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Analyzing the drivers behind the distribution patterns of the southern white rhinoceros across the South African savanna landscape

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SOUTHERN AFRICAN
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“ The rhinoceros is accounted the second wonder in Nature [after the elephant]; being a beast in every way as admirable for its outward shape and greatness, as also for its inward courage, disposition and mildness ”

– Prose of 1684, author unknown

Foreword

I promise that no rhino were harmed in the making of this thesis. I do hope however, that the results found in this thesis are able to inspire others to continue studying the white rhino so we can together help academics, conservationists, rangers and everyone else protect this magnificent species from going extinct today and in the future.

That being said, I would first of all like to thank my supervisor and first reader, Joris Cromsigt for giving me the opportunity to travel to South Africa to learn and experience first hand the extent of the current rhino poaching crisis. Thank you for being enthusiastic, for inspiring me and pushing me to do beyond what I thought I was capable of.

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Madelief Verdaasdonk,
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Summary

The increase in demand for ivory has in recent years triggered an upsurge in the number of white rhinoceros poached in South Africa. This has not only altered the conservation status of the rhino to near threatened but also gravely threatens the savanna ecosystems in which they thrive. As a result, there is an urgent need to implement more effective conservation strategies to help protect the rhino from poaching and prevent a further demise in its conservation status. It has been suggested that to achieve this a better understanding is needed on the environmental factors that drive rhino distribution in the landscape. This will allow for conservationists to anticipate where the rhino are likely to be in the landscape and adjust management and protection plans accordingly. This research makes a preliminary analysis on understanding these dynamics with a select few indicators including vegetation cover, waterholes, wallows, temperature, precipitation, canopy cover, fire occurrence, and interaction with the African elephant. Through the use of four-year rhino distribution data this research is able to tentatively quantify for potential relationships to exist between rhino and various environmental indicators. By including an interaction effect of seasonality allows to further test how strongly each variable influences rhino distribution per season. The results show for NDVI, canopy cover, waterholes, precipitation, temperature and fire with a 6-month delay to be potential drivers of rhino distribution in the landscape. Nevertheless, no significant interactions were found to exist between rhino and wallows in the landscape. In addition, a strong interaction was found between rhino and elephants in the landscape, and especially between rhino and elephant bulls in the summer season. Although some clear relationships are found to exist, it is not possible yet to make sound conclusions due to a variety of limitations associated with this research including but not limited to the influence of confounding effects and the lack of sufficient data. While it remains to be further tested if the defined indicators truly effect rhino distribution in the landscape, this research does provide empirical evidence on potential relationships that may exist and should therefore be seen an exploratory study on which other research should be based.

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1. Introduction

1.1. *The rhino poaching crisis*

There is no doubt that the sixth mass extinction on Earth is underway. While life on Earth has been marked with several periods of mass extinctions before, where more than 75% of species disappeared, the sixth one is notably different. For the first time extinction is being driven by humanity instead of by natural disasters. At the current rate, species are going extinct 100 times faster than any period before humanity (Ceballos et al., 2015; Estes et al., 2011). Threatened by climate disruptions, population growth, pollution, urbanization, hunting and poaching, this extinction period has been characterized specifically by the loss of larger mammals and apex consumers (Estes et al., 2011).

Apex consumers are located at the top of the food chain and are therefore largely immune to any non-human predation (Cromsigt & te Beest, 2014; Landman, Schoeman, & Kerley, 2013; Owen-Smith, 1988). This means that only the resources available on land regulate their survival. Megaherbivores, species with a body mass greater than 1000kg are characterized as being apex consumers largely because of their ability to tolerate lower-quality food and dominate biomass in the landscape (Owen-Smith, 1988). It has therefore been suggested for megaherbivores to play an important role in the functioning of ecosystems especially because they can alter the vegetation structure to benefit smaller mammals (Cromsigt & te Beest, 2014; Landman et al., 2013; Owen-Smith, 1988; Waldram, Bond, & Stock, 2008). The square-lipped white rhinoceros (*Ceratotherium simum simum*), from here on referred to as white rhino, is an example of a megaherbivore, potentially acting as a major driver in the functioning and structure of savanna ecosystems in Southern Africa (Cromsigt & te Beest, 2014). Specifically, according to Waldram, Bond and Stock (2008), the wide mouth of the white rhino allows it to be an efficient grazer, as it prefers to consume shorter grasslands to taller ones. By maintaining patches of short grass lawns, the white rhino acts as a ecosystem engineer by creating habitats for other species (Waldram et al., 2008).

There are two subspecies of white rhino, the northern and southern. The northern white rhino (*Ceratotherium simum cottoni*) previously widespread in countries including Uganda, Chad, Sudan and the Central African Republic has gone extinct from the wild due to excessive hunting and poaching (Emslie, 2011a). The southern white rhino on the other hand remains in the wild, albeit having been given a near-threatened status by the International Union for the Conservation of Nature (IUCN) (Emslie, 2011b; Ripple et al., 2015). South Africa currently has the largest remaining population of the southern white rhino at approximately 20,000 individuals (Emslie, Miliken, & Talukdar, 2013). However, due to an increase in organized crime in recent years, it is likely for the white rhino in the near future to experience a downgrade in its conservation status (Emslie, 2011b; Ripple et al., 2015).

Throughout history, the survival of the white rhino has been repeatedly susceptible to hunting and poaching, so much so that in the late 19th century only a handful of species remained (Rookmaaker, 2000). Due to the implementation of effective conservation strategies and re-introduction programs, the white rhino was brought back from the brink of extinction (Rookmaaker, 2000). Yet, despite this success story, the outcome from the 16th meeting on the Convention of the International Trade of Endangered Species highlighted that since 2010, the survival of the white rhino is once again threatened by increased occurrences of poaching (Emslie et al., 2013). To put into perspective, in 2010 there were 122 total recordings of rhino poached. By 2013, this number had skyrocketed into the thousands (Büscher & Ramutsindela, 2015; Emslie et al., 2013). This increase is particularly attributed to the surge in demand for the rhino horn in Asian markets, where it is prescribed as traditional medicine able to cure a range of diseases, from hangovers to cancer (Hanley, Sheremet, Bozzola, & MacMillan, 2017). Specifically, in Vietnam, possessing white rhino horn is seen as a symbol of wealth for the middle-class (Hanley et al., 2017). In order to curb the increase in demand for rhino horn more effective conservation strategies are needed especially ones that cannot be undermined by poaching. To do this, a greater understanding is needed not only on the distribution of the white rhino in the

landscape but more on what natural factors drive their distribution. Enhancing this understanding will not only provide more accurate data for conservation practitioners to base decisions off of but it will also allow to determine which areas are in need of greater protection. Moreover, understanding rhino distribution in one area can help towards making predictions on distribution in similar regions for which little to no data is available (Lawler, Wiersma, & Huettmann, 2011)

1.2. Natural drivers behind rhino distribution

Evidence for key drivers influencing rhino distribution has been scarce; partly because collecting extensive data on white rhino locations is often time consuming and costly. The majority of studies have thus far focused on perceiving the behavior of a handful of rhino across small spatial scales. Nevertheless, analysis of these observations allows for some preliminary conclusions to be drawn on the potential drivers behind white rhino distribution.

Upon studying the behavior and habitat selection of fifteen white rhino in Kruger National Park (KNP), Pienaar (1994) found for the white rhino to exhibit a high selectivity in habitat requirements. Rhino are a water-dependent species meaning they require regular access to surface water and therefore prefer habitats where the annual rainfall is greater than 400mm. It was also found for there to be an avoidance of both landscapes where the woody vegetation is very dense and landscapes which are devoid of any canopy cover (Pienaar, 1994). Jordaan et al. (2015) reaches similar conclusions when observing the habitat use of the white rhino in the Free State Province in South Africa. The authors found for the three most inhabited grassland landscapes to include those that have at least some degree of canopy cover (Jordaan, Brown, & Slater, 2015). A preference is given towards habitats with at least some degree of tree coverage as it can help the white rhino deal with thermoregulatory processes, including protection from extreme temperatures and cold winds (Jordaan et al., 2015).

Vegetation cover in terms of the consumption of grasses is also found to be a driver behind the distribution of the white rhino and is strongly correlated to the wet and dry season (Owen-Smith, 1988; Shrader, Owen-Smith, & Ogutu, 2006; White, Seaisgood, & Czekala, 2007). When observing rhino in the Hluhluwe-iMfolozi Park (HiP), Owen-Smith (1988) found for the grassland type on which the white rhino grazes to shift depending on the season. During the wet season, the rhino were found to feed on shorter grasslands, whereas during the dry season they shifted towards grazing on grasses situated in more wooded areas (Owen-Smith, 1988). According to Shrader and Perrin (2006), the shift in grassland preference is for the most part dependent on the prevailing weather conditions. When for example, an area has above-average rainfall no difference has been recorded on there being an exact shift in grassland preference. This is likely attributed to the fact that when rainfall is abundant, sufficient vegetation can grow throughout the year and no dietary shift is needed by the white rhino to compensate (Shrader & Perrin, 2006).

Fire in savannah grasslands has also been found to be a potential driver behind white rhino distribution. Specifically, fire and white rhino grazing interactions work whereby once a fire has taken place, rhino have been recorded to move to these areas and graze on the newly emerged grasses, which tend to be much more nutritious than other grasses (Archibald, Bond, Stock, & Fairbanks, 2005). Further some literature on the effect of fire in savannah landscapes has illustrated that it takes about 3-8 months for plant density to increase after a fire has taken place, depending on the intensity of the fire (Morgan, 1999). This means rhino are likely to shift their distribution to these areas a couple months after a fire has taken place.

Finally field observations have reported for the white rhino to possibly alter its distribution contingent on the presence of the African elephant (*Loxodonta africana*). Specifically, interactions between the bull (male) elephant has in the past resulted in the mortality of the white rhino (Slotow et al., 2000; Slotow & van Dyk, 2001). This is predominantly the result of an increase in aggressive behavior or musth state which arises within young male elephants due to a lack of hierarchal support from older males (Slotow & van Dyk, 2001). In addition, tensions between the

species have also been noted to arise when they have to share resources such as waterholes which often results in the elephant chasing away the white rhino (Landman et al., 2013).

2. Knowledge Gap

From the literature it becomes clear that up to now most long-term studies have focused predominantly on understanding the behavior or habitat selection of a small sample of white rhino in various landscapes. To my knowledge, no previous studies have focused exclusively on understanding the drivers behind rhino distribution nor modeled the influence of these drivers acting at the same time on rhino distribution in a landscape. In addition, the majority of the research available on white rhino comes from HiP located in the KwaZulu Natal province in South Africa. Unlike the greater Kruger area on which this research is based, HiP is a smaller, very fertile and fenced national park with the highest density of rhino per square kilometer. The greater Kruger area on the other hand is unfenced, much bigger, is significantly less fertile and has far fewer rhino present per square kilometer. As a result, it may be that rhino have to distribute across greater distances to obtain favorable conditions than what is documented in HiP. Due to the differences in landscape configuration between parks in South Africa, it becomes of interest to focus efforts on different areas such as the greater Kruger to obtain a more holistic indication on what drives rhino distribution in different landscapes. In addition, considering the environmental drivers are scale dependent, understanding rhino distribution across time and space will allow for conservation efforts to be geared towards areas found to be most essential for protecting the white rhino.

3. The Theoretical Framework

The objective of this research is to investigate the extent to which defined environmental indicators influence white rhino distribution in the greater Kruger National Park area. The indicators that are examined are the ones deemed most important from the literature above. It should be noted these are just a subset of the many drivers influencing rhino distribution and the drivers are thus not limited to the ones presented here. The indicators outlined in figure 1 include temperature, precipitation, fire occurrence, vegetation cover, waterhole and wallow presence, canopy cover, and interaction with elephant bulls and with elephant herds. A hierarchical model is presented because temperature and precipitation have both a direct and an indirect effect on white rhino distribution. Indirectly, temperature and precipitation can impact the distribution of vegetation across a landscape as well as influence the occurrence of fire, the location and frequency of waterholes and wallows and the degree of canopy cover. Directly, certain degrees of temperature or volumes of precipitation can be more preferred by the white rhino and subsequently influence its distribution. Moreover, density will be used as a proxy for rhino distribution in the landscape as it allows to measure the total number of a species present in a given landscape at a defined spatial and temporal scale (Boulinier, Nichols, Sauer, Hines, & Pollock, 1998; Keiter et al., 2017)

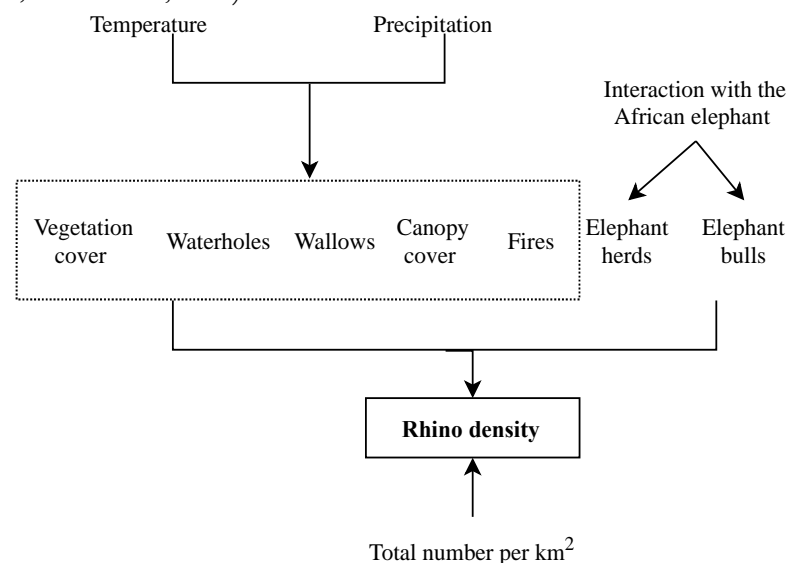


Figure 1: Conceptual framework on the environmental indicators used in this study

4. Research Questions

Based on the theoretical framework, the following main research question is proposed:

To what extent do the defined environmental indicators influence the density of the white rhinoceros across the South African savanna?

In order to fully ascertain the relationship between each individual driver and rhino density, the following sub-questions are proposed:

Sub-question 1: To what extent does rhino density relate to changes in vegetation cover, canopy cover, waterholes, wallows, precipitation, temperature, and fire occurrence?

Sub-question 2: To what extent does rhino density relate to the density of the African elephant bulls and African elephant herds?

Hypothesis

Sub-question 1: Research question two is associated with multiple variables, each which will be analyzed for their possible influence on rhino density:

1. *Temperature:* Areas (measured per km²) with consistently high average temperatures are expected to have lower rhino densities because the species there will struggle more in maintaining an ideal body temperature. The influence of temperature on body heat is expected to have a greater influence in the summer than the winter.
2. *Precipitation:* Areas (measured per km²) that have a high volume of total rainfall are expected to have higher densities in rhino because they are water dependent. Precipitation is expected to play a lesser role during the wet season.
3. *Vegetation cover:* Rhino density will be higher in areas that contain a certain bandwidth of NDVI values in the landscape; the values are expected to be around 0.5.
4. *Canopy cover:* It is expected for the white rhino to avoid areas, which overall have high canopy covers, such as areas (measured per km²) with more than 50% tree cover.
5. *Waterholes:* A higher number of waterholes present per km² is expected to correlate with a higher rhino density.
6. *Wallows:* Areas with a greater number of wallows present per km² are expected to have an overall higher white rhino density.
7. *Fire Occurrence:* Rhino density is expected to increase in those areas a couple of months after a fire has taken place.

Sub-question 2: African bulls will have a greater impact on rhino density, where an increase in elephant bulls in an area will result in a decline in rhino density. Regarding herds it is predicted that the greater the herd size, the lower the rhino density per km².

5. Methodology

5.1. Study region

The study area for this research is located in the greater Kruger region in the Mpumalanga province in South Africa. As seen in figure 2, the study region, shown in pink is approximately 1,440 square kilometers and covers multiple game reserves including Kruger National Park, Timbavati game reserve, Thorny Bush private game reserve and the Klaserie private nature reserve. As mentioned, the study region is an open system without any fencing, allowing for species to move between the different game and nature reserves. This means that this research will not only deal with rhino inside the study area but also rhino moving in and out of the region.

The climate is divided into a wet and dry season. The wet season lasts from November to April and coincides with the summer season. The dry season runs from May to October and coincides with the winter season. Although all four seasons occur in South Africa, it is not uncommon for the spring and the autumn to be very short and thus more of an extension of the summer and winter seasons. Nevertheless, the meteorological seasons run opposite to those in the Northern Hemisphere meaning spring runs from September to November, summer from December to February, autumn from March to May and winter from June to August.

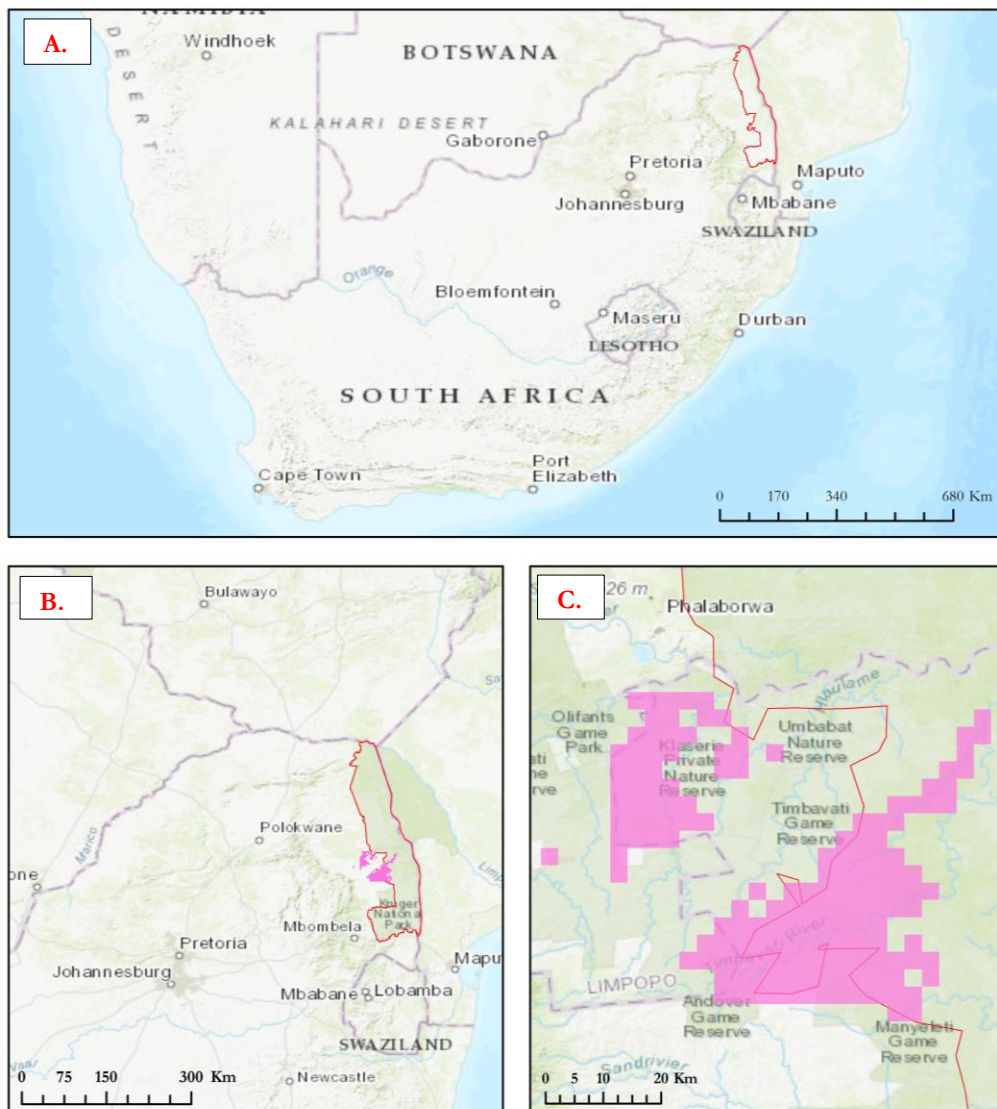


Figure 2: Panel A illustrates South Africa and the location of Kruger National Park as outlined in red. Panel B zooms in on the study area in pink and where in Kruger it is located. Panel C focuses on the study region and the reserves in the Greater Kruger region it encompasses.

5.2. Data providers

Table 1 briefly outlines the data structure including data type, data provider, sampling method, and temporal and spatial resolution for each variable that was outlined in the conceptual framework in figure 1. Section 5.4 gives more detailed information on how the data for each variable is collected and how it is analyzed.

Table 1: Overview of the type of data acquired for all environmental predictors indicating data type, data provider, sampling method, temporal resolution and spatial resolution

Environmental Variable	Data Gathering				
	Data type	Data provider	Sampling method	Temporal resolution	Spatial resolution
White rhino	Point data	SAWC ¹	Fixed wing airplane	Median: 9 days Mode: 7 days	250m
Elephant	Point data	SAWC	Aerial count using fixed wing airplane	Mean: 20 days SD: 48.63 days	250m
Fire MODIS	Point	FIRMS ² NASA	Satellite imagery	Once per day	1 km
Fire VIIRS	Data		Satellite imagery	Once per day	375 m
NDVI for vegetation cover	Raster grid	LANDSAT 7 LANDSAT 8	Satellite imagery	Seasonal	30 m
Waterhole & Wallows	Point data	Google Earth	Satellite imagery	07/09/2016	1x1 km ²
Canopy Cover	Raster grid	Google Earth Digital Globe	Satellite imagery	03/12/2015	1x1 km ²
Temperature	Point data	Wunderground historic archive	Weather station	Monthly average	1x1 km ²
Precipitation	Point data	SAEON ³ SANParks ⁴	Weather station	Monthly sum	1x1 km ²

¹SAWC: South African Wildlife College

²FIRMS: Fire Information for Resource Management System

³SAEON: South African Environmental Observation Network

⁴SANParks: South African National Parks

5.3. The spatial and temporal extent of research

Determining the spatial extent for this research is difficult to do because each environmental variable influences white rhino distribution at a different scales. Climate for example does not change significantly across small distances but instead governs the distribution of species at more continental scales (Fournier, Barbet-Massin, Rome, & Courchamp, 2017). The proximity of waterholes on the other hand is more likely to drive the distribution of a species at smaller spatial resolutions. However, due to time constraints, this research is only able to look at the effect of the environmental drivers at one spatial scale. As a result, whilst it is unlikely for precipitation and temperature to alter significantly at small resolutions, it still is decided to use the smallest resolution possible to get the most detailed results. Based on the spatial resolutions presented in table 1, it becomes clear that the minimum size at which each environmental variable can be analyzed is at a scale of 1x1 km².

The temporal resolution used for analysis in this research is based predominantly on three factors. First, the temporal time scale is dependent on the period for which the data is available. The white rhino location data is provided by the Southern African Wildlife College (SAWC) and is recorded using a fixed-wing airplane. On average, the measurements are taken every 9 days from February 2014 until February 2018. Second, as seen in figure 3 the flight paths taken over the study area to collect rhino and elephant data vary considerably throughout the landscape, where some cells are flown over more frequently than others. With a temporal scale of 1 month the majority of cells are at least flown over twice allowing for a difference in distribution to be measured. Third, the distribution of the while rhino and elephant may vary in the landscape on a day-to-day basis, but it takes time to detect noticeable changes in a majority of the environmental variables. For example, significant variation in vegetation cover or temperature is unlikely to

occur at very fine temporal scales. As a result, analyzing the data on a monthly basis is expected to result also in detectable changes in the environmental variables. Nevertheless, as further explained in section 5.4, it should be noted that for some variables such as vegetation cover, canopy cover, waterhole and wallows the data was not available on a monthly basis.

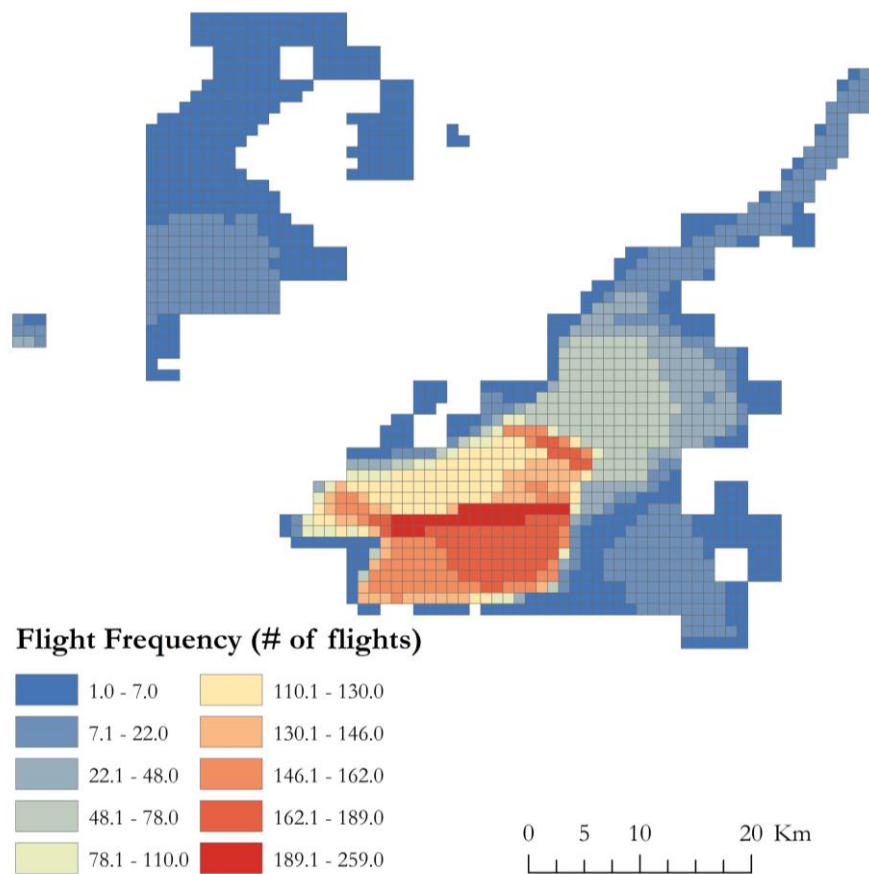


Figure 3: Flight frequency or total number of flights taken across each cell from February 2014 – February 2018

5.4. Data analysis

The aim of this section is to provide a more comprehensive overview on the environmental variables and how the data was transformed to obtain aggregate values for each cell each month.

5.4.1. *White rhino and African elephant census data*

As mentioned, the data on the distribution of the white rhino and the elephant was made available by the SAWC from February 2014 until February 2018. The sampling method used includes aerial counts from a fixed wing airplane, that covers the study area using different flight path transects. The pilot flies at an altitude of approximately 500 meters and has a visibility of 250 meters on either side of the plane. The data comes in the form of GPS points giving not only information on the location of a species in the landscape but also on how many rhino or elephants are present at a particular GPS point. Since the data is given in a point format, a ‘point-to-grid’ method is employed to translate the data to the 1x1 km² grid. This type of mapping allows to overlay point observations on a defined grid and determine the values for each individual cell (Graham & Hijmans, 2006). The total species density for a grid cell is calculated by adding the total recorded observations for each species per month.

Nevertheless, as seen in figure 4 a potential error arises with the fact that the sampling frequency used to collect the species distribution data varies considerably throughout the study region. The overall median revisit time per cell is around 9 days, but this is linked with an overall standard deviation of 48.63 days. In addition, an observational error arises from the flight path transect

chosen by the pilot, which causes some cells to have a higher total coverage than others. For example, if in cell A (figure 4), two white rhino are spotted then one can be fairly sure only two species are present as the cell has a coverage of around 100%. Cell B on the other hand, tells a different story. If two white rhino were spotted in this cell, it cannot be certain that all species were recorded because only a small percentage of the cell is flown over. As a result, a correction factor is added to the data whereby flight path area coverage is taken into account when calculating total species density per grid cell per month. The total coverage is calculated by adding the flight path area including the 250 meters the pilot can see on either side of the plane, as illustrated by the blue buffer. Thus, the final monthly rhino and elephant count for each cell is calculated by dividing the total species count per cell by the average flight path area per month for each cell.

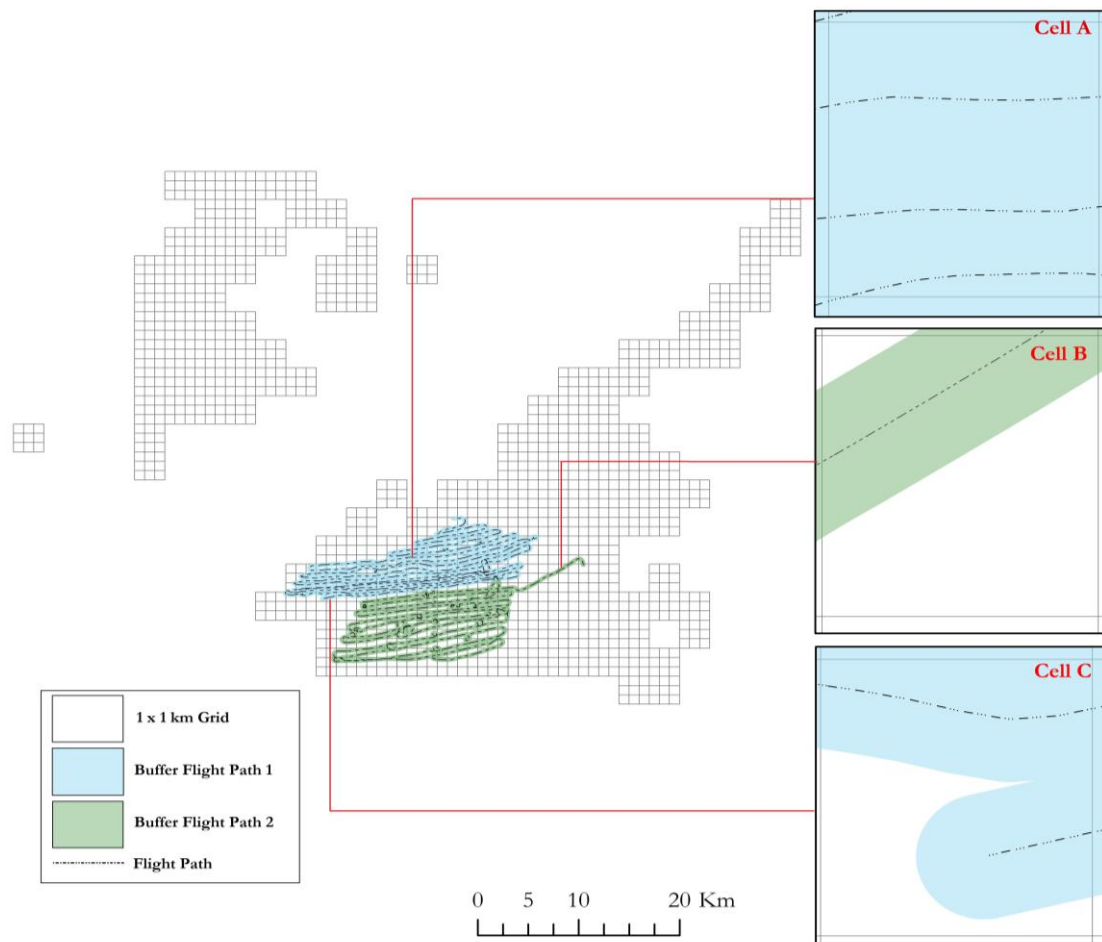


Figure 4: Example of flight transects used by the pilot to cover the study region. The blue and green lines subsequently represent the buffers of the 250 meters the pilot can see from the airplane. This buffer is used to quantify the total coverage in a cell.

5.4.2. Fire Occurrence

Data on the location and frequency of fires in the landscape is a combination of recordings from the Moderate Resolution Imaging Spectroradiometer (MODIS) and the Visible Infrared Imaging Radiometer (VIIRS). Both satellites record near real time active fire data, the former has a spatial resolution of 1km, the latter of 375m. It was decided to combine the data from both satellites as MODIS and VIIRS each detect fires missed by the other. The data is given in GPS point format, geo-referenced to an area in the study region. Moreover, each fire data point is accompanied with confidence intervals set either set to low, normal or high. Fire data with low confidence intervals were omitted from the data because they are typically sun glints assumed by the satellite to be a fire.

5.4.3. Vegetation Cover

The normalized difference vegetation index (NDVI) is a graphical indicator reflecting the health and density of vegetation. Some studies have suggested that an important link exists between NDVI and species distribution, whereby the chosen home ranges of some species is positively correlated with higher NDVI values (Pettorelli et al., 2005, 2011; Zinner, Peláez, & Torkler, 2002). For example, the home range of the grivet monkey in Eritrea shows to have overall higher NDVI values as compared to neighboring areas (Pettorelli et al., 2005; Zinner et al., 2002). In addition, a study analyzing the relationship between the NDVI and the African elephant in the savanna found for significant changes to arise in the density of the elephant in areas which had higher primary productivity and thus NDVI values (Duffy, Pettoelli, Duffy, & Pettoelli, 2012). As a result, the NDVI is used in this research as a proxy for vegetation cover and is calculated from LANDSAT satellite imagery by using the visible red and near infrared (NIR) reflectance bands. These reflectance bands are used because vegetation typically absorbs visible blue and red light and reflects green visible light and NIR. By using the equation,

$$\frac{(\text{NIR light} - \text{Red light})}{(\text{NIR light} + \text{Red light})}$$

an indication is gained on the health of the vegetation and how this changes overtime (Pettorelli et al., 2011). NDVI values range between -1 and +1. Areas with dense and healthy vegetation such as forests have NDVI values closer to +1, whereas areas with no vegetation such as barren rock or deserts have NDVI values closer to -1 (Pettorelli et al., 2005, 2011). The LANDSAT satellite imagery used in this study is available only on a seasonal basis meaning the months that fall into the same season will have the same NDVI value. To get a value per grid cell per month, the total NDVI values present in a cell are averaged.

5.4.4. Waterholes and Wallows

Information on waterhole and mud wallow locations is provided by the SAWC, and obtained from Google Earth satellite imagery. To ensure the validity of the waterhole and wallow locations, some have been visually verified in the field. Nevertheless, due to high-resolution satellite data not being available for all four years, it is only possible to obtain data for one month of one year, namely September 2016. Thus, the water layer data incorporating waterhole and wallow locations is definitive, meaning there is no change in either for the entire study period. The monthly values therefore stay the same for the entire study period and are calculated by taking the sum of all waterholes or wallows present in a cell.

5.4.5. Canopy Cover

The Tree Cover Mapping (TCM) tool developed by the U.S. Geological Survey is used to measure canopy cover in the study area (Cotillon & Mathis, 2016). As seen in figures 5-7, the tool creates two grids; the first is a systematic grid in this case defined to be 1x1km² in size. The second is a sample grid consisting of 100 red points placed at regularly spaced intervals, which defines the precision and resolution of the output map. Tree cover per grid cell is calculated by adding all the red points which land on a tree giving a value out of a 100 and hence a percentage of cover. Again due to lack of high-resolution satellite imagery, only one layer representing canopy cover is created for the entire study period. Hence, the monthly cell value for each year is the percentage canopy cover calculated for each cell.

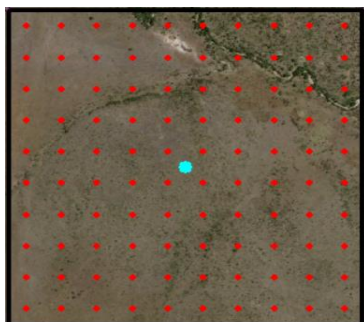


Figure 5: < 15% canopy

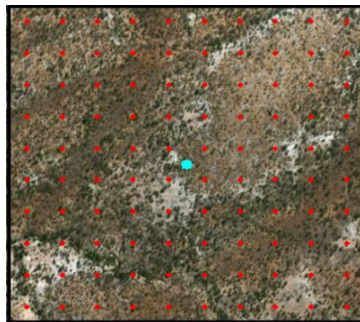


Figure 6: between 15 – 50% canopy cover

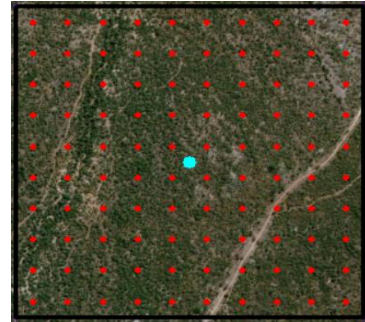


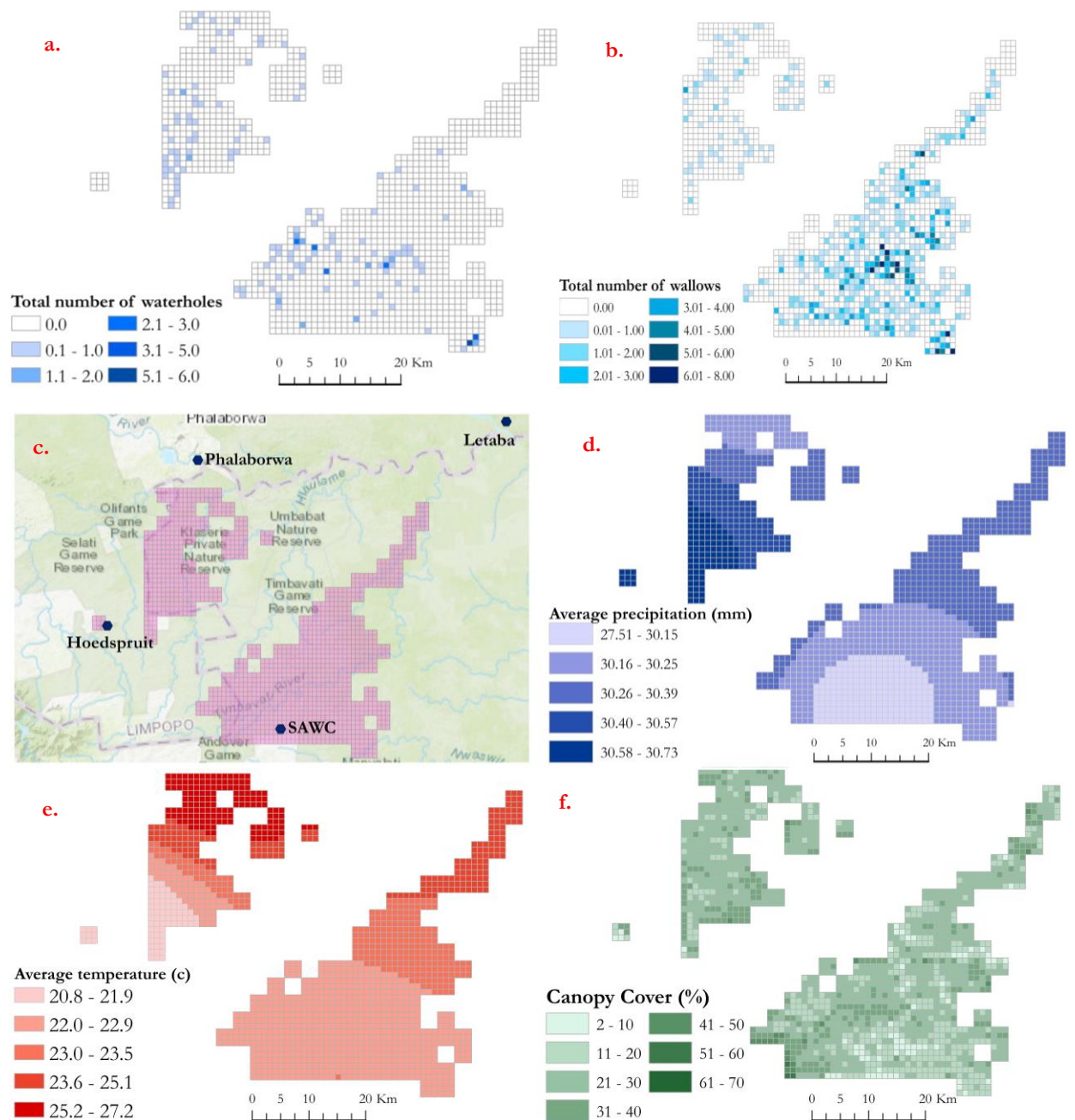
Figure 7: > 50% canopy cover

5.4.6. Temperature and Precipitation

Temperature and precipitation data is collected from a variety of sources. The SAWC is the only weather station located within the study region for which temperature and precipitation data for the entire time period is made available. The rest of the data comes from weather stations just outside, as shown in figure 8c. Further, data for some months is missing due to technological problems with the weather stations and is regarded as NA within the data. In order to get an indication on what the temperature and precipitation may be like within the study region, the data is interpolated. As a result, the value per grid cell per month for temperature is the interpolated monthly average. For precipitation it becomes the interpolated total volume per cell per month.

5.4.7. Distribution of the data in the study region

In order to get a more comprehensive view on the distribution of the data in the study region, a series of maps are generated which illustrate the four-year average value for each environmental indicator for each cell, seen in figure 8a – 8h.



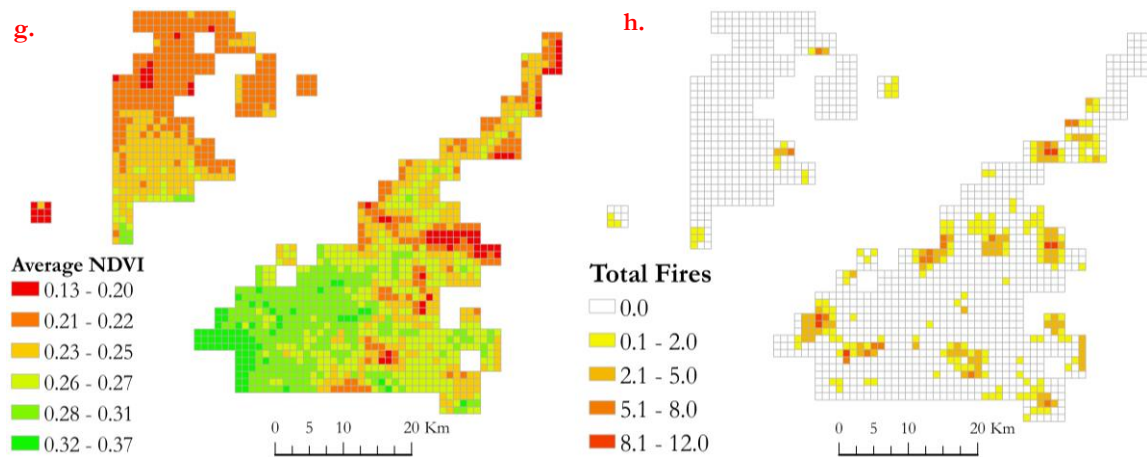


Figure 8: Figures 8a – 8h depict the total and average values for each indicator from 2014 – 2018. 8a illustrates the total number of waterholes present in each cell and 8b illustrates the total wallows present per cell. 8c shows the locations of the four weather stations used to obtain the interpolated rainfall and temperature data. These locations include the SAWC, Hoedspruit, Letaba and Phalaborwa. 8d and 8e respectively show the interpolated average precipitation (mm) and average temperature (°C) data from 2014 until 2018. 8f depicts the total canopy coverage (%) per cell. 8g conveys the average NDVI per cell from 2014 – 2018. Finally, 8h exemplifies the total number of fires that took place in each cell over the four-year study period.

Figure 8g illustrates the average NDVI value for each cell across the four-year study period. However, by taking the average NDVI, the results become oversimplified when in fact NDVI values tend to alter significantly between the dry and wet season. As a result, figure 9 displays a more holistic overview on how NDVI alters between the wet and dry season every year.

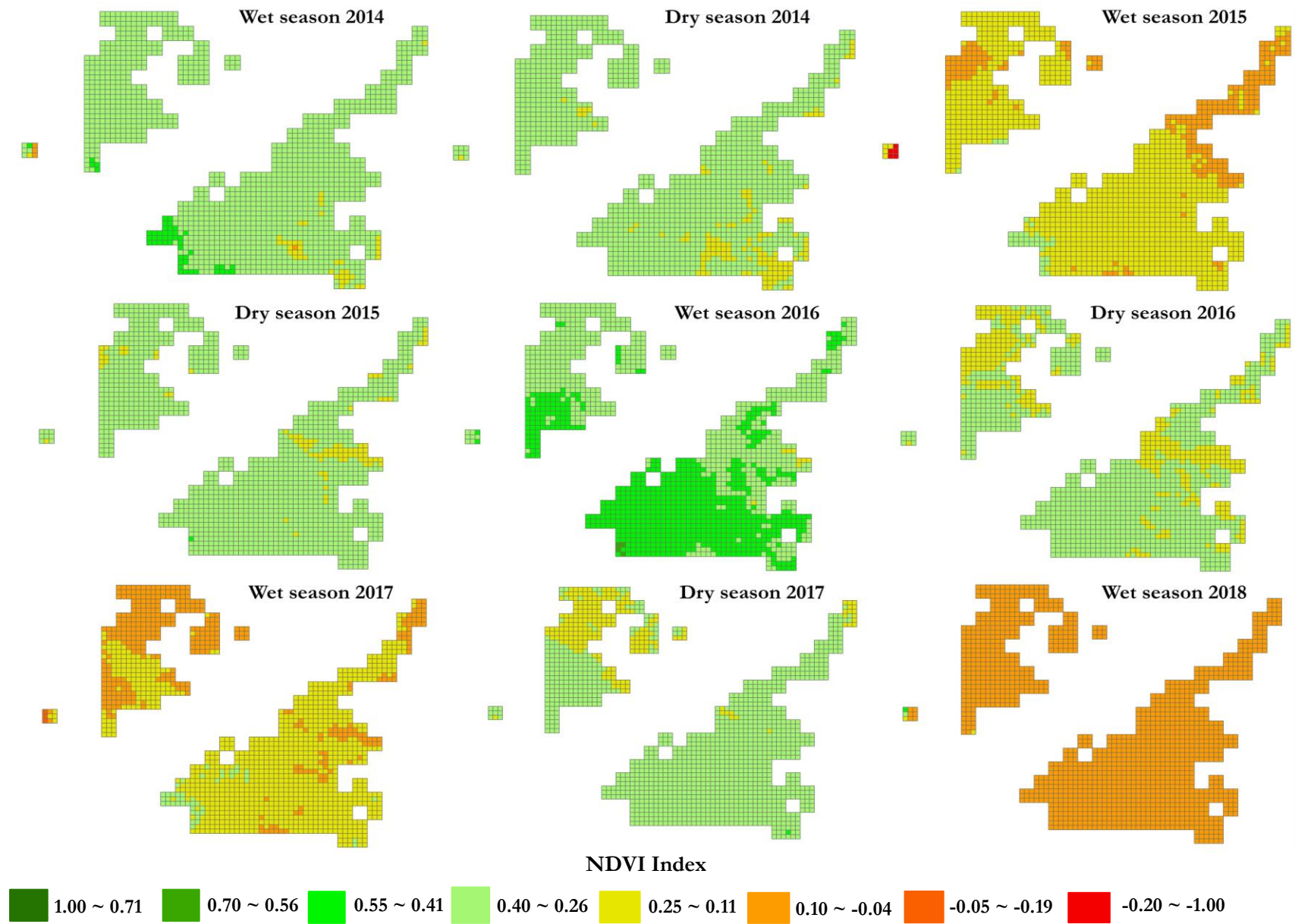


Figure 9: The average NDVI values for the dry and wet season from 2014 until 2018.

5.5. Statistical analysis

The statistical analysis in this research is comprised of a variety of steps. First, a preliminary analysis is undertaken to understand the distribution of the data using scatterplots. Second, a correlation matrix is devised to evaluate both the association between rhino density and each environmental indicator and the relationship between the indicators themselves. In addition, it is believed for a positive bias to potentially exist with the rhino count data that has been adjusted for flight path area. This positive bias assumes that the greater the area that is flown over, the more rhino is expected to be present, which may influence the overall statistical results. To ensure this will not be the case, it is verified through linear regression models whether it is better to use the original non-adjusted rhino count or the adjusted for flight path area rhino count. Moreover, multicollinearity tests are executed in order to ensure that all variables can be used within the mixed-effect models.

5.5.1. Scatterplots and quadratic relationships

There is a potential for polynomial relationships to exist between rhino density and some environmental indicators. For example, the literature establishes that certain NDVI values correspond with more favorable habitats for species. As a result, it is hypothesized for an optimum range of values to correlate more strongly with rhino density than others. This may indicate for a potential quadratic or parabolic relationship to exist rather than a linear one. This will be verified from the scatterplots identified previously. If a quadratic relationship is found to exist between rhino density and an environmental indicator, then for use in the statistical models, the environmental indicator will have to be matched with a new variable that is the quadratic term of the original values. For example, if NDVI indeed has a quadratic relationship with rhino density, then the original value $NDVI$ will be matched with the quadratic $NDVI^2$.

While the results from the scatterplots may identify for potential quadratic relationships to exist, it further becomes necessary to verify that they actually provide for a better model fit. The corrected for small sample size Akaike's information criterion (AICc) tool is implemented to measure the information lost (Akaike, 1988). In other words, a model with a better fit will show to have a minimum loss in information and the AICc score will be the smallest (Akaike, 1988; Snipes & Taylor, 2014). Therefore, the model with the lowest AICc, whether including or excluding the quadratic will be used in the model. It is important to select the correct variables for use in the models as problems of under and over fitting easily arise (Snipes & Taylor, 2014). Under-fitting occurs when the variables in the model do not portray true variability (Snipes & Taylor, 2014). Over-fitting arises when too many variables are removed and the model is oversimplified (Snipes & Taylor, 2014).

5.5.2. Multicollinearity tests

It is further necessary to test for multicollinearity between variables. Multicollinearity arises when two explanatory variables, in this case the environmental indicators, are related to one another. If two variables are collinear and are left in the model it will create misleading model results (Crawley, 2007). In other words, the problem of confounding effects arises where highly correlated variables distort the effect on the response variable (i.e. rhino density) and the model will not be able to detect which variable is creating the effect on the response variable (Johnston, Jones, & Manley, 2017).

Multicollinearity is tested using the variance inflation factor (VIF) tool, which tests by how much the variance in a model is inflated among the environmental predictors (Murray, Nguyen, Lee, Remmenga, & Smith, 2012). The general rule of thumb is if the VIF value is greater than 4, then multicollinearity may exist and further investigation is needed. If the found VIF value is greater than 10, then multicollinearity unquestionably exists and needs to be corrected (The Pennsylvania State University, 2018).

5.5.3. Mixed-effect models

The second part of the statistical analysis includes computing mixed effect models within r-script software. This thesis proposes the use of these statistical models because they deal with the issue

of repeated measurements. Within this research, the 1x1 km² grid cells are being repeatedly measured on monthly basis for four consecutive years. The repeated measurement causes the cells to not be truly independent from one another. If the problem of pseudo-replication is not dealt with then the outcomes of the statistical model will be distorted (Crawley, 2007; Winter, 2014).

As seen in figure 10 three different mixed-effect models are tested, answering one of the aforementioned sub-questions. The first and second model test for the relationship between changes in rhino density and those changes in the environmental variables including waterholes, wallows, temperature, precipitation, fire, canopy cover and NDVI. An interaction effect is also added into the model, which tests for the strength of each relationship throughout the four seasons. The third mixed effect model analyses the association between rhino density and elephant bull and herd density, also checking for the interaction effect of seasonality.

The mixed models are split into three due to discrepancies within the raw data. First, two models are created to answer sub-question 1 because the temperature data has many missing data points. This is because of irregularities with the data recording equipment of each weather station. Data is found to be missing for the months of April and May 2014, June 2015 and July 2017. The problem that arises with missing this data is that these months for all variables are omitted from the analysis. As a result, two mixed effect models are created to test whether the model including all explanatory variables has a better model fit compared to the model excluding temperature as a variable.

It is decided to remove the elephant bulls and herds as an explanatory variable in the first two models due to the impact of having many zeros within the data. The absence or presence of a rhino in a particular area can be the cause of many factors. By having a significant amount of zeros in the data influences the understanding on rhino and elephant interaction. Since the aim of sub-question two is to determine whether the presence of an elephant(s) has an effect on rhino density, it becomes plausible to remove all zeros for which there is no interaction. Thus, the only data rows that are considered in the model either have (1) a rhino present but no elephant (2) elephant present but no rhino or (3) both elephant and rhino present.

The results for each model are presented in two tables. The first table highlights the parameters of the different models tested. These include the AICc score, the change (Δ) in AICc between models, as well as conditional r^2 . The conditional r^2 describes the variation explained by both the fixed and random factors in the model. The criteria on which it is decided whether a model has a best fit or to reject it and continue with backward elimination is based on three factors. First, when the AICc score increases instead of decreases then the model no longer has a better fit. Second, when the conditional r^2 significantly reduces in size, then the model explains lesser variance and third, when only statistically significant variables remain the model has a better fit because no variables can then be removed. As mentioned, backwards elimination is used to take out the variables with the highest p-values. The second table presented illustrates the final estimates of the best fitting model, which include the explanatory variables and their estimates, the standard error, the t-value and the p-values. The significant level of the p-values is reported as $p < 0.05 = *$, $p < 0.01 = **$ and $p < 0.001 = ***$, and the p-value is reported if found to not be significant.

Finally, from the literature it is determined that it may take a couple of months for new grasses to emerge after a fire has taken place. As a result, a simple mixed effect model including a delay effect for up to 8 months is presented. The aim is to determine whether a significant interaction between rhino density and the months after a fire has taken place exists.

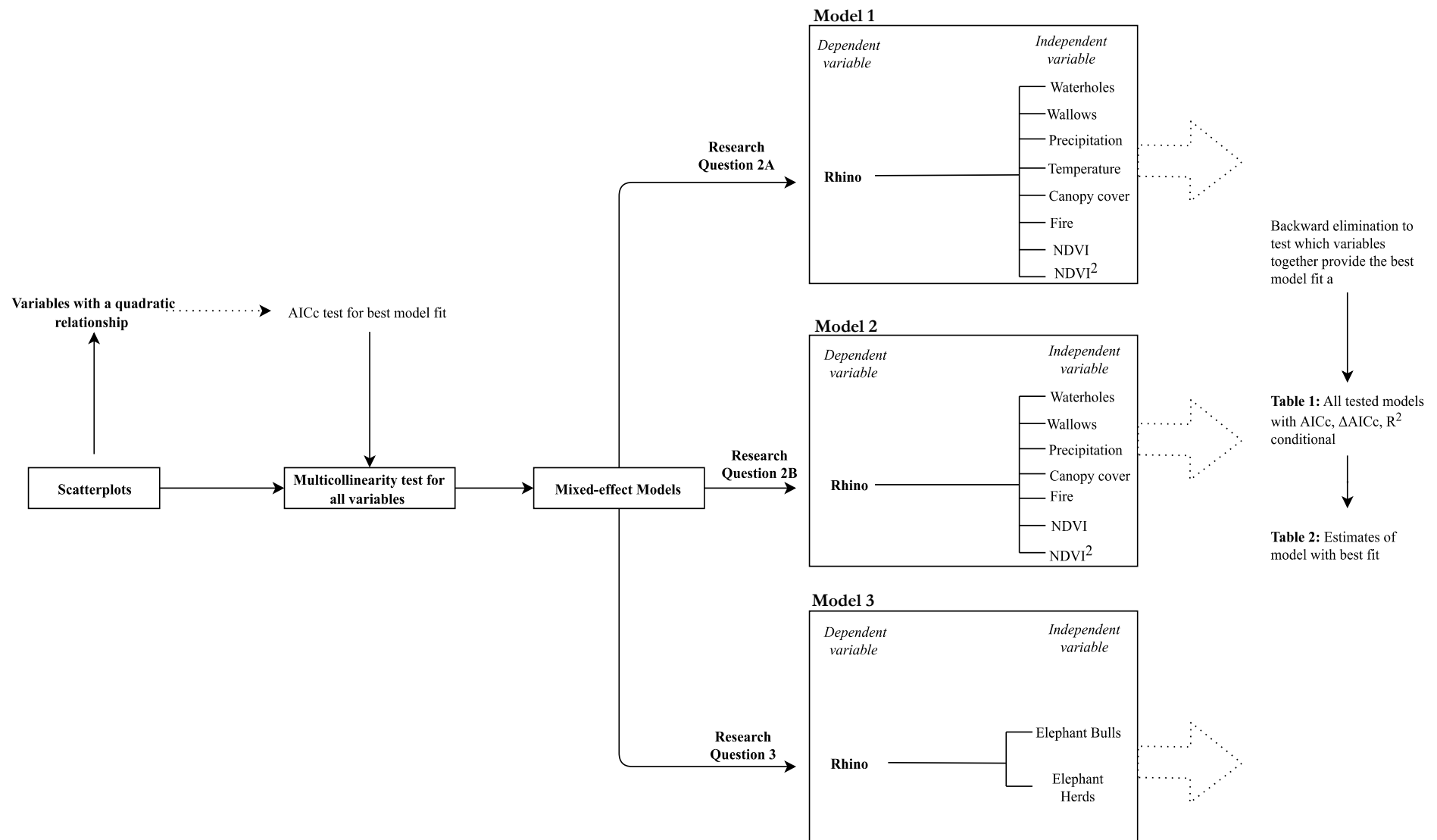


Figure 10: The statistical methodological framework that will be used to assess each research question. Model 1 and model 2 aim to answer sub-question 1 whereas model 3 aims to answer sub-question 2.

6. Results

6.1. Data pre-analysis

Table 2 illustrates the linear model outcomes for the uncorrected total observed rhino count and the rhino count data that has been corrected for flight path area.

Table 2: Linear regression for adjusted rhino count and observed rhino count

	Estimate	Std. Error	T-value	Pr(> t)
Adjusted for flight path area rhino count				
Intercept	0.28060	0.03770	7.444	1.01e-13
Average Fight Path	0.87161	0.06021	14.477	< 2e-16 ***
Observed rhino count				
Intercept	-0.09701	0.02341	-4.143	3.43e-05
Average flight path	1.05042	0.03740	28.090	< 2e-16 ***

The results show for there to be a positive significant relationship in the adjusted for flight path rhino count meaning the greater the area that is flown over, the more rhino are expected to be present in the landscape. This creates a positive bias where some cells have unrealistically high rhino counts. To correct for this, the outliers will have to be taken out of the data, which is unfavorable because the outliers play an important role in explaining rhino distribution in the landscape. It thus becomes questionable whether the use of the corrected rhino count is most favorable for the analysis.

Evidently, as also seen in table 2 the original observed rhino count, which has not been adjusted for flight path area, also shows to have a positive significant relationship. Considering the original rhino counts are real-world observations and the adjusted rhino count is exposed to a bias, it is preferable to continue with the original rhino count. Further, figure 11 depicts a histogram of the average cell coverage that has been witnessed by the pilot during each flight path. A coverage of 1.0 means the entire cell has been witnessed. The results show that approximately 70% of all cells have area coverage by the plane that is greater than 50%. It is thereby assumed that the majority of cells have sufficient coverage to adequately observe the total rhino presence without having to correct for flight path area.

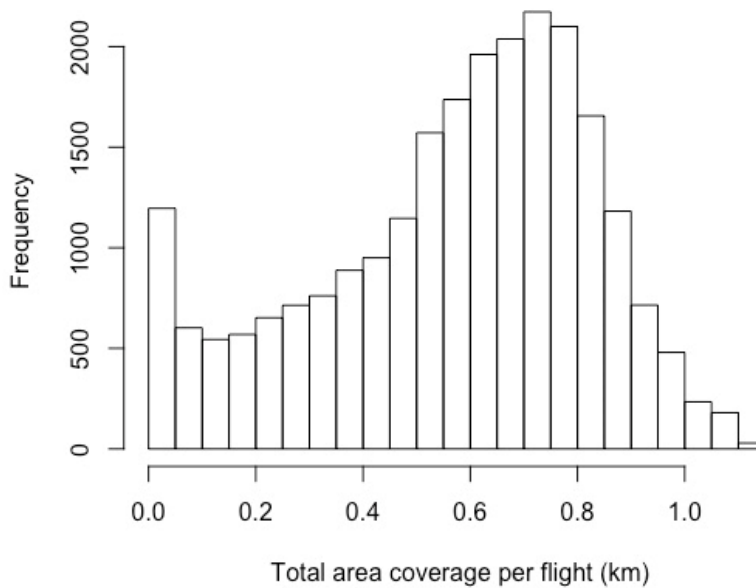


Figure 11: The average area of a cell that has been witnessed during a flight. A coverage of 1 means the entire cell has been witnessed.

6.2. Scatterplots

From the scatterplots which are presented in the results section 6.4 and 6.6, linear relationships are found to exist for rhino and elephant bulls, elephant herds, wallows, waterholes, fire occurrence and precipitation. Quadratic relationships are found to exist with rhino and canopy cover, temperature and NDVI. The quadratic relation indicates that rhino density is the highest at intermediate levels of each predictor. To test whether the variables with a quadratic relationship provide a better model fit, they are tested using the AICc function, the results of which are shown in table 3.

Table 3: AIC results for canopy cover and canopy cover², NDVI and NDVI² and Temperature and Temperature²

Model variables	AICc
Canopy cover	88764.16
Canopy Cover and Canopy cover ²	88763.18
NDVI	88753.35
NDVI and NDVI ²	88722.71
Temperature	84304.08
Temperature and Temperature ²	84306.07

The results show that a better model fit exists when regarding NDVI as a quadratic function. This observation is however not realized for temperature and canopy cover, as the AICc without the quadratic function is better. As a result only NDVI and its squared counterpart will be used in further analysis, whereas the squared counterparts for canopy cover and temperature will not be included.

6.3. Correlation and multicollinearity between all variables

A correlation matrix illustrating the relationship between variables is outlined in table 4. For the most part weak relationships are found to exist between variables. Nevertheless, relationships of moderate strength are found to exist between rhino and elephant bulls and rhino and elephant herds. In addition, a strong relationship is found to exist between elephant bulls and elephant herds. Table 5 presents the results for the multicollinearity test for all variables. The values show to all be around 1 meaning no collinearity exists and all can be used for analysis in the mixed-effect models.

Table 4: Pearson's correlation matrix

	Rhino	Bulls	Herds	Water holes	Wallows	Precipitation	Canopy Cover	NDVI	Fire	Temperature
Rhino	1.000									
Bulls	-0.400	1.000								
Herd	-0.459	-0.604	1.000							
Waterholes	-0.042	-0.002	0.011	1.000						
Wallows	-0.007	0.007	0.0002	-0.010	1.000					
Precipitation	-0.041	-0.033	-0.064	0.004	-0.003	1.000				
Canopy Cover	-0.020	0.014	0.040	0.032	-0.076	0.005	1.000			
NDVI	0.040	0.026	0.048	0.019	0.041	-0.138	0.084	1.000		
Fire	-0.009	-0.108	-0.007	0.000	0.004	-0.052	-0.010	0.006	1.000	
Temperature	-0.025	-0.040	-0.009	-0.039	-0.047	0.567	0.031	-0.120	-0.048	1.000

Table 5: Multicollinearity (VIF) test for all variables

Variable	Waterholes	Wallows	Precipitation	Temperature	Canopy Cover
VIF value	1.030499	1.025208	1.437963	1.448605	1.015070
Variable	Fire	Elephant Bulls	Elephant herds	NDVI	NDVI ²
VIF value	1.001894	1.027776	1.032101	1.177554	1.276324

6.4. Model 1: Rhino and environmental indicators

The outcomes for the mixed-effect model 1 for rhino and all environmental variables are presented below in table 6. It should be noted that the interaction effect of fire and the summer season are not included in the model because no fires took place during the summer months. The results from table 6 show that when adding the interaction effect of seasonality into the model, the model fit increases as the AICc declines and the variance explained by the model increases from 6.8% to 7.7%. Model 13 provides the best model fit, as the models after all show to have declines in conditional r^2 .

Table 6: The models tested including the model structure, the associated AICc, Δ AICc, and conditional r^2

#	Variables	AICc	Δ AICc	$r^2_{\text{conditional}}$
13	Model minus wallows*summer	83100.5	0	0.077
12	Model minus wallows*autumn	83116.98	16.48	0.077
11	Model minus wallows*spring	83123.52	6.54	0.077
10	Model minus waterholes*summer	83130.38	6.86	0.077
9	Model minus fire*autumn	83135.41	5.03	0.077
8	Model minus waterholes*spring	83144.81	9.40	0.077
7	Model minus fire*spring	83150.06	5.25	0.077
6	Model minus temperature*summer	83150.5	0.44	0.077
5	Rhino ~ waterholes + precipitation + canopy cover + NDVI + waterholes*spring + waterholes*summer + waterholes*autumn + wallows*spring + wallows*summer + wallows*autumn + temperature*spring + temperature*summer + temperature*autumn + precipitation*spring + precipitation*summer + precipitation*autumn + fire*spring + fire*autumn + canopycover*spring + canopycover*summer + canopycover*autumn + NDVI*spring + NDVI*summer + NDVI*autumn	83157.64	7.14	0.077
4	Rhino ~ waterholes + precipitation + canopy cover + NDVI	83258.01	100.37	0.068
3	Rhino ~ waterholes + precipitation + fire + canopy cover + NDVI	83261.24	3.23	0.068
2	Rhino ~ waterholes + temperature + precipitation + fire + canopy cover + NDVI	83272.2	10.96	0.068
1	Rhino ~ waterholes + wallows + temperature + precipitation + fire + canopy cover + NDVI	83281.09	8.89	0.068

Table 7 illustrates the final parameter values for model 13. No significant interaction is found to exist between rhino density and wallow distribution in the landscape nor between rhino density and fire occurrence. Figures 12 - 16 illustrate the scatterplots of raw data between each variable and rhino density, as well as the effect of each variable per season on rhino density.

Table 7: Estimates of model with best fit. The significance level is reported at $P < 0.05 = *$, $P < 0.01 = **$, $P < 0.001 = ***$. The p-value is reported if not significant

Variables	Estimates	Std. Error	t-value	Pr(> t)
Intercept	-0.128793	0.302306	-0.426	0.670086
Waterholes	-0.142184	0.041268	-3.445	***
Precipitation	0.018245	0.006827	2.672	**
Canopy cover	-0.025563	0.003547	-7.207	***
NDVI	7.114004	0.798460	8.910	***
NDVI ²	-13.519498	11.817464	-1.144	0.252625
Autumn	-0.112657	0.411476	-0.274	0.784250
Spring	1.232247	0.487833	2.526	*
Summer	-0.870978	0.139951	-6.223	***
Temperature	0.059123	0.015143	3.904	***
Autumn: waterholes	0.107191	0.055678	1.925	0.054215
Spring: Precipitation	-0.022307	0.006947	-3.211	**
Summer: Precipitation	-0.017832	0.006845	-2.605	**
Autumn: Precipitation	-0.019553	0.006855	-2.852	**
Spring: Temperature	-0.071279	0.021831	-3.265	**
Autumn: Temperature	-0.037922	0.019108	-1.985	*
Spring: canopy cover	0.020728	0.004101	5.054	***

Summer: canopy cover	0.023293	0.003853	6.046	***
Autumn: canopy cover	0.019817	0.004040	4.905	***
Spring: NDVI	-6.860185	1.065994	-6.435	***
Summer: NDVI	-6.397165	0.822410	-7.779	***
Autumn: NDVI	-5.638682	0.896868	-6.287	***
Spring: NDVI ²	-14.741149	14.943648	-0.986	0.323923
Summer: NDVI ²	13.708654	11.829780	1.159	0.246539
Autumn: NDVI ²	12.206378	11.824979	1.032	0.301964

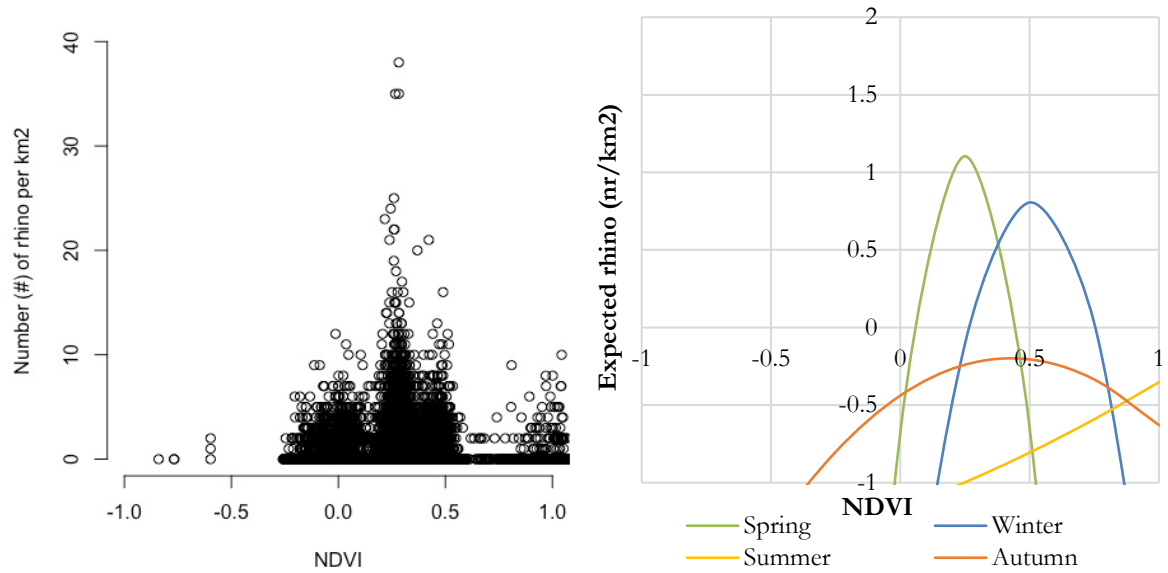


Figure 12: The left panel illustrates a scatterplot of the raw data of the NDVI and total rhino present per km². The right panel illustrates the plotted function for the total rhino that are expected to be present in a cell for a certain NDVI value during the spring, winter, summer and autumn

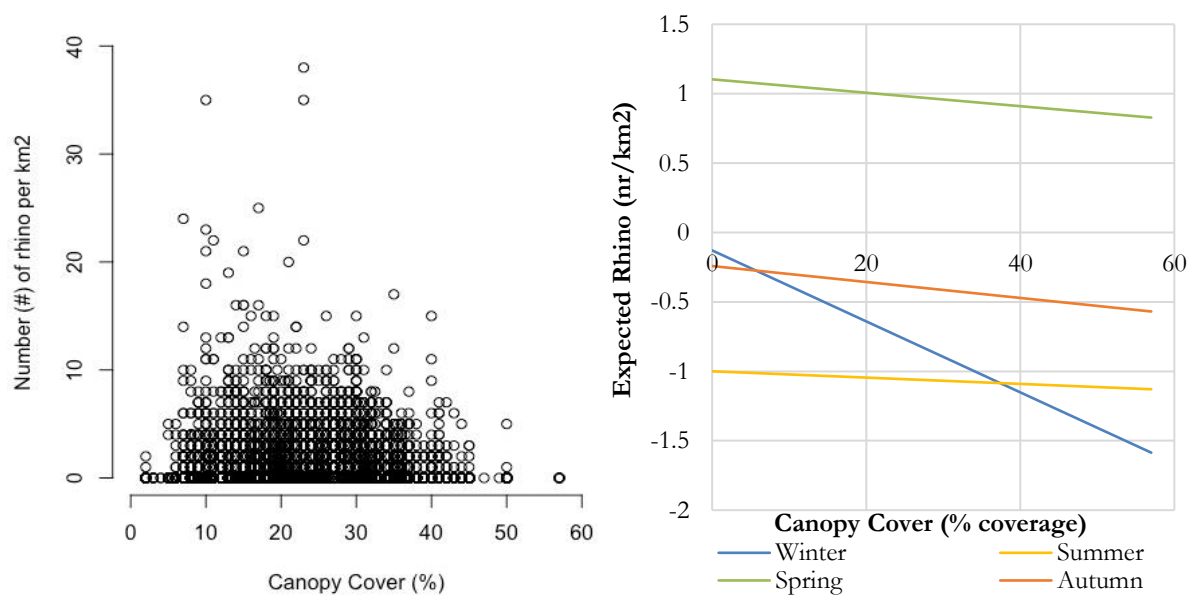


Figure 13: The left panel presents the scatterplot of the raw data between the canopy coverage per cell and the total rhino present per km². The right panel is the plotted function for the total rhino that are expected to be present in a cell for a certain canopy cover percentage (%) during a defined season

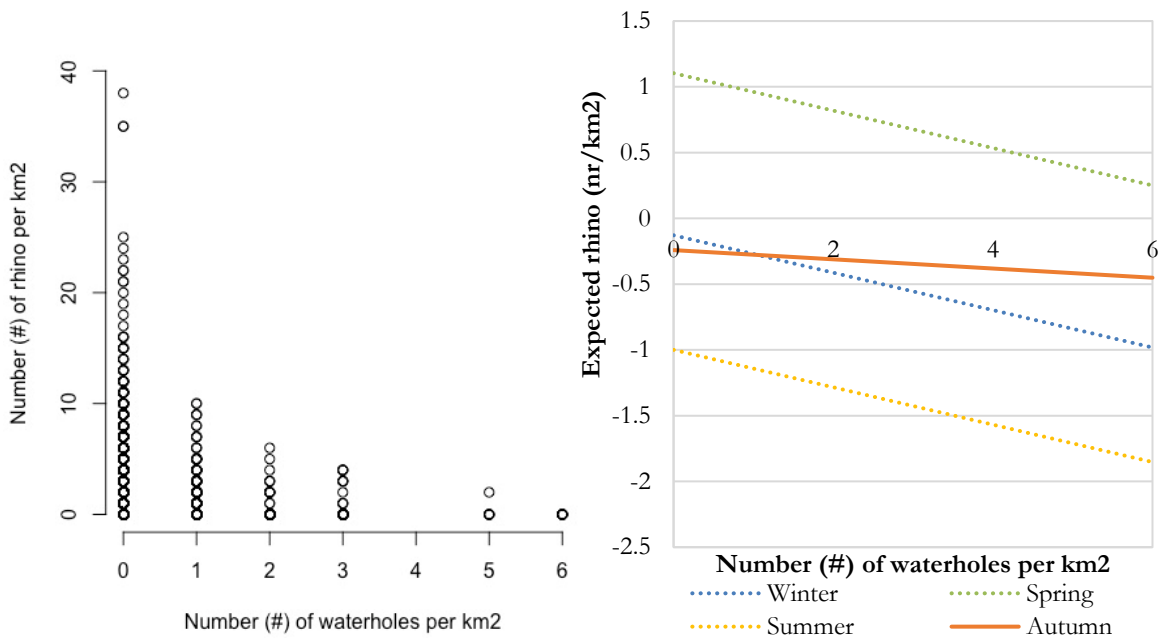


Figure 14: The left panel shows a scatterplot of the total waterholes present per cell and total rhino present per km². The right panel is a plotted function for the total rhino that are expected to be present in a cell for a number of waterholes during the winter, spring, summer and autumn seasons.

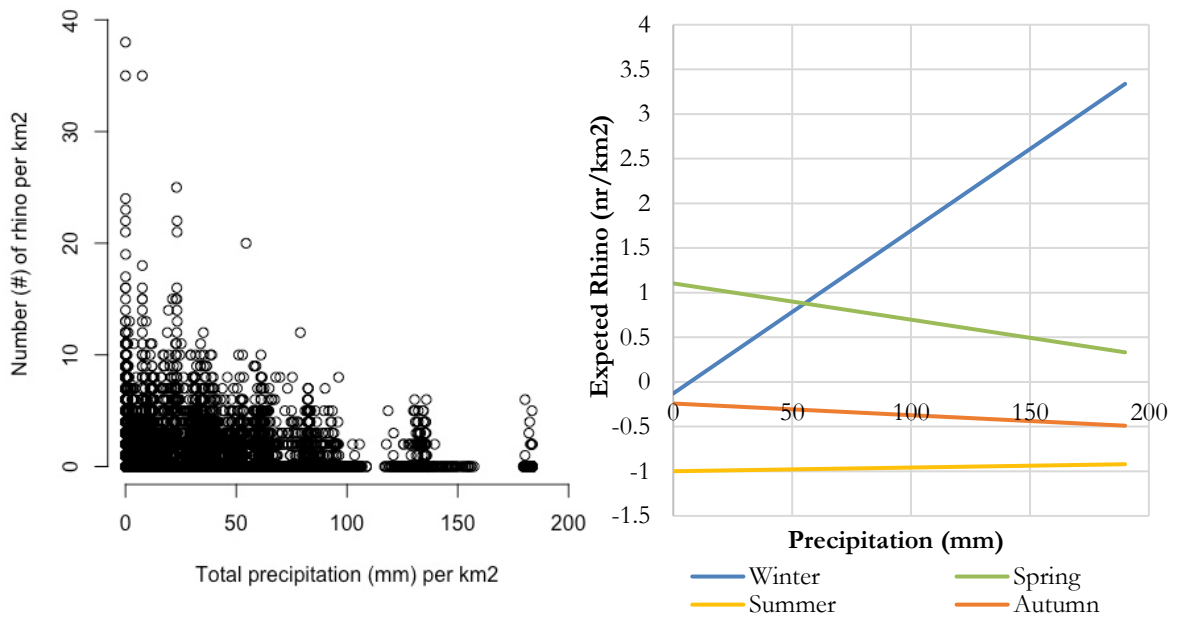


Figure 15: The left panel depicts a scatterplot of the total volume of precipitation in a cell and total rhino present per km². The right panel is a plotted function for the total rhino that are expected to be present in a cell for a certain volume of precipitation (mm) during the winter, spring, summer and autumn

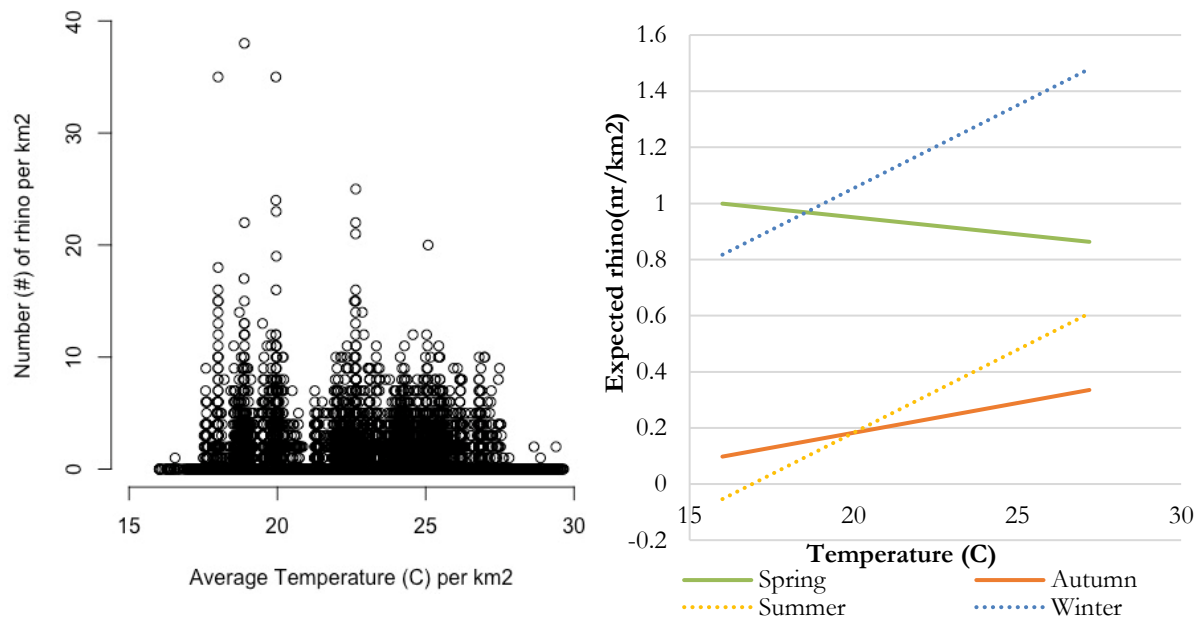


Figure 16: The left panel is the scatterplot of the temperature (°C) and total rhino present per km². The right panel depicts the plotted function of the total rhino that are expected to be present in a cell for a certain temperature (°C) during a defined season.

A quadratic relationship is found to exist between white rhino density and the NDVI. As seen by the scatterplot in figure 12 this means that for a certain bandwidth of NDVI values rhino presence is expected to be the highest. From the scatterplot this can be seen to be present between NDVI values of 0.2 and 0.5. This relationship is also reflected for the spring, winter and autumn seasons. During the spring, the results show for an optimum to exist at an NDVI value of around 0.2, where the total rhino expected to be present in a cell is 1. The influence of expected rhino subsequently drops after the threshold of 0.2 is reached. During the summer months, no parabolic relationship can be identified. For these months the data shows for a negative relationship to exist between expected rhino and NDVI. Nevertheless, as seen, the magnitude of the negative effect on expected white rhino quantities is reduced for higher NDVI values. It should be noted that having a negative expected rhino in this research does not refer to absolute declines in white rhino but instead shows that for any indicator value the impact on the expected amount of white rhino is negative. The winter season also shows to have an optimum value, where at an NDVI value of around 0.5 the highest number of rhino is expected to be present. Finally, the autumn months also show for a parabolic relationship to exist. Yet, the influence on expected white rhino presence remains negative throughout the season.

A significant relationship is also found for white rhino density and canopy cover for each season. A weak negative relationship can be derived from the scatterplot in figure 13 which shows for more rhino to be present in cells that overall have lower canopy cover percentages. This observation also exists for the winter months as plotted in the line graph, where the higher the canopy coverage, the higher the absolute decrease in rhino per square kilometer. The winter months also show to have a much more rapid rate of decrease compared to the other seasons. Canopy cover is found to play less of a role during the spring, summer and autumn months as the overall declines in expected white rhino as canopy cover increases is minor.

Although a significant relationship is found between rhino and waterholes, a seasonal significance was only found during the autumn period. From the scatterplot illustrated in figure 14, a negative relationship between rhino and waterhole abundance is seen. This exemplifies that the greater the

number of waterholes in a cell, the lower the expected white rhino. Essentially the addition of 1 waterhole in a cell leads to a -0.14 decline in expected rhino. A similar observation can be made during the autumn season, where although minimal, a negative relationship is also found. The other seasons, although not significant are added into the figure as dashed lines to provide a holistic understanding of their effect on expected rhino.

As defined by the scatterplot in figure 15, a negative linear relationship is seen where an increase in precipitation is found to correspond to a lower presence of rhino in a cell. This observation is however not found to be true for the winter months. Instead, during this period, the higher the volume of precipitation the more rhino is expected to be present in a cell. At the maximum precipitation rate of 190mm per month, there is an expected increase of 3.3 rhino per cell. During the summer and autumn months precipitation can be assumed to have a small effect, as the change in expected rhino is minimal. For the spring season however, the opposite effect is observed compared to the winter. In this case, the higher the precipitation, the lower the expected white rhino.

The scatterplot between white rhino density and temperature (figure 16) indicates a slight decline in rhino density at higher temperatures. This interaction during the seasons is found to be significant only for the spring and autumn months, which show opposite trends. In the autumn temperature has a reinforcing effect where the higher the temperature, the higher the expected rhino. The opposite is seen for the spring season. Nevertheless, the magnitude on expected rhino during these months seem to be minimal. For example, during the autumn at 16 degrees the total expected rhino is around 0.10, at 25 degrees this increases to 0.34 rhino. Similarly, during the spring the expected rhino present at 16 degrees is 1 whereas at 25 degrees this declines to 0.86. These values only show small overall declines in expected rhino.

6.5. Model 2: Rhino and environmental indicators without temperature

Due to the missing temperature data, it is decided to create two mixed-effect models, one with and one without temperature, to determine which one explains greater variance and thus has a better model fit. The result for the mixed effect model, which excludes temperature, only accounts for 7.3% variance compared to the 7.7% explained by the model including temperature. It can therefore be concluded that model 1 has a better fit and thus better explains the relationship between rhino density and each indicator. The model results, as well as the final parameter values can be found in appendix 1.

6.6. Model 3: Rhino and elephant interaction

Model 3 aims to explore the relationship between rhino density and the density of elephant bulls and elephant herds. The results from table 8 illustrate that model 4 is found to be the best model fit for the interaction between the rhino, elephants and seasonality. Table 9 gives the final parameter values for model 4.

Table 8: The models tested including the model structure, the associated AICc, Δ AICc, and conditional r^2

Model	Variables	AICc	Δ AICc	r^2 conditional
4	Rhino ~ elephant bulls + elephant herds + elephant bulls*spring + elephant bulls*summer + elephant bulls*autumn + elephant herds*spring + elephant herds*summer	22748.52	0	0.12
3	Rhino ~ elephant bulls + elephant herds + elephantbulls*spring + elephantbulls*summer + elephantbulls*autumn + elephantherds*spring	22757.43	8.91	0.12
2	Rhino ~ elephant bulls + elephant herds + elephantbulls*spring + elephantbulls*summer + elephantbulls*autumn + elephantherds*spring + Elephant herds*summer + elephant herds*autumn	22767.11	9.68	0.12
1	Rhino ~ elephant bulls + elephant herds	22793.74	26.63	0.11

Table 9: Estimates of model 4. The significance level is reported as $P < 0.05 = *$, $P < 0.01 = **$ and $P < 0.001 = ***$. The p-value is reported if not significant.

Variables	Estimates	Std. Error	t-value	Pr ($> t $)
Intercept	2.997017	0.081109	36.950	***
Bull	-0.225189	0.091455	-2.462	*
Herd	-0.048110	0.003834	-12.549	***
Spring	-0.227610	0.106750	-2.132	*
Summer	-0.571224	0.104261	-5.479	***
Autumn	-0.653984	0.104936	-6.232	***
Summer: Bull	-0.413239	0.145659	-2.837	**
Autumn: Bull	-0.257557	0.133124	-1.935	0.05308
Spring: Bull	-0.243163	0.141619	-1.717	0.08604
Spring: Herd	0.015037	0.008141	1.847	0.06479

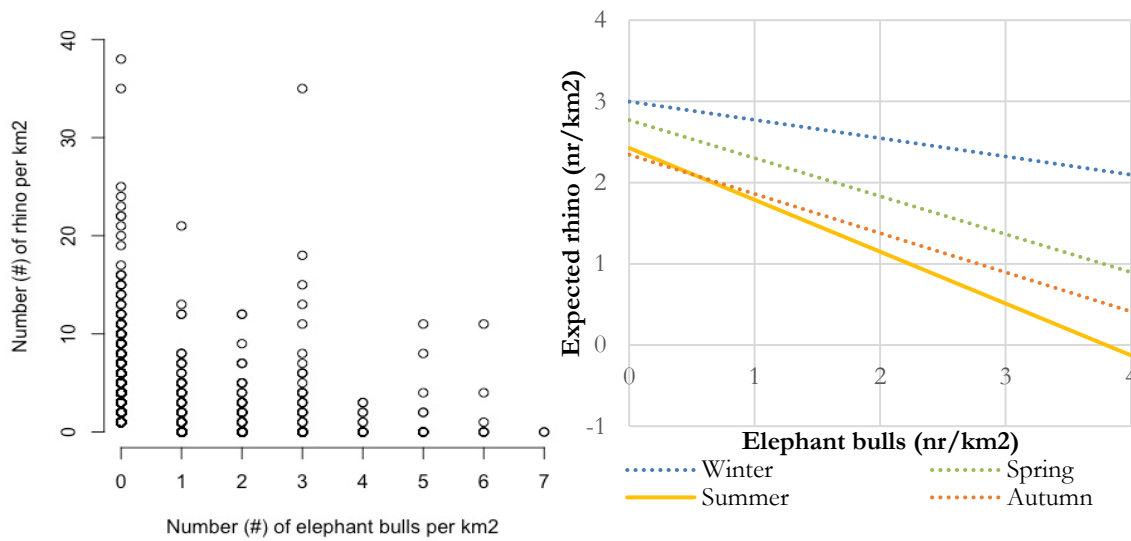


Figure 17: The left panel shows the scatterplot illustrating the total number (#) of elephant bulls in a cell and the total rhino number (#) of rhino present per km². The right panel is the plotted function for the total rhino that are expected to be present in a cell for a certain number of elephant bulls during a particular season.

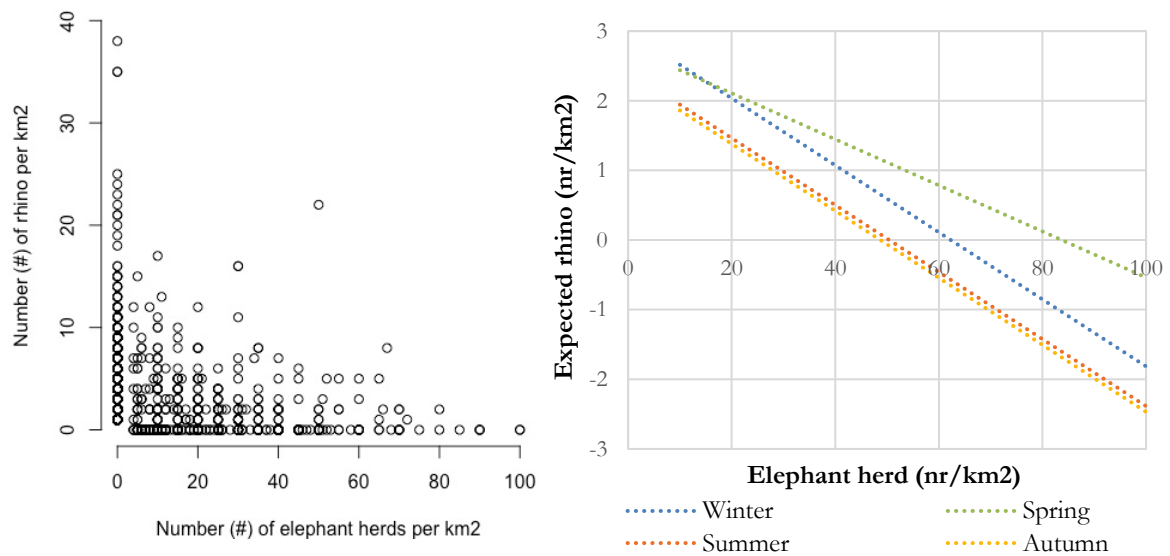


Figure 18: The left panel shows the scatterplot illustrating the total number (#) of elephant herds in a cell and the total rhino number (#) of rhino present per km². The right panel is the plotted function for the total rhino that are expected to be present in a cell for a certain number of elephant herds during a

Overall, in broad terms the relationship between rhino density and the density of the elephant herds and elephant bulls in the landscape shows to have a negative relationship meaning the higher the presence of each in the landscape, the lower the number of rhino. Between rhino and elephant bulls the relationship was found to be significant only for the summer months, yet the autumn was found to be almost significant. During the summer the addition of 1 elephant bull is found to result in an expected rhino presence of 2.9. If however, 4 bulls were present in one cell, no rhino are expected to be present. Although the relationship between rhino and elephant herds is also found to be negative, no significance is found during the seasons.

6.7. Fire with delay effect

Table 10 illustrates the results for the mixed effect model which tests for the association between rhino density and 1 to 8 months after a fire has taken place within a cell. A significance level is only found to exist 6 months after a fire, which shows for the expected white rhino to increase by 0.224 rhino.

Table 10: The mixed-effect model parameter results for the impact on expected rhino density 6 months after a fire has taken place in a cell

Variables	Estimates	Std. Error	t-value	Pr (> t)
Intercept	0.3940	0.01624	24.259	***
Fire delay 6 months	0.2240	0.04459	5.023	***

7. Discussion

The main research question is, “*to what extent do the defined environmental indicators influence the density of the white rhinoceros across the South African savanna?*” While this study is the first to provide insights into the relationships that exist between selected indicators and rhino distribution, it is not possible at this point to generalize beyond the study region. Specifically, the results for sub-question one show for NDVI, canopy cover, waterholes, precipitation, temperature and fire with a 6-month delay to be potential influencers on rhino density. No significant interaction was found to exist with wallows or fire without delay in the landscape. By adding seasonality into the model a better understanding is gained on how the effect of each variable on rhino density varies between the seasons. For example, precipitation during the winter seems to have a bigger influence on rhino density compared to the other months. Furthermore, the results for sub-question two show for a relatively strong interaction to exist between rhino and elephant density in the landscape. In this case, an increase in the presence of an elephant bull or an increase in the size of an elephant herd results in a decline in rhino density. This effect is predominantly found to be the strongest between rhino and bulls during the summer seasons. This study hereby suggests that certain drivers may indeed influence the distribution of the white rhino in the greater Kruger landscape yet their impact is found to vary throughout the seasons. While an influence is found, the extent of their influence is also limited as the variance explained by model 1 and model 3 are respectively 7.7% and 12% advocating that it is likely for many other factors not included in the analysis to play a role in altering rhino density. Thus, while environmental drivers are found to influence the density of the white rhino in the landscape, the extent of their influence is minimal likely attributed to the unidentified presence of confounding variables and other limitations that will be discussed below.

7.1. Rhino and Environmental Indicators

7.1.1. Rhino density and vegetation cover (NDVI)

The results for rhino density and the NDVI show that compared to the other seasons, a much weaker relationship exists between the variables during the summer. During this time, for all NDVI values, expected rhino is found to stay below zero, meaning there is no relationship between NDVI and rhino density. This result can be attributed to the idea that during the summer, which is also the wet season, favorable grasses for the rhino are able to grow more widespread across the landscape, allowing for vegetation to not become a limiting factor. As a result, no clustering by rhino in areas with specific NDVI values is needed. During the autumn season, the results show for an optimum to start rising, but the expected rhino remains negative. This may be related to the fact that late-summer rainfall can allow for green forage to remain abundant for a longer period of time (Archibald & Scholes, 2007; Chamaille-Jammes, Fritz, & Murindagomo, 2006). The winter and spring season on the other hand, both show to have two clear optimum values at which the expected rhino presence is the highest. During the winter the optimum is around 0.5 as compared to the spring where the optimum is around 0.2. The higher expected rhino identified during the winter season may be related to the fact that during this time period, rainfall is a limiting factor and many grasslands start to lose their nutritional value. As a result, rhino may choose to cluster in areas, which still have flushes of healthy green grasses (Shrader et al., 2006). In addition, during the dry period rhino have also been observed to graze on green grasses from areas that have previously been burnt, which tend to have an overall high reflectance and thus NDVI value (Shrader et al., 2006). Finally, rhino have also been observed to consume more woodland grasslands during the dry season (Shrader et al., 2006). These areas may be comprised of evergreen forests, which do not lose their leaves during the winter and thus remain to have a higher NDVI value. The finding of having a lower optimum during the spring is attributed to the date of satellite imagery used. Since the wet season starts during the spring, it is expected for the optimum to be the highest during this period as new healthy grasses will start emerging. Nevertheless, if the satellite image use was taken before any rainfall took place then the grasses in the landscape will still be of lesser nutritional value and indicate lower NDVI values.

All in all, due to a variety of limitations associated with the NDVI, it becomes difficult to

pinpoint exactly the relationship between rhino density and NDVI within this study. Specifically, the NDVI values derived from the satellite image can be influenced by a number of factors including but not limited to atmospheric conditions, vegetation moisture, soil moisture, differences in soil type and land management type (Pettorelli, 2013). Whilst it is possible to control for some factors such as atmospheric conditions, it is not possible to account for others. In addition, the NDVI also becomes less sensitive as the above ground biomass increases. Essentially this means that, as the density of vegetation in the landscape increases, the change in NDVI decreases. The results may therefore only detect a small change in NDVI in highly dense areas when in fact there may actually be a significant change in vegetation (Pettorelli, 2013).

7.1.2. Rhino density and Canopy cover

Significant interactions are found to exist between rhino density and canopy cover for all seasons. The overall effect shows a decrease in expected rhino as canopy cover increases. Whilst this decrease is minimal for the spring, autumn and summer seasons, it becomes more substantial for the winter. Although limited research is available on how the rhino utilizes canopy cover in the landscape, it has been suggested that rhino typically prefer a landscape to have some degree of tree coverage (Owen-Smith, 1988). A second study however analyses the habitat preferences of white rhino in the HiP game reserve and found for vegetation structure to be the least determinant factor influencing habitat selection (Perrin & Brereton-Stiles, 1999). While the landscape in HiP is notably different with much denser vegetation compared to the Greater Kruger area, it may still be the case that tree cover in the greater Kruger is also less of a determining factor for rhino distribution. This may explain why the changes in expected rhino in the summer, spring and autumn are minimal. The significant difference in the winter can be attributed to a number of reasons. First, relating back to the idea of having an open system essentially means that there may have been a shift of species out of the region. Thus, there may not actually be an avoidance of rhino with canopy cover but just less rhino present in the study region at this time. Second, contrary to the literature, it may be that the grasses below the canopy are unfavorable during the winter season resulting in an avoidance. It should further be noted that the current data on canopy cover in the study region is unsuitable for making any sound conclusions. The current data used to depict the canopy cover is biased towards the summer season. This evidently distorts the results because during the dry and winter season many trees shed their leaves meaning the canopy coverage is likely to be much lower compared to the summer season. Furthermore, the method used to identify canopy coverage does not visualize the distribution of trees in a cell. For example, in one cell the trees may be more clustered in an area compared to another cell where the trees may be more evenly dispersed making it difficult to establish the true density of coverage.

7.1.3. Rhino density, waterholes and wallows

Whilst the results between rhino density and waterhole distribution are significant, they are found to only be significant for the autumn season. Specifically, during this time a negative relationship is found to be present where the higher the number of waterholes, the lower the expected rhino, although the effect is minimal. This is contrary to what is expected, as one would assume that the greater the number of waterholes present in the landscape, the higher the overall expected rhino. Nevertheless, it actually becomes more logical to have a higher expected rhino in areas with lower waterhole densities because rhino will have to cluster more to one point to access water. In cells where there are multiple waterholes present less sharing of resources is needed, allowing them to be more dispersed. This observation has significant implications for conservation strategies as the question arises whether it is better to create a management plan which allows for many waterholes to be present in the landscape, or if it's better to have a limited number. By having many waterholes in an area allows for the rhino to be more dispersed so it becomes difficult for poachers to find them, yet at the same time it also becomes more difficult for conservationists and rangers to protect them. When having a limited number of waterholes in an area, the rhino become more clustered and thus easier to protect. But, it then also becomes easier for poachers to find them. This is a major implication that needs to be considered by conservationists when creating management plans.

The results showed for no significant interaction to exist between rhino density and wallows in the landscape. As seen in figure 8b, this can firstly be related to the fact that wallows in the landscape are much more abundant and widespread compared to the waterholes, so they may not become a limiting factor for rhino distribution. Secondly, the results found may also be caused by the lack of sufficient data for waterhole and wallow presence. As with canopy cover, both variables are subjected to a bias for the summer season. The waterhole and wallow data are fixed layers as they have only been measured once during the four-year time period. By being a fixed layer there is essentially no change in the variables throughout the study period. The implications that this brings are that the results may be grossly overestimated for the other seasons. For example, the measurements for the waterhole and wallow locations are accumulated during the wet season. During this time there are typically many more wallows and waterholes present in the landscape that tend to gradually deplete as the dry season advances. This has not been taken into account in the model. In addition, throughout the four-year study period there has been a prevailing drought meaning many more waterholes and wallows may have disappeared thereby limiting the conclusions that can be made on the relationship between rhino density, waterholes and wallows.

7.1.4. Rhino, temperature and precipitation

The results between rhino and precipitation show from the scatterplot for a linear relationship to exist where the higher the precipitation, the lower the number of rhino present in an area. However, when analyzing these results per season the winter shows to have a significant increase in expected rhino as precipitation increases. This can firstly be related to the idea of rhino being a water dependent species (Owen-Smith, 1988; Pienaar, 1994). Considering water is a limiting factor during the dry season it could mean that when it does finally rain in the winter, rhino will tend to gravitate more towards those areas with higher rainfall. During the wet season in the summer, the effect of precipitation on rhino density is almost nonexistent. This is because precipitation is plentiful during the summer thereby preventing it from becoming a limiting factor. Furthermore, the issue of having an open system study arises again as the increase in rhino during the winter may also be due to a higher influx of rhino from outside the study period

The results show for the interaction effect between rhino and temperature to only be significant for the spring and autumn seasons, which show contradicting effects. Unfortunately, by using data that has been interpolated over a very large spatial scale, the differences between each cell become minimal. From the literature it would be assumed for the relationship between temperature and rhino to differ in the summer and winter due to thermoregulatory processes. Although no studies have yet focused on the white rhino, research on the effect of temperature on the elephant show that it has a preference for certain landscapes to lower or raise their body temperature (Kinahan, Pimm, & van Aarde, 2007; Riek & Geiser, 2013). Specifically, in the summer the species tends to choose areas that warm up slowly and in the winter choose areas that cool down more slowly (Kinahan et al., 2007). This allows the elephant to manipulate the rate at which they exchange heat with their environment. As the physiological features of elephants somewhat resemble that of the white rhino, it may be the case for the rhino to use the landscape in a similar manner. But for this to be tested, much more detailed weather data needs to be collected.

A significant limitation associated with using the temperature and precipitation data is that the data used is from weather stations outside the study region. This causes for the interpolated weather data to become very static for each cell, meaning not much difference in temperature or precipitation is found between cells. This makes it difficult to determine whether a strong link exists between rhino density, precipitation and/or temperature.

7.1.5. Rhino and Fire occurrence

The fire data that is used within the model is real-world data that takes into account the exact time a fire takes place. Logically, this would not make sense, as it is unlikely for a rhino to go to an area when a fire is taking place. As a result, it was decided to include a time delay into a model to tests whether rhino density alters 1 to 8 months after a fire has taken place. The linear mixed

model results show that at the point of 6 months, there is a significant positive interaction with rhino density. Specifically, rhino density increases at this point. This is likely because it takes around 6 months for new flushes of green grasses to emerge in these areas, which attract rhino into the area. This result has significant implications for creating rhino conservation strategies as it is likely for more rhino to be present in areas 5-7 months after a fire has taken place, meaning it becomes favorable to increase protection.

7.2. *Rhino and the Elephant*

The second part of this research focuses on the interaction between the rhino and the elephant. The model results show for a there to especially be a strong interaction between rhino and bulls in the summer season whereby the higher the number of bulls in a cell, the greater the avoidance by the rhino. This type of avoidance was also found to be present between the elephant and the black rhino (*Diceros bicornis*), where studies show for the black rhino to graze more selectivity in the absence of the elephant. When the elephants are present, it becomes likely for them to monopolize favorable food niches and preventing the black rhino from accessing it (Landman et al., 2013). While the white rhino and black rhino clearly have different physiological features this observation may hint towards a similar phenomenon occurring between the white rhino and the elephant in the greater Kruger region. In this case, the elephant may monopolize landscapes, which are also favorable for the white rhino. Nevertheless it is believed for the greatest avoidance to occur during the summer-wet season because both vegetation and water are more present in the landscape and are thus not limiting factors by which the species are forced together. This evidently makes it easier for the white rhino to avoid interaction with the elephant. When the dry season emerges however, both water and vegetation become limited and the species may have to share resources thereby increasing interaction.

The relationship between rhino and elephant herds is more difficult to analyze as even though significance is found, no significant interaction effect is found per season. This could indicate that rhino will avoid any sort of interaction with the elephant herds regardless of the season. This may also be related to the relative size of each herd, a very large herd which in this study was found to reach up to 100 individuals will likely result in a loss of resources for the white rhino as the herd monopolizes the landscape resulting in an avoidance by the rhino.

7.3. *Limitations and Future Research*

There is a necessity to balance the results found in this study against several limitations. While some limitations have already been mentioned relating for example to inadequate data collection and the caveats associated with having an open system, others still need to be addressed or explained in more detail. First, the problem of having an open system is that it allows for rhino and elephants to move freely to and from the study region. The results assessing the relationship between changes in rhino density and the defined environmental indicators can therefore not be seen as definitive interactions. This is because it is not known whether the effect found is because of an interaction with the environmental indicator or if it arises due to an in or out flow of species. A specific example of this is seen with precipitation during the winter season where a significant increase in expected rhino is found as the total volume of precipitation rises. This finding is not because all the rhino shifted towards the area with the highest precipitation but instead it is more likely for there to have been an influx of rhino from outside the system which caused the effect of higher expected rhino.

Second, there is the problem of human error associated with the method undertaken to collect the rhino and elephant location data. Specifically, when flying at a high altitude it becomes difficult to record all rhino and elephants in the landscape. This becomes even more so in areas which have a high canopy cover density as it makes it more difficult to spot the species. In addition, through the use of transect flying it also becomes difficult to know when flying over a cell whether the same rhino is counted twice or if it is a new uncounted rhino. This error can be resolved by using alternative methods such as using collard data to observe species in the landscape. Using collared data is also a more effective measure of understanding the interaction between the rhino and the landscape as well as between the rhino and the elephant to verify if

they do in fact avoid each other or if other confounding effects are playing a role. Having collared data is furthermore beneficial because by tracking a select-few rhino in the landscape over a defined period of time will help to verify why they may be in a particular cell at a particular time. In addition, it can also again deal with the issue of confounding effects. Confounding effects refers to the idea where other variables not included in this study are wholly or partially accountable for the results found. The only way to resolve for this is to include more variables into the model, yet it should keep in mind not to create problems with over fitting the data.

8. Conclusion

Due to the prevailing rhino poaching crisis in South Africa, there is a need to create more efficient conservation strategies to better protect the rhino and prevent its extinction. It has been suggested that in order to do this, a more enhanced understanding is needed on the relationship between the rhino and the landscape; specifically what natural factors drive rhino distribution. This research makes a first attempt at understanding these dynamics with a select few indicators. The results show for some clear significant relationships to exist yet due to the various limitations presented in this research it is not possible to make any sound conclusions on how the environmental drivers can alter the distribution of the white rhino in the savannah landscape. Instead this research should be seen as more of an empirical exploratory study that makes a first attempt at understanding the dynamics between rhino and its landscape. In order to improve this research and in the future be able to give conclusions on which conservation decisions can be based off of, it is primarily important to obtain higher quality raw data for canopy cover, waterholes, wallows, temperature and precipitation and include more potential environmental drivers into the model. The findings in this study should therefore be used as building blocks to be used in future research and give an indication on which limitations need to be taken into consideration.

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Appendix 1

The two tables below are the results for model 2 which analyses the relationship between rhino distribution and all environmental variables minus temperature. Table (x) and (x) illustrates the results for the mixed-effect models which excludes temperature as a variable.

Table (11): The models tested including the model structure, the associated AICc, Δ AICc, and conditional r^2

#	Variables	AICc	Δ AICc	$r^2_{\text{conditional}}$
12	Model minus wallows*autumn	87513.55	0	0.073
11	Model minus wallows*summer	87529.78	16.23	0.073
10	Model minus wallows*spring	87536.56	6.78	0.073
9	Model minus waterholes*summer	87543.55	5.44	0.073
8	Model minus fire*autumn	87548.99	9.82	0.073
7	Model minus waterholes*spring	87558.81	5.35	0.073
6	Model minus fire*spring	87564.16	0.44	0.073
5	Rhino ~ waterholes + precipitation + canopy cover + NDVI + waterholes*spring + waterholes*summer + waterholes*autumn + wallows*spring + wallows*summer + wallows*autumn + precipitation*spring + precipitation*summer + precipitation*autumn + fire*spring + fire*autumn + canopycover*spring + canopycover*summer + canopycover*autumn + NDVI*spring + NDVI*summer + NDVI*autumn	87564.6	82.98	0.073
3	Rhino ~ waterholes + precipitation + canopy cover + NDVI	87647.58	2.78	0.067
2	Rhino ~ waterholes + temperature + precipitation + fire + canopy cover + NDVI	87650.36	8.91	0.067
1	Rhino ~ waterholes + wallows + precipitation + fire + canopy cover + NDVI	87659.27		0.067

Table (12): Estimates of model with best fit. The significance level is reported as $P < 0.05 = *$, $P < 0.01 = **$ and $P < 0.001 = ***$. The p-value is reported if not significant.

Variables	Estimates	Std. Error	t-value	Pr ($> t $)
Intercept	0.908401	0.079489	11.428	***
Waterholes	-0.142903	0.040955	-3.489	***
Precipitation	0.020966	0.006804	3.082	**
Canopy Cover	-0.022840	0.003474	-6.575	***
NDVI	6.774585	0.793727	8.535	***
NDVI ²	-8.985916	11.664402	-0.770	0.441088
Autumn	-0.614034	0.104115	-5.898	***
Spring	-0.095956	0.096357	-0.996	0.319340
Summer	-0.376995	0.094903	-3.972	***
Autumn: Waterholes	0.084957	0.052899	1.606	0.108281
Spring: Precipitation	-0.024708	0.006900	-3.581	***
Summer: Precipitation	-0.020956	0.006825	-3.070	**
Autumn: Precipitation	-0.022778	0.006828	-3.336	***
Spring: canopy cover	0.018239	0.004048	4.505	***
Summer: canopy cover	0.020731	0.003797	5.460	***
Autumn: canopy cover	0.015256	0.003864	3.948	***
Spring: NDVI	-6.450064	1.065843	-6.052	***
Summer: NDVI	-5.838376	0.818467	-7.133	***
Autumn: NDVI	-5.055295	0.880765	-5.740	***
Spring: NDVI ²	-20.134687	14.816691	-1.359	0.162558
Summer: NDVI ²	9.581296	11.677702	0.820	0.441400
Autumn: NDVI ²	7.504294	11.670084	0.643	0.550440