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The distribution patterns of African elephant (*Loxodonta africana*) and white rhinoceros (*Ceratotherium simum simum*) in relation to waterhole availability in a South African savanna

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FOREWORD

What a pleasure to be able to delve into the livelihoods and home of the elephant and rhino. I hope that this research can motivate others to notice the intricacies of the savanna, as well as nature in its entirety. It certainly inspired me and I shall never forget the feeling of seeing elephants right outside my door every day.

I would not have been able to embark on such a compelling project without Joris Cromsigt, my supervisor and first reader, who gave me the opportunity to travel to South Africa and helped me when I couldn't see the wood through the trees. Many thanks also go to those that helped me at Southern African Wildlife College, including those that supported me academically, including Cleo Graf and Alan Gardiner, and those that trundled relentlessly through the bush with me, including Gawie Lindeque and Bruce McDonald, as well as my good friends Peter, Laurens and Nic. Not only did you help me collect data, but you also got me through some of the more trialling moments.

Lastly, I must thank my family for always supporting and encouraging me to achieve my dreams, despite being terrified that I may be eaten by a leopard. Having you all visit me in Kruger made the experience even more special.

– Rosemary Wool
Budapest, 2 August 2019

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SUMMARY

Anthropogenic activities, including the illegal poaching trade, have been threatening the global populations of elephants and rhinoceros for decades. Rigorous studies into the ecology of these megaherbivores are imperative for conservation strategies. I studied the relationship between water availability, and the African elephant and the southern white rhinoceros. Water resources are crucial environmental determinants of animal distribution within semi-arid habitats, particularly during the dry season when water is relatively scarce. I hypothesised that elephant and rhino would spend more time in water-present areas during the dry season and high temperatures. During the dry season, I predicted that elephant and rhino would prefer permanent sources of waterholes that were mostly artificial. I also expected that the herbivores would select for waterholes large enough for full-submergence, and lastly, I hypothesised that elephants (mixed-feeders) would spend more time around waterholes with high shrub and grass cover, and rhinos (grazer) with more grass cover. In Kempiana, an area within Greater Kruger, South Africa, waterhole occurrence was identified using satellite imagery and ground-truthing by foot and aeroplane. Waterhole characteristics were also classified using satellite imagery, and animal density data was provided from Southern African Wildlife College in the form of aerial counts between 2016 and 2018. Generalised linear mixed-effect models were used to deduce the best-fit models for animal presence and density. Elephant presence was significantly found to increase in areas of water occurrence as temperatures rose. In water-present areas, both elephant and rhino utilised medium- and small-sized waterholes more during the dry season, with elephants utilising medium and rhinos preferring small. Elephants also associated more with permanent waterholes but less with temporary waterholes during the dry season, and rhino density around waterholes of neutral permanence was higher during the dry season. Shrub cover positively predicted elephant and rhino density during the wet season, whilst grass cover negatively predicted elephant density. Rhinos preferred natural waterholes for both seasons, and elephant density was significantly higher at artificial waterholes during the dry season (and the opposite trend for the wet season). These results suggest differences in thermoregulation strategies of elephant and rhino, with elephant depending more on water. It also supports the notion that elephants utilise artificial waterholes considerably more during the dry season, which may propagate their distribution and population numbers. Lastly, species-specific preferences for waterhole characteristics may also indicate that displacement between rhino and elephant has led to waterhole niche partitioning.

Contents

1 INTRODUCTION

1.1 Biodiversity loss

Over the past five centuries anthropogenic activities have generated a surge of global biodiversity loss (Rockström *et al.,* 2009). Such losses are parallel to historic mass extinction events, and therefore scientists have labelled this epoch the sixth extinction. One group of animals that is notably affected by human-driven activities are large herbivores (≥100 kg); around 60% are threatened with extinction owing to land-use change, competition for habitat and resources with livestock, and hunting (Ripple *et al.,* 2015). Firstly, estimates of range contractions for elephant, hippopotamus, and black rhinoceros in Africa have shown that large herbivores currently occupy only 19% of their historical ranges on average. This is principally related to the greater area requirements of larger species, which have been disrupted through human encroachment (e.g. road building, urbanisation), habitat loss, cultivation, and deforestation. Secondly, livestock encroachment on areas colonised by wild herbivores has resulted in more competition for food and water (Ripple *et al.,* 2015; Mallon & Zhigang, 2009). Lastly is extensive over-hunting, which is the most significant driver of terrestrial herbivore decline (Milner-Gulland & Bennett, 2003; Craigie *et al.,* 2010; Lindsey *et al.,* 2013). Poaching of body parts is one aspect of this, which facilitates international organised crime (Ripple *et al.,* 2015).

One region where poaching of megaherbivores is particularly prevalent is the continent of Africa, where bush and forest elephants (*Loxodonta africana* and *Loxodonta cyclotis* respectively) are hunted for their ivory tusks, and rhinoceros species (*Cerathotherum simum* and *Diceros bicornis*) are pursued for their horn. Consequently, the poaching of the northern white rhinoceros (*Ceratotherium simum cottoni)* led to this species functional extinction in 2011 (Emslie, 2011). The southern white rhinoceros (*Ceratotherium simum simum)* remains in the wild, but is classified as near-threatened according to International Union for the Conservation of Nature (IUCN) status (Emslie, 2011; Ripple *et al.,* 2015). Between 2014 and 2017, over 100,000 African elephants were also slaughtered for ivory, and this species is considered to have a vulnerable status according to the IUCN (Blanc, 2008). The loss of megaherbivores, such as elephants and rhinos, can lead to cascading effects on other species, including predators, scavengers and mesoherbivores, and ecological processes involving vegetation, hydrology, nutrient cycling and fire regimes (Ripple *et al.,* 2015). Correspondingly, extensive conservation efforts have gone into protecting remaining megaherbivores. Many of these conservation programs have been initiated in South Africa as the largest remaining population of the southern white rhino resides there (Emslie & Brooks, 1999). In Kruger National Park, the southern white rhinos became locally extinct in the early 1900s until their reintroduction in the 1960s (Pienaar, 1993). Consequently, white rhino numbers were estimated at 10,621 individuals in 2010 (Ferreira *et al.,* 2012). Furthermore, African elephant populations in South Africa have recovered from a low of 120 individuals in the 1920s, to over 28,000 individuals in 2015 (CITES, n.d.; Yolanda *et al.,* 2018).

Whilst the growing numbers of rhino and elephants is positive, there has also been a growing rate of poaching. Poaching rates increased from 122 rhinos in 2009 to 1,338 in 2015, and a continental decline was seen in African elephant numbers between 2007 and 2016 owing to a surge in ivory poaching (Thouless *et al.,* 2016). This is mainly linked to the increasing demand for ivory and rhino horn in Asian markets, where such commodities are prescribed as traditional medicine to treat a variety of maladies including cancer, as well as indicating wealth and social status (Hanley *et al.,* 2017). Correspondingly, conservation efforts are imperative to the continuation of megaherbivore populations in Africa, and to be most effective these efforts must steadily improve and adapt to increasing ecological knowledge of these species. Understanding the ways in which species, including African bush elephants and Southern white rhinoceros', move according to environmental variables, such as water availability, is an important aspect of this (Owen-Smith, 1989).

1.2 Scientific background

1.2.1 Water availability in Kruger

In semi-arid savanna systems, such as Kruger National Park (KNP) in South Africa, the distribution patterns of water-dependent herbivores are predominantly restricted by the availability of surface water (Western, 1975; Redfern *et al.,* 2003). During the wet season when temperatures can reach high-30s (°C), water is fundamental to elephants and rhinos for thermoregulation and for drinking (Zambatis, 2006). However, during the dry season when rainfall is much lower, animals are limited to very scarce water availability. As water is so important in this environment, water management and policy changes within KNP has been highly debated within conservation for several decades. A policy was passed authorising the construction of 350 artificial waterholes in the 1980s to allow wildlife to always be within a 5 km radius of a water source (Gaylard *et al.,* 2003; Smit *et al.,* 2007b). This was partly related to the presence of fences around KNP, which limited water accessibility to animals during the dry season (Sutherland *et al.,* 2018). The goal of this policy was to provide wildlife with more water sources during dry periods, to improve rare antelope numbers, to sustain a habitat for migratory species, and to accumulate wildlife in focal areas to increase tourism revenue (Pienaar, 1983; Smit & Grant, 2009). The use of artificial waterholes was debated as their presence could have led to the depletion of forage due to high concentration of animals utilising an area they previously did not frequent (Rosenstock *et al.,* 1999; Smit *et al.,* 2007b). Furthermore, a drought during the 1980s highlighted local ecosystem concerns including the reduction in rare antelope numbers (Owen-Smith, 1996). This was largely related to water-dependent ungulates, which are the main prey of carnivores, moving into artificial waterhole areas that were initially only used by water-independent ungulates. This resulted in a shift from predation of water-dependent ungulates to more water-independent ungulates, such as antelopes, and also increased competition for food. As a result, the water policy of KNP was revised (the 'Systems Approach'; Smit *et al*., 2013), and now aims to close these artificial waterholes in order to restore natural variations in the landscape (Sutherland *et al.,* 2018).

1.2.2 Rhino and water relationship

African elephants (from here on called elephant) and southern white rhinos (from here on called rhino) are considered water-dependent species (Owen-Smith, 1989), and understanding how these animals have responded to changes in water availability and characteristics is now of substantial importance to their conservation. Literature on the drivers of rhino distribution is scarce, however, the pioneering work of Owen-Smith (1989) has formulated a basis of knowledge regarding the determinants of rhino distribution. Pienaar (1994) also contributes an important insight specifically into rhino habitat preferences within KNP. This empirical data highlighted the short-term and daily movement patterns of the rhino, which were governed by four primary activities including feeding and searching for graze, travelling, resting, and other movement behaviours such as drinking, wallowing (rolling in mud to keep cool), grooming, and interacting with conspecifics (Owen-Smith, 1989). As a large-bodied grazer, rhinos require a considerable amount of grass and therefore allocate the majority of their time to foraging. In one study that observed six rhinos that were translocated from Kenya and the U.S.A. to Uganda, rhinos allocated more than triple their time budget to grazing than they did to drinking, and even more time in comparison to bathing (Sheil & Kirkby, 2018).

Nevertheless, rhinos require regular access to surface water throughout the year for both cooling and drinking purposes (Pienaar, 1994). During the wet season rhinos drink once to twice daily (Owen-Smith, 1989). Owing to the high availability of water during this period, rhinos have been found to remain in smaller areas during the wet season (Owen-Smith, 1989; Pienaar, 1994; Pedersen, 2009). In the dry season, rhinos are forced to travel further and are only found to drink once every two to four days (Pienaar, 1994). Bathing in pools generally occurs in warmer conditions during midday, and can sometimes follow a period of drinking (Sheil & Kirkby, 2018). It has also been found that rhinos will lay in water during cooler parts of the day, and that drinking occurs during the night (Owen-Smith, 1973; Pienaar, 1994). These opposing findings may indicate that rhino dependence on water varies temporally (diurnally and seasonally) and spatially depending on the occurrence and location of water. It could also suggest that rhinos use waterholes for drinking and bathing at different times of the day, however, Smith (2016) found that rhino did not use waterholes for cooling down at all during his study and it was solely used for drinking.

Besides waterhole occurrence, very little is known about the specific characteristics of waterholes that rhinos are attracted to and why. Waterhole size, which is important as it could vary from a small puddle to a large dam, has only been analysed in one paper, of which found that waterhole size did not predict animal density (Smith, 2016). In terms of how permanent these water sources are, several papers have indicated that rhinos prefer permanent and longer-lasting water sources, particularly during the dry season when other temporary waterholes have dried up (Pedersen, 2009; Owen-Smith, 1989), however, these papers lack a robust, empirical approach to test the effect of waterhole permanence on rhino distribution. One paper has studied the source type of waterholes preferred by rhino, however this only focussed on artificial waterholes where rhinos preferred pans and troughs in Greater Kruger (Smith, 2016). This study highlighted that rhinos selected for artificial waterholes with lower slopes on its banks as other artificial waterholes, such as reservoirs, can often be inaccessible to the smaller-bodied rhino in comparison to the elephant (Smith, 2016; Kasiringua, 2010). Conversely, some papers have described the tendency of rhinos to graze in drainage lines, which is also where many natural waterholes occur (Perrin & Brereton-Stiles, 1999; Pedersen, 2009). However, whether rhinos utilise the natural waterholes more as a result of foraging on nearby vegetation has not been scientifically tested. During the dry season, rhinos will often move away from these drainage lines to seek taller grasslands on hillslopes in KNP as the lowlands and drainage lines no longer provide a high quantity of grass (Pienaar, 1994). Rhinos will also utilise shady trees on hillslopes to cool themselves during the midday heat (Sheil & Kirkby, 2018).

1.2.3 Elephant and water relationship

Drivers of elephant distribution and movement have been studied much more extensively than rhino, and there are several papers that document their relationship with waterholes. As with rhino, elephants spend a large proportion (around 75%) of their time feeding (Eltringham, 1982). They also allocate a lot of their time to resting, particularly in shaded areas during the hotter times of the day, travelling, and socialising (Sikes, 1971). Socialising is an important aspect of this species as they form large matriarch herds. On average, a herd size is ten elephants, but several family units can join to form a ‘clan’ consisting of up to 70 or more members (Lee & Moss, 1986). This social structure is important as these groups synchronise their activity, including waterhole use. Hayward & Hayward (2012) highlighted that elephants utilise water more than rhinos, and consequently are found to drink one to three times daily during the wet season (Owen-Smith, 1989). During the dry season, they can survive for periods of two to three days between waterholes visits and can travel up to 40 km to reach a water source (Pratt & Gwynne, 1977; Thaker *et al.,* 2019). Waterhole use peaks during the dry season, and they repeatedly utilise the same local waterholes (Stokke & du Toit, 2002; Thomas *et al.,* 2008; Grainger *et al.,* 2005; Hayward & Hayward, 2012). Similarly to rhinos, elephants will remain closest to water sources during hotter periods to enable thermoregulation (Thaker *et al.,* 2019; Purdon & van Aarde, 2017), but are found to rely on waterholes more for cooling purposes than rhinos do (Smith, 2016).

As with rhinos, waterhole size preferences of elephant has scarcely been covered. Some papers have looked at waterhole fidelity, highlighting that elephants stay in a smaller area and use the same waterholes in the dry season (Loarie *et al.,* 2009). However, another more recent paper showed the opposite and found that elephants show low fidelity to the same water source (Thaker *et al.,* 2019). It is clear that the literature on the size and permanence of waterholes is very minimal, despite these possibly being important aspects of waterholes to large herd sizes of elephants. There are more papers on waterhole source type and this is largely related to the recent conservation debate relating to the artificial waterhole openings in the KNP in the 1980s (Smith, 2016; Sutherland *et al.,* 2018; Smit *et al.,* 2007a; Smit *et al.,* 2007b; Smit *et al.,* 2009; Purdon & van Aarde, 2017; Loarie *et al.,* 2009; Kasiringua, 2010; Hayward & Hayward, 2012; Gaylard *et al.,* 2003; De Beer & van Aarde, 2008). It is believed by many that the introduction of the artificial waterholes contributed towards an increase in elephant numbers and that their dependence on these waterholes during the dry season may have had profound consequences on their distribution patterns (Chamaille-Jammes *et al.,* 2007; de Beer & van Aarde, 2008; Smit *et al.,* 2007a,b; Thomas *et al.,* 2008; Viljoen, 1989; Loarie *et al.,* 2009). However, it is argued that elephants prefer riverine habitat owing to the availability of abundant and high-quality forage, and that they will select rivers over waterholes (de Boer *et al.,* 2000; Harris *et al.,* 2008; MacFadyen et al., 2019; Purdon & van Aarde, 2017; Smit *et al.,* 2007a).

Several studies have looked at the importance of vegetation around waterholes to elephants, which contrasts the absence of literature on this topic for rhino. Radial gradients of vegetation degradation exist around waterholes and these are called piospheres (Lange, 1969; Thrash & Derry, 1999). Piospheres indicate the level of impact of herbivores utilising the water source, and bare ground cover generally increases under high trampling pressure. Conversely, the presence of shrubs and trees around waterholes indicates less trampling by herbivores, suggesting that the area is not used as intensively. Elephants are mixed-feeders, meaning that they eat a combination of grass and shrub and adjust their reliance on these food sources depending on seasonal availability (van der Merwe & Marshal, 2014). Landman *et al.* (2012) and Brits *et al.* (2002) found that shrub volume within piospheres increased as elephants moved further away from waterholes, and this is likely related to the elephants consuming these shrubs. Furthermore, tree cover was found to be directly proportional to elephant distance from waterholes (Thrash & Derry, 1999), which could be because debarking decreased around waterholes as elephants moved further away (Fullman, 2009). In studies in both Zimbabwe (Chamaille-Jammes *et al.,* 2009) and Malawi (Wienand, 2013) elephant abundance was not associated with woody cover around waterholes. A seasonal difference in foraging around waterholes has also been identified, whereby elephants increase their browsing levels close to water points during the dry season (Mukwashi *et al.,* 2012).

Elephants do not solely use waterholes for drinking and cooling but also have other behavioural coping mechanisms. They have evolved large ears to enable the animal to cool itself down by waving their ears back and forth. They also undertake dust bathing and wallowing, whereby they use mud to cool themselves. In terms of drinking, elephants are able to access water by digging wells with their feet and trunks in the dry sand of low-lying areas where groundwater resides near the surface (Rarney *et al.,* 2013). Two papers even found that elephants may dig wells adjacent to water pools rather than drinking from those readily available water sources (Payne, 1998; Rarney *et al.,* 2013).

1.3 Knowledge gap

It is clear from the literature that the current knowledge of environmental determinants of rhino distribution is minimal. Much of the research originates from the Hluhluwe-iMfolozi Park (HiP) in southern South Africa 30 years ago (Owen-Smith, 1989), and from KNP around 25 years ago (Pienaar, 1994). Whilst this research forms an important foundation for understanding drivers of rhino movement, it is important to build and expand on this research. More specifically, there is even less data focussing on rhino preferences of waterhole characteristics with most papers lacking long-term quantitative data in response to variations in water. Many studies have focussed on individual waterholes or rhinos rather than providing a measurement of rhino distribution patterns across a larger landscape with a network of waterholes.

In comparison, there is a wider coverage of elephant movement ecology, however there are aspects relating to waterhole characteristics that also lack including analysing the effect of waterhole size and permanence on elephant preferences for waterholes. The most explored area for waterhole characteristics includes that of artificial water sources, yet there is relatively little knowledge of elephant use of natural waterholes and how this compares to the utilisation of artificial sources. Comparing the dependence that herbivores have on artificial and natural waterholes across a seasonal gradient, as well as in relation to specific water characteristics (such as permanence and surrounding vegetation structure) is important in revealing why the animals are drawn to either source types, and may clarify the role that artificial waterholes are playing in governing animal distribution patterns and populations.

Vegetation around waterholes, or more specifically the piosphere effect, has been poorly described in terms of rhinos, however there are several key studies about the relationship between elephants and the piosphere effect (Landman *et al.,* 2012). By researching the relationship between the piosphere effect and the two species, this enables an interesting comparison for two herbivores with different feeding strategies. Understanding how other waterhole characteristics, such as waterhole permanence, impact the piosphere effect may be crucial in assessing the relationship between elephant and rhino and the piosphere effect at a more detailed level.

It is evident that there are several knowledge gaps within the scientific field regarding the preferences of rhino and elephants for specific waterhole characteristics. By researching two of the most poached megaherbivores at a landscape level, it enables a more holistic understanding of waterhole utilisation that can contribute to waterhole management in KNP and the surrounding area.

1.4 Theoretical framework

Season is mainly governed by climate variations, particularly temperature and precipitation within the semi-arid ecosystem found in South Africa (figure 1). These variables have an indirect and direct effect on elephant and rhino distribution. Directly, elephants and rhinos have preferences for varying levels of temperature and precipitation and this will consequently alter their distribution. Indirectly, temperature and precipitation govern characteristics of waterholes, including the size and permanence (through evaporation of water and rainfall flowing to waterholes), the source type (as artificial water sources are known to be more permanent and less impacted by evaporation) and vegetation type (as plant desiccation occurs at high temperatures and low rainfall levels). Waterhole permanence and size may also play a role in the piosphere effect, as vegetation around waterholes that are continuously fluctuating in size will have to tolerate more frequent inundation than vegetation around more permanent waterholes, and larger waterholes may be more frequently visited and thus have a higher trampling rate. Waterhole permanence may also be impacted by source type, as artificial waterholes are generally believed to be the more permanent and reliable sources of water in comparison to natural waterholes. By looking at these relationships between waterhole characteristics, this could help in interpreting the preferences of elephant and rhino densities for certain waterhole characteristics. The aforementioned relationships are visualised in figure 1.

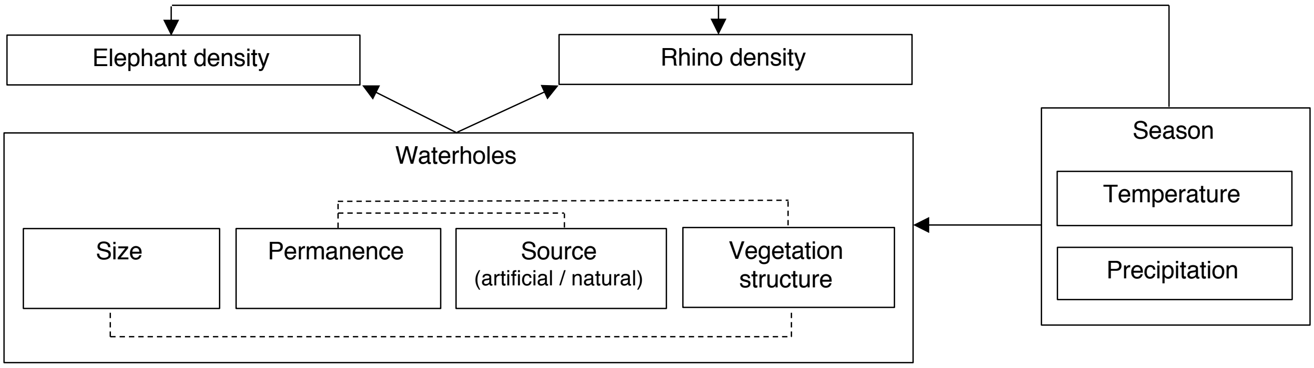


Figure 1. Theoretical framework of waterholes and their characteristics and its impact on elephant and rhino distribution as well as vegetation structure, where arrows indicate direct effects

1.5 Research questions

<u>Main research question</u>

To what extent does elephant and rhino distribution relate to the occurrence and defined characteristics of waterholes in Kempiana on a seasonal scale?

<u>Research sub-questions</u>

Owing to the variety of factors that were considered to fully understand the species' relationship with waterholes, several sub-questions were addressed:

1a. How does waterhole permanence and size influence grass and shrub cover surrounding waterholes?
1b. How does waterhole permanence relate to waterhole source type (natural or artificial)?
2a. How does waterhole occurrence influence the presence of elephants and rhinos?
2b. How does temperature and precipitation influence the relationship between waterhole occurrence and the presence of elephants and rhinos?
2c. How does waterhole size influence the distribution and density of elephants and rhinos?
2d. How does waterhole permanence influence the distribution and density of elephants and rhinos?
2e. How does waterhole source type (natural or artificial) influence the distribution and density of elephants and rhinos?
2f. How does the surrounding vegetation structure influence the distribution and density of elephants and rhinos near waterholes?

<u>Hypotheses</u>

In response to the research sub-questions regarding the effects of several waterhole parameters on elephant and rhino density, the respective hypotheses were drawn:

1a. Waterhole permanence and vegetation. Permanent waterholes will have higher trampling rate and therefore shrub and grass cover will be lower here than at more temporary waterholes.

1a. Waterhole size and vegetation. Larger waterhole areas will have higher trampling rate and therefore shrub and grass cover will be lower here than at smaller waterhole areas.

1b. Waterhole permanence and source type. Artificial waterholes will be more permanent than natural waterholes.

2a. Waterhole occurrence. Elephant and rhino will be distributed in areas with water, and will spend more time closer to waterholes during the dry season.

2b. Temperature and precipitation. Elephant and rhino will use waterholes more during seasons with high temperatures and less during seasons with high rainfalls.

2c. Waterhole size. Elephant and rhino will select for waterholes large enough for them (individuals as well as groups) to bathe in.

2d. Waterhole permanence. Elephant and rhino will select for more permanent waterholes during the dry season when water is most limiting, and will show a neutral response to waterhole permanence in the wet season when water is highly available.

2e. Waterhole source type. Elephants and rhinos will show preference for artificial waterholes as they are more available in the dry season, and will show a neutral response to waterhole source type in the wet season when both artificial and natural waterholes are present.

2f. Surrounding vegetation. Elephant will select for with high shrub and grass cover as they are mixed feeders. Rhinos will select for waterholes with high grass cover as they are grazers.

2 METHODS

2.1 Study region

I conducted this study in the Kempiana reserve in Greater Kruger, which is located in the Mpumpalanga province of South Africa (figure 2). Kempiana has been owned by the World Wide Fund for Nature (WWF-SA) since 1990, and is managed by the Kempiana Management Committee. It is around 130 km^2 in size, and is located immediately west of Orpen Gate, an entrance to KNP, and south of the Timbavati Private Nature Reserve (figure 2b). There are no fences between Kempiana and KNP or Timbavati, enabling free movement of animals. In the southern part of Kempiana, there is the Southern African Wildlife College (SAWC). The area is considered Lowveld Savanna, and is mostly underlain by granite and in some parts ancient gneiss (Pieterson, 1998). The Timbavati river runs west to east through the southern half of Kempiana, however, it runs dry for 99% of the year (Tula, 2014). At least six artificial earthen dams were built across the years in Kempiana, and there were also several disused gravel borrow pits in the southern area of which some have also been converted into dams (Pieterson, 1998).

The climate of Kempiana is similar to that of the adjoining area of KNP, with an average annual rainfall of 521 ± 215 mm and temperature of 21 ± 3 °C (Pieterson, 1998; WorldWeatherOnline, 2019). Summers generally have high temperatures and rainfall, peaking during the months of December to February. Winter is relatively cool and much drier, and occurs around June to August. Spring and Autumn also occur during October to November, and March to May respectively, however are not as extreme in weather conditions as Summer and Winter. As such, seasonal variation can also be divided in terms of wet and dry season, which is largely governed by rainfall and temperatures. The dry season generally lasts during the Winter period, and experiences an average seasonal rainfall of 19 mm and temperature of 17 °C (WorldWeatherOnline, 2019). Meanwhile, the wet season typically represents November to March and experiences an average seasonal rainfall of 421 mm and temperature of 23 °C (WorldWeatherOnline, 2019).

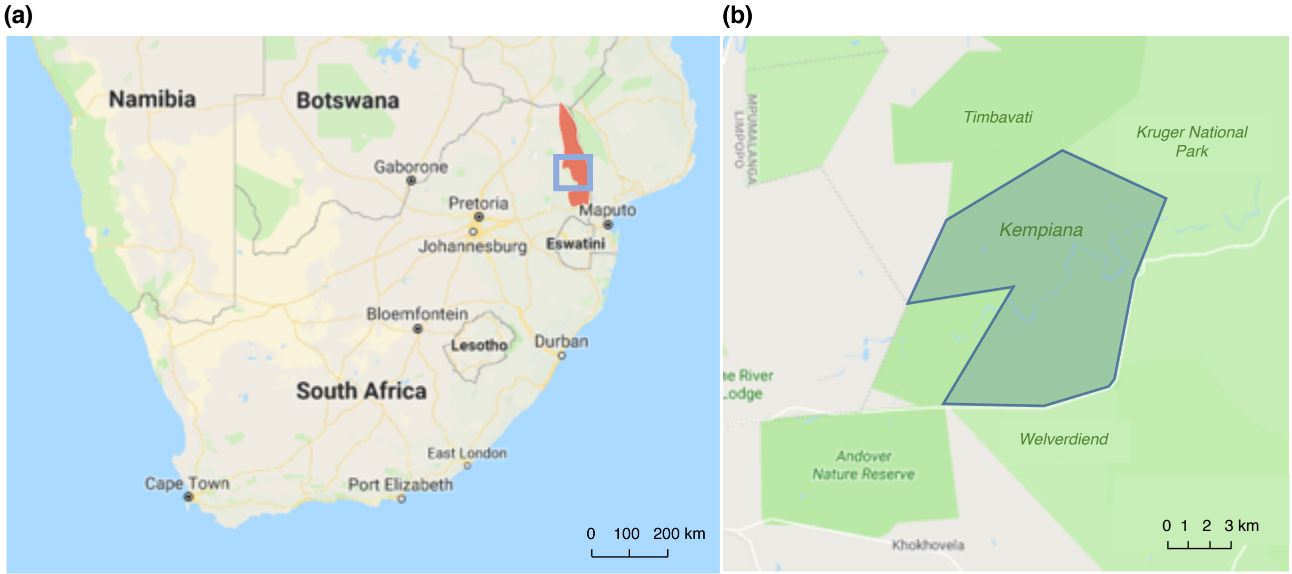


Figure 2. (a) Map of South Africa and surrounding countries, where the red area represents Kruger National Park and the blue square represents the general region of Kempiana, and; (b) detailed map of Kempiana study area

2.2 Spatial and temporal scale

The temporal scale of this study was largely related to the data that was available, particularly the waterhole data. Waterhole data, which includes waterhole size, permanence and the surrounding vegetation, was attained from Google Earth satellite imagery. A total of 10 days of satellite data were available between 2016 to 2018 where useful imagery of water availability (for example, not excessive cloud cover) overlapped with data on rhino and elephant distribution. Animal GPS data was collected by SAWC and was recorded using a fixed-wing aeroplane. On average, the animal GPS data was collected every 9 days from February 2014 to February 2019. However, only the animal data that coincided with the water data collected from Google Earth could be considered, which began in March 2016. As a result, it was decided that the data would be considered at a seasonal level. Whilst this could have been at a higher temporal resolution of one month, the resolution I could attain for water availability fit best with seasonal data of animal distributions. Using a seasonal scale also meant that it increased the reliability of the animal and water data (table 1). Water data was condensed down into seasons, often meaning that seasons consisted of a mean of several time periods. Equally, using a seasonal scale for animal data improved the reliability of the data, as often a temporal resolution of one month or less would present too few flight sessions to cover the whole study area (figure 3).

In terms of spatial resolution, I identified waterhole location to their specific GPS location. Elephant and rhino numbers and distribution was collected through an aerial survey from a fixed-wing aeroplane and any animals observed within 250 m either side of the aeroplane were included. This created a 500 m buffer around the aeroplane during its flights. Whilst this meant that the minimum size at which the data could be analysed was 0.5x0.5 km^2, a size of 1x1 km^2 was used. I used this coarser scale because at a scale of 0.5x0.5 km^2, over 80% of grid cells had neither water occurrence nor animal presence. As elephant and rhino are found to traverse long distances for water, it was decided that using a scale of 1x1 km^2 would not greatly impact the results found but would aid in removing large quantities of grid cells without water and animal presence. Not all grid cells were the same size on the edges of Kempiana owing to its irregular shape (seen in figure 5), however this was accounted for during the analysis (as discussed further in section 2.3.7).

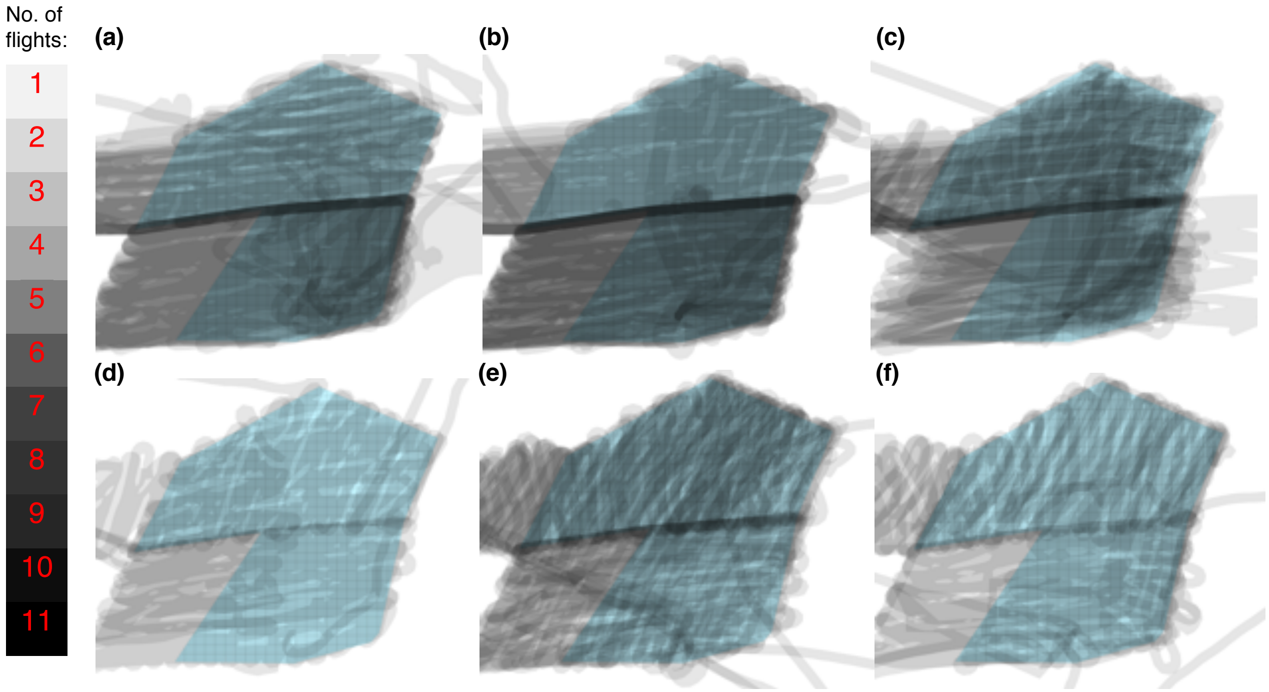


Figure 3. Flight cover, with a 500 m buffer, of the Kempiana region (in blue) during animal distribution data collection in (a) Autumn 2016; (b) Winter 2016; (c) Autumn 2017; (d) Winter 2017; (e) Summer 2017/2018, and; (f) Spring 2018

Table 1. Data available per season for water (dates featuring satellite imagery on Google Earth) and animal distribution (total flight time dedicated to collecting animal data)

Season	*Satellite imagery dates*	*Total flight time (hh:mm)*
Autumn 2016	07/03/2016	19:20
Winter 2016	11/06/2016, 26/06/2016, 09/07/2016	06:31
Autumn 2017	18/04/2017, 07/05/2017	20:37
Winter 2017	24/07/2017	18:52
Summer 2017-2018	01/01/2018	13:38
Spring 2018	14/11/2018, 26/11/2018	08:17

2.3 Data collection

2.3.1 Waterhole occurrence

I identified waterhole presence initially using Google Earth. The entirety of Kempiana was analysed for all ten dates of satellite imagery, and anything that resembled a waterhole or similar was noted. To check waterhole legitimacy, I undertook ground-truthing by foot and by aeroplane. Owing to the dense nature of some parts of the savanna system and the lack of infrastructure, ground truthing waterholes by foot was highly time consuming, and as a result only fourteen waterholes were checked. Aerial ground-truthing proved more efficient and the entire region of Kempiana was covered by flight during March 2019. This was conducted with an experienced pilot that collects the animal GPS data and is highly knowledgeable about the Kempiana area. This aided in identifying the waterholes flown over, and photos and GPS readings were taken for each waterhole (examples of waterholes can be seen in figure 4). These GPS readings were then relayed into Google Earth. All waterholes that were initially identified, but had not been confirmed during ground-truthing were assessed again by comparing their satellite images to that of confirmed waterholes to see how closely they resembled the latter. Those that were initially identified using satellite imagery but were discarded in the end were predominantly wallows as confirmed during ground-truthing. Conclusively, I identified 144 waterholes in Kempiana (see figure 5). These waterholes were then allocated to a grid cell, as discussed in section 2.2. Rather than using number of waterholes per grid cell, the cells were labelled with either water presence or absence for this part of the study.

Figure 4. (a) Example of a Google Earth satellite image of waterhole 1 identified prior to ground-truthing; (b) Image of waterhole 1 taken from aerial ground-truthing; (c) Example of a Google Earth satellite image of a waterhole 2 identified prior to ground-truthing, and; (d) Image of waterhole 2 taken from ground-truthing by foot

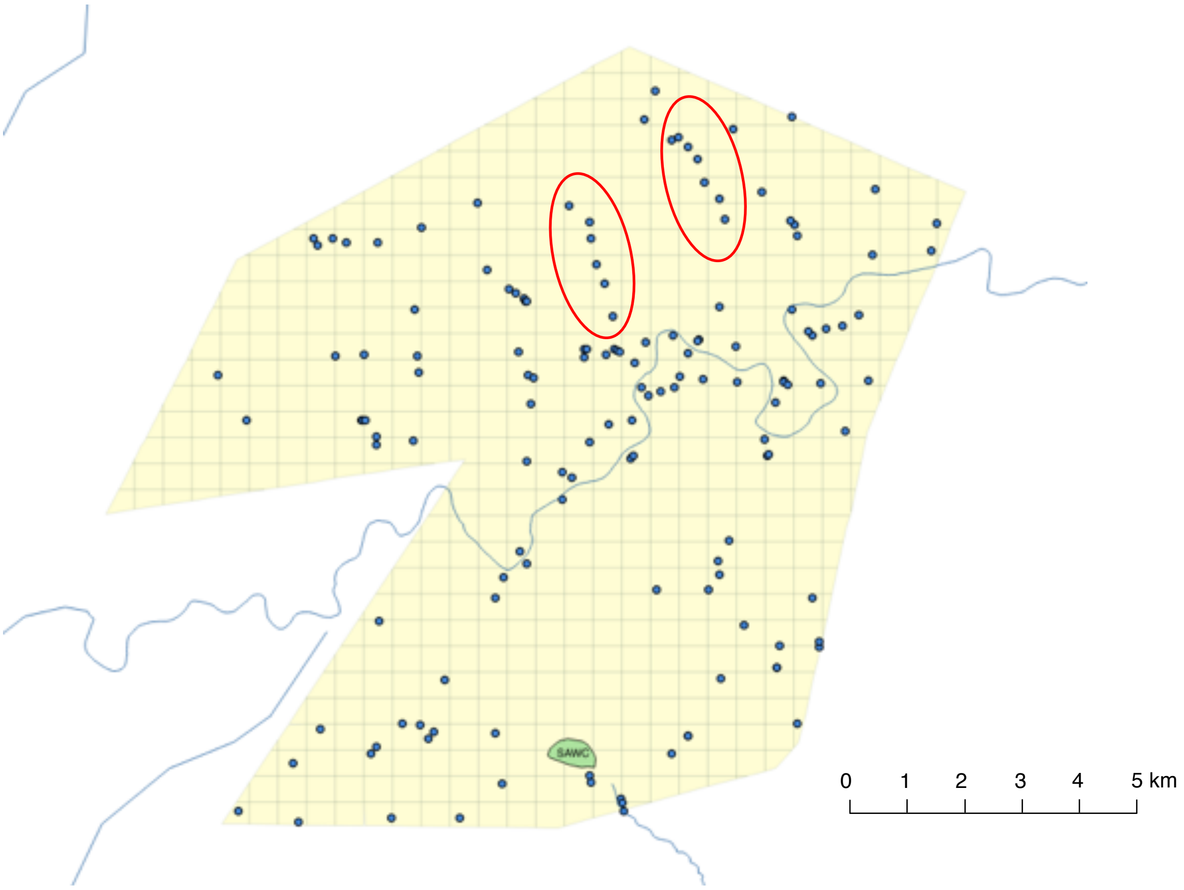


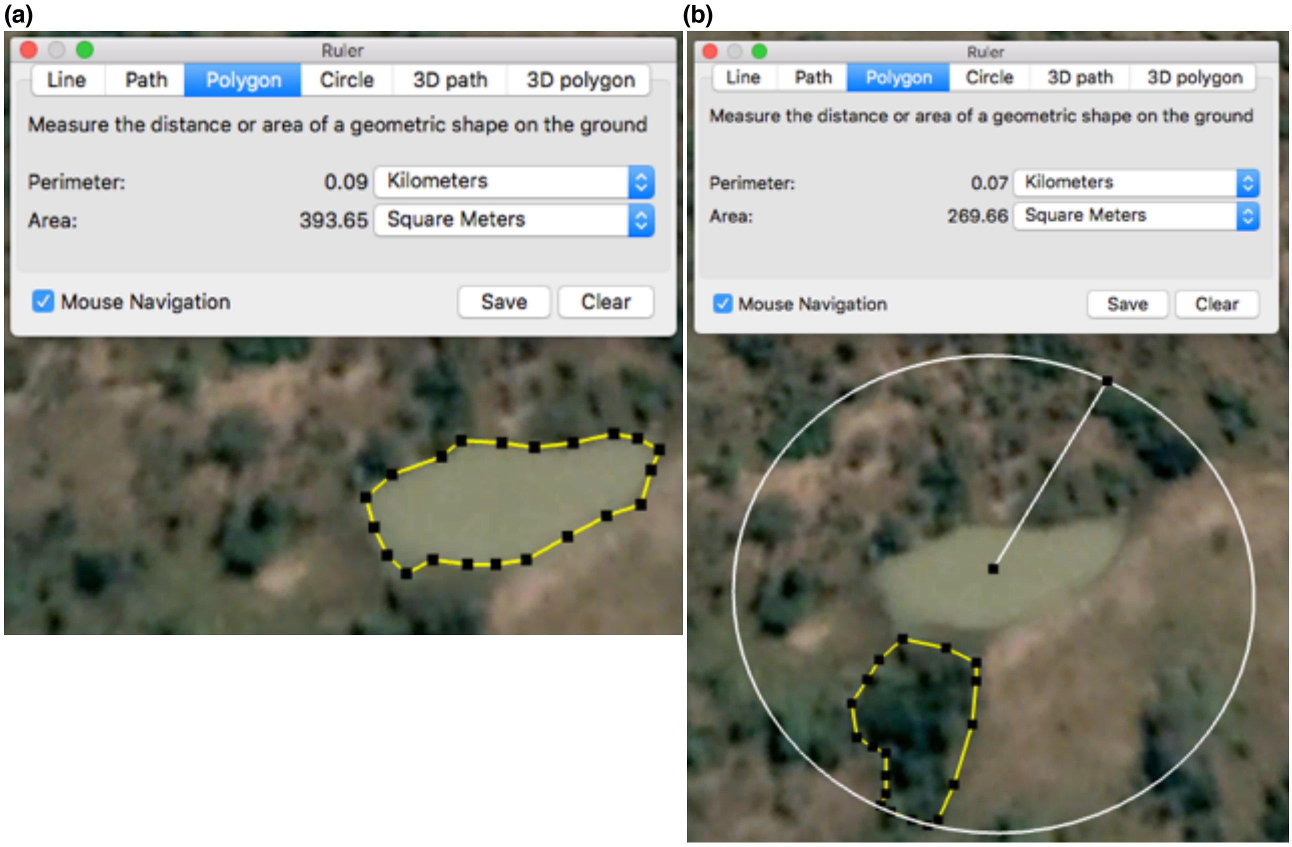
Figure 5. Locations of waterholes (blue markers) present in the Kempiana region between 2016 and 2018, with the Timbavati River running through the centre and the SAWC campus in the southern region (red circles represent two examples of drainage areas with natural waterholes)

2.3.2 Weather

Weather data was extracted from two weather stations, one North of Kempiana and one South of Kempiana. The Northern weather station came from the Timbavati Private Nature Reserve around 3 km away from the Kempiana border, and the Southern weather station came from Welverdiend, a small community also around 3 km away from the Kempiana border (see figure 2b for locations of both places). The Timbavati data was acquired from the main ecologist of the reserve, and the Welverdiend data was provided by WorldWeatherOnline (2019). Whilst Kempiana had their own weather station, data was incomplete for several seasons that I had studied, and there were no other weather stations within close distance of the remote Kempiana region. I received monthly values of total precipitation and average temperature from both weather stations. To calculate seasonal values, I summed monthly precipitation values that fell within the season at question, and I determined the mean of monthly temperature levels that fell within the season at question. For example, if it was precipitation during Winter 2016, then a sum of the rainfall during June to August 2016 was calculated, and if it was temperature then a mean for these months was taken. Whilst Kempiana is small and therefore the weather is not expected to vary greatly from the northern to the southern region, an interpolation was still calculated to allow for some variation across the region. The grid was broken up into five regions on a latitudinal basis, and the precipitation and temperature was calculated for that section by varying the weight of the averages. Winter, Autumn, Spring and Summer were then either assigned to be part of the dry and wet season according to temperature and precipitation levels.

2.3.3 Waterhole size

I calculated the size of each waterhole on Google Earth satellite imagery. I used the ruler feature and assumed the waterhole to be a polygon in order to trace the entirety of the water's edge, giving the total water area in square metres (figure 6). As mentioned in section 2.2, this was done for all dates available on Google Earth, which amounted to ten dates. In total, around 2000 measurements were taken for waterhole area across the 144 waterholes and 10 days of available Google Earth imagery. The outline of the waterholes were generally discernible in Google Earth (as seen in figure 4), making it easy to distinguish where the waterhole started. Occasionally vegetation would be within waterholes, such as large bushes in the centre, and the area of this vegetation (calculated in the same way as water area) was simply subtracted from the total area. As previously discussed, each waterhole was allocated to its grid cell, and therefore the area of the waterhole was also designated to the same grid cell. If there was more than one waterhole in a grid cell, then the sum of waterhole area was calculated to represent the total water availability in that cell. Subsequently, the data was broken up into six seasons (as also discussed in section 2.2) between 2016 and 2018. When a season featured waterhole area data from more than one day's worth of data from Google Earth, the mean was calculated. For example, if there were three days during Winter 2016 where a specific grid cell had 100 m², 320 m² and 240 m², then an average of these three figures would be taken for that grid cell during Winter 2016. Conclusively, each grid cell had 6 seasons worth of waterhole area data.



(a)

Measure the distance or area of a geometric shape on the ground

Perimeter: 0.09 Kilometers

Area: 393.65 Square Meters

(b)

Measure the distance or area of a geometric shape on the ground

Perimeter: 0.07 Kilometers

Area: 269.66 Square Meters

Figure 6. (a) Example of measuring waterhole size (yellow outline) using the ruler feature in Google Earth, where the area used in the study would be 393.65 m² in this case, and; (b) Example of measuring vegetation cover (e.g. tree cover in yellow outline is 269.66 m²) within an area surrounding a waterhole (white circle)

2.3.4 Waterhole permanence

To calculate waterhole permanence, I took the waterhole area data for all six seasons for each grid cell. I then undertook a standard deviation calculation across these water area figures for each cell to indicate how much that grid cell temporally varied in waterhole area (as a proxy for variation in water availability). A large standard deviation value represented a grid cell with great fluctuation in water availability, and was generally considered to be a more temporary water source. A small standard deviation value indicated a grid cell with greater permanence of water availability.

2.3.5 Waterhole source type

I classified waterholes as either artificial or natural origin using the "Kempiana Management Plan" by Pieterson (1998). Whilst this document is not up to date, it highlighted the location of several artificial waterholes in the form of both earth dams and borrow pits (see appendix 1). Waterholes that I had identified were compared to the map from the management plan to establish which water sources were artificial. The management plan also featured a map of drainage lines throughout Kempiana (see appendix 1). As many natural waterholes were known to be present in these areas owing to the low-lying nature of them, I denoted the waterholes in drainage lines as natural sources. An example of a drainage line featuring natural waterholes is highlighted in red in figure 5. I could not identify some waterholes that were neither known as artificial nor were in drainage areas, and therefore these waterholes were left without classification. When grid cells featured more than one waterhole and they were of differing or unknown sources, I left this grid cell without water source type classification. This meant that there was less data for waterhole source type than there was for the other data regarding water characteristics, and this will be discussed further in section 2.4.

2.3.6 Surrounding vegetation

The vegetation I considered in this project included bare ground cover, grass cover, shrub cover and tree cover. Calculating the cover of each vegetation type was again done in Google Earth. I used the day where each waterhole was at its largest, and an area that was ten times as large as the waterhole was analysed for surrounding vegetation (for example, if a waterhole was 310 m^2 on the day it was largest, then an area of 3100 m^2 was examined for vegetation). This area of examination was chosen as waterholes varied greatly in size and therefore using a standard area would not be suitable for all waterholes. Whilst an area of this size may not include the entire piosphere, it focuses on the area with the strongest piosphere effect including the sacrifice zone as well as its surrounding area (Landman *et al.,* 2012). Furthermore, whilst utilising a more general map of vegetation types across the Kempiana area would have been straight-forward, it would not have been detailed enough to understand how the usage of waterholes had impacted surrounding vegetation and the piosphere effect.

To estimate the vegetation cover, I drew a circle that was ten times the size of the waterhole from the centre of the waterhole in Google Earth using the circle function in the ruler feature. The area (m^2) covered by each vegetation type was then calculated using the ruler function in the same way that was done for waterhole size. I assumed that the vegetation areas were polygon shaped, and I drew around the outline of a vegetation patch (see figure 6b). As the same type of vegetation often did not grow in a continuous area but rather in patches, the sum of all patch areas for that vegetation type was calculated. Bare ground and grass were easy to distinguish as bare ground was often a sandy colour, whilst grass was green in colour. Whilst the colour of grass did depend on the time of year that the image was taken, the waterholes were always their largest during the wet season when grass was very green. Shrubs and trees were often more difficult to decipher owing to similarities in their appearance, however the photos taken during ground-truthing of the waterholes were used to confirm whether vegetation was either shrub or tree. I then calculated the percent cover of each vegetation by subtracting the waterhole area from the analysed vegetation circle area, and calculating the percentage that each vegetation type made up of the remaining area.

2.3.7 Animal density

As discussed in section 2.2, the distribution data of the rhino and elephant was collected by fixed wing aeroplane, and all flights undertaken during the seasons aforementioned were used. The data collected from the flights came in the form of GPS coordinates of observations for which the species (elephant or rhino) and number of individuals were noted. Since the data was given in a point format, a point-to-grid method was utilised to join the animal data to the 1x1 km^2 grid used for the previous water measurements. This was done in ArcGIS using the spatial join feature, giving each cell a total of density of observed elephants and rhinos during that season.

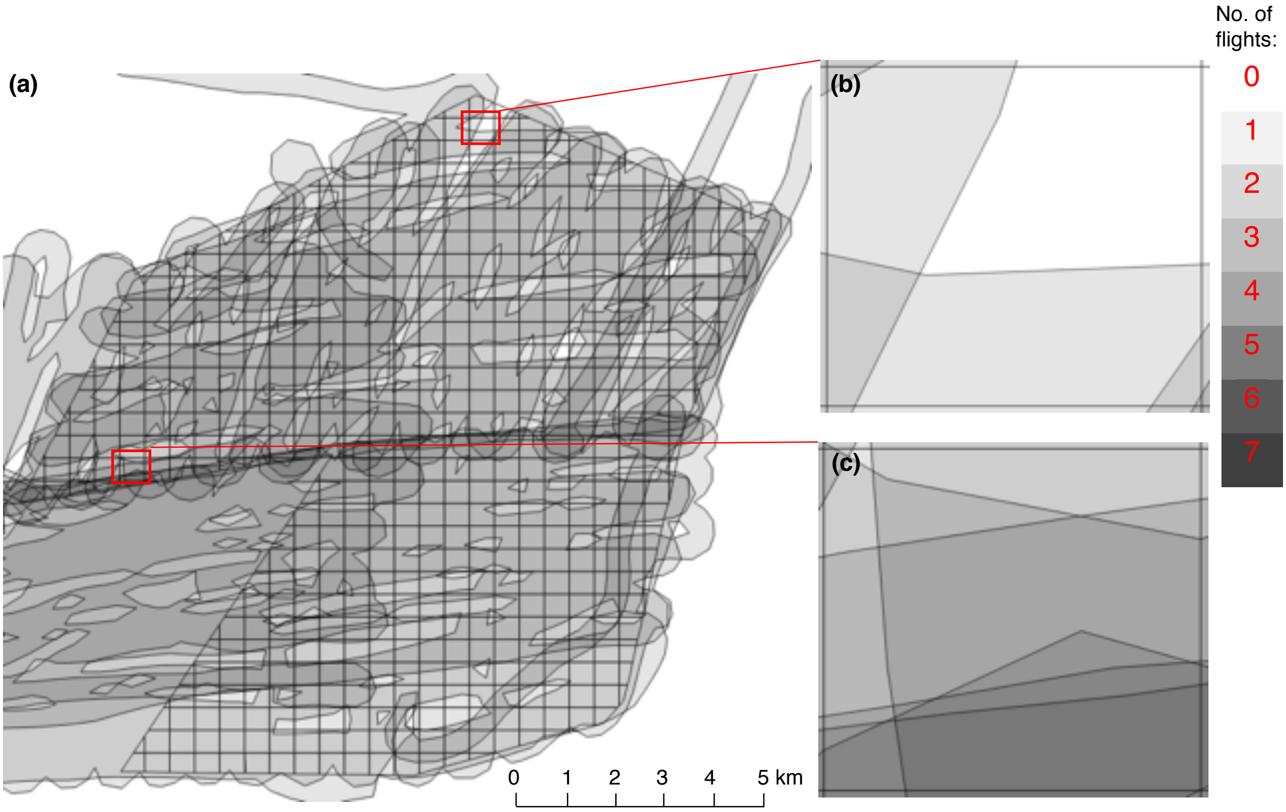


Figure 7. (a) Flight transects during Winter 2017 across the grid of Kempiana study region where the darker the area the more flight coverage; (b) an example of a cell that has not been fully covered; (c) an example of a cell that has been covered entirely and on multiple occasions

Several limitations associated with this data included the fluctuations in flight hours and paths over time, as well as the visibility from the aeroplane to collect animal data. Firstly, the pilot did not undertake standardised flights on a temporal basis and therefore there was a disparity in the flight frequencies. Secondly, flight paths also varied throughout time. As flights began from the college grounds and Kempiana was a focal area in the animal distribution data collection, the study region was largely covered in compared to surrounding areas. Nonetheless, the variation in flight frequencies and cover created a bias in sampling intensity of grid cells and thus the animal density estimates, and this had to be accounted for. The flights ran at an altitude of 500 m and had a 250 m visibility either side of the aeroplane, creating a buffer of 500 m. This buffer also had to be accounted for as it indicated the area that was observed during the flight. To account for both of these aspects, all flight paths undertaken during a season were fitted with a buffer of 500 m, and were overlaid on the 1x1 km^2 grid. The tabulate intersection tool in ArcGIS was then used to calculate how many times, and what extent of, each grid cell had been covered by flight. This can be seen in figure 7, where there is great variation in flight paths and cover. This tool in ArcGIS gave each cell a percentage cover, where 1100% would indicate that the entire cell was flown over on eleven occasions, and 100% would indicate that the cell was only entirely flown over once during that season. This percentage value became what was considered the correction factor or offset in the statistical analyses, which will be discussed further in section 2.4. Overall, all cells during each season had a coverage of over 100%, meaning that all cells were entirely covered during that season at least once.

2.4 Statistical analyses

For the statistical analyses, I used R Studio software and Matrix and lme4 packages to undertake several generalised linear-mixed effect models (R Core Team, 2012; Bates *et al.,* 2012). To identify the type of models to use, elephant and rhino density (including the correction factor for varying flight cover) were firstly checked for normal distribution. The residual errors of the models were not normally distributed, and were strongly left-skewed. As a result, binomial and poisson regressions were used to analyse the data. These models featured the correction factor for varying flight cover over individual cells as the offset, allowing the difference in effort levels for collecting animal GPS data to be accounted for in the models. The cell ID was used as a random factor in these models to control for random variability and repeated measurements of the same cells during different seasons. A complete overview of all statistical tests run can be seen in figure 8.

First, I ran binomial generalised linear-mixed effect models to look at how animal presence was related to water presence (research sub-question 2a) and whether temperature and precipitation played a role in this (research sub-question 2b). Water occurrence, temperature, precipitation and season were included as fixed effects, and interactions between water occurrence and temperature, precipitation and season was included. This was done for both elephant and rhino and can be seen in test 1 of figure 8.

Then, I used poisson regressions on a reduced dataset of only grid cells where water was present to look further into how waterhole characteristics influenced animal density. The first poisson regression model included waterhole area size, permanence and all vegetation covers (research sub-questions 2c, d & f). Within the same model was also interactions between season and these aforementioned fixed effects, of which can be seen in test 3 of figure 8. In this model, waterhole area size and permanence were entered as binomial variables owing to several substantial outliers in the data that impacted statistical analysis. The categories used can be seen in table 2.

As previously discussed in section 2.3.5, waterhole source type was a smaller dataset than the general water dataset owing to unidentifiable data, and therefore could not be included in the other poisson model. As a result, the second poisson model I ran included waterhole source type and season, both as individual fixed effects and also with an interaction (test 3 in figure 8; research sub-question 2e).

The remaining models focussed on the relationships between waterhole characteristics (research sub-questions 1a & b). I ran four models, including the relationship between waterhole permanence and size with vegetation (test 4 and 5 in figure 8) and the relationship between waterhole permanence with waterhole source type (test 6 in figure 8). Cell ID was again used as a random effect here in order to allow for repetition of vegetation cover in each cell. Waterhole permanence were used as continuous variables (rather than their binomial categories) in models where they featured as the response variables (test 6).

With all models previously discussed, I deduced the best-fit model to explain animal presence or density (or a waterhole characteristic for tests 4 to 6) through a process of simplification. The fixed effect with the highest p-value, and therefore the least significance, was removed. A likelihood ratio test was then conducted. For test 1 and 2 (figure 8), I used the Akaike Information Criterion (AIC) values of the original model and the new model with the fixed effect removed. This process was continued until only significant variables were left within the model. The AIC values of all models were then compared using ΔAIC, which is the difference between the model with the lowest AIC value and another model. Whilst the model with the lowest AIC value is generally considered to be the best-fit, models with ΔAIC of 2 or less cannot be differentiated in terms of quality and explanatory power. According to the principle of Occam's razor (Blumer *et al.,* 1987), the best model to select with a ΔAIC value of less than 2 is the one that is the simplest. For tests 3, 4, 5 and 6, likelihood ratio tests were again conducted. The chi-square (X_2) value and p-value of the comparisons between models were used to examine whether a fixed effect was included in the best-fit model. The summaries of the best-fit models from tests 1, 2 and 3 (figure 8) have been included in tables in the results section. For test 2, individuals models of each fixed effect (across season) were also run in order to clearly see estimates, standard error and p-values. This was done as the test 2 models were often more complex with many interactions. Therefore, those values that are cited in text and are not referenced to any tables in the results section come from these individuals models conducted. The significance level of the p-values are reported as $p < 0.05$ = (*), and $p < 0.001$ = (**), and the p value is reported if it is not significant.

Table 2. Categories of waterhole size and permanence used in tests 1-6 of figure 8

Fixed effect	*Category*	*Size (m^2)*
Waterhole permanence	Permanent	< 79
	Semi-permanent	80 – 299
	Semi-temporary	300 – 599
	Temporary	> 600
Waterhole size	Small	< 199
	Medium	200 – 999
	Large	> 1000

2.4.1 Methodological framework

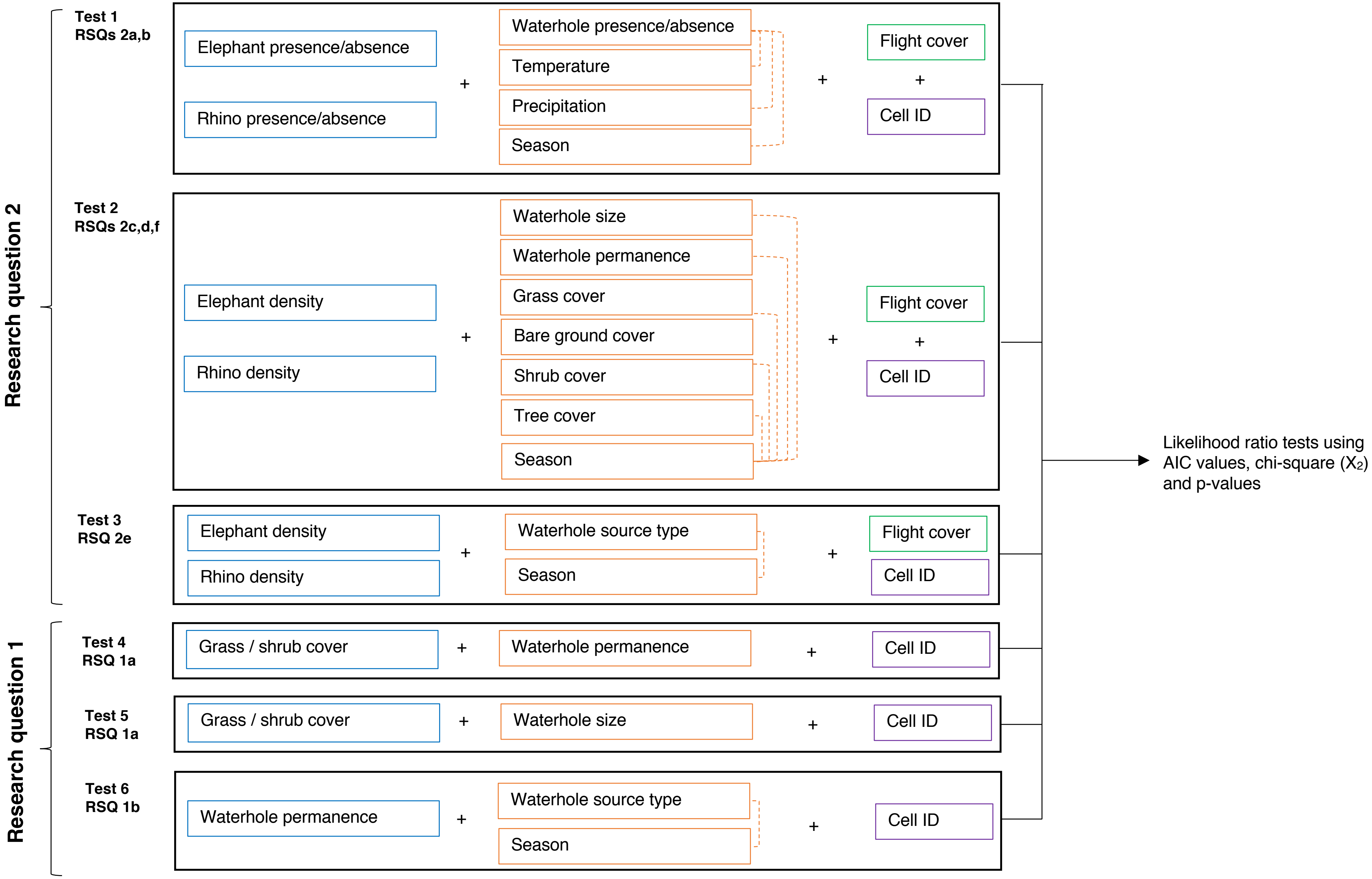


Figure 8. Statistical methodological framework denoting the models used, where blue boxes represent response variables, orange boxes represent fixed effects (and dashed lines indicate interactions), green boxes represent the offset, and the purple box represents the random effect

3 RESULTS

To identify which seasons fell within the dry and wet period, the temperature and precipitation levels were studied. It revealed that both weather variables were highest during Summer months, with similar temperatures maintained during Spring (figures 9). In comparison, Winter temperatures were around 8 °C lower than Spring and Summer, and precipitation levels were considerably lower than all other seasons. Autumn precipitation and temperature levels were intermediate compared to other seasons, however had a much higher rainfall level than that of Winter (over 100 mm) and a very wide standard deviation. As a result, it was decided that Spring, Summer and Autumn would constitute as the wet season, and Winter as the dry season.

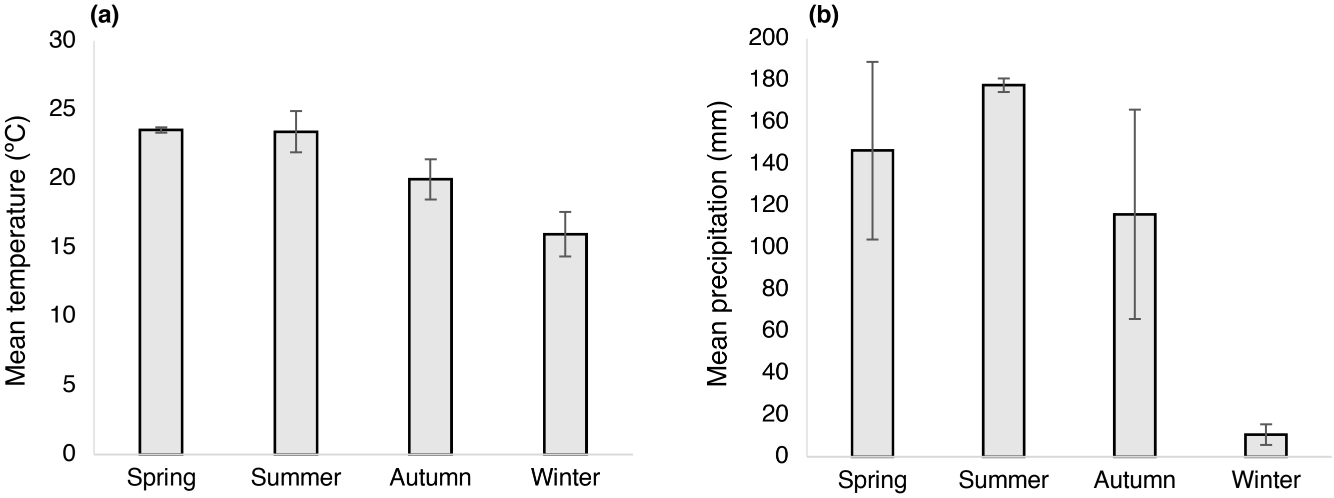


Figure 9. (a) Mean temperature and; (b) mean precipitation levels for Spring 2018, Summer 2017/2018, Autumn 2016 and 2017, and Winter 2016 and 2017

Overall, observed elephant density was much higher than observed rhino density, with a mean of 18 ± 51 elephants and 4 ± 8 rhinos in each km^2 area (figure 10). Both elephant and rhino observed density was found to be highest during the dry season, especially for rhino where density more than doubled in comparison to the wet season. As seen by the standard deviation, elephant and rhino mean density varied substantially across cells.

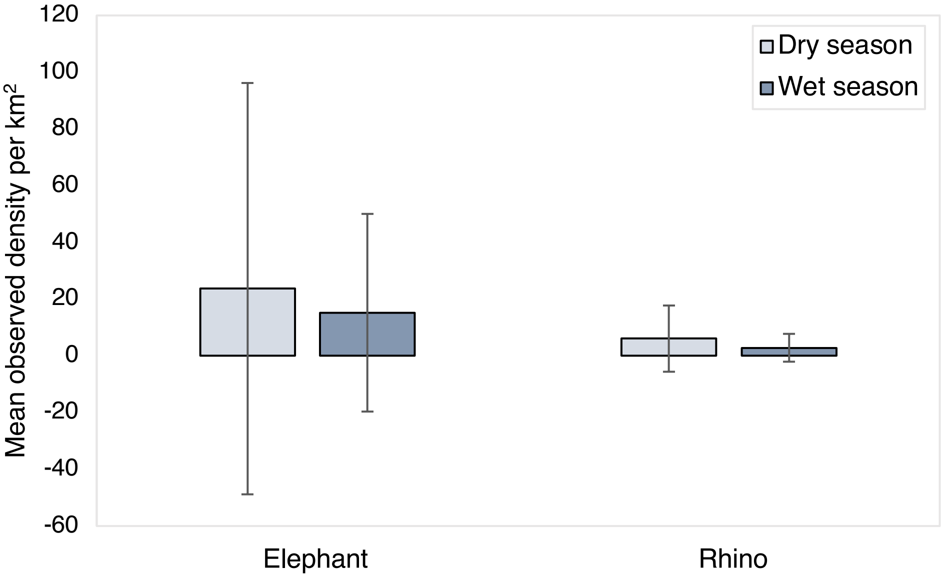


Figure 10. Mean elephant and rhino observed density per cell across seasons as corrected for by flight path cover

A seasonal difference was seen in terms of waterhole size, with large and medium waterhole cover remaining much higher during the wet season, whilst the cover of smaller waterholes was slightly higher in the dry season (figure 11a). The cover of all permanence level types remained highest during the wet season (figure 11b). The total cover of temporary waterholes varied the least across a seasonal gradient, whilst semi-permanent waterholes varied the most. The percentage of cells in the study region featuring natural and artificial waterholes was similar during the dry period. However, during the wet season there was a considerable difference in cover, with natural water sources being substantially higher (figure 11c). Lastly, the most prominent vegetation type around waterholes was identified as grass, and the scarcest was tree (figure 11d). Across a seasonal scale, bare ground and tree cover were higher during the dry season whilst grass and shrub cover were higher during the wet season. None of the vegetation types drastically changed across seasons, with the largest difference being between wet and dry seasonal covers of bare ground (31.89% and 35.16% respectively).

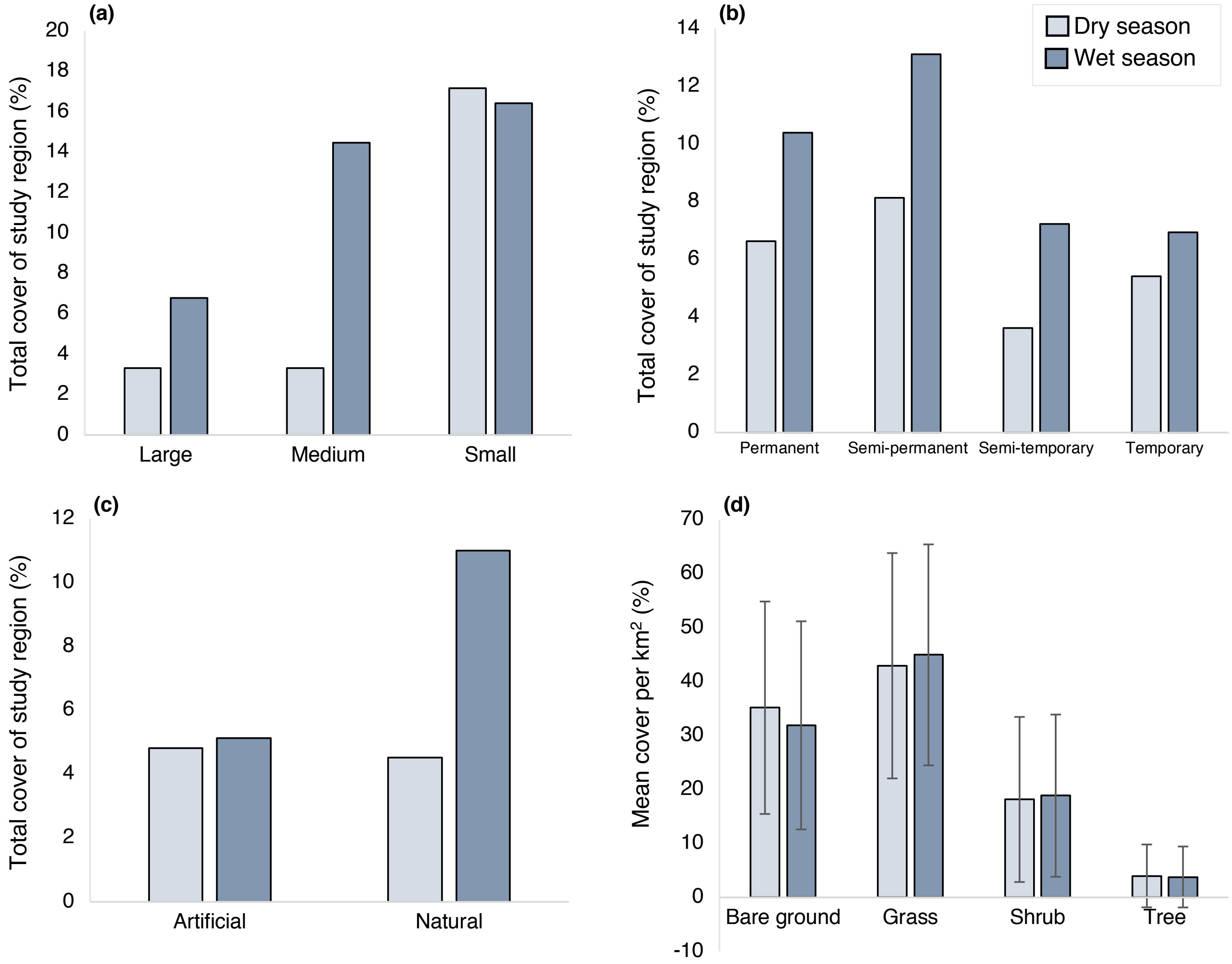


Figure 11. (a) Total seasonal percentage of cells in the study region featuring different sizes of waterholes; (b) different permanence levels of waterholes, and; (c) different source types, and; (d) mean seasonal cover of vegetation types surrounding waterholes per grid cell

3.1 Interactions between waterhole characteristics

Waterhole size did not significantly predict grass cover ($X_2 = 0.025$, $p = 0.988$) or shrub cover ($X_2 = 0.176$, $p = 0.916$). However, waterhole permanence predicted shrub cover ($X_2 = 9.139$, $p < 0.05$). Shrub cover was significantly higher around temporary waterholes than permanent waterholes (figure 12, table 3). In terms of permanence, waterhole source type did not predict waterhole permanence ($X_2 = 3.782$, $p = 0.057$), and the effect of source type on waterhole permanence did not significantly vary between the seasons ($X_2 = 0$, $p = 1$).

Table 3. Summary of model run between mean shrub cover and water permanence, where (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	2.062	0.231	8.922	< 0.001**
Semi-permanent	0.410	0.303	1.354	0.176
Semi-temporary	0.692	0.355	1.950	0.051
Temporary	1.070	0.362	2.959	< 0.05*

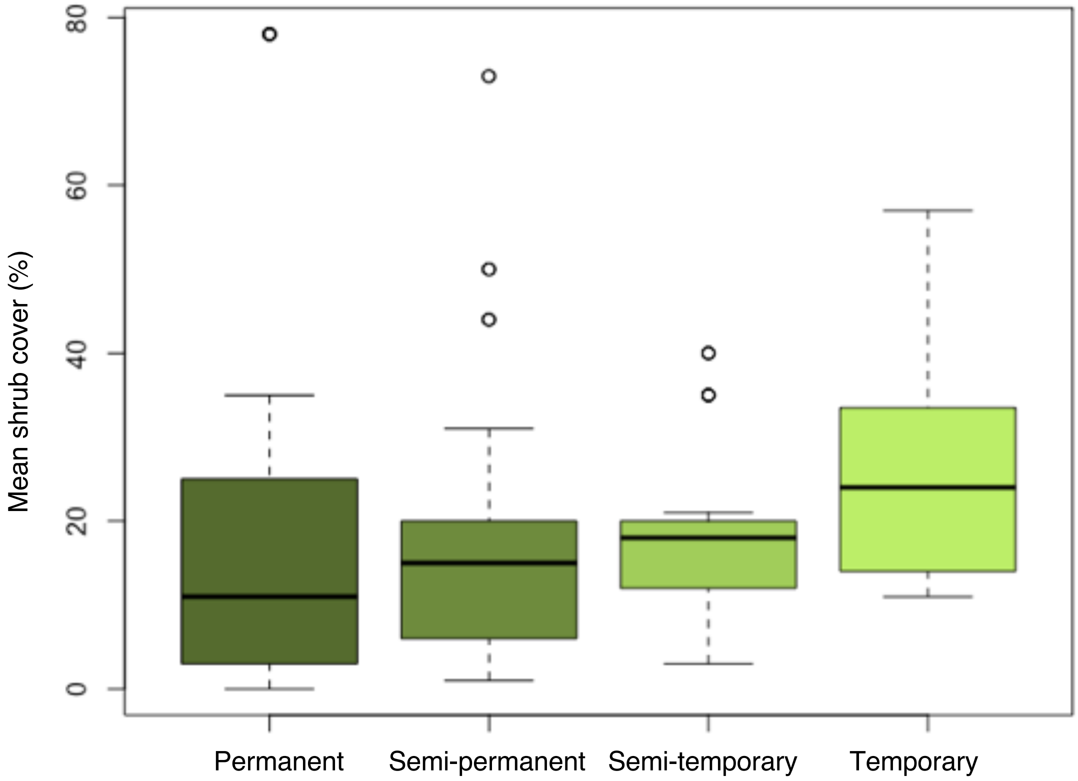


Figure 12. Mean shrub cover according to varying levels of water permanence

3.2 Elephant

3.2.1 Waterhole occurrence

Observed elephant presence was best predicted by a model containing temperature, water occurrence and an interaction between these effects (model 4, table 4). Elephant presence was highest in areas without water in comparison to areas with water (table 5). However when considered over a temperature gradient, observed elephant presence was higher in areas with water (estimate = -0.758, std. error = 0.021, p = 0.809) than without water (estimate = -0.776, std. error = 0.021, p = 0.546). In temperatures over 24 °C, elephant presence increased in areas with water (figure 14).

Table 4. Models tested for elephant presence/absence and water occurrence, where the results of likelihood ratio tests between models can be found in table 1, appendix 2

Model	*Variables*	*AIC*	*ΔAIC*
3	Model 1 minus water occurrence:precipitation, water occurrence:season	1258.3	0
4	**Model 1 minus precipitation, season, water occurrence:precipitation, water occurrence:season**	**1258.5**	**0.2**
5	Model 1 minus temperature, season, water occurrence:temperature, water occurrence:precipitation, water occurrence:season	1260.1	1.8
2	Model 1 minus water occurrence:precipitation	1260.2	1.9
6	Model 1 minus water occurrence, season, water occurrence:temperature, water occurrence:precipitation, water occurrence:season	1261.9	3.6
1	Elephant ~ water occurrence + temperature + precipitation + season + water occurrence:temperature + water occurrence:precipitation + water occurrence:season	1262.1	3.8

Table 5. Summary of model 4 in table 5, where (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	-0.354	0.490	-0.723	0.470
Water presence	-1.413	0.907	-1.557	0.119
Temperature	-0.033	0.025	-1.328	0.184
Water presence: temperature	0.086	0.045	1.935	< 0.05*

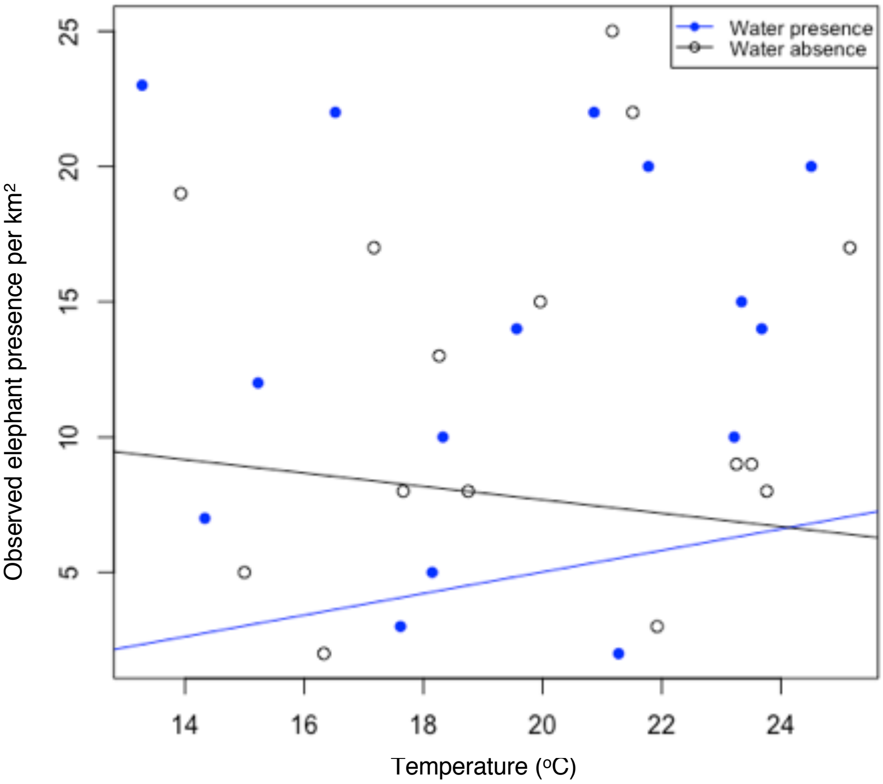


Figure 14. Observed elephant presence across a temperature gradient in water present and absent cells

3.2.2 Waterhole characteristics

Observed elephant density was best predicted by a model featuring all fixed effects, including season, waterhole area size, permanence, and grass, tree, shrub and bare ground cover all across a seasonal gradient (model 1, table 6). A breakdown of each fixed effect can be seen in table 7.

Table 6. Models tested for elephant density and water characteristic variables, where the results of likelihood ratio tests between models can be found in table 2, appendix 2

Model	*Variables*	*AIC*	*ΔAIC*
1	**Elephant ~ season + water area + permanance + grass cover + tree cover + shrub cover + bare ground cover + water area:season + permanence:season + grass cover:season + tree cover:season + shrub cover:season + bare ground cover:season**	**5071.4**	**0**
5	Model 1 minus permanence:season and permanence	5147.1	75.7
4	Model 1 minus permanence:season	5149.3	77.9
3	Model 1 minus water area:season and water area	5149.5	78.1
2	Model 1 minus water area:season	5220.2	148.8
13	Model 1 minus shrub cover:season and shrub cover	5242.2	170.8
12	Model 1 minus shrub cover:season	5243.8	172.4
6	Model 1 minus grass cover:season	5246.0	174.6
7	Model 1 minus grass cover:season and grass cover	5246.2	174.8
11	Model 1 minus bare ground cover:season and bare ground cover	5264.0	192.6
10	Model 1 minus bare ground cover:season	5265.5	194.1
9	Model 1 minus grass cover:season and tree cover	5284.7	213.3
8	Model 1 minus tree cover:season	5285.6	214.2

Table 7. Summary of model 4 in table 7, where (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	37.077	4.317	8.589	< 0.001**
Wet season	-34.689	2.788	-12.442	< 0.001**
Medium water area	3.488	0.340	10.247	< 0.001**
Small water area	2.471	0.311	7.952	< 0.001**
Semi-permanent water	1.082	0.539	2.006	< 0.05*
Semi-temporary water	0.601	0.638	0.942	0.346
Temporary water	1.158	0.646	1.792	0.073
Grass cover	-0.397	0.044	-8.975	< 0.001**
Bare ground cover	-0.406	0.046	-8.875	< 0.001**
Tree cover	-0.391	0.058	-6.779	< 0.001**
Shrub cover	-0.363	0.045	-8.019	< 0.001**
Wet season: medium water area	-2.858	0.347	-8.244	< 0.001**
Wet season: small water area	-2.233	0.318	-7.014	< 0.001**
Wet season: semi-permanent water	-1.415	0.190	-7.444	< 0.001**
Wet season: semi-temporary water	-0.539	0.213	-2.534	< 0.05*
Wet season: temporary water	-0.072	0.210	-0.345	0.730
Wet season: grass cover	0.358	0.029	12.219	< 0.001**
Wet season: bare ground cover	0.390	0.030	12.893	< 0.001**
Wet season: tree cover	0.460	0.034	13.510	< 0.001**
Wet season: shrub cover	0.352	0.029	12.159	< 0.001**

Observed elephant density was highest at medium waterhole areas and lowest at large waterhole areas for both seasons (table 7; figure 15). Medium waterhole areas attracted a significantly ($p < 0.001$) higher elephant density during the dry season (estimate = 1.655, std. error = 0.122) in comparison to the wet season (estimate = 0.929, std. error = 0.227). The same was seen for small waterhole areas; elephant density was significantly ($p < 0.001$) higher at small waterholes during the dry season (estimate = 0.690, std. error = 0.067) compared to the wet season (estimate = 0.440, std. error = 0.227). The opposite was seen for large waterhole areas, as elephant density was significantly ($p < 0.001$) lower during the dry season (estimate = -0.655, std. error = 0.165) compared to the wet season (estimate = 0.311, std. error = 0.240).

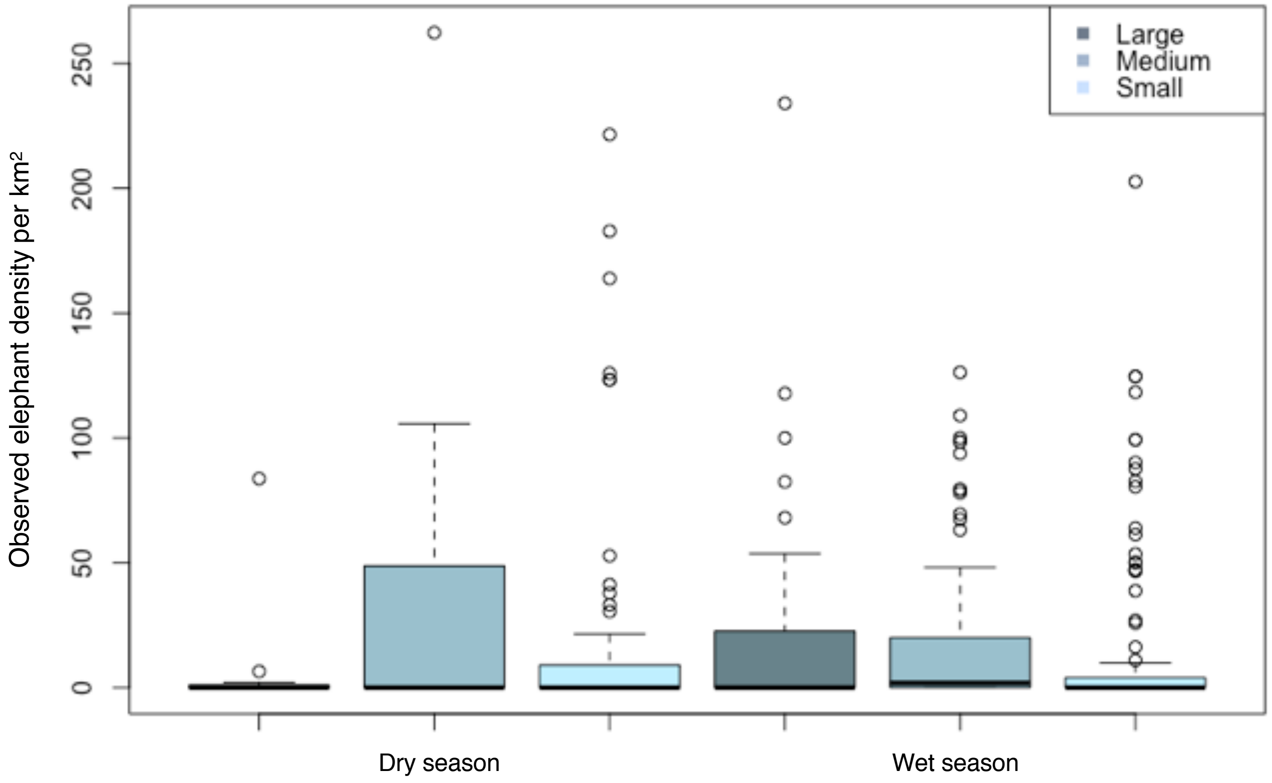


Figure 15. Observed elephant density at 1x1 km^2 grid cells of varying waterhole area sizes

Observed elephant density was highest around temporary waterhole areas and lowest around permanent waterhole areas for both seasons (table 7; figure 16). Elephant density was significantly ($p < 0.001$) lower at temporary waterholes during the dry season (estimate = 1.144, std. error = 0.103) compared to the wet season (estimate = 1.586, std. error = 0.488). We saw the same trend with semi-temporary as elephant density was significantly ($p < 0.05$) lower at semi-temporary waterholes (estimate = 0.688, std. error = 0.118) during the dry season compared to the wet season (estimate = 0.957, std. error = 0.478). Conversely, the opposite pattern was seen for permanent and semi-permanent waterhole areas. Elephant density was significantly ($p < 0.001$) higher around semi-permanent waterholes during the dry season (estimate = 0.859, std. error = 0.083) than during the wet season (estimate = 0.382, std. error = 0.354), and elephant densities around permanent waterholes were also significantly ($p < 0.05$) higher during the dry season (estimate = 0.394, std. error = 0.097) than the wet season (estimate = 0.139, std. error = 0.408).

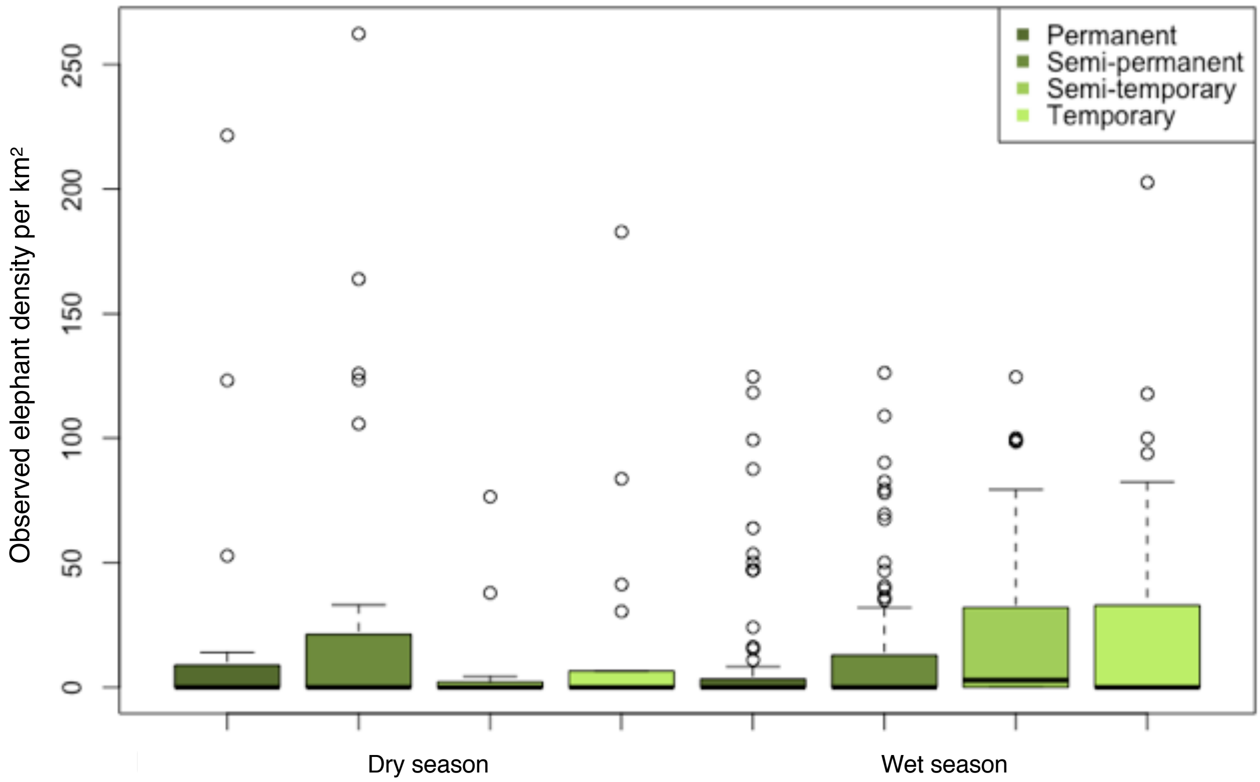


Figure 16. Observed elephant density at 1x1 km^2 grid cells of varying water permanence levels

Elephant density varied depending on the type of vegetation surrounding waterholes (table 7; figure 17). Grass cover significantly predicted elephant density during the wet season (estimate = -0.022, std. error = 0.010, $p < 0.05$), however did not significant predict elephant density during the dry season (estimate = -0.020, std. error = 0.010, $p = 0.054$). Bare ground cover did not significantly predict elephant density across seasons (wet: estimate = 0.003, std. error = 0.011, $p = 0.774$; dry: estimate = 0.002, std. error = 0.011, $p = 0.869$). However, elephant density did significantly vary between seasons, being higher during the wet season ($p < 0.001$). Tree cover also did not predict elephant density across seasons (wet: estimate = 0.068, std. error = 0.036, $p = 0.061$; dry: estimate = 0.048, std. error = 0.037, $p = 0.192$). However, elephant density did significantly vary between seasons, being higher during the wet season ($p < 0.001$). Lastly, shrub cover also did not significantly predict elephant density across seasons (wet: estimate = 0.017, std. error = 0.014, $p = 0.243$; dry: estimate = 0.022, std. error = 0.014, $p = 0.243$), being higher during the dry season ($p < 0.001$).

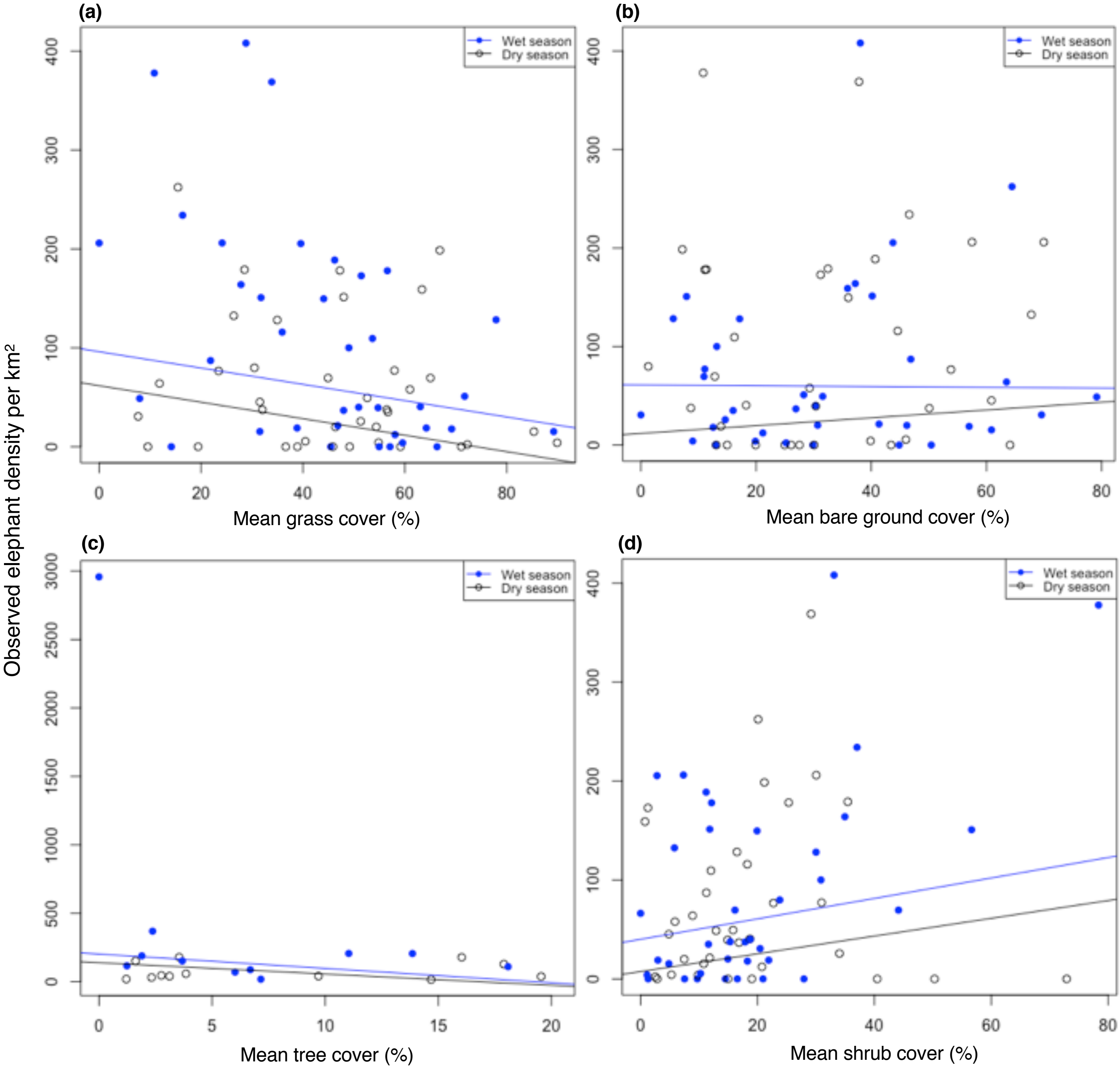


Figure 17. (a) Seasonal observed elephant density according to mean grass cover; (b) bare ground cover; (c) tree cover, and; (d) shrub cover

Water source type alone did not predict a significant effect on elephant density ($X_2 = 0.02$, $p = 0.88$), however when included as an interaction with season there was a significant effect ($X_2 = 42.31$, $p < 0.001$). During the wet season, elephant density was lower at artificial waterholes than at natural waterholes (table 8; figure 18). However, during the dry season elephant density was higher at artificial waterholes than at natural waterholes.

Table 8. Summary of model including effect of water source type and season on elephant density, where (*) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	1.131	0.543	2.111	< 0.05*
Natural water	-0.098	0.645	-0.144	0.891
Wet season	-0.687	0.123	-5.887	< 0.05*
Natural water: wet season	0.413	0.151	2.835	< 0.05*

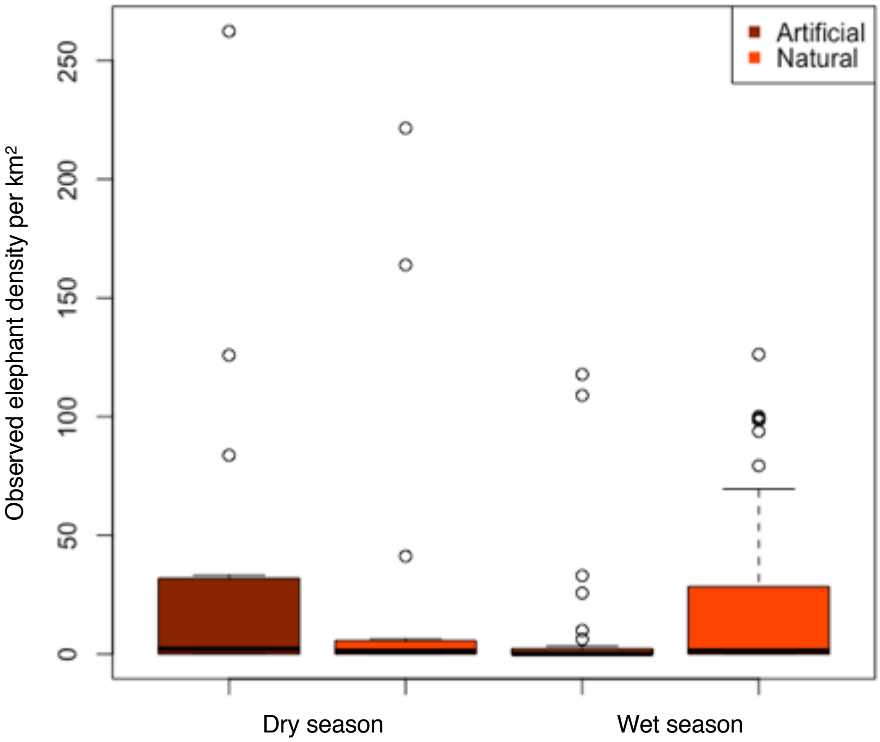


Figure 18. Observed elephant density at 1x1 km^2 grid cells of artificial and natural water source types

3.3 Rhino

3.3.1 Waterhole occurrence

Rhino presence was found to be best predicted by a model containing precipitation and temperature, and did not feature water occurrence nor season (model 6, table 9). As seen in figure 19, rhinos presence decreased as temperature increased, but increased as precipitation increased (table 10).

Table 9. Models tested for rhino presence/absence and water occurrence, where the results of likelihood ratio tests between models can be found in table 3, appendix 2

Model	*Variables*	*AIC*	*ΔAIC*
6	**Model 1 minus water occurrence, season, water occurrence:temperature, water occurrence:precipitation, water occurrence:season**	**1217.4**	**0**
5	Model 1 minus water occurrence, season, water occurrence:temperature, water occurrence:season	1218.1	0.7
4	Model 1 minus water occurrence, water occurrence:temperature, water occurrence:season	1219.0	1.6
3	Model 1 minus water occurrence:temperature, water occurrence:season	1220.6	3.2
2	Model 1 minus water occurrence:temperature	1221.7	4.3
1	Rhino ~ water occurrence + temperature + precipitation + season + water occurrence:temperature + water occurrence:precipitation + water occurrence:season	1223.6	6.2
7	Model 1 minus water occurrence, precipitation, season, water occurrence:temperature, water occurrence:precipitation, water occurrence:season	1224.5	7.1

Table 10. Summary of model 6 in table X, where the estimates and standard errors of individual variables and interactions can be seen and (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	1.881	0.675	2.784	< 0.001**
Temperature	-0.169	0.042	-4.065	< 0.001**
Precipitation	0.055	0.018	2.985	< 0.001**

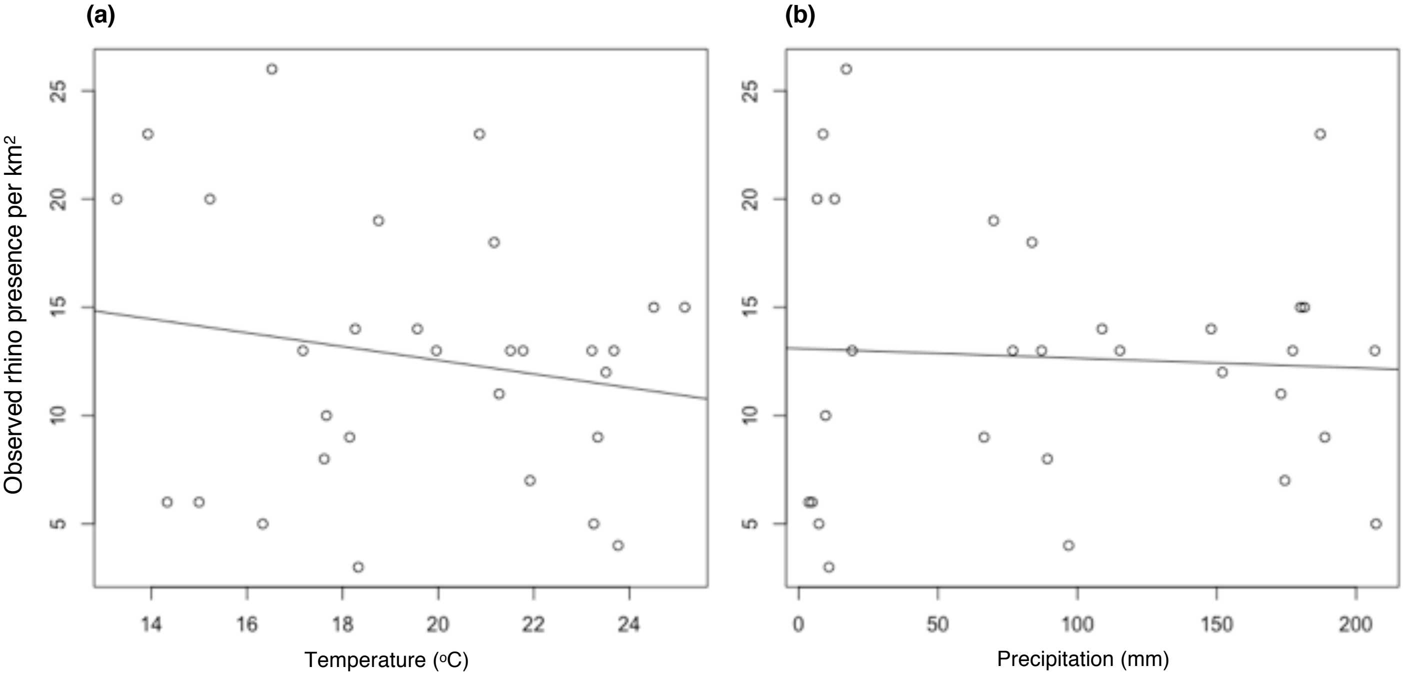


Figure 19. (a) Rhino presence per 1x1 km² grid cell across a temperature gradient in water present and water absent areas; (b) rhino presence per 1x1 km² grid cell across a precipitation gradient

3.3.2 Waterhole characteristics

Model 9 of table 11 provided the best fit model to explain observed rhino density. This model included waterhole area size, permanence, shrub cover and bare ground cover and the interactions of these variables across a seasonal gradient. Grass and tree cover, both overall and seasonally, were not included in the model of best fit as they did not have a substantial role in determining rhino density. A breakdown of each fixed effect can be seen in table 12.

Table 11. Models tested for rhino density and water characteristic variables, where the results of likelihood ratio tests between models can be found in table 4, appendix 2

Model	*Variables*	*AIC*	*ΔAIC*
7	Model 1 minus grass cover:season, grass cover	1385.8	0
6	Model 1 minus grass cover:season	1385.8	0
9	**Model 1 minus grass cover:season, grass cover, tree cover:season, tree cover**	**1387.3**	**1.5**
1	Rhino ~ season + water area + permanance + grass cover + tree cover + shrub cover + bare ground cover + water area:season + permanence:season + grass cover:season + tree cover:season + shrub cover:season + bare ground cover:season	1387.3	1.5
8	Model 1 minus tree cover:season, grass cover:season, grass cover	1387.7	1.9
13	Model 1 minus grass cover:season, grass cover, tree cover:season, tree cover, shrub cover:season, shrub cover	1390.9	5.1
12	Model 1 minus grass cover:season, grass cover, tree cover:season, tree cover, shrub cover:season	1392.8	7.0
10	Model 1 minus grass cover:season, grass cover, tree cover:season, tree cover, bare ground cover:season	1394.6	8.8
11	Model 1 minus grass cover:season, grass cover, tree cover:season, tree cover, bare ground cover:season and bare ground cover	1395.5	9.7
4	Model 1 minus permanence:season	1401.4	15.6
5	Model 1 minus permanence:season and permanence	1401.7	15.9
3	Model 1 minus water area:season and water area	1406.0	20.2
2	Model 1 minus water area:season	1408.7	22.9

Table 12. Summary of model 9 in table X, where (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	-1.452	0.809	-1.795	0.073
Wet season	2.463	0.803	3.067	< 0.05*
Medium water area	0.472	0.749	0.630	0.529
Small water area	1.490	0.677	2.202	< 0.05*
Semi-permanent water	0.995	0.346	2.878	< 0.05*
Semi-temporary water	1.330	0.420	3.170	< 0.05*
Temporary water	0.062	0.510	0.122	0.903
Bare ground cover	0.002	0.008	0.286	0.775
Shrub cover	-0.021	0.011	-1.921	0.055
Wet season: medium water area	-1.175	0.800	-1.469	0.142
Wet season: small water area	-2.476	0.730	-3.391	< 0.001**
Wet season: semi-permanent water	-1.352	0.292	-4.973	< 0.001**
Wet season: semi-temporary water	-1.712	0.341	-5.021	< 0.001**
Wet season: temporary water	-1.330	0.522	-2.549	< 0.05*
Wet season: bare ground cover	-0.017	0.006	-3.050	< 0.05*
Wet season: shrub cover	0.023	0.009	2.556	< 0.05*

As seen in figure 20, the variation in rhino densities across waterhole size is much bigger during the dry season compared to the wet season. During the wet season, observed rhino density was highest at large waterhole areas (estimate = -0.173, std. error = 0.242) and lowest at medium waterhole areas (estimate = -0.411, std. error = 0.142). During the dry season, observed rhino density was highest at small waterhole areas (estimate = 0.528, std. error = 0.118) and lowest at large waterholes (estimate = -1.181, std. error = 0.624). As a result, small waterhole areas were significantly ($p < 0.001$) different across seasons in predicting rhino density, being higher during the dry season. Medium waterhole areas were also significantly ($p < 0.001$) different across seasons in predicting rhino density, also being higher during the dry season. On the other hand, large waterhole areas were not significantly ($p = 0.089$) different across seasons.

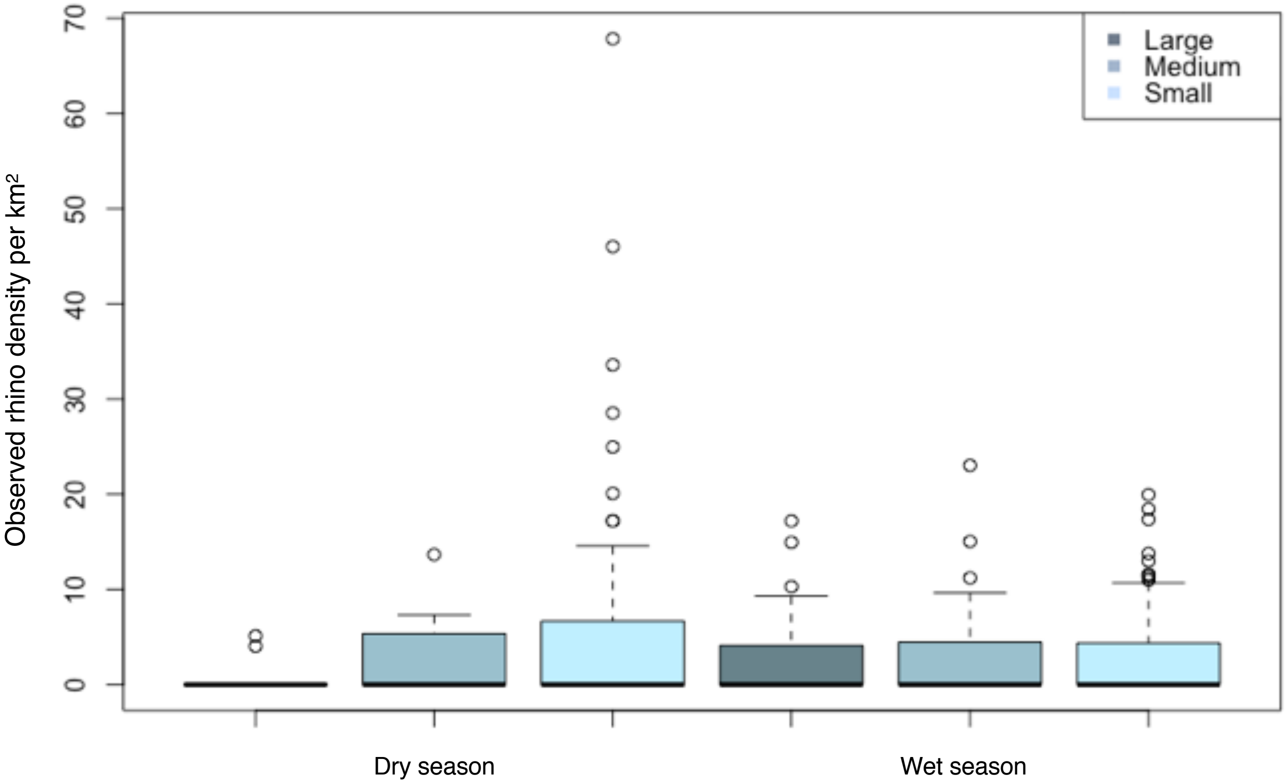


Figure 20. Observed rhino density at 1x1 km^2 grid cells of varying waterhole area sizes

In terms of water permanence, rhino density was highest at semi-temporary (estimate = 1.067, std. error = 0.423) and lowest at temporary (estimate = -0.026, std. error = 0.311) waterholes during the dry season (figure 21). Conversely, rhino density was highest around permanent waterholes (estimate = -0.383, std. error = 0.381) and lowest around temporary waterholes (estimate = -0.723, std. error = 0.311). Rhino density did not significantly differ at temporary waterholes between seasons ($p = 0.928$), and nor did it at permanent waterholes across seasons ($p = 0.553$). Rhino density around semi-temporary waterholes did significantly ($p < 0.001$) differ across seasons, being much higher during the dry season. Semi-permanent waterholes also significantly ($p < 0.001$) varied in predicting rhino density across seasons, and was also higher during the dry season.

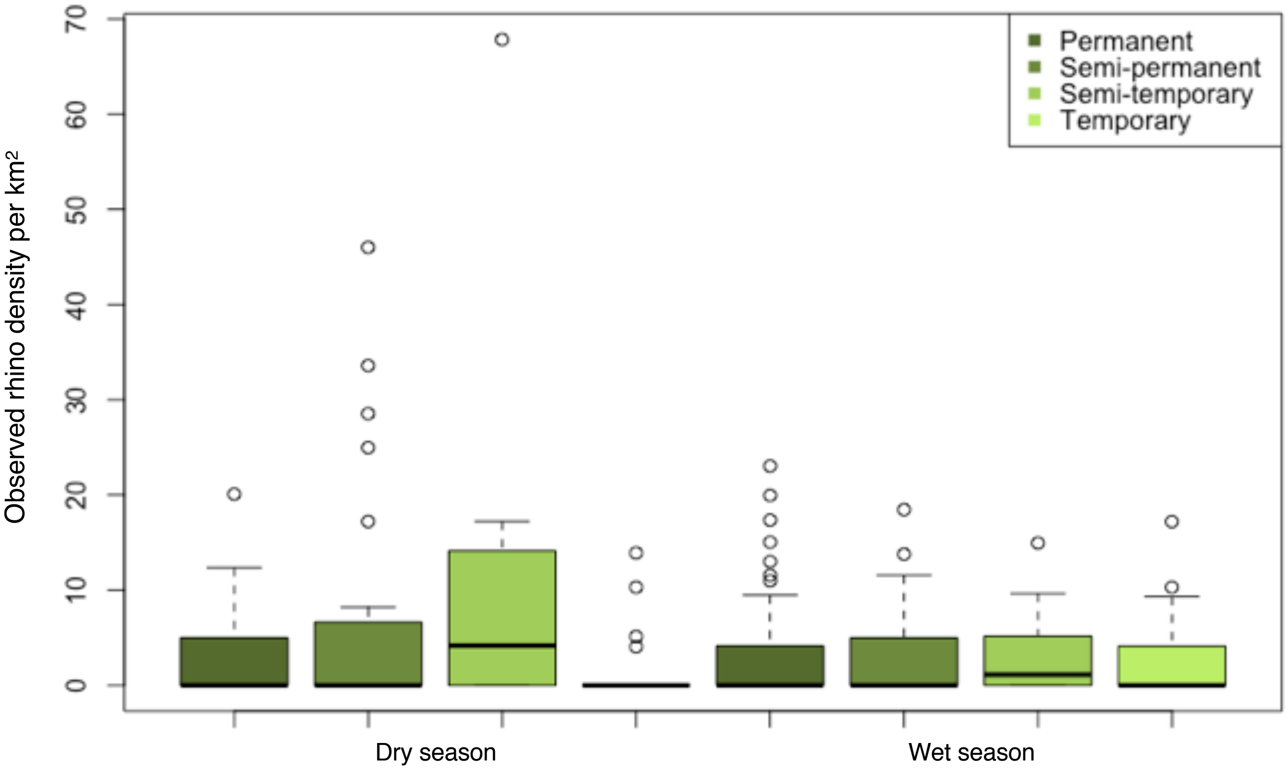


Figure 21. Observed elephant density at 1x1 km² grid cells of varying water permanence levels

Rhino density was predicted by bare ground and shrub cover in the model of best fit (figure 22). Bare ground cover significantly predicted rhino density during the wet season (estimate = -0.017, std. error = 0.007, $p < 0.001$) but did not during the dry season (estimate = 0.011, std. error = 0.007, $p = 0.104$). Rhino density also significantly varied between seasons, with density being lower during the wet season ($p < 0.001$). Shrub cover did not predict rhino density across seasons (wet: estimate = -0.009, std. error = 0.008, $p = 0.289$; dry: estimate = 0.010, std. error = 0.008, $p = 0.215$). However, rhino density did significantly vary between seasons, being higher during the wet season ($p < 0.001$).

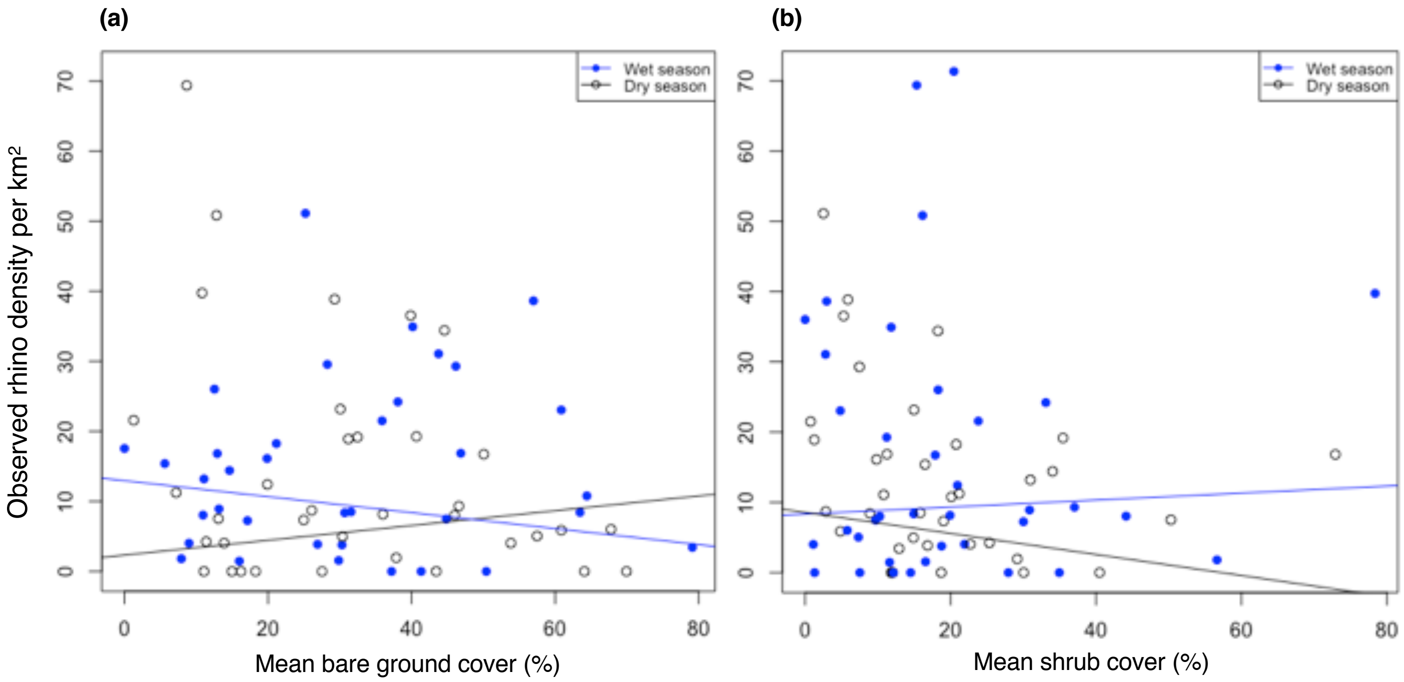


Figure 22. (a) Seasonal observed rhino density according to mean bare ground cover, and; (b) shrub cover

The effect of water source type had a significant effect on rhino density both when alone in a model ($X_2 = 7.46$, $p < 0.001$), as well as between seasons ($X_2 = 19.23$, $p < 0.001$). Overall, a lower density of rhino was observed for artificial waterholes in comparison to natural waterholes (table 13). This was also seen for both wet and dry season (table 14; figure 23). During the wet season, the difference between rhino density at artificial and natural waterholes was much larger, and rhino showed an increased use of artificial waterholes and a decreased use of natural waterholes during the dry season in comparison to the wet season.

Table 13. Summary of model including effect of water source type on rhino density, where the estimates and standard errors of individual variables and interactions can be seen and (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Artificial water source	-0.99	0.29	-3.46	< 0.001*
Natural water source	-0.04	0.95	0.33	< 0.001*

Table 14. Summary of model including effect of water source type and season on rhino density, where the estimates and standard errors of individual variables and interactions can be seen and (*) and (**) represents significant p values

Fixed effect	*Estimate*	*Std. error*	*Z value*	*Pr(>lzl)*
Intercept	-0.81	0.36	-2.27	< 0.05*
Natural water	1.43	0.41	3.47	< 0.001**
Wet season	-0.26	0.34	-0.76	0.45
Natural water: wet season	-0.51	0.39	-1.32	0.19

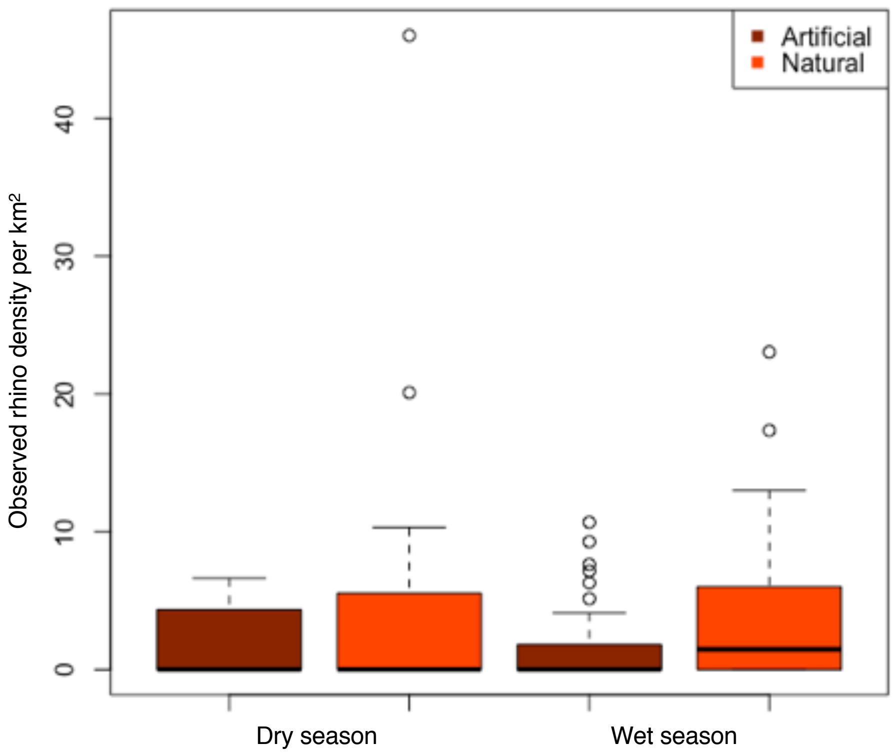


Figure 23. Observed rhino density at 1x1 km^2 grid cells of artificial and natural water source types

4 DISCUSSION

This study aimed to investigate *the extent to which elephant and rhino distribution relates to the occurrence and defined characteristics of waterholes in Greater Kruger on a seasonal scale*. To summarise the results, whilst season did not significantly predict the presence of elephant and rhino, weather variables did. Rhino presence increased with rainfall levels and decreased with temperature, however this was not found to be related to water occurrence. Elephant presence was however related to water occurrence: during seasons with high temperatures elephant presence was more likely in grid cells where waterholes were present than where waterholes were absent. In only water-present areas, elephants and rhinos selected for medium- and small-sized waterholes significantly more in the dry season than the wet season (with elephant density being highest at medium-sized waterholes (for both seasons) and rhinos at small-sized waterholes during the dry season). Elephant density significantly increased around large-sized waterholes during the wet season whilst still remaining the highest at medium-sized waterholes. Conversely, rhino density was highest around large-sized waterholes during the wet season, but this did not significantly differ from rhino density around large-sized waterholes during the dry season. During the dry season, elephant density was significantly higher around permanent waterholes, and significantly lower around temporary waterholes compared to the wet season. Meanwhile, rhino density around waterholes of neutral permanence (semi-temporary and semi-permanent waterholes) was significantly higher during the dry season. Rhinos preferred natural waterholes on an annual scale, whilst elephant density was significantly higher at artificial waterholes than at natural waterholes during the dry season (and the opposite trend during the wet season). In terms of vegetation, grass cover significantly and negatively predicted elephant density during the wet season. Bare ground, tree and shrub cover significantly differed in elephant density across seasons, with bare ground and tree cover being higher during the wet season and shrub cover during the dry season. Bare ground cover significantly and negatively predicted rhino density during the wet season, and rhino density was significantly higher around waterholes featuring shrub cover during the wet season. Lastly and in terms of interactions between waterhole characteristics, shrub cover was proportional to the permanence of waterholes, being highest at temporary waterholes and lowest at permanent waterholes.

4.1 Waterhole occurrence

I predicted that animal presence would be stronger around areas with waterholes during the dry season as water is more limited in this period. However, there was no seasonal difference of animal presence relating to water occurrence. This lack of seasonal distinction supports the popular notion that artificial water presence has a profound effect on ranging patterns in the dry season, and drastically decreases the differences between dry and wet distributions (de Beer & van Aarde, 2008; Smit *et al.,* 2007a,b; Thomas *et al.,* 2008; Viljoen, 1989; Loarie *et al.,* 2009). It was also expected that rhino would utilise waterholes more during periods of high temperatures and rainfall, however it was found that water occurrence was not important to rhino presence at all. This could be related to the timing of data collection not representing rhino dependence on waterholes: aerial counts of animals were undertaken during the morning and early afternoon when rhinos have previously been found to move upwards to midslopes and ridgecrests to seek out shady trees during the hottest period of the day (Pienaar, 1994). Rhinos are then known to move into open, lower-lying areas during cooler periods, and also during the late afternoon and night to use waterholes (Pienaar, 1994). This research equally supports my finding that rhino presence decreased with temperature, which could be explained by their tendency to move to shaded, closed habitats in hot temperatures where they are less visible to the pilot collecting animal data. Contrarily, elephant presence increased in water-present areas during hotter temperatures. This indicates that elephants were more present than rhinos in open areas by waterholes during the aerial data collection. As discussed by Hayward & Hayward (2012), it may be that elephants are more water-dependent than rhinos are, and that this dependence may also be related to climate variables. For example, Dunkin *et al.* (2013) proposes that the magnitude of elephant water-dependence is highly dependent on the climate, and that in periods of high temperatures elephants will have to visit more waterholes as other thermoregulatory behaviours and physiological processes are not substantial enough to cool them. By remaining close to water in hot weather, elephants can then benefit from both direct (evaporation) and indirect (reducing water debt from cutaneous evaporative water loss) cooling, since water is the fastest way for large herbivores to lose heat (Dunkin et al., 2013; Thaker *et al.,* 2019; Purdon & van Aarde, 2017). The same could be said for rhino, however, and therefore it is surprising that we do not see rhino presence increase in waterhole-present areas at high temperatures. An alternative explanation for this could be that elephant and rhino differentiate in their thermoregulation strategies, where elephant utilise water to cool down during hot periods, whilst rhinos take advantage of shaded, woody areas. This interpretation is further supported by Smith (2016), who studied the use of waterholes by several herbivores in Greater Kruger and found that white rhino did not use waterholes for the purpose of cooling down, in comparison to elephant.

4.2 Waterhole characteristics

4.2.1 Waterhole size

I hypothesised that animals would select for waterholes that were large enough to enable full-body submergence. In areas of waterhole presence, elephant and rhino density was found to increase at medium- and small-sized waterholes during the dry season. Elephant density was highest in areas with medium-sized waterholes, whilst rhino density was highest around small-sized waterholes. I expect that these smaller waterholes were large enough to accommodate for the rhinos, particularly because the average density of rhinos to visit these waterholes was around 0.5 individuals and small waterholes varied between 10 and 200 m^2. Similarly, medium-sized waterholes (between 200 and 1000 m^2) would have been able to support a mean density of 1.7 elephants. The reliance on small- and medium-sized waterholes during the dry season was likely related to the availability of these waterholes, as these waterholes constituted 20% of the Kempiana area during the dry period compared to only 3% for large-sized waterholes. Furthermore, elephant density significantly increased around large-sized waterholes during the wet season compared to the dry season (despite still being the highest at medium-sized waterholes). The shift of elephant density from medium- and small-sized waterholes to large waterholes during the wet season indicates that elephants will utilise larger waterholes when they are more available. Large waterholes covered 7% of the Kempiana region (increasing by 4% from the dry season) whilst small- and medium-sized waterholes covered a total of 21% of the study area in the wet season (only increasing by 1% from the dry season). Rhino density was also highest around large waterholes during the wet season, however this density did not significantly differ from the dry season density at large waterholes.

Another interesting aspect related to the results regarding water size is the possibility of displacement between elephant and rhino. Whilst elephant and rhino both utilised small- and medium-sized waterholes more during the dry period than the wet period, elephant density was highest at medium-sized waterholes and rhino density was highest at small-sized waterholes. Furthermore, elephant density increased significantly at large-sized waterholes during the wet period, and whilst rhino density was the highest at this size of waterhole, it did not increase significantly more than during the dry period indicating that rhinos did not want to heavily rely on larger waterholes. According to Berger & Cunningham (1998), displacement as a result of interspecies competition, is often based on body size, indicating that when elephants co-exist with rhinos, the rhinos are displaced. It could be that when elephant density was highest in an area, it often consisted of large groups of elephants that were taking up too much space for rhinos to also utilise the waterhole. This is corroborated by Berger & Cunningham (1998), who found that competition at waterholes is linked to gender and group size, with elephant cows (which make up the majority of large herds) being less tolerant of other waterhole users and dominating waterholes in comparison to elephant bulls (Smith, 2016).

4.2.2 Waterhole permanence

It was hypothesised that elephant and rhino density would be highest at permanent waterholes during the dry season but that the animals would not exhibit a preference for permanence in the wet season when water was highly available. Whilst elephant density was highest at temporary waterholes and lowest at permanent waterholes throughout both seasons, elephant density significantly increased around permanent waterholes and decreased around temporary waterholes during the dry season. Furthermore, elephant density was higher at semi-permanent waterholes than semi-temporary waterholes during the dry season (which was the opposite during the wet season). These results show some partial shift to more permanent waterholes in the dry period, and therefore in part confirms my hypothesis for elephants.

Whilst I did not hypothesise that elephants would rely significantly more on temporary waterholes during the wet season, there are several feasible reasons why we may be seeing this. Firstly, it is a better use of energy to take advantage of the many temporary waterholes that emerge during the wet season than to travel further distances to permanent sources of water in extreme heat. Low fidelity to water sources in Kruger National Park has been identified before, and whilst this does not look at permanence of water, minimal attachment to specific waterholes indicates that elephants would have also been open to temporary waterholes in that study (Thaker *et al.,* 2019). However, as seen in the results, the amount of temporary waterholes did not drastically increase from the dry season to the wet season and therefore there may be an alternative explanation for why elephant density is highest at temporary waterholes in the wet season. I found that shrub cover peaked around temporary water sources but remained the lowest around permanent water. From this result, it seems that elephants take advantage of more ephemeral water sources with better forage quality during the wet season rather than more permanent water sources that have a stronger piosphere effect. The high density of elephants may represent many individual elephants utilising these temporary waterholes, but it may also portray larger herds of elephants. The latter possibility correlates with the discovery of Smith (2016), whereby increasing group size led to longer durations of waterhole visits because individuals not only drank and bathed, but also foraged and socialised. Therefore, increasing elephant density comes with an increase in foraging around waterholes as individuals will be waiting for conspecifics to finish drinking and bathing in the waterholes, and as a result elephants will select for the waterholes with the most productive forage. This is also associated with the finding by Smit *et al.* (2007b) that mixed herds of elephants prefer riverine habitats for their good forage as they will do a combination of eating, bathing and drinking, in comparison to bull groups, which are considerably smaller (up to around three individuals), which show a preference for artificial waterholes.

Rhino density around waterholes of neutral permanence (semi-permanent and -temporary) was significantly higher during the dry season, which also in part supports my hypothesis that rhino will select for more permanent sources of water. This was further corroborated by the finding that rhino density was the lowest at temporary waterholes during the dry season, as well as during the wet season. As with the discussion regarding animal preference of waterhole size, the reason why rhinos avoid temporary waterholes so strongly whilst elephants select for them on an annual scale could be related to displacement. This could also be seen again during the wet season, where rhino density and elephant density in regard to water permanence had the opposite trend: at permanent waterholes, rhino density was highest and elephant density was lowest, and at temporary waterholes, rhino density was lowest and elephant density was highest. It is also interesting to note that although rhino density was also significantly related to high shrub cover in the wet season, rhinos still avoided temporary waterholes in this season despite the high shrub cover associated with it. One paper suggests that species impacted by interference competition with elephants shift their temporal niches at waterholes to avoid overlap with elephants (Valeix *et al.,* 2007). However, in this study it could be that instead of a temporal change, we see rhinos select for different types of waterholes that elephants are less likely to frequent, as seen with both the avoidance of medium sized waterholes throughout the year, temporary waterholes in the wet period and permanent waterholes in the dry period.

4.2.3 Waterhole source type

As previously mentioned, past research on elephants has highlighted their preference for water from riverine areas owing to the productive vegetation there (Purdon & van Aarde, 2017; Smit *et al.,* 2007b). However, as Kempiana does not feature a flowing river, this study provided an interesting insight into the preferred waterhole source type of elephants and rhino when the animals would have to travel further distances to access rivers. I hypothesised that elephants and rhinos would show a preference for artificial waterholes in the dry season as they are more reliable than natural waterholes. However, we found that source type did not predict the permanence of a waterhole, indicating that artificial waterholes may not be more reliable than natural waterholes. Nonetheless, elephant density was highest around artificial waterholes, and rhino density (whilst still higher around natural waterholes) became higher around artificial waterholes in the dry season in comparison to the wet season. One important reason why we may be seeing that there is no difference in permanence between source types is related to the fluctuation in some very large artificial waterholes as a result of anthropogenic changes to them (Pieterson, 1998), perhaps creating some bias in the data. Another interesting factor to note is the number of waterholes of different source types available for each season: during the dry season 9.64% of grid cells featured artificial waterholes and 9.04% featured natural waterholes, which shows that there was a similar amount of each waterhole source type. Conversely, during the wet season, 20.48% of grid cells featured artificial waterholes and 43.98% featured natural waterholes, exhibiting a considerable difference between availability of each waterhole source type. It could be that elephants utilised artificial waterholes much more than natural waterholes during the dry season not because their size varies less over time (i.e. their permanence), but simply because their relative availability is more certain. This has been discussed by many other papers, which indicate that artificial waterholes are more reliable in the dry season in comparison to their natural counterparts (Sutherland *et al.,* 2018; Loarie *et al.,* 2009; Smit *et al.,* 2007a,b; Smit & Ferreira, 2010; De Beer & van Aarde, 2008; Thomas *et al.,* 2008; Viljoen, 1989). This again highlights that artificial waterhole provision narrows the gap between wet and dry seasonal ranging patterns of elephant, and enables the population to thrive throughout the winter period. Artificial waterholes could, therefore, be used as a potential tool to regulate elephant distribution and to limit their impact throughout the landscape (Chamaille-Jammes *et al.,* 2007).

Whilst rhino density showed a marginal increase in artificial waterholes during the dry season in comparison to the wet season, rhino still preferred natural waterholes. As discussed before, this could partly be related to the high numbers of elephants around artificial waterholes in the dry season which are displacing the rhinos to natural waterholes (Smith, 2016). Another possible explanation for the lack of artificial waterhole selection of rhinos may be the design of the water sources. Several papers have indicated that artificial waterholes have high sides that only favour large animals, such as elephants, and are too steep for the smaller-bodied rhino (Smith, 2016; Kasiringua, 2010). Some of the larger dams in Kempiana do have arduous slopes leading to them, meanwhile natural waterholes are in low-lying areas that are accessible to a more diverse array of species. This was further supported by Smith (2016) who identified that when white rhinos utilise artificial waterholes they select most for pans and troughs, which are characterised by their low sides in comparison to reservoirs that have much higher banks. The lack of reliance on artificial waterholes during the dry season also suggest that these man-made water sources are not as influential on seasonal rhino distribution as they are on elephant. This could be critical to water management in Kruger, as altering artificial waterholes provision could have differing effects on elephant and rhino and could be used to monitor their populations accordingly. During the wet season, when water availability is considerably more widespread, elephants were found to shift to natural waterholes. As discussed before, this is likely because they are much more available than artificial waterholes. Whilst natural waterholes were not associated with any different piosphere effects than artificial waterholes, it may also be linked to other aspects of natural waterholes that are favourable in comparison to artificial waterholes, such as enhanced water quality or better accessibility.

4.2.4 Surrounding vegetation

I predicted that elephant and rhino density would be higher around waterholes that featured their food type (shrub and grass, and grass respectively). This is because the feeding strategies of elephant (mixed-feeder) and rhino (grazer) are essential aspects of interpreting the relationships between elephant and rhino density and vegetation cover. Elephants switch between grazing on grass and browsing on leaves and shoots of shrubs throughout the year, and this shift is often underpinned by changing environmental conditions (van der Merwe & Marshal, 2014). In Kempiana during the wet season, elephant density around waterholes was predicted by low grass cover. Elephant density also significantly increased around waterholes with high shrub cover in the same season, of which supported my hypothesis. Elephant preference for high shrub cover in the wet season was predicted as it is an important aspect of their diet. This shows that elephants are not excessively grazing on these shrubs to the point where they are reducing its availability, which has been seen in another study in Addo Elephant National Park in South Africa (Landman *et al.,* 2012), where over-grazing may have been more prominent.

The relationship between low elephant density and high grass cover could be because of their reliance on browse. Codron *et al.* (2006) found that elephants in more southern KNP, including an area called Satara which is located close to Kempiana, consume much less grass than elephants in the north. Grass ranged between 10 to 50% of their diet, and was particularly low during the dry season (Vogel *et al.,* 1990). This was also found by Redfern *et al.* (2003) who found that elephant faeces contained a high proportion of browse, particularly during the dry season. Furthermore, Owen-Smith & Chafota (2012) highlighted a pivotal element that, whilst elephants are classified as mixed feeders along the grass-browse continuum, savanna-inhabiting elephants are actually distinct in that they depend on bark, twigs and roots much more than on foliage and fruits, and that this helps to reduce the overlapping of diet with other animals. It could also be linked to the quality of shrub around waterholes; shrubs thrived best in waterholes that were continually fluctuating and this indicates high productivity of the shrubs in this area, whilst grass around waterholes is often subjected to intense trampling (Jawuoro *et al.,* 2017; Mattchet, 2010). Another important factor of interpreting these results regards the method of data collection. By using satellite imagery to calculate the cover of each vegetation type, the layer of grass below shrubs and trees are not visible and are therefore not included, which underestimates the amount of grass in the area. Furthermore, by using percent cover, a positive effect of shrubs on elephants would likely result in a negative effect of grass on elephants, and this may be what we have seen here. Therefore it may not be that elephants are selecting for waterholes with low grass cover, but because they are selecting for areas with shrub cover then this accordingly presents a negative relationship with grass.

I did not hypothesise that elephant density would be related to tree cover as this vegetation tends not to be part of elephant diet. However, elephant density significantly decreased with tree cover during the dry season compared to the wet season. This was supported by Thrash & Derry (1999), which found that tree cover was directly proportional to elephant distance from waterholes and that in the absence of elephants an increase in woody plant density and canopy cover occurs in a zone just beyond the sacrifice area of a piosphere. This may be related to the tendency of elephants to debark trees (Fullman, 2009). Elephants have been found to do this to marula trees (*Sclerocarya birrea*) in KNP, where around half of the marula population sampled experienced substantial damage from elephants, which often resulted in a decrease in plant height (Biggs & Jacobs, 2002).

In terms of rhino, I expected rhinos to select for waterholes with high grass cover, however grass did not feature in the model of best fit. Instead, rhino density significantly increased with shrub cover in the wet season compared to the dry season. Interestingly, both elephant and rhino density was predicted by high shrub cover in the wet season despite the apparent presence of competition regarding other waterhole characteristics. The reason why we may not be seeing displacement in terms of shrub cover could be related to the different ways in which rhino and elephant use shrub: elephants likely consume it, whilst rhinos prefer the ideal habitat it provides. Pienaar (1994) concluded from his study that rhinos select for habitats with moderate-high shrubs of around 2 to 4 m as they help to support moderate to dense grass cover with a high proportion of palatable grass species. The shrubs identified in Kempiana were classified of up to 6 m, so it could be that the majority were these shrubs that support better quality and cover of grass. As described previously, this attractive grass beneath the shrubs would not have been included in this study owing to the use of satellite imagery to classify vegetation cover, and this may be why we did not see a relationship between rhino density and grass cover. As rhinos are known to take advantage of shaded areas under woody cover when it is hot, it may also be that shrubs provide areas where rhinos can cool down when utilising waterholes during the wet period. Shrubs that were taller than rhinos, which are typically between 1.5 to 1.8 m, would be sufficient to provide the shade that the rhinos may need (Owen-Smith, 1989). Whilst tree cover could have provided shade, I did not identify a relationship between rhino density and tree cover. This may because tree cover was generally low (with the highest cover being 21%), which suggests that trees were randomly distributed and that there was only one or two trees in that area. The shade provided by trees therefore represented a poor amount of shade in comparison to high shrub cover, which could constitute up to 78% of the vegetation.

In the dry season, rhino density was found to decrease significantly around waterholes with high shrub cover. This finding could also be explained by the finding of Pienaar (1994): rhinos shift their grazing areas of medium-tall *Themeda* grassland in lower areas to hillslopes where there are reserves of taller grassland during the dry season when grass in lower areas is poorer in quality. This indicates that rhinos did not utilise waterhole areas for foraging during the dry season as food quality was better in different areas. Rhino and elephant density also increased in waterhole areas with high bare ground cover in the dry season compared to the wet season. It is likely that this is the consequence of low productivity of vegetation during the dry season, and that neither elephant nor rhino directly selected for this poor vegetation.

4.3 Limitations and future research

Some limitations of this research have been deliberated throughout this discussion, however it is important to highlight those that have not been discussed and to consider them in more detail. Firstly, a seasonal scale had to be utilised in this study owing to the limited amount of data available from Google Earth. Six seasons were analysed, and whilst giving an important insight into detailed characteristics of waterholes, it did mean that more detailed temporal scales could not be assessed. For example, seasonal temperature and precipitation levels were utilised and therefore hourly or daily changes in these climate variables could not be assessed. As a result, daily movements of rhinos and elephants to waterholes on account of heat or rain could only be generally discussed. Secondly, Kempiana is an open system to both other private reserves as well as the national park, and as a result animals are able to move in and out of the area as they desire. Therefore, relationships found between water occurrence and characteristics, and animal distribution, are not definitive. For example, when rhino presence is higher in low temperatures and rainfall levels then this does not represent increased mortality of rhinos or even that they move to more covered, wooded areas, but perhaps that they simply move out of the area. Thirdly, the use of percent cover for vegetation types led to possible correlations between these fixed effects, therefore impacting the results drawn from the statistical models. Lastly, and as previously discussed in the methods section, the animal data collection method is limited by several factors. The visibility of animals to the pilot is restricted by topographical features, for example high canopy covers or slopes may prevent the pilot from observing the animals. On the other hand, the pilot could also count the same group several times if they have moved from one area to another. Furthermore, whilst a correction method was applied to the animal density data to deter differences in flight path cover, it was still biased especially against areas where no animals were observed as a correction factor can only be applied to animal densities above zero.

Despite the limitations of the study, it remains that many insightful results were identified that contribute towards the current scientific knowledge. To examine these results in more detail, it would be interesting to apply similar research questions to animal density data that is collected using GPS collar data. By attaching these collars to several individuals and taking automatic readings of locations on an hourly basis, the animal data would eliminate a large proportion of the bias currently seen in this study. It would also be useful to utilise this improved quality of data to research the relationship between elephants and rhinos in terms of waterhole usage. Elephants and rhinos were found to have several opposing responses to types of waterholes that they select for, and the possibility of a shift in specific waterholes used by these species as a result of displacement has not yet been studied. Identifying if elephants are causing rhinos to move elsewhere for water could have substantial impacts on the distribution patterns of rhinos and their subsequent population.

5 CONCLUSION

During periods of water scarcity, elephants and rhinos were found to rely more on smaller-sized waterholes. This may be related to the deficit of large-sized waterhole availability during the dry season, as elephants increased their density around larger waterholes during the wet season when their occurrence increased. Despite similar seasonal changes in preferences of waterhole size in elephant and rhino, we may have seen niche partitioning as rhino density was predominantly highest around waterholes where elephant density was not high. Similarly, elephants and rhinos showed a shift in reliance to more permanent waterholes during the dry season, however their preferences also differed: rhino density increased around waterholes of neutral permanence (semi-temporary and -permanent), whilst elephant density increased around permanent waterholes. Differences between source type preference was also observed, with elephant density significantly increasing around artificial waterholes and decreasing around natural waterholes in the dry period, meanwhile rhino density remained higher at natural waterholes. Whilst this could be explained by the displacement argument, it could also be related to waterhole design whereby artificial waterholes are less accessible to the smaller-bodied rhino. As a result, the presence of artificial waterholes may have a substantial impact on elephant distribution during the dry season whilst having relatively little effect on rhinos. Lastly, elephant and rhino densities was predicted by high shrub cover during the wet season. We may be seeing this because competition in terms of shrub cover may be considerably low in comparison to all of the aforementioned waterhole characteristics as elephant and rhino exploit shrub differently to each other owing to different feeding strategies.

This research adds to a body of scientific knowledge both by contributing to pre-existing theories, but also by providing novel insights into the types of waterholes that are preferred by these megaherbivores. Not only are these preferences seemingly governed by species-specific feeding strategies, body and group size, or thermoregulation strategies, but also inter-species competition. This thesis may reveal the importance of waterhole niche partitioning between rhino and elephant, which may subsequently impact their availability to waterholes. This study could, therefore, be useful to the management of water sources and animal populations in Kruger National Park and the surrounding areas. It could also provide crucial information into the likelihood of animal whereabouts, thus aiding to avert poaching threats of these highly-threatened herbivores.

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7 APPENDICES

7.1 Appendix 1: Waterhole management maps

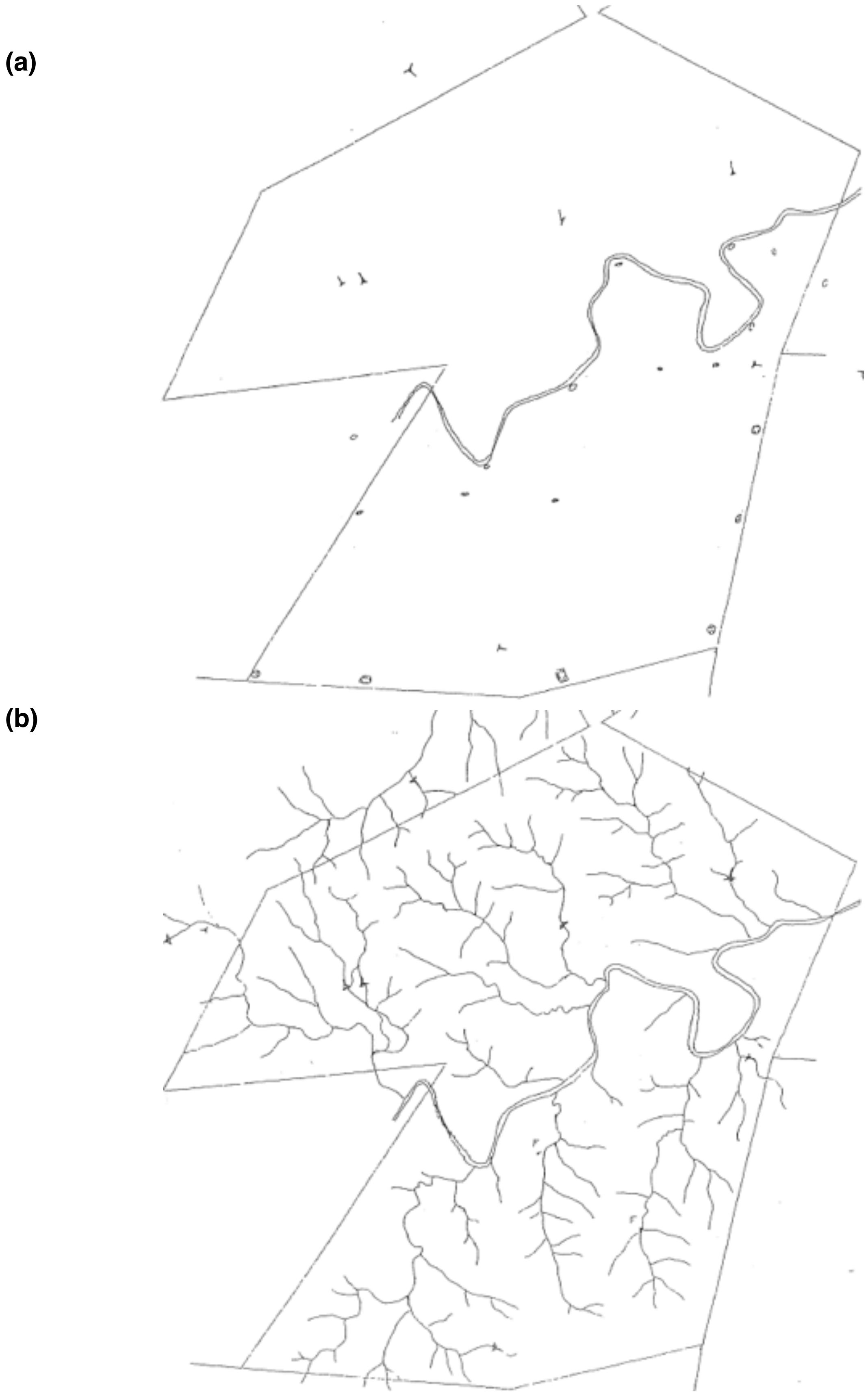

Figure 1. (a) Locations of artificial waterholes in Kempiana; (b) Drainage lines throughout Kempiana that indicate natural waterhole presence (taken from the Kempiana Management Plan by Pieterson, 1998)

7.2 Appendix 2: Likelihood ratio tests

Table 1. Likelihood ratio tests whereby two models (from table 5 under section 3.2.1) were compared using an anova to provide a chi-square (X_2) result and a p value, where (*) and (**) represents significant p values

Model comparisons	1	2	3
2	$X_2 = 0.10$, $p = 0.76$		
3		$X_2 = 4.55$, $p = 0.21$	
4			$X_2 = 2.13$, $p = 0.14$
5			$X_2 = 5.81$, $p = 0.06$
6			$X_2 = 7.58$, $p < 0.05$*

Table 2. Likelihood ratio tests whereby two models (from table 7 under section 3.2.2) were compared using an anova to provide a chi-square (X_2) result and a p value, where (*) and (**) represents significant p values

Model comparisons	1
2	$X_2 = 156.82$, $p < 0.001$**
3	$X_2 = 82{,}11$, $p < 0.001$**
4	$X_2 = 83.96$, $p < 0.001$**
5	$X_2 = 87.754$, $p < 0.001$**
6	$X_2 = 176.65$, $p < 0.001$**
7	$X_2 = 178.78$, $p < 0.001$**
8	$X_2 = 216.22$, $p < 0.001$**
9	$X_2 = 217.29$, $p < 0.001$**
10	$X_2 = 196.1$, $p < 0.001$**
11	$X_2 = 196.66$, $p < 0.001$**
12	$X_2 = 174.44$, $p < 0.001$**
13	$X_2 = 174.8$, $p < 0.001$**

Table 3. Likelihood ratio tests whereby two models (from table 10 under section 3.3.1) were compared using an anova to provide a chi-square (X_2) result and a p value, where (*) and (**) represents significant p values

Model comparisons	1	2	3	4	5	6
2	$X_2 = 0.11$, $p = 0.74$					
3		$X_2 = 0.87$, $p = 0.35$				
4			$X_2 = 0.40$, $p = 0.53$			
5				$X_2 = 1.13$, $p = 0.29$		
6					$X_2 = 1.29$, $p = 0.26$	
7						$X_2 = 9.12$, $p < 0.05$*

Table 4. Likelihood ratio tests whereby two models (from table 12 under section 3.3.2) were compared using an anova to provide a chi-square (X_2) result and a p value, where (*) and (**) represents significant p values

Model comparisons	1	6	7	8	9
2	X_2 = 25.433, p < 0.001**				
3	X_2 = 26.719, p < 0.001**				
4	X_2 = 20.126, p < 0.001**				
5	X_2 = 26.410, p < 0.001**				
6	X_2 = 0.518, p = 0.472				
7		X_2 = 1.983, p = 0.159			
8			X_2 = 3.891, p < 0.05*		
9				X_2 = 1.641, p = 0.200	
10					X_2 = 9.225, p < 0.001**
11					X_2 = 12.11, p < 0.001**
12					X_2 = 7.502, p < 0.001**
13					X_2 = 7.559, p < 0.05*