforts by improving predictions of spatial distributions. Additionally, having a model predicting the future distributions of rhino as a response to climate change will help local policymakers develop conservation schemes in relation to the predicted rise in peak temperatures across the region.

To achieve this, I will address the following main research question:

To what extent are spatial and temporal distribution of the Southern white rhinoceros determined by the variation in local and regional ambient temperature?

H_1: Rhinos will show a spatial response to high daily temperatures, during which they will retreat to cooler areas.

This research question can be divided into the following sub questions with hypotheses below:

- How does overhead canopy affect local temperature?

H_1: *Increased overhead canopy will have a cooling effect.*

- How does shrubby vegetation density affect local temperature?

H_1: *More open vegetation will have a cooling effect by increasing wind chill.*

H_2: *More dense vegetation will have a warming effect by reducing wind chill.*

- How does slope affect local temperature?

H_1: *Northern slopes will be warmest on average. Southern slopes will be coolest on average. East-facing and west-facing will have similar effects on temperature during peak heat.*

- How does air temperature relate to surface temperature as measured in the MOD11A1 product by the MODIS project?

H_1: *Higher air temperatures will correlate with higher surface temperatures.*

- How do the aforementioned ecological variables affect rhino distribution?

H_1: *During relatively hot days, rhinos will predominantly be in areas with ecological variables associated with lower temperatures: southern slopes, patches with high canopy and patches without dense woody vegetation.*

3. Study site

The study location is approximately 14,000 ha, located in the Kempiana reserve, Greater Kruger Area. Figure 1 shows the study area in which I collected my data on the rhino movement patterns. The study region has an open connection to the Kruger National Park and to the surrounding privately-owned nature reserves, allowing for animals to move between these different game and nature reserves. The study area is relatively low in traffic and tourism, and none of the roads are tarred.

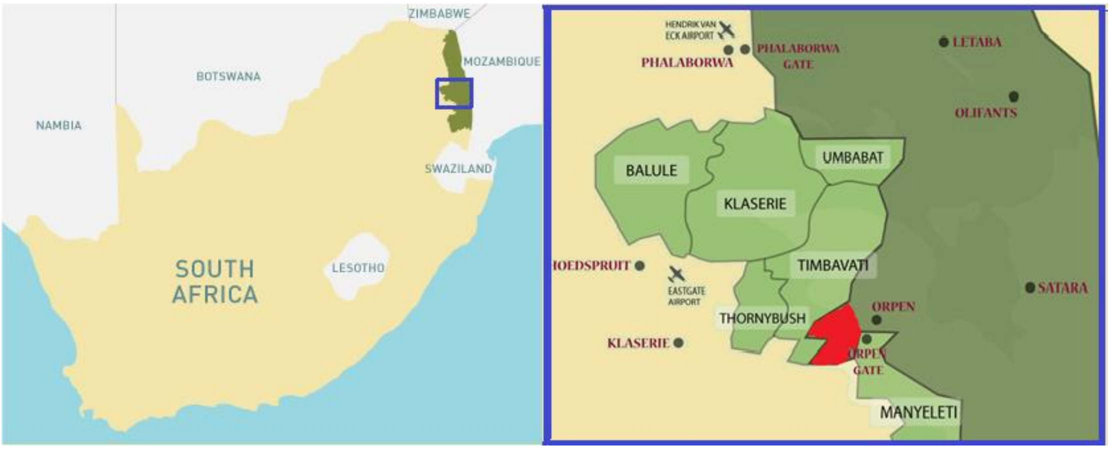

Figure 1: Greater Kruger Area (dark green in image left). Kempiana reserve depicted in red in image right.

Open woodlands with several woody species of the *Acacia*, *Terminalia*, *Combretum* genera, interspersed with patches of grasses (e.g. *Megathyrsus*, *Hyparrhenia* and *Themeda* genera) dominate the area. The Timbavati river runs through the centre of Kempiana, with more dense patches of tall riverine vegetation along its edges. The bedrock in most of the area consists of quartz-feldspar-biotite gneiss, with some smaller sections of gabbro and biotite gneiss.

The temperature and precipitation are very seasonal in the area, with a hot and wet season occurring in December, January and February (28.6 ± 3.9 °C standard error (SE), 239.7 ± 132.6 mm SE), and a graduate cooling and drying of the landscape in March, April and May (26.2 ± 3.6 °C SE, 90.1 ± 17.3 mm SE). The cooler dry season occurs in June, July and August (22.7 ± 3.4 °C SE, 23.9 ± 35.6 mm SE), with temperatures and precipitation increasing over the months of September, October and November (26.6 ± 4.9 °C SE, 134.8 ± 77.8 mm SE).

The southern part of Kempiana is used by the Southern African Wildlife College (SAWC) for educational and ranger-training purposes, since that area is not accessible to tourists. I collected the temperature data on the training grounds of SAWC, as a representative area of the greater study area (figure 2).

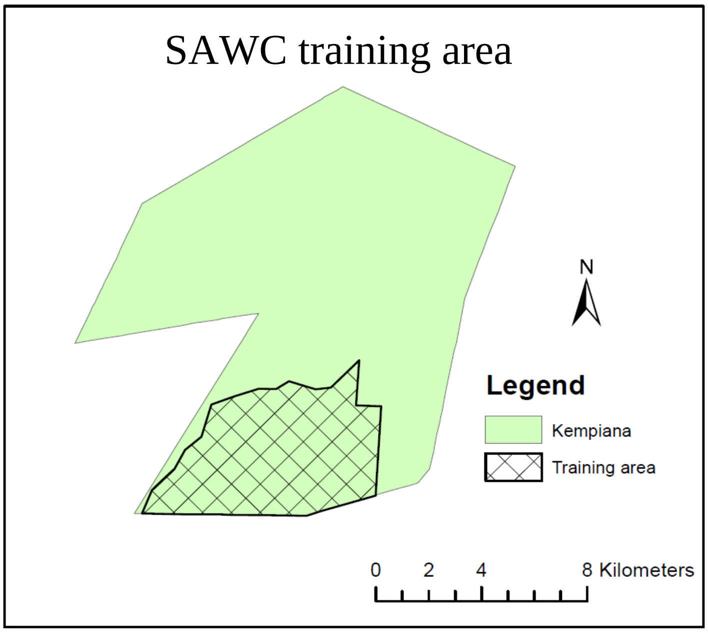

Figure 2: Training area in Kempiana reserve

4. Methods

4.1 Temperature collection

I measured the effect of separate landscape features on temperature by placing 24 iButton thermochron DS1921G (www.ibuttonlink.com) thermometers in the field in two groups of 12 thermometers in contrasting conditions. The experiments were conducted in March and April 2019. These thermometers have a 0.5 °C accuracy. The iButtons were placed in the field for 7-10 consecutive days for each experiment, depending on guard availability (the work was conducted in a big game area and work on foot is only permitted with the accompaniment of an armed guard). During this period, the thermometers logged temperature readings every 10 minutes. I performed experiments to investigate the effect of 3 different landscape features on local temperature: direct overhead canopy cover, woody vegetation density and dominant slope aspect. At the end of each experiment, I collected the iButtons and documented landscape features of each site where a thermometer was placed with the Cybertracker android app (www.cybertracker.org). Woody vegetation cover, dominant slope aspect (north, east, south or west-facing), dominant woody vegetation species, dominant vegetation height, and whether the thermometer was attached to a tree under its canopy or to a pole with no overhead canopy (figure 3) were documented as an average for a circle with a 5 meters radius around every iButton. For woody vegetation cover, I made a distinction between 'dense' and ‘sparse’ vegetation cover. I defined ‘dense’ as >50% woody vegetation cover of between 1 and 2 meters height, and ‘sparse’ as <25% woody vegetation cover between 1 and 2 meters height. I chose the 1-2 meters mark because vegetation could impact wind speed around the thermometer most at this height. For dominant slope aspect, I used a compass to assess in which direction the slope angled. If I could not see a slope in any direction, dominant slope was defined as ‘flat’. Dominant woody vegetation species was defined as the 3 species that covered the greatest area. I defined 3 groups for dominant vegetation height: ‘ground’, ‘low’ and ‘high’ to distinguish which vegetation height covered most area at each site. ‘Ground’ meant predominantly grasses or bare soil, ‘low’ meant <3m woody vegetation and ‘high’ as >3m. I filled in a ‘special circumstances’ field when applicable, for example when vegetation density was difficult to assess, or when an animal had damaged or knocked over the thermometer. Every iButton was also photographed in 2 directions, as a backup to the field data collection.

Figure 3: examples of thermometers in the field attached to a pole (left) and a tree (right).

In all experiments concerning the effects of landscape features on temperature, I placed the thermometers in pairs that were located 10 meters from one another. One of the thermometers would be attached to a tree, 15 cm from the trunk, and the other on a pole 10 meters in a random direction as long as this resulted in a 0-canopy situation. This way, the average degree of canopy cover was equal for both groups of interest in every separate experiment, as half of the thermometers in each group was shaded, and the other half was not shaded. Each pair of thermometers was placed at least 50 meters apart. All iButtons were located at a height of 170 cm above the ground. This height was chosen as rhino head height, and so similar to where a rhino might register air temperature.

I attached all iButtons to either trees or poles by a metal wire, depending on whether they were part of the shaded (tree) or non-shaded (pole) group (figure 3). The reason for attaching the shaded iButtons to the tree rather than a pole next to the tree was to limit visibility to passing elephants and/or baboons that may interfere with the set up. I attached hazard tape to the poles to help find them again. The poles were secured by first hammering a metal stake into the ground and placing the pole over the top. I secured the metal wire to the trees using rope. A photo directly overhead of each thermometer was also taken. I used CanopyApp, developed by the University of New Hampshire, to assess overhead canopy closure based on this photo. Only trees with >50% canopy closure were selected.

4.1.1 Vegetation density

I first assessed vegetation density through ESRI World Imagery maps and Google Earth. In this initial assessment, areas of 400 m^2 with a >70% woody vegetation coverage were considered 'dense vegetation', and areas with >20% woody vegetation coverage were considered 'sparse vegetation'. I picked 3 locations at random for both dense and open vegetation. At each of these locations, I put two pairs of thermometers into place, located between 50 and 150 meters from each other. I decided to contrast plots differing in both canopy cover and vegetation density to separate the effects of solar irradiation and wind chill. A lone tree in a grassland provides canopy cover and thus shelter against irradiation, but is not surrounded by dense vegetation so allows for wind chill. A square meter of grass in a dense patch of bushes does not provide canopy cover but is surrounded by dense vegetation so reduces wind chill.

4.1.2 Slope aspect

I first assessed general slope aspect through the 'elevation profile' function in Google Earth. I measured east-west as well as north-south slope ratios across the SAWC training area, at 250m intervals. First, I selected points with steep (>5%) north-facing or south-facing slopes while having weak (<1%) west-facing or east-facing slopes. Similarly, I selected points with steep (>5%) east-facing or west-facing slopes while having weak (<1%) north-facing or south-facing slopes. This made sure that all slopes used for analysis were facing cardinal directions (north, east, south or west), without including intercardinal slopes (e.g. north-east or south-west). This way, north-facing slopes could be compared with south-facing slopes, and east-facing slopes could be compared with west-facing slopes. I chose these direct comparisons in order to have a what was deemed adequate number of thermometers per test group. If all cardinal directions were compared simultaneously, only 6 thermometers would be available per group, still with a chance of thermometers being disturbed by animals which would reduce this number even more. In the setup as was followed, this number of thermometers was 12 per group.

4.2 Rhino distribution

4.2.1 Rhino location data

The data on rhino and elephant locations was provided by SAWC. SAWC has been monitoring the locations of rhinos by means of aerial surveys since February 2014, with varying temporal resolution throughout the area, ranging from multiple times a week to less than once a month. In addition to the animal location, the flightpath of the airplane was also tracked. During the surveys, the pilot recorded the GPS location of every sighting, and noted the number of rhinos in every sighting. However, for the purpose of this research I have chosen to view every sighting as a single encounter regardless of group size, because I assumed rhino landscape use as an response to temperature to be independent of rhino group size.

Since the focus of this research was on high peak temperatures, only rhino location data collected during summer months was included (December, January & February). A weather station at SAWC (figure 4) measured hourly temperatures over the entire period of available rhino location data, which was used to assess which days were relatively hot, and which days were relatively cool. By cross-referencing this weather data with dates for which rhino location data are available, the 25% hottest and 25% coolest days (named 'hot group' and 'cold group', respectively, from here on) were selected for analysis. By comparing hot days with cold days, the effect of temperature in the hot season on rhino distribution can be calculated and visualised.

The accuracy of the rhino locations was around 500 meters. This is because locations are taken from a moving aircraft, so the location once a rhino is seen is documented rather than the actual location of the animals on the ground (up to 250 meters to either side of the plane). Therefore, I constructed a 500*500m grid using the 'create fishnet' tool in ArcGIS, to which I could add landscape features and rhino locations.

4.2.2 Correction for flight paths

For all dates for which rhino location data were provided, a detailed flightpath of the spotter airplane was also included. Since the airplane did not always cover the entirety of Kempiana, and some cells were therefore visited more often than others, I used this flightpath to construct a new cell raster showing rhinos per km^2 rather than the simple rhinos spotted per cell.

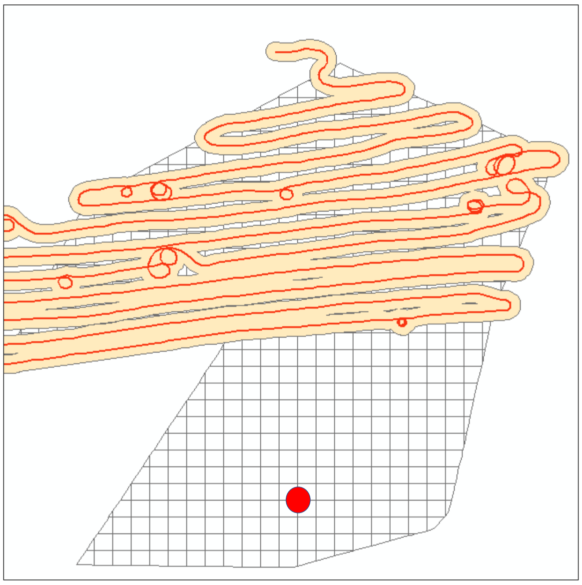

Figure 4: Kempiana grid with example of original flightpath (red line), constructed buffer (orange area) and weather station (red dot).

To achieve this, the 'buffer' tool in ArcGIS was used to create buffer areas with a distance of 250 meters from the original flightpaths (figure 4). These buffers were then combined with the 500*500m raster with the 'Tabulate intersection' tool in ArcGIS to calculate the area flown for every single cell. The number of rhino encounters in each cell was then divided by the cell coverage to get to a measurement of rhino density as 'rhino per km^2'. Cell coverage here is defined as percentage of cell area the spotter plane has seen over a certain period of time. This can therefore be greater than 100% when a cell has been covered multiple times, and smaller than 100% if the cell was only partly covered. This process was done separately for the 'hot' and 'cold' groups.

4.3 Remote sensing

4.3.1 Tree cover and vegetation density

For tree cover mapping, I used the database constructed by Hansen et al. (2013). This map provided tree (defined as >5m height) cover mapping at a 30m resolution, showing areas with 0-25% and 25-50% tree cover, and in some riverine exceptions 50-75% tree cover in the Kempiana area (M. C. Hansen et al., 2013). I used the 'Raster to point' tool to create points at the middle of each existing cell of Hansen's map. Then I used the 'Spatial join' tool to calculate the percentages of points coinciding with each of my 500*500m raster. Using the 'Extract values to table' tool in ArcGIS, I added this tree cover map as a new column to my 500*500m raster. This measure of tall vegetation was, as an explanatory variable for rhino density, used as a proxy for shade as well as vegetation density.

4.3.2 Elevation and Aspect

The 30m resolution ASTER-elevation map (Tachikawa et al., 2009) was used to map elevation throughout the study region. I used the 'Raster to point' tool to get points with elevation values for each cell of the ASTER-elevation map. I calculated mean elevation per 500*500m cell through the 'tabulate intersection' tool in ArcGIS and I used the 'Extract values to table' tool to add elevation as a new column to the 500x500m Kempiana grid. Aspect was calculated using the same dataset. First, the 'Aspect' tool in ArcGIS was used to get a new dataset with aspect in degrees (0° - 360°). Then, this dataset was converted into the four cardinal directions, with 0° - 45° and 316° - 360° as North, 46° - 135° as East, 136° - 225° as South and 226° - 315° as West. By using the 'Tabulate intersection' tool, the most prevalent aspect was identified as the 'dominant aspect' of every 500*500m cell. Slope gradient was excluded from the analysis.

4.3.3 Dominant vegetation

A vegetation map of the area was available at SAWC, as produced by Timbavati Nature Reserve Management (figure 5). This map showed 18 distinct vegetation types, with 'Dolorite' and 'Disturbed areas' being relatively devoid of vegetation. Using a similar approach as when determining aspect, the 'Tabulate intersection' tool was used to find the vegetation type that covered the largest area for each cell, which was then assumed to be the 'dominant vegetation type'. Since only the dominant vegetation types were used, some of the smaller groups were not found in the coarser 500*500m vegetation map. For the purpose of the analysis, the vegetation map created in the 500*500m grid was further simplified into 'Open woodland', 'Lowland savanna', 'Woodland' 'Riverbeds', 'Thicket' and 'Disturbed/rocky' to increase predictive value of the created model.

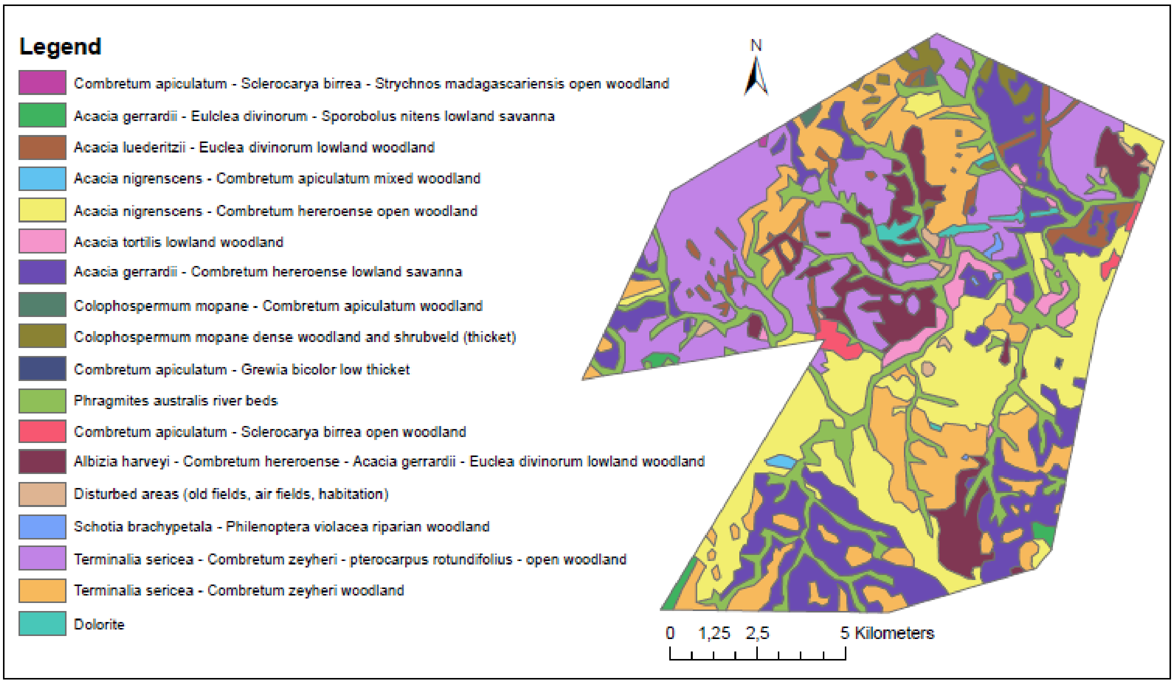

Figure 5: Vegetation map by Timbavati Nature Reserve Management

4.3.4 Waterholes

Waterholes were also included as a variable to explain rhino densities. The collection of data on waterholes and wallows was done by R. A. Wool during the same study period as this research (Wool, 2019). Initial identification of waterholes was done using Google Maps, with aerial confirmation as well as confirmation of a selection of waterholes on foot. Artificial as well as natural waterholes were included. For a detailed description of the methods used in this regard, I would like to refer to Wool (2019).

I used the 'Spatial join' tool in ArcGIS to assess which of the 500*500m cells contained waterholes, disregarding the exact number of waterholes in each cell, thereby creating a waterhole presence/absence map. For detailed relationships between waterhole number and sizes and rhino densities I again refer readers to Wool (2019).

4.4 MODIS temperature

To check for correlations between the MODIS satellite surface temperature and the temperatures logged by the iButtons in this study, I requested MODIS data before each experiment. This data is delivered in a raster of 1x1 km^2, showing surface temperatures for each of these cells at 10:00 AM. I then identified the 2 most different (i.e. the hottest and coldest) cells located in the SAWC training area. For each experiment, the plots used were at different locations. Within each cell, 9 iButtons were placed 250 meters apart (figure 6) to get a random sample for each cell. Unlike the previous experiments, the MODIS experiments did not utilize tree-mounted iButtons because the locations required were never directly on a tree trunk. Similar to the landscape feature experiments, the length of each MODIS experiment varied based on guard availability.

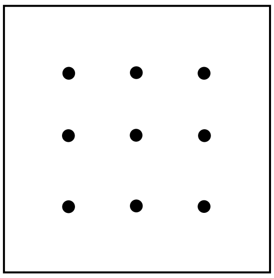

Figure 6: 1 km^{2,} 9 iButtons (dots) 250 meters apart

I performed 4 separate experiments on 4 pairs of cells, over a period of 6, 8, 12 and 6 days for each consecutive experiment. Cloud cover caused 2, 1, 7 and 2 days to be unusable from analysis for each experiment, respectively, because no MODIS data is available for clouded cells.

4.5 Statistical design

4.5.1 Temperature explained by the environment

I used t-tests to determine the effect of the separate environmental variables (shading, vegetation density and slope) on temperature using R software (https://www.r-project.org/about.html). I used the average temperatures of each multiple-day experiment of the times between 11:00 AM and 15:00 PM, thus using a single mean temperature per thermometer for each experiment. This resulted in 2 groups of 12 temperature values to compare for vegetation density, canopy closure, and both aspect analyses. In some cases, pole-mounted thermometers were knocked over by wildlife. In these instances, I excluded an equal number of random tree-mounted thermometers in the same experimental group from the analysis in order to keep equal shaded and non-shaded conditions. The temperature data from the vegetation density experiment was used for the analysis of the effect of both canopy cover and vegetation density on temperature.

4.5.2 Rhino density explained by the environment

For the environmental variables to explain rhino densities, I used generalised linear mixed-effect models (GLMM). This approach can account for random effects in the model. In this case the random factor was the location of the cell (cell ID – the name of each cell that was used twice: once in the 'hot' group, and once in the 'cold' group). All variables mentioned in section 4.3 were assigned to each 500*500m cell and used in the GLMM as separate fixed effects to model rhino density. This was done in 2 ways. First as a presence-absence approach using a binomial regression: rhino data was categorised as rhinos either being present or absent in each cell. In this case, rhino densities were approached as an 'encounter probability', meaning the probability of encountering rhino at least once based on the number of flights. The second approach used only cells where rhinos were present and included actual rhino densities in those cells. Here, I used a Gaussian process regression.

4.5.3 MODIS comparison

For the iButton data used to compare to MODIS temperatures, I averaged temperatures measured at 09:50 AM, 10:00 AM and 10:10 AM for all 9 thermometers per plot. This then resulted in a single temperature measurement per day for both plots in each experiment. Available MODIS satellite temperature data was always a single measurement per plot, at 10:00 AM. I used a Pearson correlation to check for consistency between measured data and MODIS satellite surface temperature data. This was done in 2 ways. First, a general correlation for temperatures of each of the days the thermometers were in the field. Second, a correlation between the temperature differences measured between the hot and cold cells investigated in each experiment. The reason for this second method is to get an idea of how consistent iButton data and MODIS data are with regard to showing which of two cells is has the highest temperature. Even if there is a strong positive correlation, a low R²-value for the second method might indicate a qualitative difference between MODIS and iButton data when trying to measure which cell has higher temperatures.

5. Results

5.1 Temperature explained by the environment

5.1.1 Canopy closure

The effect of canopy cover on local air temperature was measured over a 7-day period. The open canopy group showed the highest temperatures. (figure 7). The 95% confidence interval of difference between measured means was 0.60±0.41 °C, with the 'Open canopy' group estimated at 26.3±0.15 °C SE and the 'Closed canopy group estimated at 26.9±0.12 °C SE.

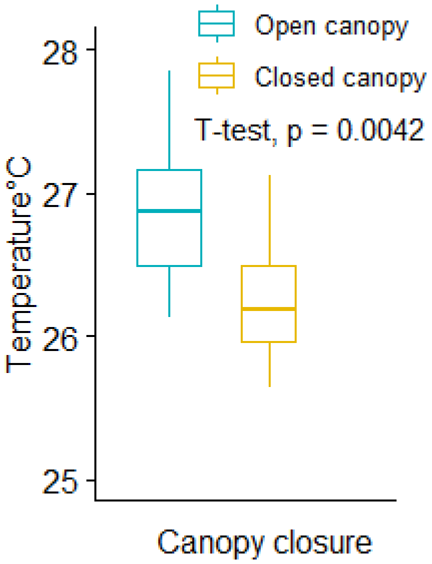

Figure 7: Midday temperatures by canopy closure. Means estimates are 26.3 (Open canopy) and 26.9 (Closed canopy).

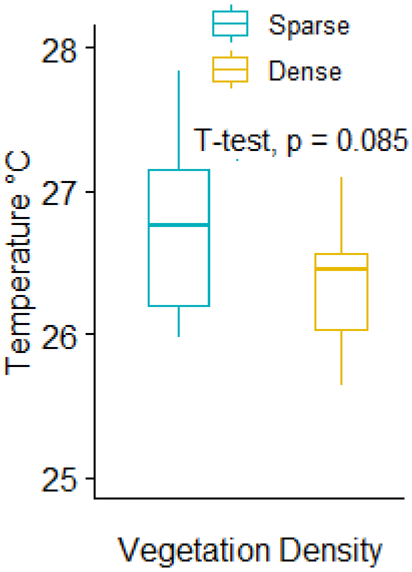

Figure 8: Midday temperatures by woody vegetation density. Means estimates are 26.7 (Sparse vegetation) and 26.3 (Dense vegetation).

5.1.2 Vegetation density

Using the same dataset as used for canopy cover, the effect of vegetation density was measured over the same 7-day period. There was a clear trend towards a temperature difference between the dense and open vegetation groups, with a t-test resulting in a p-value of 0.085 (figure 8). Estimates of the means of temperatures were 26.3±0.11 °C SE (Dense woody vegetation) and 26.7 ±0.17 °C SE (Sparse woody vegetation). The 95% confidence interval for the difference in means was 0.4±0.45 °C.

5.1.3 Aspect North-South

The effect of north and south-facing slopes on temperature was measured during an 11-day period. There were no significant differences found between the groups, with a t-test resulting in a p-value of 0.65 (figure 9). Estimates of the means of temperatures were 27.7±0.23 °C SE (North-facing slope) and 27.9±0.29 °C SE (South-facing slope). The 95% confidence interval for the difference in means was 0.17±0.78 °C.

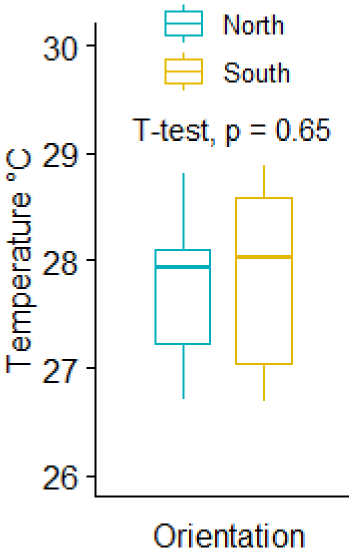

Figure 9: Midday temperatures by North-facing and South-facing slopes. Means estimates are 27.7 (North) and 27.9 (South).

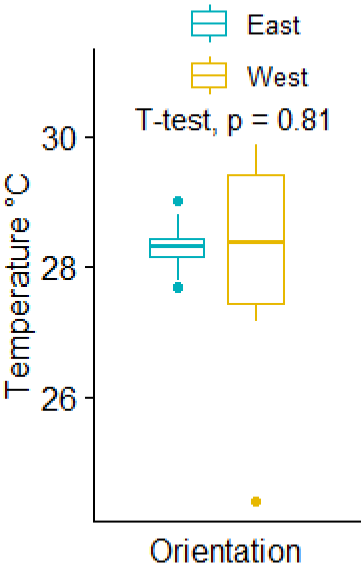

Figure 10: Midday temperatures by East-facing and West-facing slopes. Means estimated at 28.2 (East) and 28.3 (West).

.5.1.4 Aspect East-West

The experiment conducted to assess the difference in temperatures between east-facing and west-facing slopes lasted 7 days. No significant differences between the groups were found. Estimates of the means of temperatures were 28.3±0.16 °C SE (East-facing slope) and 28.2±0.52 °C SE (West-facing slope). The 95% confidence interval for the difference in means was 0.17±0.78 °C.

	Landscape features	
	Open canopy	*Closed canopy*
Mean	26,86	26,23
SD	0,15	0,12
P-value	***0,004****	
	Sparse woody vegetation	*Dense woody vegetation*
Mean	26,72	26,33
SD	0,17	0,26
P-value	0,085	
	South-facing slope	*North-facing slope*
Mean	27,9	27,72
SD	0,29	0,23
P-value	0,65	
	East-facing slope	*West-facing slope*
Mean	28,3	28,17
SD	0,16	0,52
P-value	0,81	

Table 1: Summary statistics for t-tests of the effect of landscape features on local temperature.

5.2 Environmental mapping & rhino density

5.2.1 Woody vegetation density map

Relatively dense (25-50%) tall vegetation (>5m height) was more dominant in the western parts of Kempiana (figure 11). The remaining percentage of individual cells was in almost all cases filled with 0-25% tall vegetation cover. 7 cells included some area of 50-75% tall vegetation coverage, but this was rarely more than 5% per cell.

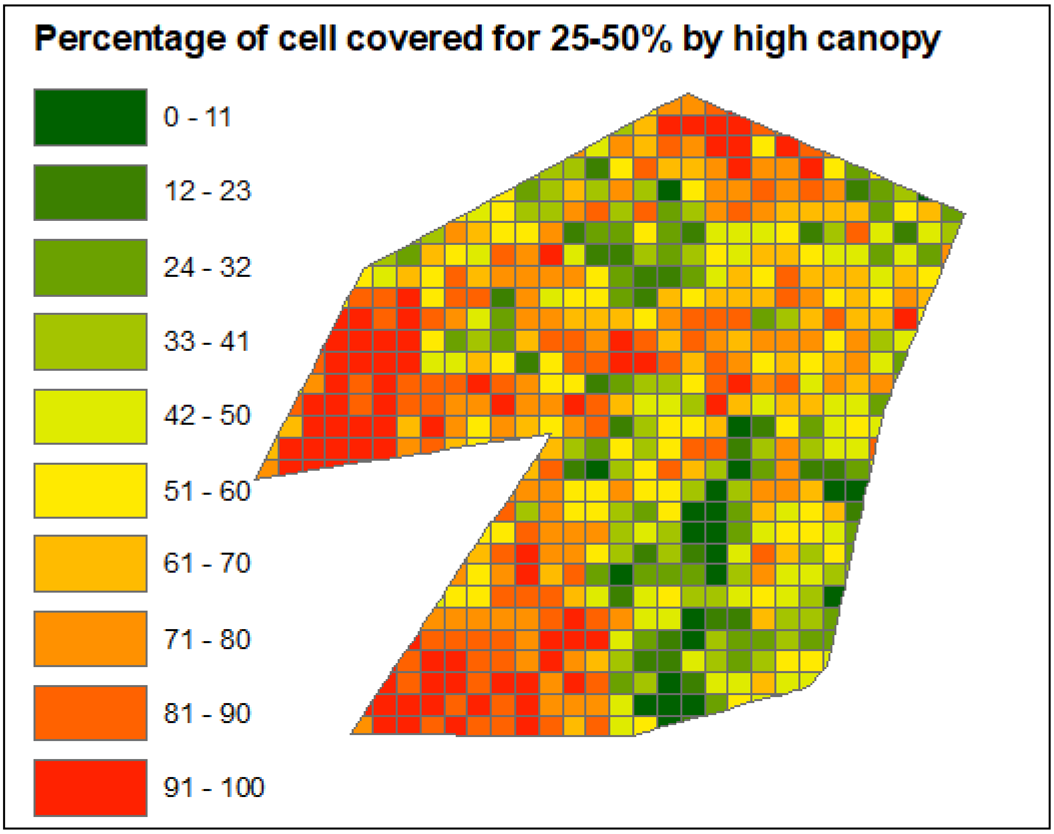

*Figure 11: Percentage of each 500*500m grid cell covered for 25-50% by high canopy, based on Hansen et al. (2013).*

5.2.2 Elevation

Elevation in the region ranged from 397 to 523 meters above sea level (figure 12). The north-western and south-eastern sections of the study area are higher than the centre and north-eastern section.

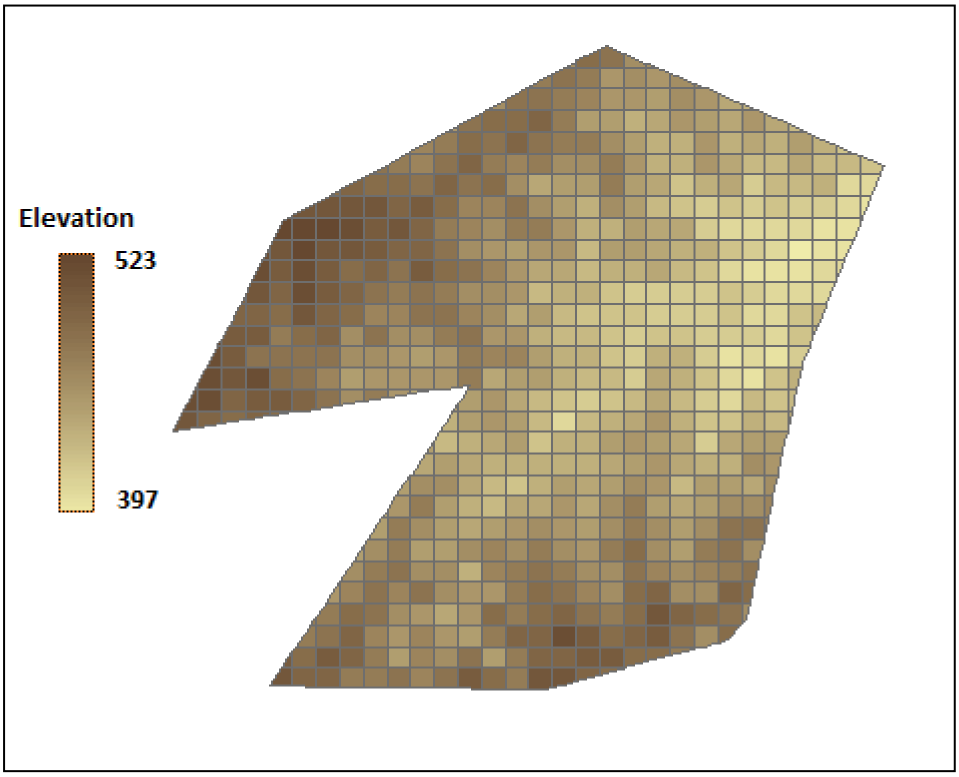

*Figure 12: Elevation of each 500*500m grid cell. Based on Tachikawa et al. (2009).*

5.2.3 Dominant aspect

Dominant slope aspect seemed to be relatively evenly distributed throughout the study region (figure 13). Predominantly North, East, South and West-facing slopes accounted for 29%, 25%, 27% and 19%, respectively. West-facing slopes seemed to be most abundant in the southern part of Kempiana.

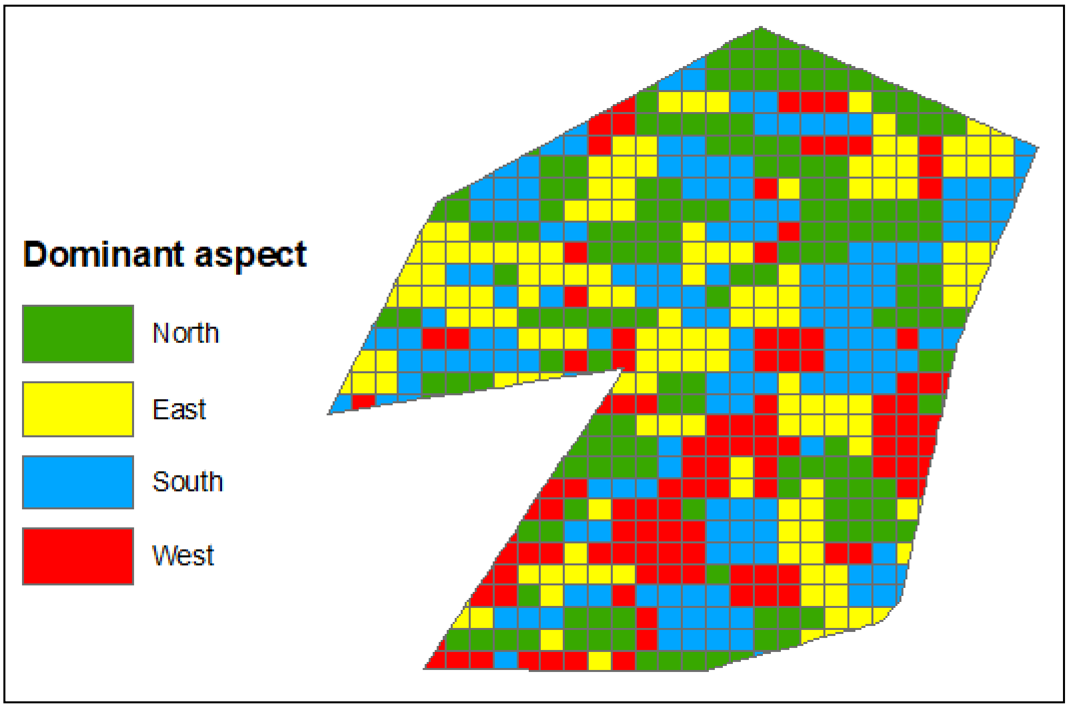

Figure 13: Dominant aspect of each 500x500m grid cell. Based on Tachikawa et al. (2009).

5.2.4 Dominant vegetation

The most dominant vegetation types in the Kempiana reserve were the 'Open woodland', 'Woodland' and 'Lowland savanna' groups, with 43%, 26% and 17%, respectively. The 'Disturbed or rocky' and 'Thicket' groups covered less than 1% of the area.

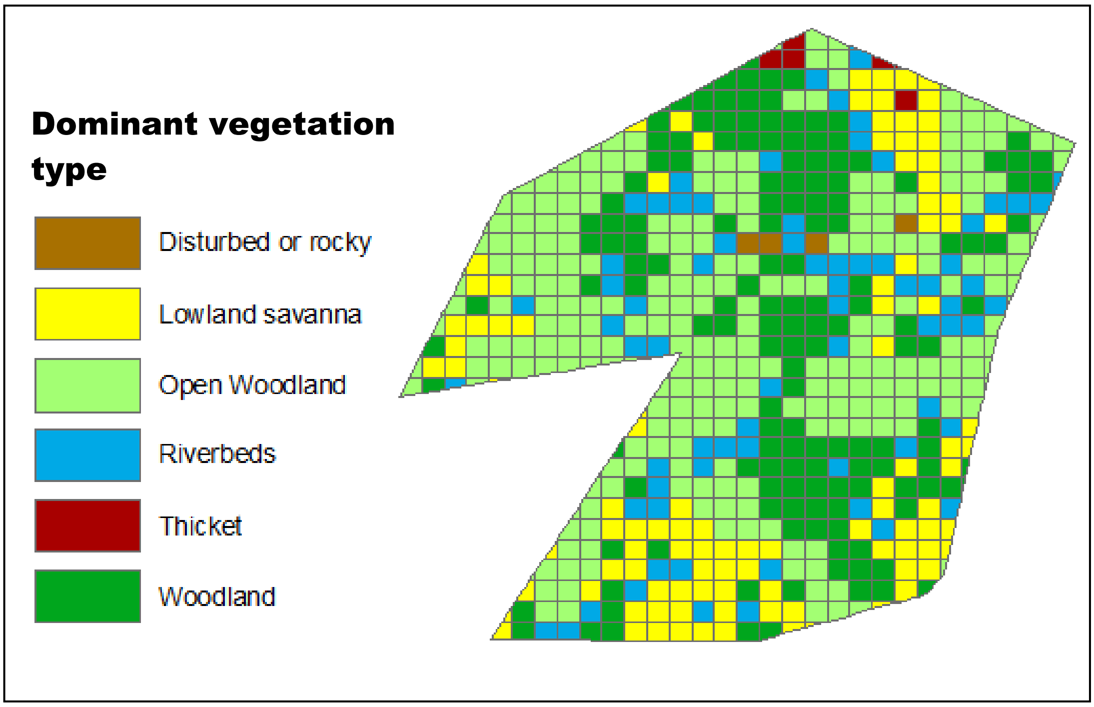

*Figure 14: Dominant simplified vegetation for each 500*500m grid cell. Based on figure 5.*

5.2.5 Waterholes

Either natural or artificial waterholes were present in 18% of the cells in the study area, of which 14% had only one waterhole, and 4% more than one waterhole (figure 15). The maximum number of waterholes per cell was 5.

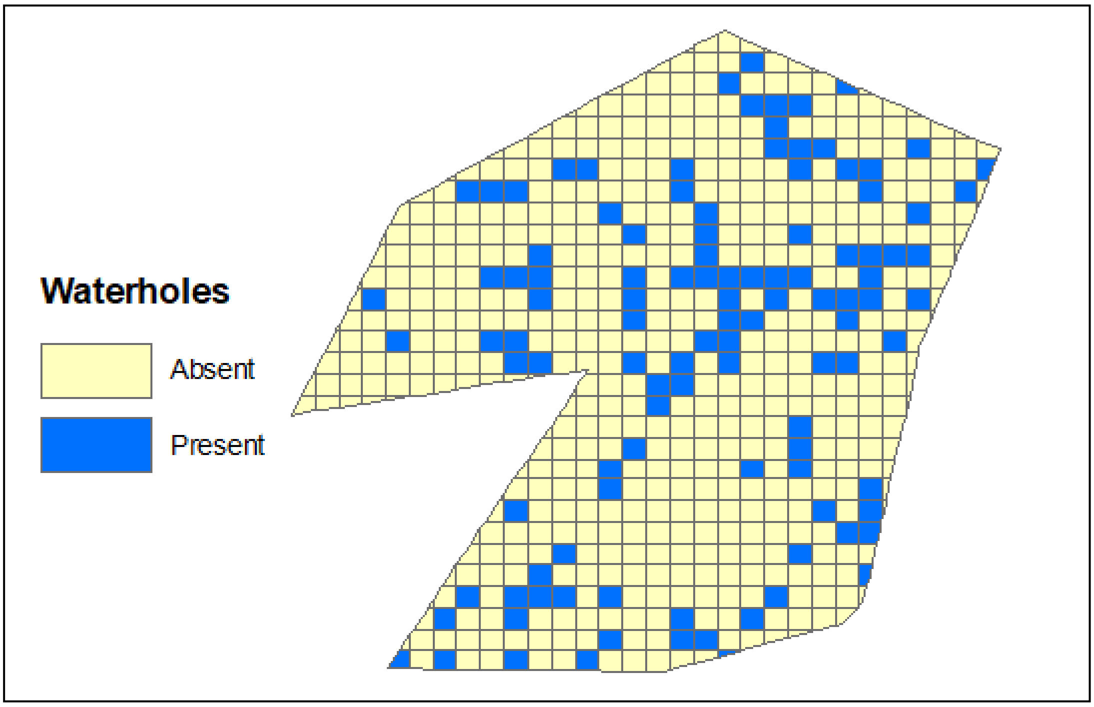

*Figure 15: Waterhole presence per 500*500m grid cell. Based on Wool (2019).*

5.2.6 Rhino densities by landscape features

Due to rhino security measures, I am not allowed to include maps depicting rhino densities in this report. Therefore, I only present statistical relationships. The temperatures on the hot and cold days (used for the hot and cold groups, respectively) were significantly different from each other with a p-value of $2.6*10^{-10}$ (figure 16). For the hot group, average temperature as measured by the SAWC weather station was 32.5±0.3 °C SE. For the cold group, this was 25.9±0.5 °C SE.

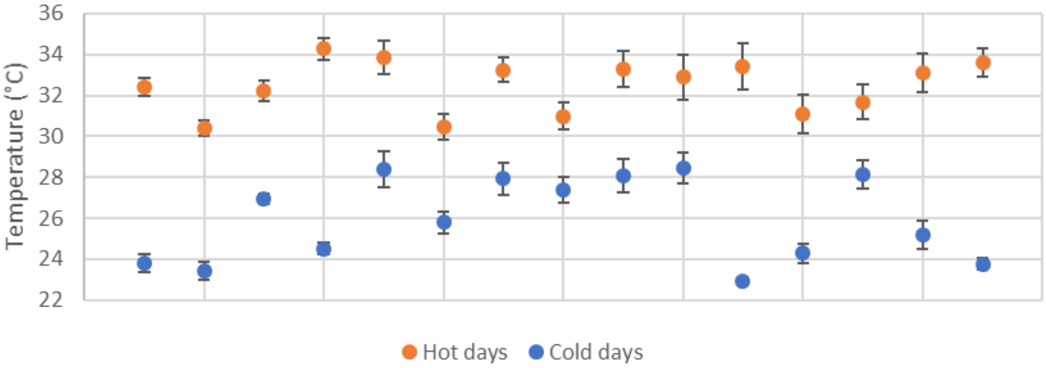

Figure 16: Temperatures of the days where the cold and hot groups were picked with SE bars

Cells were on average covered for 550% and 650% in the hot and cold groups, respectively, in 15 flights each. Both the presence-absence GLMM and the presence-only GLMM yielded insignificant differences in effects of the ecological variables on rhino density between the hot and cold groups. Summary statistics for each model can be found in table 2 and table 3 at the end of this section. Graphs showing the results of the presence-absence GLMM are provided here first (figures 17-21). This is followed by graphs of the results of the presence-only GLMM (figures 22-26).

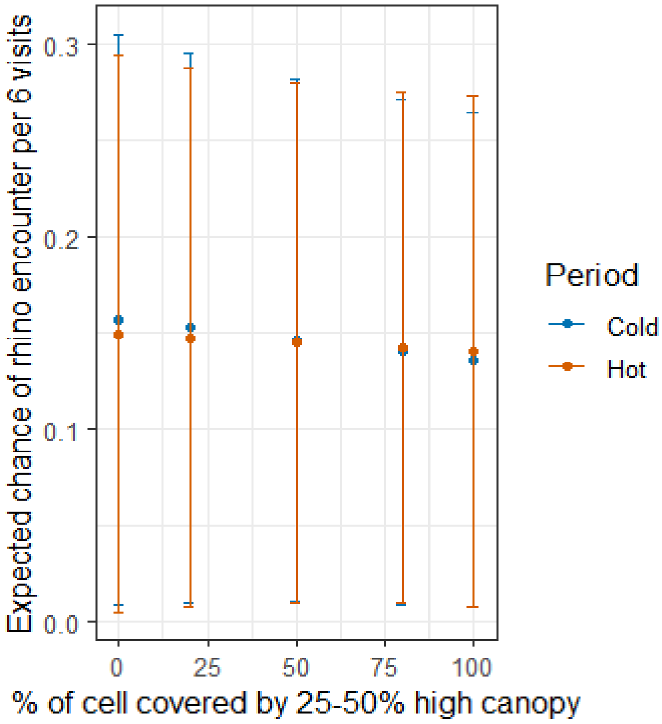

Figure 17: Expected probability of encountering a rhino per 6 observation flights by canopy closure. Based on presence-absence data.

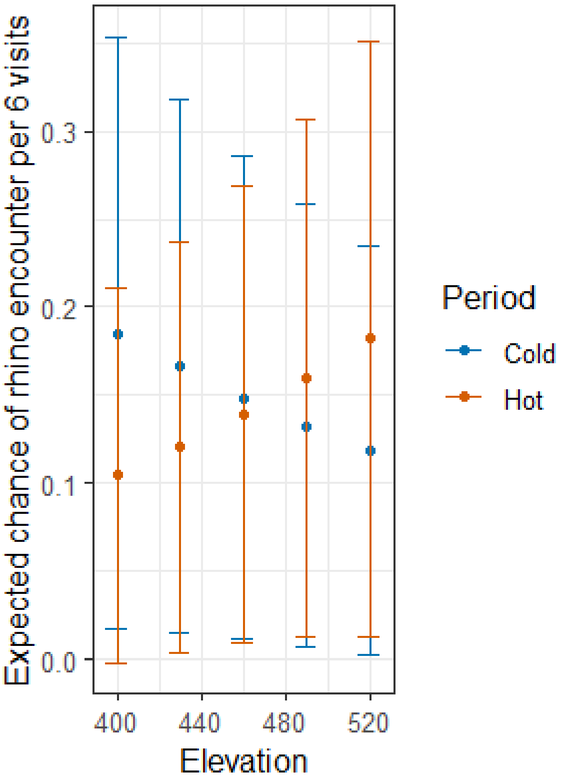

Figure 18: Expected probability of encountering a rhino per 6 observation flights by elevation. Based on presence-absence data.

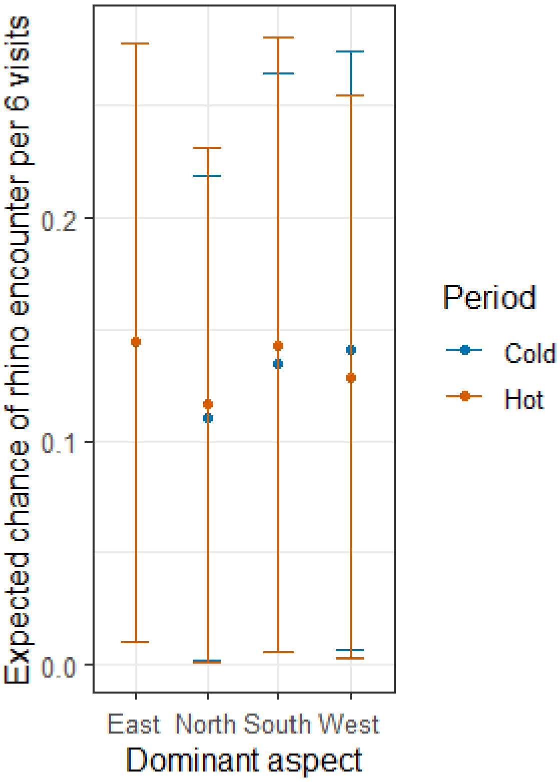

Figure 19: Expected probability of encountering a rhino per 6 observation flights by dominant aspect. Based on presence-absence data.

Dominant aspect had little differences between the hot and cold groups (figure 19). There is a trend, however, of rhino presence being low on western slopes as compared to eastern slopes for the hot group (p-value = 0.09).

For dominant vegetation, no rhinos were spotted in any of the 'Thicket' vegetation type in hot or cold periods. Similarly, in case of the 'Disturbed or rocky' group, no rhinos were spotted on the cold days, and only 1 rhino was spotted on the hot days. The remaining vegetation types show no differences in trends between vegetation types of the hot and cold groups (figure 20).

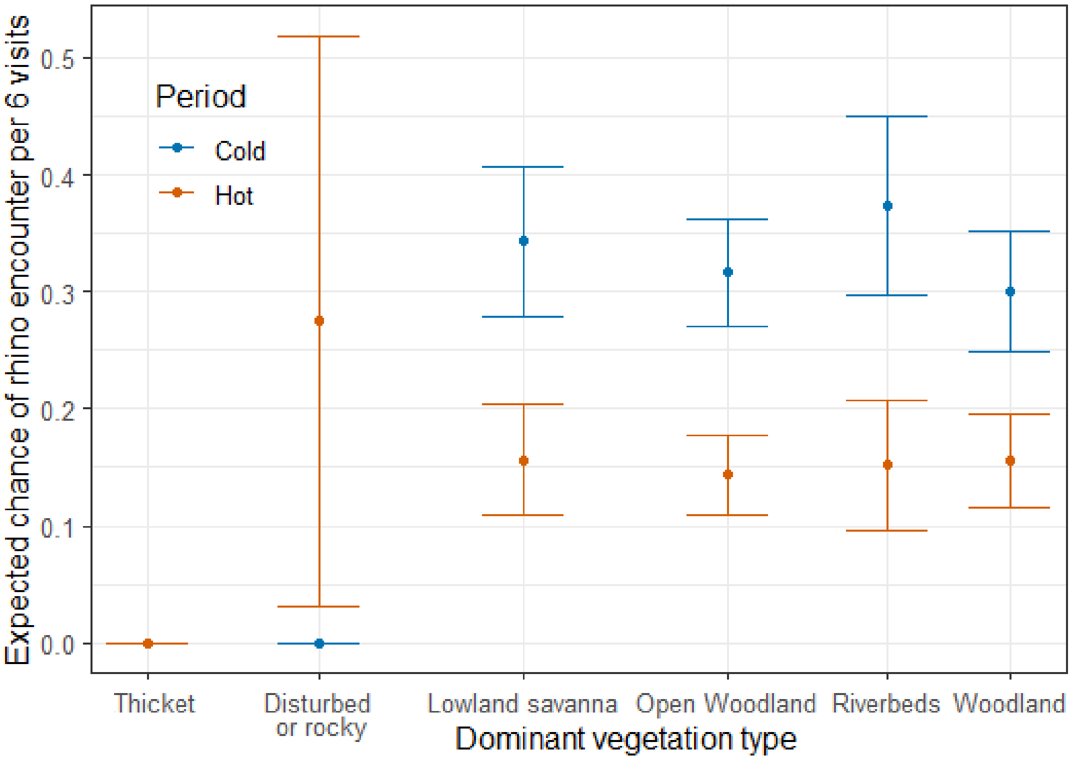

Figure 20: Expected probability of encountering a rhino per 6 observation flights by dominant vegetation type. Based on presence-absence data.

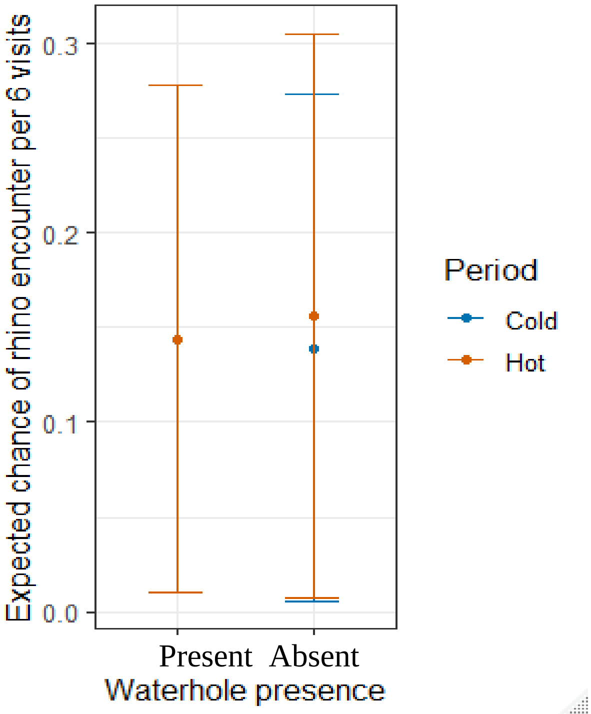

Figure 21: Expected probability of encountering a rhino per 6 observation flights by waterhole presence. Based on presence-absence data.

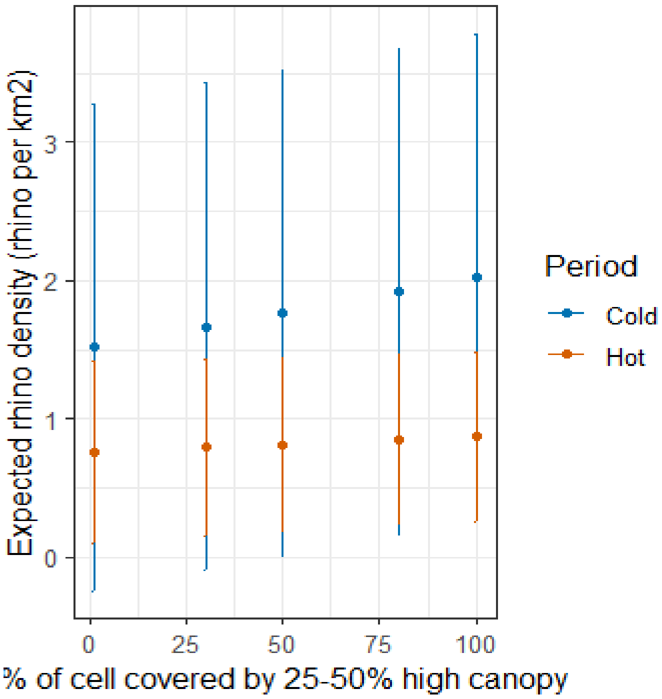

Figure 22: Expected rhino density per km^2 by canopy closure. Based on presence-only data.

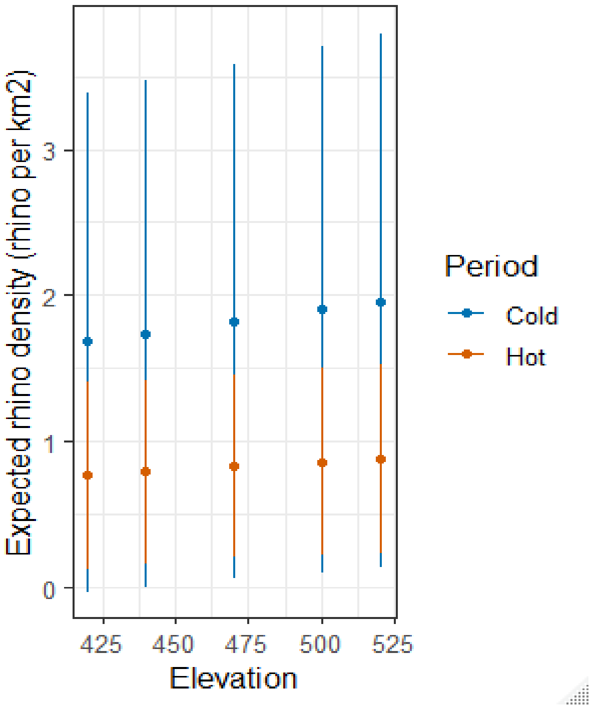

Figure 23: Expected rhino density per km^2 by elevation. Based on presence-only data.

Dominant aspect shows a decrease in expected rhino density for the west-facing slopes for the cold group (p-value = 0.004) (figure 24).

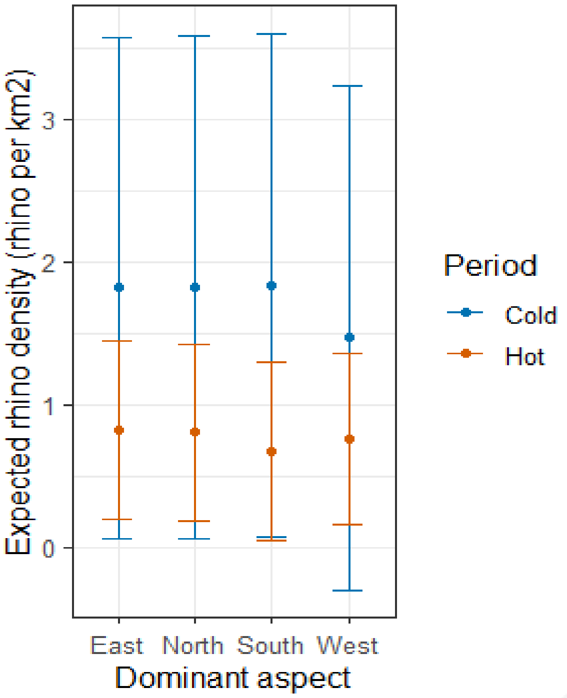

Figure 24: Expected rhino density per km^2 by dominant aspect. Based on presence-only data.

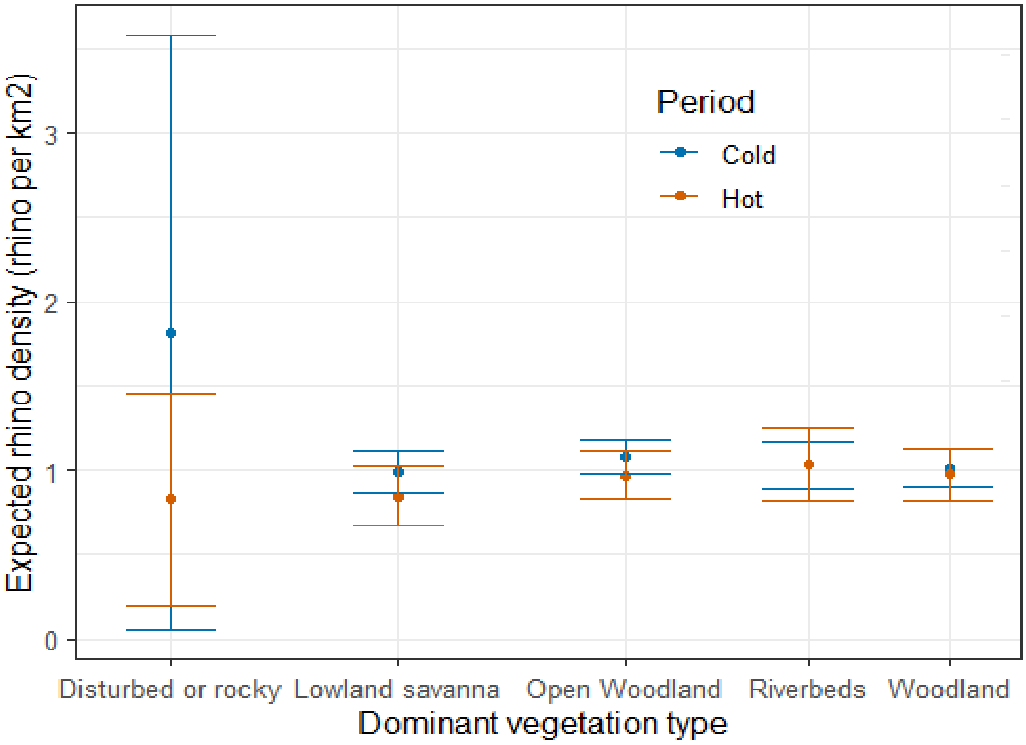

Figure 25: Expected rhino density per km^2 by dominant vegetation type. Based on presence-only data.

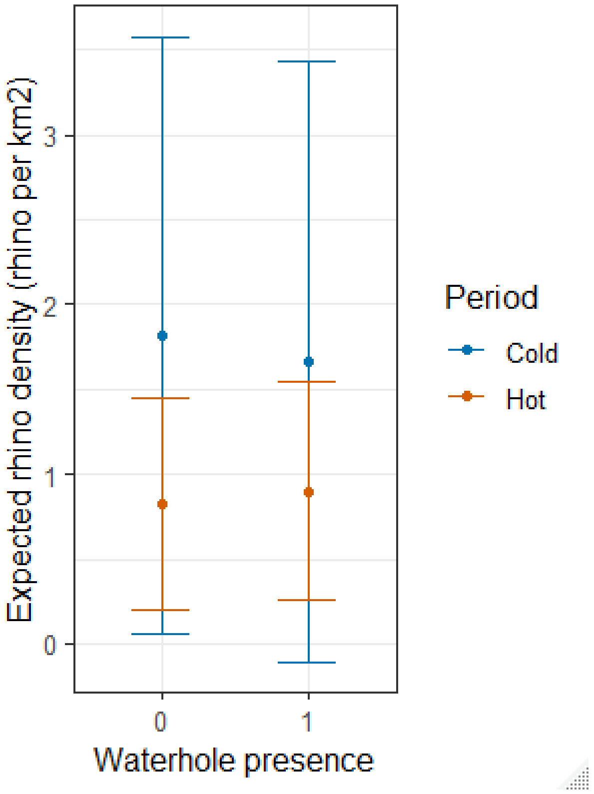

Figure 26: Expected rhino density per km^2 by waterhole presence. Based on presence-only data.

MODEL INFORMATION:
Observations: 1216
Dependent Variable: Rhino presence or absence
Type: Mixed effects generalized linear regression
Error Distribution: binomial
Link function: logit

MODEL FIT:
Pseudo-R² (fixed effects) = 0.55
Pseudo-R² (total) = 0.59
Intraclass Correlation Coefficient = 0.08

Compared to	Period	Landscape feature	Estimate	SE	z-value	p-value
NA	NA	(Intercept)	-1,21	0,17	-7,12	0
NA	Cold	*Tree cover*	-0,03	0,1	-0,33	0,74
	Hot	*Tree cover*	-0,03	0,12	-0,23	0,82
NA	Cold	*Elevation*	-0,09	0,1	-0,93	0,35
	Hot	*Elevation*	0,1	0,12	0,83	0,41
South-facing slope	Cold	*Northern slope*	0,08	0,23	0,34	0,74
	Hot	*Northern slope*	-0,65	0,28	-2,3	***0,02****
East-facing slope	Cold	*Western slope*	0,32	0,26	1,2	0,23
	Hot	*Western slope*	-0,54	0,32	-1,68	***0,09***
Open woodland	Cold	*Disturbed/rocky*	-13,14	596,77	-0,02	0,98
	Hot	*Disturbed/rocky*	0,42	1,22	0,34	0,73
	Cold	*Lowland savanna*	0,28	0,26	1,07	0,29
	Hot	*Lowland savanna*	-0,15	0,32	-0,46	0,65
	Cold	*Riverbeds*	0,4	0,3	1,33	0,18
	Hot	*Riverbeds*	-0,15	0,4	-0,39	0,7
	Cold	*Thicket*	-14,35	985,79	-0,01	0,99
	Hot	*Thicket*	-23,08	99570,9	0	1
	Cold	*Woodland*	0,11	0,23	0,49	0,62
	Hot	*Woodland*	-0,19	0,28	-0,7	0,48
Waterhole absence	Cold	*Waterhole presence*	0,04	0,24	0,15	0,88
	Hot	*Waterhole presence*	-0,01	0,31	-0,04	0,97

Table 2: Summary statistics for GLMM with presence-absence rhino data showing estimate and standard error of the effect of landscape features on rhino presence.

MODEL INFORMATION:
Observations: 279
Dependent Variable: For presence only: rhino per observed km^2
Type: Mixed effects linear regression

MODEL FIT:
Pseudo-R² (fixed effects) = 0.105
Pseudo-R² (total) = 0.528
Intraclass Correlation coefficient = 0.472

Compared to	Period	Landscape feature	Estimate	SE	t-value	df	p-value
NA	NA	(Intercept)	-0,33	0,92	-0,36	207,69	0,72
NA	Cold	*Tree cover*	0,002	0,002	2,97	258,56	0,22
	Hot	*Tree cover*	0,001	0,002	0,55	198,97	0,58
NA	Cold	*Elevation*	0,002	0,002	1,22	210,34	0,22
	Hot	*Elevation*	0,002	0,002	1,12	204,76	0,26
South-facing slope	Cold	*North-facing slope*	-0,04	0,12	-0,37	256,41	0,71
	Hot	*North-facing slope*	0,15	0,17	0,91	218,03	0,36
East-facing slope	Cold	*West-facing slope*	-0,36	0,13	-2,87	257,52	***0,004****
	Hot	*West-facing slope*	-0,03	0,19	-1,80	1229,25	0,86
Open woodland	Cold	*Disturbed/rocky*	NA	NA	NA	NA	NA
	Hot	*Disturbed/rocky*	-0,12	0,62	-0,19	244,58	0,85
	Cold	*Lowland savanna*	-0,07	0,12	-0,56	258,98	0,58
	Hot	*Lowland savanna*	-0,11	0,17	-0,65	196,20	0,52
	Cold	*Riverbeds*	-0,05	0,13	-0,39	256,54	0,69
	Hot	*Riverbeds*	0,11	0,21	0,52	159,20	0,60
	Cold	*Woodland*	-0,06	0,11	-0,52	258,50	0,60
	Hot	*Woodland*	0,01	0,15	0,07	210,27	0,95
Waterhole absence	Cold	*Waterhole presence*	-0,18	0,11	-1,65	259,00	***0,10***
	Hot	*Waterhole presence*	0,10	0,16	0,66	177,65	0,51

Table 3: Summary statistics for GLMM with presence-only rhino data showing estimate and standard error of the effect of landscape features on rhino presence.

5.3 MODIS comparison

For the comparison between MODIS data and measured temperatures, there was a strong positive correlation between the MODIS satellite data and means the measured iButton data (R^2=0.71, p=2.3*10^{-7}) (figure 27a).

A comparison of temperature difference between the investigated cells, a positive correlation was also found (R^2=0.46, p<0.05) (figure 27b).

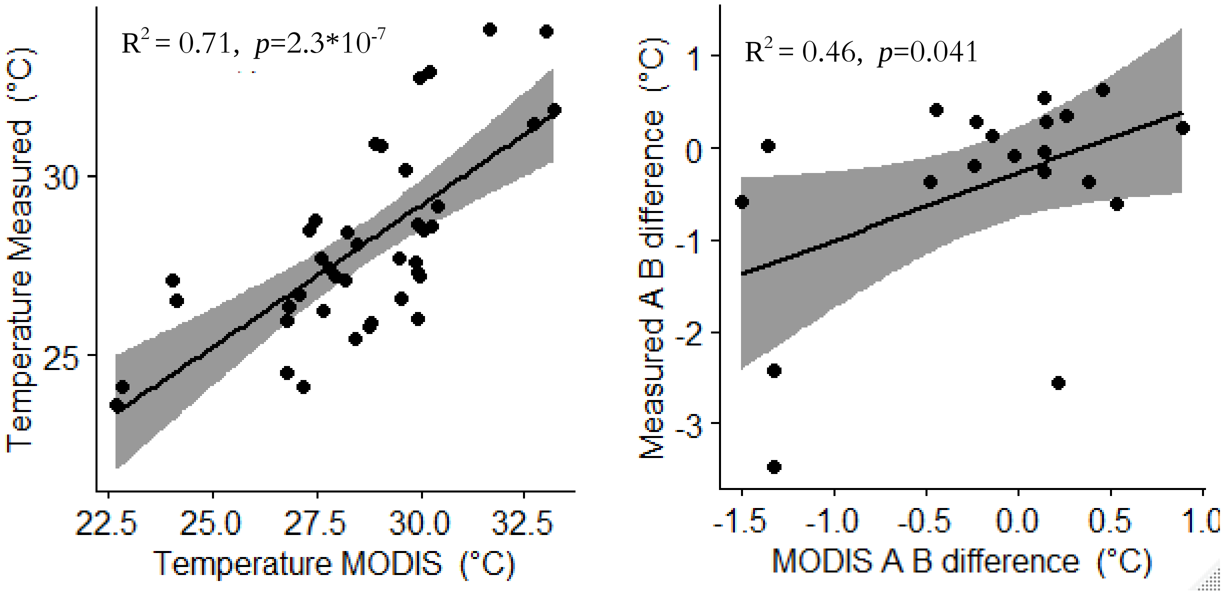

Figure 27a (left) and 27b (right): MODIS satellite land surface temperatures compared with measured iButton air temperature through Pearson correlation. 11a shows direct temperature comparison, 11b shows differences in temperature between cells.

6. Discussion

6.1 Temperature & rhino densities

Out of the environmental variables investigated in this study, only direct overhead canopy cover had a significant impact on local temperature. Based on this result, a denser canopy should result in a cooling of the local environment. The temperature difference here was 0.5 °C. Whether this effect is ecologically significant to rhinos is debatable. At some point, when peak temperatures are reaching a critical threshold for rhinos, this could be the case. Vegetation density also tended to influence temperature ($p=0.085$). I had predicted vegetation density to have a stronger effect, because the dense vegetation shelters against wind, thereby trapping heat. The limited effect of vegetation density on local temperature can be explained by more densely vegetated areas having higher evapotranspiration through plant respiration, decreasing warming of the direct surroundings (Dai et al., 1999). Alternatively, denser vegetation could provide more shade throughout the day. I do not expect the latter to be the case in my experiment though, since overhead canopy closure for the 'dense vegetation' and 'sparse vegetation' groups were similar, and I only used temperatures of when the sun was relatively high in the sky (11:00 – 15:00). The aspect of slopes had no clear effect on temperature, although this was unexpected for the north-south comparison in particular. However, air temperature and near-surface temperature have been found to differ greatly under sunny conditions (Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008), so the effect of slope might be more visible at the surface. This could mean that, temperature-wise, slope has neither beneficial nor adverse effects on large animals, which can help to develop a model without using slope in future projects. Differences in temperatures between east-facing and west-facing slopes could be more prominent when the sun is lower, in the early morning and late afternoon. Solar irradiation will be relatively high in the morning for east-facing slopes, and relatively high in the late afternoon for west-facing slopes. This could still affect animal movement, but not peak temperatures since they occur more around midday to early in the afternoon.

Since none of the variables had an effect on rhino densities or rhino encounter probability between hot and cold days, the null hypothesis that rhinos do not change their distribution based on temperature cannot be rejected. That having been said, some variables do show interesting trends: presence-absence in combination with elevation most prominently so. Expected rhino densities increased with elevation during hot days and decreased with elevation during cold days. The distribution of animals on the hot days occurring more on higher elevations could be explained by higher areas being cooler. However, the effect of elevation on temperature in the area was not measured during the study period due to limited accessibility of appropriate locations for measurements. Previous literature does show that temperature can decrease by 0.4 (for saturated air) to 0.9 (for dry air) on average per 100 meters increased elevation in more mountainous regions (Dodson & Marks, 1997), which does give an indication that the elevational differences of around 130 meters in the study area may affect local air temperature. Like the temperature difference measured between open canopy and closed canopy groups, whether the temperature effect of elevation is ecologically relevant within the study area is debatable. Similar to the effect of elevation on temperature, the effect of dominant vegetation types on local temperature was not measured in the field due to limited accessibility. The effect of water on local temperature was also not included in the analysis. The reason for this is that even though water may play a role in determining local temperature (Fridley, 2009), using a waterhole or wallow to take a (mud)bath will arguably decrease animals' body temperature to a far greater extent than any potential air cooling correlating with water proximity. The fact that rhinos do wallow regularly (Vanschoenwinkel et al., 2011) could therefore make the cooling effect water has on local air temperature redundant for the sake of cooling down during hot spells.

Cells with 'Thicket' as their dominant vegetation type had no rhino sightings. Cells with 'Disturbed or rocky' as their dominant vegetation type had only one rhino sighting for during the hot days, and no sightings during the cold days. 'Thicket', however, was the dominant vegetation type of only 6 cells, (<1% of the study area). Similarly, 'Disturbed or rocky' was the dominant vegetation type only 4 cells. The absence of rhinos in cells of where these vegetation types were dominant could therefore be coincidental.

Although the effect of landscape features on rhino densities did not differ between hot and cold days, the study area as a whole did have a dramatic increase in rhino presence during the cold days as compared to the hot days. The pilot spotted rhinos in 31% of the cells during the 15 coldest summer days, compared to only in 15% of the cells during the 15 warmest summer days. The rhino density per cell where rhinos were encountered was similar between the cold and hot group (on average 0.94 and 0.89 animals per observed km^2, respectively). This higher rhino density in the colder period might partly be caused by the increased airplane coverage per cell (550% and 650% for the hot and cold periods, respectively). Because of this, the graphs presented based on presence-absence data can be expected to show a somewhat higher number of rhino encounters in the cold group since sampling effort was only corrected for in the presence-only data. For the presence-only data this higher visiting frequency is not causing differences, because for every cell this is corrected for by using spotted rhinos per spotted km^2. Since this relatively small difference in airplane coverage between hot and cold days should not cause a doubling in rhino sightings, this higher rhino density in the cold period might indicate that, on a larger scale, rhinos do move driven by temperature. This could be the case, if local temperature differences as measured in this research are indeed not ecologically significant to a rhino while larger regional differences have greater effect on temperature. If Kempiana as a whole is a relatively hot area within the larger region, rhinos might avoid it during the hottest days. On colder days, the animals could select for different ecological features than temperature, for example grass availability. This would explain the greater number of cells containing rhinos during colder days: especially grassy patches will have little canopy cover and thus an even higher temperature within the hot landscape.

Alternatively, this result of fewer rhinos spotted during hotter days could mean that rhinos are more dominantly present under dense canopies in hot periods, making them more difficult to spot. This would correspond with the hypothesis that rhinos will select for shaded places in hot temperatures. Another explanation for fewer rhino sightings during hotter days would be that large mammals are less active during hotter times (Lewis, 1977; Maloney et al., 2005; N. Owen-Smith & Goodall, 2014; Shrestha et al., 2014), which could result in reduced visibility since an active rhino will be easier to spot than one keeping still.

6.2 Limitations to the study

One limitation to this study was the timing of the temperature measurements. Experiments were done in the period March-May 2019, just after the hottest months of December-February. Effects of landscape features on temperature might be more prominently visible in more extreme temperatures. Timing within the study period was also limited, since only midday temperatures (11:00 – 15:00) were used. Early morning or late afternoon temperatures could be affected in a different way by the landscape features investigated in this research.

The resolution at which this research has been conducted is arguably too coarse. In previous research, 50*50 meter grid cells have been documented as being fine scale for the purpose of temperature mapping in topographically complex landscapes (Chung & Yun, 2004; Fridley, 2009). This could mean that the grid cells used in this research – 100 times larger than 50*50m – are fairly coarse for the purpose of temperature mapping. This special resolution might make it hard to find fine-scale relationships between rhino density and the local environment. Canopy cover could vary greatly within each 500*500m cell, for example. The degree of variation is not exposed in these large cells: a cell that has 50% completely open canopy and 50% completely closed canopy, for example, cannot be distinguished from a cell that has a more patchy canopy. Ecologically, these 2 examples can be very different for a rhino in terms of food availability and shade proximity. It might be easier for rhino to spatially respond to high temperatures by moving to cooler patches (Terrien et al., 2011) when shade and food are in close proximity of one another. A higher resolution of rhino locations could therefore have resulted in clearer trends in rhino distribution based on the landscape features used. That having been said, since rhinos were spotted in more grid cells during the colder period, maybe a coarser temperature approximation is exactly what is needed to predict rhino distribution based on temperature.

The temporal resolution causes some of the cells in the study area to be only visited once every few months. This results in missing data for at least part of the days with the most extreme temperatures, both high and low. Especially these highest and lowest temperature extremes could show any effect that temperature has on rhino distribution. In addition to this, the rhino location data was only collected during mornings, leaving rhino locations unknown for the hottest part of the day. Night-time rhino locations are also unknown. A night-time dataset would have been interesting to investigate whether rhino move into different cells when the environment cools down.

6.3 MODIS data

The MODIS data and iButton measurements show a very strong correlation. This indicates that, at least to some degree, surface temperature and air temperature at 160-170 cm height are linked on the 1*1km scale. However, the iButtons and MODIS results differed to some degree in terms of identifying which of the 2 cells was the hottest and which was the coldest. This means that although there was a correlation between the two measurement techniques ($R^2=0.46$), they do not always show the same cell to be hotter than the other. However, since the rhino density is vastly different for the whole of Kempiana when comparing the hot and cold periods, MODIS data might be very useful in predicting rhino densities, precisely because it is measuring temperature on a larger scale. Time constraints made it impossible to include this in this thesis.

6.4 Future research

To add to the question of how rhino distribution changes based on temperature, future research can be conducted using either a smaller grid cell size or larger grid cell size. The data on landscape features used in this report were originally available in 30*30m grid cells, which more accurately represent the environmental factors that are present in each cell than the upscaled 500x*00m grid cells used here. To use a smaller grid cell size more precise rhino location data (i.e. a location at a more exact location) is also needed. A dataset based on locations provided by GPS trackers, for example, could greatly increase both the temporal and spatial resolution of rhino locations. This could help identify how rhinos move in extreme temperatures based on very local environmental factors such as proximity to shade and water. Rhinos might move to a nearby shaded patch are during the hottest part of the day that cannot be identified on a larger scale, for example.

Alternatively, in the case of a larger grid cell size, the MODIS dataset could be used to map areas with consistently higher or lower temperatures. Based on that, hypotheses can be tested that explain those largescale spatial differences in temperature. On a larger scale, elevation and composition of dominant vegetation species might have a larger effect on temperature and/or rhino habitat choice, for example.

Another thing that could be looked into is the length of warm periods as an explanatory variable for rhino densities in certain environments. As was mentioned before, big animals may experience relatively little effect from short peak temperatures due to their high volume giving them a temperature buffer. If only longer periods of extreme temperatures are used, a stronger correlation could be found.

Originally, the plan for this research was to include elephant distribution as well as rhinos. Due to limited data availability, this was not included in the analysis. Future efforts might do well to include both species. This way, contrasting results in distribution of the 2 species could indicate behavioural or dietary preferences rather than temperature related distribution.

7. Conclusion

Based on the results presented in this report, local midday air temperature is 0.5 °C lower where overhead canopy is providing shade as opposed to conditions without overhead canopy. Aspect and vegetation density did not affect temperature. Rhino distribution differences between hot and cold periods were not significantly correlated to any of the investigated environmental variables.

The null-hypotheses that temperature varies based on environmental variables other than direct overhead canopy and that rhinos do not move according to temperature cannot be rejected based on this research.

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