Influence of surface water availability on the distribution of White Rhinoceros in central Greater Kruger

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Abstract

The population of white rhinoceros (*Ceratotherium simum simum*) is now declining in the Kruger National Park (KNP) in South Africa due to the intense poaching crisis ongoing since the early 2000s. The need for an efficient conservation effort has never been greater and requires a better understanding of white rhinoceros distribution in the landscape. As the white rhinoceros is highly water dependent, I suspected that water availability would be an important driver of its distribution. Additionally, national parks and game reserves have been changing their water management plan in the recent years towards more natural ecological processes leading to less artificial sources. Thus, there is likely discrepancies between water provisioning over the study area, encompassing a small portion of the central-western KNP and adjacent nature reserves, the Associated Private Nature Reserves (APNR).

I investigated the influence of distance to the closest waterhole and river on the mean density of white rhinoceros in the study region. I calculated the distance from cells centre to rhinoceros observations, using a 1x1 km grid cell covering the entire study area. I also researched the effect of cumulative rainfall of the 2 previous months, used as a single predictor and interacting with distance to waterholes and rivers. I had 2 datasets, one originating from a standardised game count made by aerial transect sampling and occurring once a year in September, late dry season, for 4 years. The other dataset was a count originating from aerial transects samplings and targeted towards megaherbivores species. Megaherbivores reach or exceed 1 000 kg when attaining adulthood, and this very large body size set them apart from other smaller terrestrial herbivores. They act as ecosystem engineers by promoting more nutrient-rich vegetation and a higher diversity of habitat, which is benefitting smaller species of herbivores. The white rhinoceros acts as such by creating and maintaining grazing lawns.

I analysed both datasets using zero inflated generalised linear mixed models. Distance to waterhole in correlation with rainfall was the strongest predictor of variability in mean rhinoceros density overall in the study area. In the model focusing on the dry season, white rhinoceros mean density was higher close to water sources when previous rainfall supposedly allowed for vegetation regrowth. In the same model, white rhinoceros mean density increased with distance away from water sources when there had been little to no rain. In the year-round study model, white rhinoceros density increased with distance to waterhole regardless of the season. The increase in white rhinoceros density was stronger with longer distance to water and under higher rainfall. This result implied that white rhinoceros kept away from permanent water likely due to habitat preferences, food depletion, and perhaps other pressures observed at waterholes. This study suggests that water provisioning in the study area probably alleviated the need for white rhinoceros to find water sources during the dry season, making food resources the first limiting factor and main driver of rhinoceros mean density and distribution even during the dry season.

Keywords: White Rhinoceros, *Ceratotherium simum*, water provisioning, artificial water, ecological processes, habitat selection, spatial ecology, landscape use, KNP, APNR, SAWC

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Abbreviations

APNR	Associated Private Nature Reserves
APNR region	Study area: Balule PNR, Klaserie PNR, Kempiana PNR, Timbavati PNR, section of KNP
Balule PNR	Balule Private Nature Reserve
GLMM	Generalised Linear Mixed Effects Models
Kempiana PNR	Kempiana Private Nature Reserve
Klaserie PNR	Klaserie Private Nature Reserve
KNP	Kruger National Park
SAWC	Southern African Wildlife College
Timbavati PNR	Timbavati Private Nature Reserve
ZINB	Zero-inflated Negative Binomial
ZIP	Zero-inflated Poisson

1. Introduction

The ongoing poaching crisis has curtailed conservation efforts for the persistence of rhinoceros. Although poaching rates are constant since 2017 (Ferreira *et al.* 2019b), it has, together with the 2015/2016 drought, led to a decline in the numbers of southern white rhinoceros (*Ceratotherium simum simum*, thereafter white rhino) in the Kruger National Park (KNP) (Ferreira *et al.* 2019b). In recent years, scientists have estimated that the white rhinoceros may become extinct within 20 years if current high poaching rates persist (Ferreira *et al.* 2012; Biggs *et al.* 2013).

The white rhinoceros is an important contributor to savannah heterogeneity, as it acts as an ecosystem engineer by creating and maintaining grazing lawns (Owen-Smith 1988; Waldram *et al.* 2008; Cromsigt & te Beest 2014). These grazing lawns support and shape plant and animal species communities, thus, it is essential to identify the mechanisms behind white rhinoceros distribution on landscape-scale, as their disappearance would also lead to a drastic change in the savannah ecosystems (Cromsigt & te Beest 2014). Although the white rhinoceros has been well studied, most studies were set up in rather small and fenced savannah landscapes, such as the Hluhluwe-iMfolozi Park (e.g. Owen-Smith 1988; Waldram *et al.* 2008), where the white rhinoceros density is high and never went locally extinct, unlike elsewhere. Consequently, we know little about landscape-scale distribution and impact of white rhinoceros in other systems. Similarly, to other large grazers, nutritional requirements and water needs can be expected to be the main drivers behind white rhinoceros distribution. The white rhinoceros is highly water dependent and would usually drink once or twice daily in situations where water is not limiting (Owen-Smith 1988). A white rhinoceros does not spend more than 2 to 4 days without drinking and thus always stay within a reachable distance to water, for drinking, cooling down and wallowing (Owen-Smith 1988). So far, no study has investigated the prevalence of water points in wild white rhinoceros home ranges. Studies analysing water availability in herbivores home ranges in semi-arid systems often focus on African elephants or other African herbivore species (e.g. Chamaillé-jammes *et al.* 2007; Smit & Grant 2009).

This study focused on the influence of water availability on white rhinoceros distribution in a central-western portion of the KNP and adjacent private reserves, the Association of Private Nature Reserves (APNR). In this region, fences were removed in 1993, opening an area of 20 000 km² of heterogeneous savannah for wildlife to migrate within. It hosted 8 365 – 9 337 white rhinoceros in 2015 (Ferreira *et al.* 2017) and the trend is now toward a decrease (Ferreira *et al.* 2019a). To investigate the prevalence of water as a potential driver of white rhinoceros distribution, it is important to understand the management context of the Greater Kruger. The creation of the APNR, uniting private reserves adjacent to KNP, arose from the need to coordinate the private reserves management in order to comply with the KNP management plan after the removal of the fences (Kreuter *et al.* 2010). To some extent, however, the reserves of the APNR still decide and apply their own management practices. As a result, some discrepancies exist between the APNR and the KNP management practices, especially for the matter of supplementing water. Indeed, since the revision of its water policy in 1997 (Pienaar *et al.* 1997; Redfern *et al.* 2005; Smit 2013), the KNP has closed up two-third of its previous artificial waterholes and boreholes (Smit 2013). Prior to the closure plan, management actions such as water provisioning resulted in changes in the natural environment and altered the original ecological processes (SANParks 2018). Closing down artificial waterholes, among other management interventions, aimed at mitigating the impact of human actions and restore the natural ecological processes of the system. However, the APNR does not require to follow the same plan. They have started adjusting to the KNP plan, but there are still many sources of artificial water in the APNR.

To investigate the effect of water availability on white rhinoceros distribution in this landscape, I looked at how white rhinoceros mean density varied depending on the distance to the nearest source of water. I used the number of rhinoceros in 1 km² square cells as proxy for rhinoceros density, and the distance from the centre of the 1 km² cell to the nearest source of water. The white rhinoceros data originated from 2 aerial counts, one only focussing on the dry season, the other one year-round. The survey period extended from February 2014 until June 2018. Sources of surface water included rivers and artificial or natural waterholes. I also looked at how white rhinoceros distance to waterholes varied with rainfall as an approximation for seasonality and grass availability, following Redfern *et al.* (2003). I had the following predictions for the effects of water prevalence on white rhinoceros distribution:

1. White rhinoceros density decreases with increasing distance away from surface water sources, because white rhinoceros are highly water dependent.

2. White rhinoceros density is higher during the dry season, because the availability of surface water in the Kruger National Park is likely limited, thus there might be a shift in rhinoceros distribution from the park to the adjacent private reserves (APNR), where access to water is likely more constant and less restricted.
3. White rhinoceros density is higher farther from surface water sources when rainfall values increase, because it enhances forage quality and quantity and/or creates temporary waterholes throughout the area.

2. Data user agreements

2.1. Southern African Wildlife College (SAWC)

The SAWC was the main partner of this project and provided rainfall and waterhole data for the Kempiana private nature reserve (Kempiana PNR), and part of the data on white rhinoceros. Access to this data is formalized through a memorandum of understanding between SAWC and SLU.

2.2. Associated Private Nature Reserves (APNR)

Transfrontier Africa, an NGO based in the Balule PNR, was the second partner of this project and gave me access to its local data on vegetation, rainfall, waterholes, rivers, and rhinoceros.

My study was part of two other memorandum of understanding, with Timbavati PNR and Klaserie PNR, granting me access to their data on game counts, waterholes location and rainfall values, rivers, and a vegetation map from Klaserie PNR.

2.3. SANParks Scientific Services

My project was not registered with the SANParks scientific services. I only had a data user agreement that allowed me to benefit from specific data of the SANParks scientific database that is not made publicly available. As an unregistered project I did not have access to operational and 3rd parties' data, which includes all the white rhinoceros data and the seasonal water points. Under the user agreement, SANParks scientific services gave me access to a vegetation map, and data on KNP's rivers, dams, and water points used for wildlife viewing by tourists. The rainfall data comes from SANParks public data repository[1].

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[1] Available at: http://dataknp.sanparks.org/sanparks/

3. Material and methods

3.1. Study region

3.1.1. Study location and management scales of the Greater Kruger region

This study focused on a small portion of the KNP, east of the APNR, and on Balule, Kempiana, Klaserie, and Timbavati private nature reserves (thereafter the APNR region; Figure 1). The APNR region (24.32°S, 31.31°E; Figure 1), lies in the north-eastern most part of South-Africa adjacent to the KNP bordered with Mozambique (eastern) and Zimbabwe (northern). The overall study area covers 2214 km^2 which are part of the 20 000 km^2 of the Greater Kruger region. The KNP itself, the largest park in South-Africa, accounts for 19 181.4 km^2 (SANParks 2018).

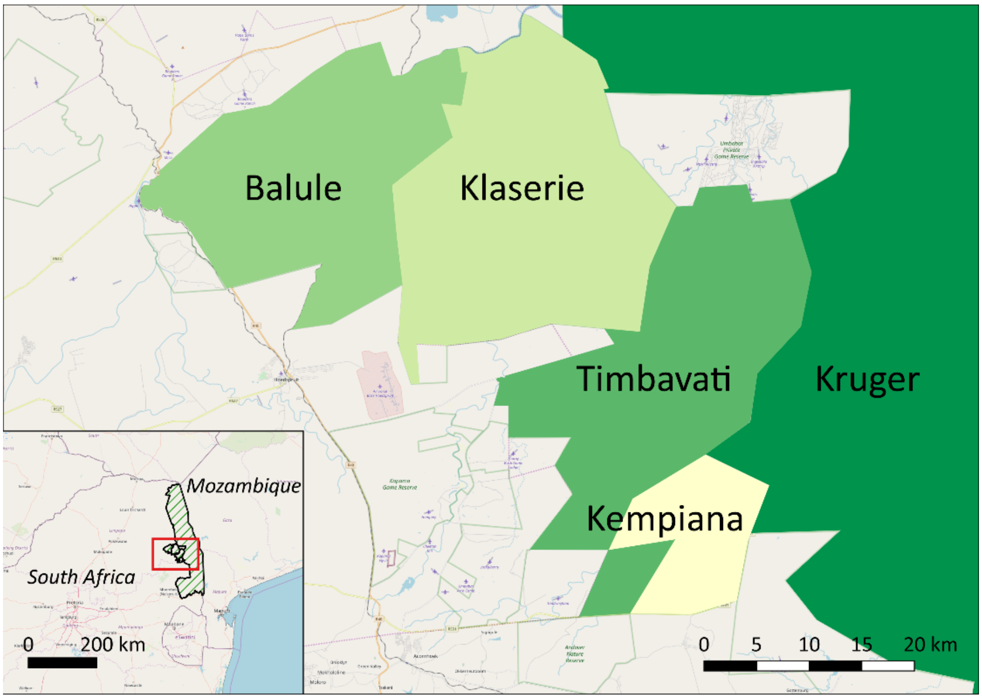

Figure 1. The Greater Kruger (green zebra) lies in north-eastern South Africa at the border with Mozambique. The study area (red rectangle) is detailed: Balule, Klaserie, Timbavati, Kempiana (SAWC) Private Nature Reserves, and the Kruger National Park.

The APNR includes the following private reserves: Timbavati (Timbavati PNR), Klaserie (Klaserie PNR), Balule (Balule PNR), Umbabat and Thornybush Private Nature Reserves, and Mjejane Game Reserve (SANParks 2018). The Kempiana Private Nature Reserve (Kempiana PNR) is not part of the APNR and is managed by the Southern African Wildlife College (SAWC). The Greater Kruger is the term used to describe the total area encompassing independent reserves such as the Kempiana PNR, the APNR and the KNP.

The emergence of more private reserves in the recent years is a result of groups of landowners incorporating their properties into private nature reserves, thus upscaling the management and conservation of natural resources (Kreuter *et al.* 2010). However, the private reserves still vary hugely in their management practices. For example, regarding water management, Balule PNR, Klaserie PNR, Timbavati PNR, and Kempiana PNR do not share the same rules[2]. In each of these reserves, landowners might have the choice to provide wildlife with artificial water resource depending on the reserve policies. While landowners are rather free to supplement in water in Balule PNR, in the other 3 private reserves, artificial waterholes are only supplemented during the dry season, and they stopped building new waterholes.

3.1.2. Biotic and abiotic characteristics of the APNR region

The KNP, and the APNR region, are covered by heterogeneous savanna, where variation in tree-grass ratios is driven by the interactions between soil types, rainfall, fire regimes, and herbivory (Venter *et al.* 2003). The Greater Kruger region is a large open savannah system where we consider that ecological interactions are unconstrained by human presence on both spatial and temporal scales (Du Toit *et al.* 2003).

The study area has among the lowest annual rainfall of the KNP ranging from 375 mm/yr. to 500 mm/yr. averaged from 1980 – 2015 (Du Toit *et al.* 2003; Peel 2015). There is a wet (October – April) season during which most of the rainfall falls, and a dry season (May – September) where monthly rainfall is close to zero (Du Toit *et al.* 2003). Summer and winter correspond to wet and dry season respectively.

The APNR region is mostly an assemblage of granitic and gabbro soils. While granitic soils are poor in nutrients and organic material and typical for *Combretum* trees assemblage, gabbro soils are rich intrusions into the granite. Richer granitic soils are usually characterized by the presence of *Acacia* mixed woodlands (Du Toit

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[2] Peel, personal communication

et al. 2003). The region is dominated by a combination of *Combretum* woodland and shrubveld, *Colophospermum* mopane woodland and shrubveld and *Acacia* veld[3] (Du Toit *et al.* 2003).

Surface water resources are perennial and seasonal rivers, permanent and seasonal waterholes that are mostly artificial but can also be natural. Olifants, Timbavati and Klaserie are perennial rivers, i.e. they often hold water year-round, mostly in the form of pools during the dry season. Other, seasonal, rivers are not providing water during the dry season. Since 1994, the KNP has changed its water policy and has been closing a large number of artificial water sources (SANParks 2018).

3.2. Data collection & processing

I processed the data and did the first steps of the analyses with a GIS software (QGIS Development Team 2019).

3.2.1. Counting rhinoceros: aerial transect sampling

I initially had three data providers but had to abandon the aerial antipoaching patrols dataset from Balule PNR. This type of sampling was management based and did not follow the common and standardised procedure for aerial sampling (Norton-Griffiths 1978). It was thus difficult to evaluate how biased was the sampling and how high was the sampling error. I decided not to use this dataset in my final analysis as the results were likely to be misleading.

The two other datasets provided me with white rhinoceros location data in my study area: 4 years of independent game counts (thereafter game count data) from 3 reserves of the APNR, i.e. Balule, Klaserie, Timbavati, and 4 years of white rhinoceros counts (thereafter rhinoceros count data) from the SAWC (Kempiana PNR).

The game count data originated from line transects sampling with helicopters following the principles of Norton-Griffiths (1978), performed yearly under daylight at the end of the dry season, in September. The time of the year allowed for the best visibility. The full area of Balule PNR, Klaserie PNR and Timbavati PNR was covered for each yearly census. Therefore, the flight coverage was spatially and temporally homogeneous, and I considered the number of rhinoceros per cell as the actual density, i.e. number of rhinoceros per km². For the Timbavati PNR game count, white and black rhinoceros (*Diceros bicornis*) were not segregated, only the

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[3] Balule PNR, Klaserie PNR, unpublished data

number of black rhinoceros was known for each census, so I used a GIS software (QGIS Development Team 2019) to create a random selection of rhinoceros observation according to the number of black rhinoceros reported for each year and deleted these observations from the dataset. These numbers being very low, it is unlikely that it influenced the outcomes of the analysis.

The SAWC designed and performed the white rhinoceros data collection. They relied on the line transect technique for aerial sampling with a fixed-wings aircraft as described in Norton-Griffiths (1978). Each flight path was a combination of parallel transect lines. The number of lines, their respective length, and the space between them varied between 2 flights but was consistent on the same line transect. These aerial surveys, focusing on white rhinoceros and African bush elephants (*Loxodonta africana*), had scientific and management purposes. They aimed at spotting all the targeted individuals present in the surveyed area. For this reason, the pilot might have circled around a specific area to check for all the animals, resulting in a route with unbalanced flight coverage (Figure 2). The pilot-observer and I used the software Cybertracker to record and extract flight routes, flight parameters and rhinoceros GPS location points. The dataset ranged from February 2014 until June 2018. Flights occurred on average 9 days per month, ranging from 1 to 13 days a month during daylight (~6 am – 5 pm).

Figure 2. Flight path (orange) with irregular coverage. The purple buffer is dissolved and does not account for more than 100% coverage/cell for one flight path.

I assumed both the game count and the rhinoceros count sampling used the following flying and counting techniques: the aircraft was a two-seater plane, flying at a constant altitude of about 500 meters, allowing for a 250 meters visibility stripe on each side of the plane, and a blind spot on the ground corresponding to a 50 meters stripe, right below the cockpit. The observer identified each 250 meters visibility frame with a physical mark on the wing. In the case of the rhinoceros count from the SAWC no actual frame was added to each side of the plane and set up for the individual observer. Rhinoceros location points had an accuracy of more or less 250 meters. The observer error was constant since the plane kept a constant altitude and the pilot was always the observer. The location points from the game counts had a similar location accuracy. Trained and experienced pilots and/or observers performed the aerial sampling, which minimized the risk of undercounting animals (Norton-Griffiths 1978; Krebs 1997).

For the rhinoceros count data from the SAWC, I used a GIS software (QGIS Development Team 2019) to create a 250 meters buffer on each side of each flight path. I chose to ignore the 50 meters blind spot that would have been an internal buffer, because it was a constant area. The resulting bias in the evaluated coverage did not have an effect on my final rhinoceros density estimates considering that I was interested in relative differences in rhinoceros density among grid cells with different distances away from water. As mentioned above, the actual flight paths followed transect lines but were likely to have circular entanglement as shown in

Figure 2, when the pilot needed to focus longer on a specific area. To correct for these patterns I allowed for a maximum cell coverage of 100%, i.e. 1 km², per flight. Thus, I had the same maximum cell coverage per flight for both the game count and the rhinoceros count.

I set the minimum coverage for the rhinoceros count at 1 km²:cell/month, i.e. all cells kept were entirely covered on a monthly scale. It insured more reliable density values as the number of rhinoceros per cell started stabilising around 1 km² covered per cell (Figure 3).

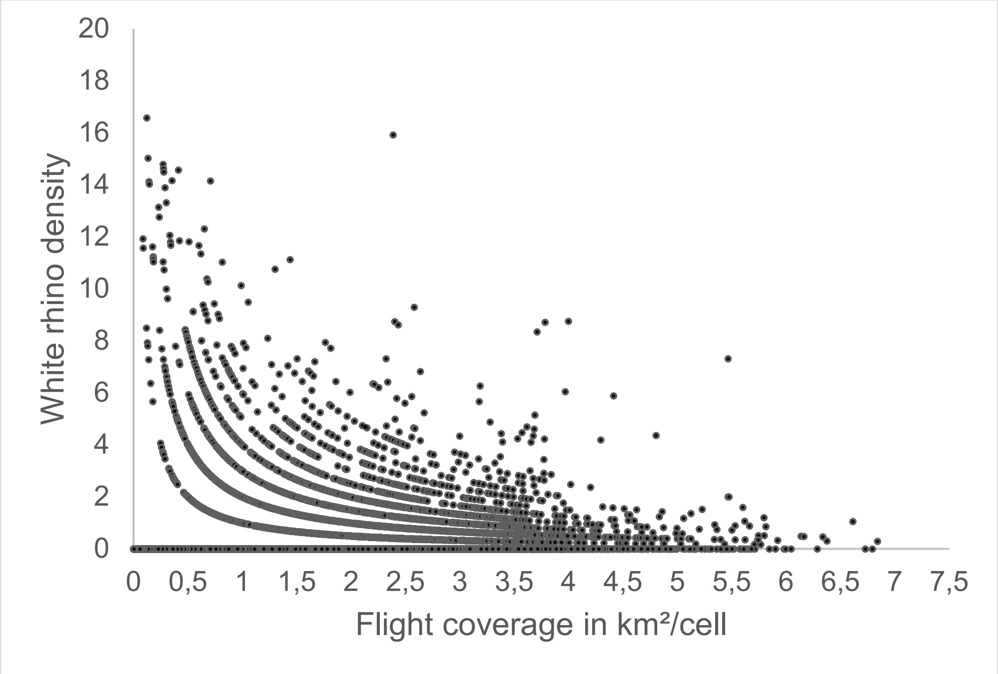

Figure 3. Influence of flight coverage in km²/cell on white rhinoceros density per cell in rhino/km². Outlying values above 20 rhino/km² are not shown.

Finally, cells within 1 km of a game fence were discarded to prevent an edge effect in the analyses. The edge effect is commonly observed in elephant behaviour and can alter its movement up to 3km from the fence (Vanak *et al.* 2010). I assumed the same might be true for white rhinoceros. I chose 1 km as it accounted at least partially for an eventual edge effect and allowed me to keep a sufficient number of observations that were often close to the fences due to the aerial sampling design.

3.2.2. Spatial and temporal frame

I based my analyses on a grid made of 1x1 km cells over the study area which is a relevant cell size for studies on waterholes' influence on herbivores (Redfern *et al.* 2005; Smit & Grant 2009). This grid was adapted from previous works done at

SAWC[4] (Verdaasdonk 2018), which created a 1x1 km grid over the area that was flown over consistently during the study period (2014-2018) to count rhinoceros.

I looked at monthly number of rhinoceros per cell. Since the game count data from the 3 reserves of the APNR was an systematic annual transect sampling (Norton-Griffiths 1978), they surveyed all cells 4 times in September between 2014 and 2017. For the white rhinoceros count data from the SAWC, I only kept cells 100% flown over through the month and which had at least 3 measurements during my study period, i.e. from February 2014 to June 2018, this to be able to perform statistical tests.

The final study area for the rhinoceros count dataset covered most of Kempiana PNR and a portion of KNP and Timbavati PNR. The game count data covered the entirety of the Balule PNR, Klaserie PNR and Timbavati PNR. Both datasets covered the discontinuous southernmost part of Timbavati. In short, observations from the rhinoceros count database included observations within KNP and in contiguous reserves, whereas observations from the game count database were strictly limited to the private reserves (APNR), and not directly adjacent to KNP for the greater part.

3.2.3. Rainfall data

Rainfall stations from Timbavati PNR, Klaserie PNR, Balule PNR, SAWC (Kempiana PNR), and the KNP[5] provided the rainfall values for the study period. Each 1 km^2 cell was given a monthly value in millimetres according to which reserve it belonged to. For Timbavati PNR and KNP, values are averages of several rainfall stations. The relevant KNP rainfall stations were Houtboschrand and Kingfisherspruit. I based this choice on their location, these two being the closest stations to my study area. Klaserie PNR, SAWC, and Balule PNR have one meteorological station each for the whole reserve. Most of the data was consistent throughout the whole study period, from 2014 to 2018, but rainfall values of KNP for 2016 and most of 2015 lacked, so for these missing months I averaged rainfall values from the two closest stations, SAWC and Timbavati PNR.

Over the entire study area, monthly rainfall ranged from 0 to 252 mm and was highly seasonal (Appendix 1). Rainfall regimes in the study area are drastically seasonal with very distinct patterns for wet and dry seasons, so I used cumulative past rainfall as a proxy for seasons. Here, I tested for the lag effect of different time periods of cumulative rainfall, no lagging (Rainfall), lagging one (Rainfall-1), two (Rainfall-2), and three months (Rainfall-3), respectively.

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[4] Nicholas Fleissner, *unpublished*.

[5] Available at: http://dataknp.sanparks.org/sanparks/

3.2.4. Waterholes

The final waterholes dataset was a combination of the data provided by Balule PNR, Klaserie PNR, Timbavati PNR, SAWC (Kempiana PNR) and the SANParks Scientific Services. I had no data on small and medium size waterpoints from Kruger, only the dams and major ponds layers were provided, as specified in the user agreement section.

The Timbavati PNR did not have data available on seasonal waterholes, while Balule and Klaserie had documented the presence of all known seasonal waterpoints, which were as numerous as the permanent waterholes. Finally, the SAWC (Kempiana) only provided information on the location of artificial sources. So, one can expect the overall proportion of waterholes to be underestimated in Kempiana, Timbavati, and Kruger in comparison to Balule, and Klaserie.

To my knowledge, no waterhole has been closed between 2014 and 2018. Only one dam in Kempiana has dried out since 2016, for this reason I decided not to include it in my waterhole dataset.

For each cell I created a “distance to the nearest waterhole” variable, measuring the shortest distance to a waterhole from the cell centre. I made two measurements: one for the dry season, and one for the wet season.

3.2.5. Rivers

I used the SANParks river map as a base and added additional features from the other reserves river dataset when needed. Olifant, Timbavati and Klaserie rivers are perennial rivers holding water discontinuously as puddles during the dry season. All other rivers were all seasonal and assumed to be dry during the dry season (May – September). As for the waterholes, I calculated the distance to the closest river for each cell centre, for both the dry and the wet season.

3.3. Statistical analysis

3.3.1. Data exploration

All statistical analyses were operated in the statistical programme software R, version 3.5.3[6]. I proceeded to data exploration following the protocol detailed by Zuur, Ieno and Elphick (2010). After choosing an appropriate distribution I followed the steps detailed in Zuur, Ieno and Elphick (2010), testing the assumptions for the

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[6] Available at: https://cran.r-project.org/bin/windows/base/old/3.5.3/

response variable and predictors. Summary tables of the data exploration process are available in Appendices 2 and 3 for the game count and the rhinoceros count datasets respectively.

Error distribution

Count data often does not comply with the assumptions for linear regression and needs a transformation to be used with linear models (e.g. Sutherland, 2006; Zuur *et al.*, 2009). However transforming the response variable does not always solve the problem and might result in different conclusion when looking at long-term effects compared to an analysis not requiring transformation (Zuur *et al.* 2009). Transforming the response variable also results in a loss of variation, which might make the predictors effects more difficult to detect (Zuur *et al.* 2010), especially in this study where the effects were already relatively low.

To avoid log-transforming the rhinoceros count and have a more appropriate model, I used distributions from the Poisson family which are the common distribution probabilities used for count data (Zuur *et al.* 2009, 2012; Crawley 2014). I either used the Poisson or the negative binomial error distribution, a special case of the Poisson distribution which allows overdispersion in the response variable (e.g. Sutherland, 2006; Zuur *et al.*, 2009; Zuur, Savaliev and Ieno, 2012). I first graphically assessed which distribution was better fitting the rhinoceros count using the “fitdistr” function (Delignette-Muller & Dutang 2015) . There was an obvious peak of 0, meaning absence of rhinoceros, and for both dataset the data was overdispersed, i.e. the variance was three-fold larger than the mean. However, overdispersion can result from outliers or zero-inflation (Zuur *et al.* 2009, 2010, 2012), which I suspected was the case in my datasets.

Outliers in the response and predictor variables

At first I kept all outliers for the game count dataset, but when validating the final model (see section 3.3.2. Model selection) it occurred best to delete outliers in the rhinoceros variable (response variable). I discarded 5 records for which the number of rhinoceros was above 7, i.e. between 8 and 10. Indeed, these records had a significant impact on the analysis, as shown by the DHARMa test for outliers (Hartig, 2019; Appendices 4, 5).

For the rhinoceros count data, I standardised the sampling rate per flight to a minimum of 100% of the cell, i.e. 1 km^2 flown area per cell. This allowed to discard the most questionable outliers. I kept all outliers left for the rhinoceros count, which originated from the response variable and all the predictors, i.e. rainfall (lagged or not), distance to river, and distance to waterhole. None of these outliers had unreasonable values, they were values that did not commonly occur but are recurrent on the long-term scale for temporal data. The outliers in distance to sources of water might originate from natural discrepancies or from differences in water provisioning. Finally, outliers in the white rhinoceros data all originated from 2016, which showed an increased in rhinoceros density compared to other years, likely due to the occurring drought (Wigley-Coetsee & Staver 2016). None of these values were extreme, and there was no difference in the result of the final model whether I included the data for 2016 or not. This was confirmed by the DHARMa test for outliers based on an exact binomial test (Hartig 2019), explained in detail in the model selection section.

Independence of the response variable

The multiple observations of each cell were likely to result in a lack of statistical independence, i.e. biased parameters estimates and increased type I error (Zuur & Ieno 2016). The observations from the same cell may have been more similar than observations from different cells. To deal with this lack of statistical independence of the replicates, i.e. pseudo replication, I employed Generalised Linear Mixed Models (GLMM), which is widely recommended when dealing with pseudo replication (Pinheiro & Bates 2000; Zuur *et al.* 2009, 2010). Specifically, random effects of the cell and the date of the observation should solve the problem of dependency.

Zero inflation

Both datasets had an extremely high number of zero observation per cell in the response variable, i.e. 72% in the rhinoceros count and 89% in the game count dataset. Relying on a regular GLMM model would have result in biased parameter estimates and standard errors, and an increased risk of type I errors (Zuur *et al.* 2010). Thus, I chose to use zero inflated models, or mixture models, and not hurdle models, because my dataset had both true and false zeros which are only modelled by the mixture models (Zuur *et al.* 2012). Indeed, the sampling design implied that a zero could arise from the count process, i.e. a rhinoceros habitat with absence of rhinoceros, these are false zeros, or from a poor design resulting in non-rhinoceros habitat area being surveyed. The latter is called true zero and is likely to have happened because the purpose of the surveys was always managemental and designed to census multiple species, and thus multiple habitats.

Relationships

None of the plot showed a noticeable relationship between the response variable and the predictors, i.e. curves were almost flat, meaning that the ecological effects of these predictors on the response variable were likely to be weak.

Collinearity

Based on a conservative generalised variation inflation factor (GVIF) of 3 (Zuur *et al.* 2010), I selected covariates with GVIF < 3 for the final model: distance to the nearest river, distance to the nearest waterhole, rainfall values.

3.3.2. Model selection

I created the plots using the "effects" package (Fox, 2003; Fox and Weisberg, 2018). Results from the ZINB and ZIP GLMM models are not back transformed.
I analysed both the game count and the rhinoceros count datasets with a zero-inflated GLMM model. The covariates solely included continuous variables, i.e. distance to the nearest river, and distance to the nearest waterhole. I also added an interaction of each of these terms with the rainfall variable. I used the R package "glmmTMB" which has been argued to be faster and more flexible than other packages to model zero-inflated GLMM (Brooks *et al.* 2017a, b). The predictors date of the observation and cell ID served as crossed random effects, which had a better fit than a 2-way nested effect for both datasets.

For each dataset I built 4 models, each one with a different rainfall variable depending on the length of the lag effect of rainfall. The variable "rainfall" was the observed rainfall during the month of the rhinoceros observation, "rainfall-1", "rainfall-2", and "rainfall-3" had cumulative rainfall values of the previous month(s), ranging from 1, 2, and 3 months prior to the rhinoceros observation respectively and did not include the rainfall amount of the ongoing month of the observation. Following the information theory approach (Zuur *et al.* 2012), I planned on selecting the best fitting model using the Akaike Information Criteria (AIC). However, there was no meaningful differences in the ΔAIC scores (Appendices 6 and 7). Thus, I chose the model with a lagged effect of rainfall from the 2 previous months for both datasets (i.e. Rainfall-2 for which rainfall was summed over the 2 months prior to the observation), because 2 months is the approximate time needed for the vegetation to regrow and for waterholes to hold water durably.

I relied on the "DHARMa" package (Hartig 2019) to validate the models (Appendices 4 and 5). I used the "simulateResiduals" function which calculated the quantile residuals and chose 1000 simulations to allow for high precision. Although the residuals against with predictors were not perfectly flat, the models for the game count data indicated no issues (Appendix 4). The rhinoceros count model was overdispersed (Appendix 5) even with the negative binomial distribution ($p = 0.034$), which I accounted for when discussing my findings.

For the game count data, I modelled the number of rhinoceros with a zero-inflated Poisson (ZIP) GLMM, with the default log link function for the Poisson regression (count part of the model), and the default logit link function for the binomial regression (zero part of the model). The final model was as follows in the R software:

$$\begin{aligned} number\ of\ rhinos \sim {} & distance\ to\ waterhole * rainfall2 + distance\ to\ river \\ & * rainfall2 + (1|\mathrm{date}) * (1|\mathrm{cell}), \\ & zero\ inflation\ formula = \sim 1, family = poisson \end{aligned}$$

I analysed the rhinoceros count dataset with a zero-inflated negative binomial (ZINB) GLMM. In fact, the initial ZIP GLMM included nested random effects but had convergence problem. I solved this issue using crossed random effects instead and the negative binomial “nbinmo2” (NB). The “nbinom2” allows for the variance to increase quadratically with the mean (Hardin & Hilbe 2007). This way, I managed to solve the convergence problem but not the overdispersion (Appendix 5).

The model for the rhinoceros count data was similar to the game count model. I only added an offset in the conditional model to account for the irregularity of flight coverage. I modelled this with the natural logarithm of the flown area in km^2 for each cell at each specific date and allowed for a different intercept for each observation (e.g. Zuur, Savaliev and Ieno, 2012). The final model was as follows in R:

$$\begin{aligned} number\ of\ rhinos \sim {} & distance\ to\ waterhole * rainfall2 + distance\ to\ river \\ & * rainfall2 + (1|\mathrm{date}) * (1|\mathrm{cell}) \\ & + offset(\log(flight\ coverage)), \\ & zero\ inflation\ formula = \sim 1, family = nbinom2 \end{aligned}$$

I evaluated the main effects of the best models with the Wald Z test with Laplace approximation used as default in the glmmTMB package and a type II Wald chi-square test which gives more reliable results.

4. Results

All cell measurements of the rhinoceros count totalised 10 358 monthly observations from February 2014 to June 2018, among which 7 477 (72%) were absence of rhinoceros. The rhinoceros count sampling occurred on average 9 times a month, ranging from 1 to 13 sampling dates. The final flight coverage for a 1 km² cell, ranged from 1.00 to 6.84 km²/cell/month, with a mean coverage of 2.52 km²/cell/month. The game count data had 6 011 observations with 5 381 absence of rhinoceros (90%). The game count flights always covered 100% of each sampled 1 km² cells.

On average, white rhinoceros observations occurred 1.28 km (0 – 11.31 km) and 1.08 km (0.05 – 2.95 km) away from water in the rhinoceros count and in the game count datasets respectively. In the rhinoceros count dataset, rhinoceros observations occurred on average within 2.11 km (0.03 – 12.18 km) and 1.89 km (0 – 13.01 km) of a waterhole and a river respectively. The game count sampling in the APNR found rhinoceros on average within 1.17 km (0.06 – 3.29 km) and 6.78 km (0.05 – 19.58 km) of a waterhole and a river respectively. Figure 4 shows that rhinoceros were more numerous around waterholes than rivers.

Tables 1 and 2 present the results of the generalised linear mixed-effect models analyses and the analyses of deviance for the game count and the rhinoceros count datasets respectively. In these tables, results for a single predictor variable have to be ignored as all significant results for single predictors also depicted a significant result when tested in interaction with another predictor variable. Thus, in this study, rhinoceros density can only be interpreted together with its associated distance to the nearest source of water and rainfall records.

Hypothesis 1 and 3 related to both analyses, the 1st one inspecting the general trend of the data and the 3rd one examining seasonal trends separately. But hypothesis 2 implied a comparison of the results between seasons, thus I could only use the rhinoceros count analysis to answer this one as the game count data was all records of the dry season.

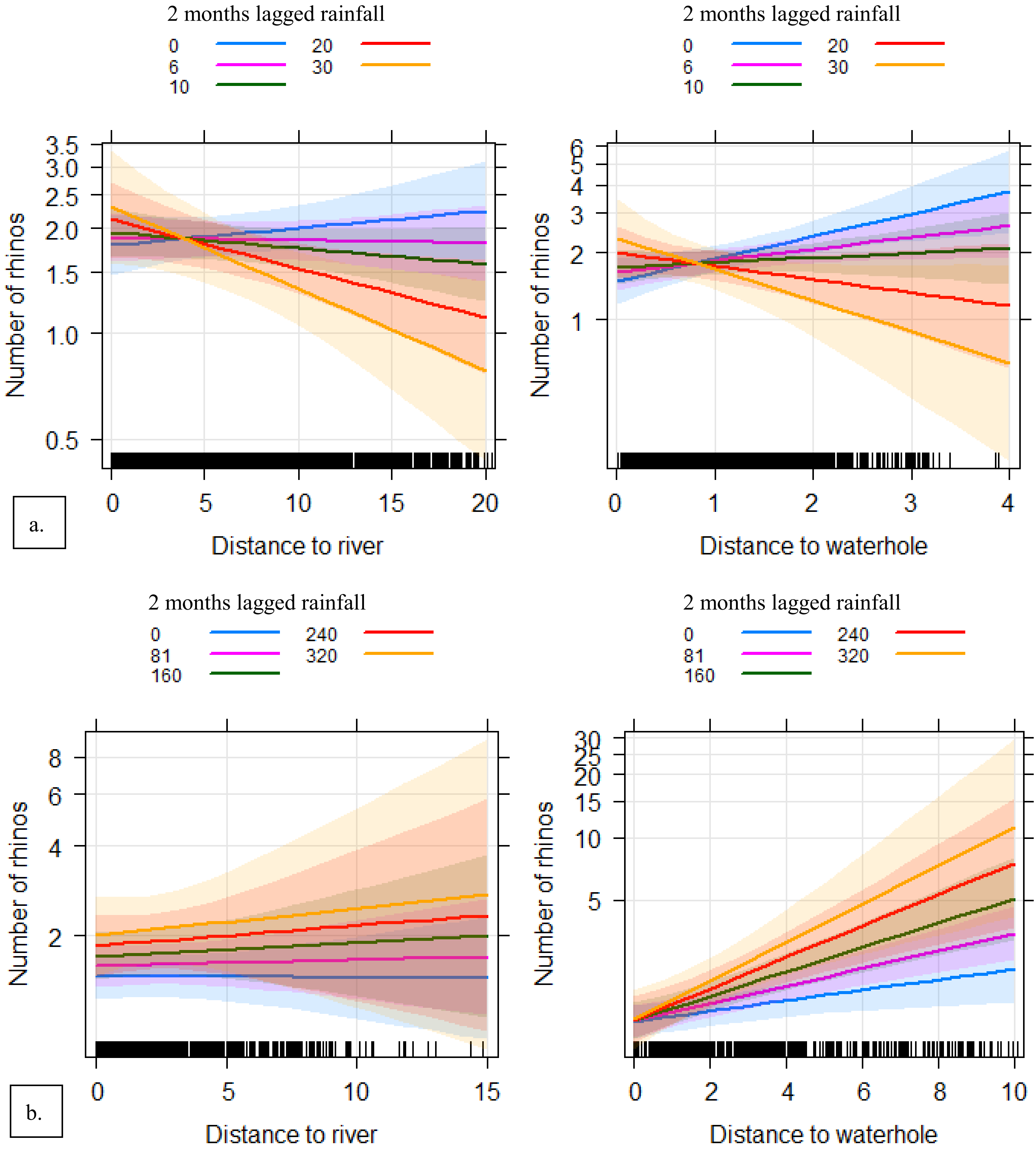

Figure 4. Interactions between the distance to the nearest river or waterhole in km and the cumulative past rainfall from the previous 2 months in mm on the number of rhino/km² (95% CI) for the game count model (a) and the rhinoceros count model (b). Black stripes on the x-axis show the number of observations, long stripes indicate more observations. (a) is solely dry season data, (b) includes dry season (0 mm curve) and wet season (81 to 320 mm curves) records.

Table 1. Summary of the ZIP GLMM and analysis of deviance results (Type II Wald chi-square test) for the game count model for white rhinoceros density. Significant results are depicted in bold.

	Summary of the Zero-Inflated Poisson Generalised Linear Mixed-Effect Model (ZIP GLMM)				*Analysis of deviance table with type II Wald χ^2 test for the ZIP GLMM*		
Fixed effects	**Estimate**	**Standard Error**	**z value**	**Pr(>|z|)**	**χ^2**	**Df**	**Pr(>χ^2)**
Distance to waterhole	0.232	0.078	2.987	**0.003**	2.832	1	0.092
Rainfall-2	0.030	0.012	2.438	**0.015**	2.741	1	0.098
Distance to river	0.011	0.012	0.981	0.327	0.713	1	0.398
Distance to waterhole:rainfall-2	-0.019	0.007	-2.631	**0.009**	6.923	1	**0.009**
Distance to river:rainfall-2	-0.002	0.001	-2.312	**0.021**	5.345	1	**0.021**

Table 2. Summary of the ZINB GLMM and analysis of deviance results (Type II Wald chi-square test) for the rhinoceros count model for white rhinoceros density. Significant results are depicted in bold.

	Summary of the Zero-Inflated Poisson Generalised Linear Mixed-Effect Model (ZIP GLMM)				*Analysis of deviance table with type II Wald χ^2 test for the ZIP GLMM*		
Fixed effects	**Estimate**	**Standard Error**	**z value**	**Pr(>|z|)**	**χ^2**	**Df**	**Pr(>χ^2)**
Distance to waterhole	0.059	0.021	2.766	**0.006**	27.989	1	**1.22E-07**
Rainfall-2	-6.02E-05	0.001	-0.101	0.919	4.225	1	**0.040**
Distance to river	-0.001	0.018	-0.057	0.954	0.028	1	0.867
Distance to waterhole:rainfall-2	4.82E-04	2.18E-04	2.204	**0.027**	4.860	1	**0.027**
Distance to river:rainfall-2	7.04E-05	1.58E-04	0.444	0.657	0.198	1	0.657

4.1. Hypothesis 1: White rhinoceros density decreased (game count) or increased (rhinoceros count) with distance away from water sources

The 1st hypothesis stating that white rhinoceros declined as distance to the nearest surface source lengthened was confirmed in the game count analysis when it had rained and rejected in the rhinoceros count analysis.

The game count analysis confirmed the hypothesis as, white rhinoceros density decreased with lengthening distance to surface water when it rained during the dry season, in the Balule, Klaserie, and Timbavati private reserves. Indeed, when rainfall records of July and August reached 10 mm or above, white rhinoceros density was the highest by rivers (Figure 4a; Table 1, GLMM estimate = - 0.002 ± 0.001, $P_Z<0.05$; $\chi^2 = 5.345$, $P_{\chi^2} < 0.05$) and waterholes (Figure 4a; Table 1, GLMM estimate = - 0.019 ± 0.007, $P_Z<0.01$; $\chi^2 = 6.923$, $P_{\chi^2} < 0.01$). And density decreased as the river, or the waterhole was further than 4 km and 0.8 km away respectively. Nevertheless, these results are supported by few rainfall records due to the sampling design, based on one day of sampling per year, so further investigations would better support this finding. Lastly, a more detailed seasonal analysis of the rhinoceros count data looking at 30 mm rainfall intervals, would allow for a more accurate comparison between the two study sites.

When looking at year-round data in the rhinoceros count, the analysis invalidated the 1st hypothesis. In fact, white rhinoceros density significantly increased as the distance to a waterhole lengthened (Figure 4b; Table 2, GLMM estimate = 4.82E-04 ± 2.18E-04, $P_Z < 0.05$; $\chi^2 = 4.860$, $P_{\chi^2} < 0.05$) contrary to what I expected. There was no change in white rhinoceros density related to their distance to the nearest river as shown graphically and statistically by the high p-value and standard error (Figure 4b, Table 2).

4.2. Hypothesis 2: White rhinoceros density was higher during the wet season

The 2nd hypothesis was rejected, i.e. white rhinoceros density was lower during the dry season than during the wet season. An increase in rainfall records translated into more rhinoceros in the study area of the rhinoceros count (Figure 4b), i.e. Kempiana PNR and the portions of the KNP and Timbavati PNR. For both interactions tested, white rhinoceros density was always higher during the wet season, whether it was nearby waterholes (Figure 4b; Table 2, GLMM estimate = 4.82E-04 ± 2.18E-04, $P_Z < 0.05$; $\chi^2 = 4.860$, $P\chi^2 < 0.05$) or rivers, although this latter inference was only graphical as there was no significant result for the interaction of lagged rainfall and distance to river on white rhinoceros density (Figure 4b, Table 2).

4.3. Hypothesis 3: White rhinoceros density increased (rhinoceros count) or decreased (game count) with distance away from surface water sources when rainfall values increased

The rhinoceros count analysis supported the 3rd hypothesis, namely, white rhinoceros density was indeed increasing with distance away from a waterhole and rising rainfall records (Figure 4; Table 2, GLMM estimate = 4.82E-04 ± 2.18E-04, $P_Z < 0.05$; $\chi^2 = 4.860$, $P_{\chi^2} < 0.05$,). In other words, white rhinoceros density was peaking at the height of the rainy season, as far as waterholes as it could be. Rhinoceros density stayed rather constant as the distance to the nearest river lengthened, and both the p-values and the standard error were high (Table 2).

The game count analysis showed opposite results in the dry season, thus rejecting the 3rd hypothesis when a rainy event occurred within the 2 previous months for both rivers (Figure 4a; Table 1, GLMM estimate = - 0.002 ± 0.001, $P_Z<0.05$; $\chi^2 = 5.345$, $P\chi^2 < 0.05$) and waterholes (Figure 4a; Table 1, GLMM estimate = - 0.019 ± 0.007, $P_Z<0.01$; $\chi^2 = 6.923$, $P\chi^2 < 0.01$) (see 4.1.). In this case of rainfall event, rhinoceros seemed more abundant (Figure 4a) from 0 to 4 km away from rivers, and 0 to 0.8 km away from waterholes than when it had not rained. At longer distances however, density dropped to its lowest values and rhinoceros were more abundant when the rainfall amount was lower or null. Nevertheless, the same caution applies with this result as stated in the 1st hypothesis result section (4.1.) regarding its reliability.

5. Discussion

This research project aimed at gaining knowledge and an understanding of how white rhinoceros use the landscape in central Greater Kruger. I focused on how the distribution of surface water sources and the amount of rainfall events impacted white rhinoceros mean density in the study area (Figure 1) encompassing private reserves of the APNR (Balule PNR, Klaserie PNR, Timbavati PNR), the Kempiana PNR and a central-western portion of the Kruger National Park. I chose to study the influence of water availability on white rhinoceros distribution as water is theoretically an important driver of rhinoceros distribution and is supplemented year-round in most of the study area. Understanding the determining factors of rhinoceros habitat selection is an important tool for parks and reserves management and anti-poaching strategies. I structured my research around 3 hypotheses; 1st hypothesis: considering white rhinoceros are highly water dependent, I assumed their mean density would decrease as their distance away from water sources increased; 2nd hypothesis: I predicted that the higher concentration of water provisioning in the APNR compared to that of the KNP, would attract more rhinoceros in the entire study area during the dry season; 3rd hypothesis: as rainfall likely generate seasonal pans and enhance forage resources, I supposed that rhinoceros would stay far away from water sources when rainfall events become heavier.

The 1st hypothesis stating that white rhinoceros density decreased with distance away from water sources was true in the APNR gamecount when it had previously rained at least 10 mm in the past 2 months. In other words, white rhinoceros stayed close to waterholes and rivers in the APNR at the end of the dry season when previous rainfalls were sufficient enough to induce vegetation regrowth in the vicinity of water sources, allowing rhinoceros to fulfil their needs in drinking and foraging. In this case, it is possible that rhinoceros used rivers in the APNR or that they used waterholes nearby rivers, which were plentiful. In this case of rainfall events during the dry season, white rhinoceros seemed to avoid being far from water sources. This finding could arise from the availability of both food and water resources close by water sources or from rhinoceros leaving the area to a preferred landscape where rain had also initiated vegetation regrowth. The positive outcomes of staying close to water at this period of resources scarcity was likely counterbalancing the negative outcomes that may rise from staying close to water sources. Indeed, the costs of piosphere effect, interference competition, predation and poaching pressures as well as other human disturbances are likely greater at waterholes and riverbanks, which make a good observation spot for tourists and are often crowded by other herbivores. In contrast, the 1st hypothesis was invalidated in the rhinoceros count study (Timbavati PNR, Kempiana PNR and a small portion of the KNP) and in case of rainfall lower than 10 mm in the APNR during the two months prior to the gamecount. In the rhino count study area, i.e. Kempiana PNR, Timbavati PNR and the portion of KNP, white rhinoceros avoided staying close to waterholes year-round. They also avoided riverbanks in the APNR gamecount study when rainfall was lower than 10mm. The results from the rhinoceros count suggests that they were not attracted to rivers in the Kempiana PNR, Timbavati PNR, and KNP study area, which might be due to the topography of the riverbanks, preventing rhinoceros from accessing it. White rhinoceros avoidance for water sources vicinity in the rhinoceros count study and when there was no sufficient rainfall in the gamecount study might be due to food resources depletion, and piosphere effect. The lack of foraging resources might have forced rhinoceros to use all available habitat to fulfil their nutritional needs. In that case, the best trade-off might have been to travel further away from permanent water sources to find food.

The results did not support the 2nd hypothesis inferring that white rhinoceros were more abundant during the dry season than during the wet season. The study area encompassing Kempiana PNR, Timbavati PNR and a portion of KNP, did not seem to attract rhinoceros more during the dry season despite the abundance of permanent water sources. This result suggests that rhinoceros habitat selection varied seasonally. I suspect that the Kempiana PNR, Timbavati PNR and the portion of KNP was a preferred landscape where white rhinoceros likely stayed when resources were not limiting, i.e. during the wet season. The drop in the number of rhinoceros during the dry season might come from the need to travel further away to satisfy their nutritional requirements. Although I doubt that surface water was limiting during the dry season considering that water provisioning in the area would still be considered in excess, rhinoceros could still have travelled western, further in the APNR, where surface water was more abundant than in this part of the study area. The peak season for tourism during the dry season could also lead rhinoceros to avoid the waterholes vicinity during park and reserves opening hours. Females with calves, could also have had to adapt to a seasonal variation in predation risk and avoid water areas at the riskiest time of year for them. The lack of influence of rivers regardless of the season likely shows that rhinoceros did not favour riverbanks in the rhino count study area.

The results of the rhinoceros count analysis supported the 3rd hypothesis stating that white rhinoceros were more attracted to the Kempiana PNR, Timbavati PNR and

KNP area at the peak of the rainy season and avoided permanent water sources vicinity. In fact, white rhinoceros probably relied on seasonal pans which they favour for wallowing. It also means that foraging opportunities might have been better further away from waterholes. Other pressures such as interference competition, predation, and poaching pressures, as well as other human disturbances might have lessened with distance to water. Rivers in this study area did not seem to be more or less attracting for white rhinoceros after heavy rainfalls probably enhanced foraging opportunities and water availability, so I suspect that rhinoceros did not favour riverbanks habitat. The 3rd hypothesis was rejected in the APNR gamecount analysis of the late dry season, i.e. rhinoceros stayed close to water sources when rainfall events had been more important. This finding hints that resources scarcity in the landscape probably led rhinoceros to stay close to water sources to fulfil both drinking and nutritional needs as mentioned previously. It might imply that rainfall events helped with vegetation regrowth but as resources were still limiting rhinoceros might have made a trade-off between staying further away and travelling more or travelling less to find good forage and water quality. Interestingly the highest number of rhinoceros was observed when there had been no rain at all since July. Perhaps food resources depletion was far more spread around water sources leading rhinoceros to go further away to find food.

Lastly, in all 3 hypotheses, white rhinoceros distribution might have been influenced by other parameters such as rhinoceros timing of behaviours, temperature and wind conditions, extreme climatic events, other habitat characteristics, namely the distribution of grazing lawns, shade availability, local topography, and soil composition. Because of rhinoceros timing of behaviours, we could have missed observations if they were active and near water sources at night.

5.1. Habitat characteristics and activity pattern

White rhinoceros habitat selection is known to vary seasonally (Wardjomto *et al.* 2019). Rhinoceros select their preferred habitat during periods of food abundance at the late wet season and use all available habitat at the late dry season when food is scarce (Wardjomto *et al.* 2019). White rhinoceros use open shrub and tree layers with moderate vegetation density (Pienaar *et al.* 1993; Pienaar 1994; White *et al.* 2007) but prefer open grasslands with moderate to dense grass cover (Pienaar *et al.* 1993; White *et al.* 2007; Thompson *et al.* 2016). Thus, the abundance of rhinoceros during the wet season might mean that the study area was a preferred landscape and the decline in rhinoceros number during the dry season could imply that rhinoceros had to travel away to find resources, using all available habitats.

Weather conditions, time of the observation, or extreme climatic events, e.g. a drought, could have affected rhinoceros distribution in both analyses. Indeed, white rhinoceros daily activity patterns is strongly shaped by weather conditions, temporal variation and habitat characteristics (Tichagwa *et al.* 2020). In case of drought, white rhinoceros might have travelled to areas they would normally avoid, to find enough food and water. However, I did not have data on climatic conditions aside from rainfalls for both study areas, and neither was I aware of the time of observation for the gamecount study. Observations in the rhinoceros count ran throughout the day between 6am and 5pm. Although rhinoceros are known to be active at night (Owen-Smith 1988), their nocturnal drinking activity pattern seem to depend on the rhinoceros population and habitat, as studies found opposite results: Owen-Smith (1973) found white rhinoceros drinking during the night when Patton *et al.* (2011) found another population of rhinoceros in a different reserve to be unlikely to drink at night. In the rhinoceros count study, it is unlikely that rhinoceros were missed during the day because of the time of observation, as it seems they can usually be found drinking either between 10 and 11 am or between 3pm and 6pm (Patton & Genade 2019) for up to an hour. As mentioned above, they might drink at night depending on the rhinoceros population, thus we might have missed rhinoceros observations at night-time. White rhinoceros activity pattern is primarily influenced by weather conditions (Tichagwa *et al.* 2020), temperature being the first factor, time of the day in interaction with habitat characteristics, and age and sex of the individuals. Although habitat selection might vary seasonally, activity budget does not seem to be influenced by the seasonality (Tichagwa *et al.* 2020). Thus, as the rhinoceros count was sampled year-round and throughout the day covering all available habitats of the study area, it is unlikely that we missed rhinoceros due to the study design, or that the observations would be biased due to a lack of representativity in the different types of factors mentioned. The rhinoceros count was designed to spot all rhinoceros in the landscape. Therefore the study area was flown over until every vegetation patch was checked for rhinoceros. Moreover, as rhinoceros prefer open habitat as mentioned previously, they would normally be easy to spot from an aircraft. So it is unlikely that observers missed rhinoceros during the day however there is still a possibility that rhinoceros were present at water sources at night as explained above and thus not accounted for in this study. The gamecount study design also allowed to survey all available habitat but the few sampling dates and the absence of the time of observation implies that the interpretation of this analysis cannot be considered as a representative sample of rhinoceros distribution throughout the day and the dry season. It is only a snapshot of a rhinoceros day and of their distribution at the end of the dry season, that gives a hint at where rhinoceros can be found in this area and allowed me to make suggestion as to why there were found there at that moment given all the factors examined in this discussion.

5.2. Food resources: a main driver of white rhinoceros distribution year-round

The smaller number of white rhinoceros during the dry season and the fact they avoided surface water areas at this time of year was most likely due to food resources depletion. Indeed, where there is water provisioning in excess, Owen-Smith (1996) showed that it leads to increased vegetation degradation due to higher herbivores pressures. Water provisioning can be considered in excess when it disrupts natural ecological processes and increases animals mortality, which is the case when water sources are 2 km apart but can be avoided when they are 10 km apart (Owen-Smith 1996). So water provisioning can be considered excessive in both study areas, as the average distance between water sources was less than 2 km. Such concentration of artificial waterholes tends to support higher ungulates density on the short term but can jeopardize ungulates populations survival in case of severe drought as it happened in 1982-1983 in the Kruger region (Owen-Smith 1996). Indeed, higher density of ungulates increases the herbivores pressure and ultimately leads to grass standing crop and biomass decline, i.e. food resources depletion (Peel & Smit 2020). In this regard, the drought of experienced during the wet season of 2015/2016 might have influenced rhinoceros population in the area and could have led to a decrease in rhinoceros numbers due to mortality, as it did in KNP (Ferreira *et al.* 2019a) and for other herbivores species in the Greater Kruger (Peel & Smit 2020), or rhinoceros migration and also influenced their habitat selection locally.

Water being the first limiting factor during the dry season in the APNR could theoretically explain the abundance of white rhinoceros by water sources following rainfall events in the previous two months. However it is quite unlikely, as in the area surveyed in the gamecount, water sources were on average 4 times closer than in the area surveyed in the rhinoceros count, which showed opposite results, i.e. rhinoceros stayed away from waterholes even during the dry season. It is more likely that food was the first limiting factor as explained above. In that case, at the end of the dry season, there would likely be not much food left, and rainfall events totalising more than 10 mm in the previous two months, might have given the chance to vegetation to regrow and provide food for rhinoceros.

5.3. Piosphere effect

Waterholes in the study area could also be affected by the piosphere effect. It is a buffer zone around natural and artificial waterholes, where herbivores impact is very high and results in a reduction in forage quality and quantity as well as changes in soil composition (Andrew 1988). Such reduced forage availability would make areas close to waterholes less suitable as foraging areas. The fact that rhinoceros mostly avoided the close proximity of waterholes suggest that they had to make a trade-off by staying further away from waterholes to satisfy their nutritional requirements, thus having to travel longer distances for drinking purpose. This result is in agreement with previous studies (Redfern *et al.* 2003; Smit & Grant 2009) which observed that when there is a high abundance of artificial waterholes, the main constraint for herbivores is nutritional needs regardless of the season, whereas during the dry season, access to water should be the main constraint under natural ecological processes (Owen-Smith 1996). During the wet season, rhinoceros could have avoided the possible piosphere effect by relying on seasonal pans, as suggests the higher number of rhinoceros away from waterholes.

5.4. Rivers habitat use

The results of the gamecount analysis showed that rhinoceros also stayed nearby rivers when there had been above 10 mm of rainfall, implying that they might have used riverbanks habitats in this study area (APNR). They might be accessible to rhinoceros which is not always the case due to broken riparian terrain being also often more densely wooded than other types of terrain (White *et al.* 2007; Thompson *et al.* 2016). Thus, they might have used rivers for drinking and feeding, as found in Pienaar (1994) where rhinoceros fed on grasses such as *Panicum maximum* in riverbanks. However, the absence of variation in the rhinoceros number linked to the distance to river in the rhinoceros count study could mean that rhinoceros presence around rivers was consistent year-round or that they did not particularly use riverbanks. As resources provided by riparian habitat are also affected by seasonal variation and herbivores pressure, one could expect rhinoceros presence to vary accordingly. Water scarcity in the landscape could theoretically attract rhinoceros to perennial riverbeds but the analysis shows otherwise, i.e. the number of rhinoceros seemed to be the lowest during the dry season. This confirms that water was not a limiting resource for rhinoceros in the study area. A likely explanation would be that riparian terrains in the rhinoceros count study area (i.e. KNP, Kempiana PNR, Timbavati PNR) were not accessible to rhinoceros because of broken terrain, abundant rocks, or dense and wooded vegetation (Pienaar *et al.* 1993; Thompson *et al.* 2016) . Graphically, the higher number of rhinoceros during the wet season might only mean that there were more rhinoceros during the wet season overall given that this was not a significant result.

5.5. Seasonal wallowing

White rhinoceros are also known for wallowing at waterholes for up to several hours during the wet season (Owen-Smith 1973; Pienaar 1994; Tichagwa *et al.*

2020). However Pienaar (1994) found that rhinoceros preferred wallowing in small seasonal pans formed at foot slopes that have their favourite mud consistency with a high clay component. In this study, they might have chosen their preferred habitat for wallowing, relying on seasonal pans perhaps also for drinking and foraging nearby, thus avoiding the direct proximity of waterholes. Wallowing only occurs during the wet season (Owen-Smith 1973; Tichagwa *et al.* 2020) and the higher number of rhinoceros during this season could come from their attraction to the area for wallowing pools.

5.6. Interference competition

When natural ecological processes are in action in this type of savannah, i.e. when there is no artificial water, interference competition would coexist with exploitation competition and make access to water a limiting factor during the dry season (Valeix *et al.* 2007). As mentioned previously, water was probably not a limiting factor in the study due to water provisioning. Thus, we can expect that exploitation did not generate enough competition as to make water the limiting factor. However, what is still likely to have happened is that animals aggregation at waterholes generated interference competition (Matsika *et al.* 2008). This translates into an increase in aggression and vigilance, and ultimately reduces the intake rate and constraints herbivores to spend a longer time at waterholes (Matsika *et al.* 2008). This would particularly be true during dry years with likely elephants crowding waterholes (Valeix *et al.* 2007). To reduce the impact of such interference, herbivores communities do temporal partitioning at waterholes, i.e. they shift their diurnal activity going by waves or coming at night (Valeix *et al.* 2007; Matsika *et al.* 2008). This choice can have indirect fitness costs as animals could be exposed to a higher predator pressure if they were going to waterholes at night, but it also reduces the interference (Valeix *et al.* 2007). White rhinoceros could have avoided waterholes during the day when they were crowded by other herbivores and especially when elephants were abundant. In that case they might come to drink at night or during the day once or twice, for up to an hour, and then leave the waterhole proximity. One can assume that during the dry season in the gamecount study area (APNR) the positive outcomes of staying close to water allowing rhinoceros to fulfil their needs outweighed the negative outcomes such as those of interference competition.

5.7. Intraspecific competition

It is unlikely that intraspecific competition played a big role in rhinoceros avoidance of waterholes as rhinoceros territories often overlap (Thompson *et al.* 2016). In fact, adult male white rhinoceros may hold exclusive territories from other males, while subadults males tend to share part of their territories with other subadults and females, while females territories often overlap with adults and subadults males territory (Thompson *et al.* 2016). There is also little aggression between rhinoceros, as Patton & Genade (2019) reported in their 10 years study, fights only occurring between adult males to establish breeding rights. Adult white rhinoceros would overall not be attracted to waterholes to find conspecifics as they are solitary animals and only associate for discontinuous consort relationship and mating (Patton & Genade 2019). In Patton and Genade (2019) study, subadults evolved through temporary groups when dispersing either solely with subadults of either sex or associating with a female and her calf (Patton & Genade 2019). These findings were similar to previous studies about rhinoceros behavioural ecology (Owen-Smith 1975; Shrader & Owen-Smith 2002). Thus, rhinoceros are overall unlikely to be attracted or avoid water areas due to the presence of conspecifics. Data on rhinoceros territories and behavioural ecology would be needed in my study to assess their relative importance in intraspecific competition but one can estimate them to have a low influence considering previous studies results and compared to the other factors aforementioned.

5.8. Predation and poaching pressures

Herbivores above 150 kg, such as white rhinoceros, are less prone to natural predation (Sinclair *et al.* 2003). Owen-Smith & Mills (2008) study in the Kruger NP confirmed that predation is not a cause of white rhinoceros adult mortality, food limitation is the sole mortality factor controlling rhinoceros abundance. Only females rhinoceros with calves might face natural predation (Owen-Smith 1973). Thus, probably only them might adapt their drinking patterns to avoid predation. Other herbivores species use a variety of strategies to cope with competition, hunting and predation, such as shifting their visits to waterholes from day hours toward night hours (Valeix *et al.* 2007; Crosmary *et al.* 2012; Sirot *et al.* 2016). Herbivores with young might shift toward night hours or not depending on how vulnerable and when they are to natural predation (Crosmary *et al.* 2012), i.e. a herbivore species which was not identified as a main prey in the study area, shifted its visits to waterholes towards night hours, although the presence of young lessened that shift (2012). Additionally, predation rates on rhinoceros might fluctuate seasonally as it did for other herbivores species in the KNP in a study by Owen-smith (2008). Thus, rhinoceros, female rhinoceros with calves, could adapt the length and time of their visits to waterholes perhaps shifting towards night hours if they are less prone to predation at night and depending on the seasonal predation pressure. The poaching risk could also vary seasonally and influence rhinoceros habitat selection accordingly.

Herbivores are also known to modulate group sizes to cope with predation and poaching in risky areas (Fortin & Fortin 2009; Sirot *et al.* 2016; Brooke *et al.* 2020). Although white rhinoceros face a low predation risk overall (Owen-Smith 1973; Sinclair *et al.* 2003; Owen-Smith & Mills 2008), they are threatened by the ongoing poaching rates (Ferreira *et al.* 2018). It would then be interesting to know whether they associate to other herbivores to alleviate predation and poaching pressures. Several studies on herbivores responses to poaching or predation risk showed that in risky areas herbivores might adjust their foraging strategies by reducing the time spent searching for optimal resources and their exploitation (Fortin & Fortin 2009; Brooke *et al.* 2020). They also observed that herbivores would select for patches of vegetation far from poaching activities (Brooke *et al.* 2020). In the end, Brooke et al. (2020) demonstrated that poaching activities hindered the optimisation of foraging strategies and shaped herbivores distribution. There are no such studies focusing specifically on white rhinoceros, but they could response to poaching pressure similarly as other herbivores and thus if waterholes are risky areas, avoid staying near them longer than necessary for drinking purpose, i.e. once or twice daily at maximum up to one hour at a time and up to two to four days intervals (Owen-Smith 1988; Pienaar 1994; Patton *et al.* 2011).

5.9. Touristic disturbances

The influence of human infrastructures and touristic activities on white rhinoceros remains unclear. On one hand, Tichagwa *et al.* (2020) found that white rhinoceros were attracted to roads, likely due to their easy access, the absence of landscape barrier, and the intense animal disturbance promoting plant species richness diversity. On the other hand, the other species of African rhinoceros the black rhinoceros (*Diceros bicornis*) is known to be sensitive to tourism disturbances and would only tolerate low and moderate levels of them (Muntifering *et al.* 2019). High disturbances reduces the habitat value and black rhinoceros would simply keep their distance from highly disturbed habitat (Muntifering *et al.* 2019). As in our study area most waterholes are kept artificially by provisioning and often close to other infrastructures (e.g. lodges, roads, observation spot, etc.), they are likely associated with human disturbances to some extent. We can only hypothesize that such disturbances might either reduce the habitat value for white rhinoceros or that they might not considered them as landscape barriers or repellent and could even prove attractive to them such as feeding sites close to roads in Tichagwa *et al.* (2020) study. Thus, if white rhinoceros were disturbed by touristic disturbances, they could have avoided the vicinity of waterholes during the peak of the touristic season, i.e. during the dry season (in June and July for 1998; Ferreira & Harmse 1999). The results shows that they could have done so in the rhinoceros count study area but perhaps not in the gamecount area. Relevant data on tourists abundance and infrastructures correlated to rhinoceros distribution could allow to research this hypothesis further.

6. Conclusion

This study suggests that food resource was the first limiting factor for rhinoceros year-round in the study area and that white rhinoceros had to make trade-offs to fulfil their nutritional and hydration needs. It appears that water provisioning in the area might still disrupt natural ecological processes, which translates into nutritional needs being the main driver of rhinoceros distribution in this landscape. The Kempiana PNR, Timbavati PNR and portion of the KNP study area also seemed to be a favoured landscape for white rhinoceros, attracting them during the wet season, likely holding preferred characteristics for main activities such as foraging and seasonal wallowing. Results are hinting that rivers might be used by rhinoceros only in the western part of the study area (APNR) and not in the portion of the KNP and the two reserves bordering it. Seasonal variations might also have influenced rhinoceros habitat selection, both directly with weather conditions, spatio-temporal availability of resources, and habitat characteristics, and indirectly with interference competition, predation pressure, poaching pressure and other human disturbances. Researching all these factors as well as intraspecific competition should provide a better understanding of white rhinoceros habitat selection, and subsequently distribution, in the central western Greater Kruger. Finally, it is difficult to assess from the results of this study whether the difference observed in rhinoceros distribution between the two study areas arose solely from the factors described above or if the scale of the analysis and the disparities in the model and data quality influenced the results and interpretation.

7. Caveat

I had the chance to be able to use data from management, but it came at a price: it was difficult to find the right statistical model that would account for all the characteristics of the different datasets and still be built around the same base, i.e. generalised linear mixed effect models. Unfortunately I could not use one of the datasets for this reason, as my results would not have been very reliable. Overcoming the difficulty of fitting a model without violating critical assumptions meant that I had to narrow my initial plan to far less testing.

Indeed, I did not manage to test for detailed temporal variability of white rhinoceros density, which is the main missing component in this study. There are a couple more hypotheses that I would have liked to investigate but did not manage to do so, due to the amount of time I spent on the zero-inflated GLMM analyses, here are 2 major ideas:

- Whether white rhinoceros are found closer to waterholes than they would be by chance
- Seasonal and annual variability in white rhinoceros density

Moreover, the discrepancies in the data quality and access to waterholes might have impacted my results and prevented me from further testing on the different use of permanent versus seasonal waterholes. The gamecount analysis only accounted for a total of 4 sampling dates in each reserve (Klaserie PNR, Balule PNR, and Timbavati PNR), i.e. 1 day/year for 4 years. Thus, this analysis is not as reliable as the one from the rhinoceros count, and further research would be needed in this study area requiring more sampling dates for rhinoceros observation throughout the dry season and a more detailed analysis of rainfall patterns linked to these observations

Due to my beginner experience in software programming, I have not been able to use “raster” layers in the GIS software, which would have allowed for more spatial analysis within the software. For the same reason, I also did not include back transformations for the GLMM analyses, which I could have used to find the real values that could be used for management purposes.

Last but not least, my analyses cover a period of drought, which might give different results than under regular climatic conditions.

8. Further research

The discrepancies in water provisioning between the KNP and the different private reserves poses the question of the likely intensified impact of herbivores in the private reserves. Indeed with the KNP pursuing its management plan toward more natural ecological processes, there is a risk that the private reserves will act as a sink for herbivores during the dry season, if not already happening. This is likely to disturb local plant and animal communities as the vegetation would not have a chance to recover from intense grazing and browsing impact. An even greater collaboration in both management and research between the reserves and with SANParks Scientific Services could help alleviate this risk and reach a new understanding of white rhinoceros and other herbivores landscape uses in the Greater Kruger region. In the light of the ever-ongoing poaching crisis and the increased risks of droughts associated with climate changes, management and research action plan are critical to white rhinoceros population . To reach a full understanding of white rhinoceros landscape use in the APNR region, more data on biotic and abiotic parameters at seasonal and annual scales would allow for in depth results. The use of software or platform allowing for satellite imagery analysis (e.g. Google Earth Engine[7]) could help localise waterpoints and perform monthly survey on their water level without having to survey each single point, only using control points. Telemetry data for rhinoceros location could also help reach an in depth understanding of white rhinoceros movement and habitat use on both smaller and wider spatio-temporal scales.

Finally, the outcomes of this project and future research could be used in agent-based model of wildlife crime, which can help understanding and preventing poaching. More generally, the findings could be taken into consideration for applied antipoaching strategies and water management plans in the APNR region.

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[7] Available at: https://earthengine.google.com

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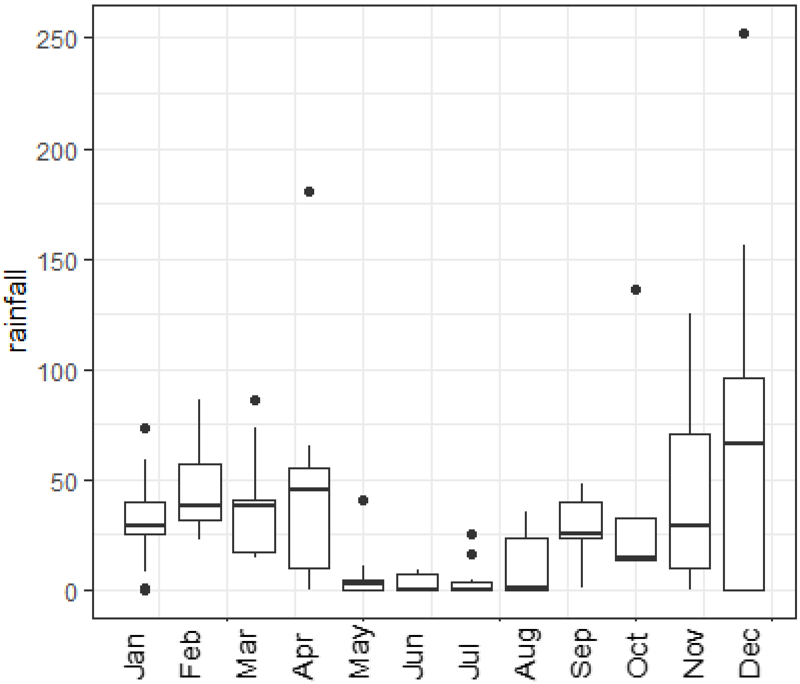
Appendix 1



Monthly rainfall values in mm averaged from January 2014 – June 2018. Outliers are represented by the black dots.

Appendix 2

Summary of data exploration for the game count data. Y refers to the response variable, X refers to the predictive variables. GVIF stands for generalised variation inflation factor, ACF stands for autocorrelation factor. Solution gives the final solution, other potential solutions later abandoned are detailed in the model selection section.

Assumptions & parameters	**Technique**	**Result**	**Solution**
Outliers presence in Y & X	Boxplot and Cleveland dotplot	Yes	5 outliers deleted in Y, resulting in rhinoceros density ≤ 7/km^2
Zero inflation Y	Frequency plot	Yes	Zero inflated model
Relationships Y & X	Multipanel scatterplot and Pearson correlation coefficients	?	No obvious relationship, flat curves
Interactions	Coplot	?	No obvious interaction, flat curves
Collinearity	GVIF & Pearson correlation coefficient	No	
Independence	ACF and plot of response against spatial variable	Yes	Crossed random effects (GLMM)

Appendix 3

Summary of data exploration for the rhinoceros count data. Y refers to the response variable, X refers to the predictive variables. GVIF stands for generalised variation inflation factor, ACF stands for autocorrelation factor. Solution gives the final solution, other potential solutions later abandoned are detailed in the model selection section.

Assumptions & parameters	**Technique**	**Result**	**Solution**
Outliers presence in Y & X	Boxplot and Cleveland dotplot	Yes	Outliers kept
Zero inflation Y	Frequency plot	Yes	Zero inflated model
Relationships Y & X	Multipanel scatterplot and Pearson correlation coefficients	?	No obvious relationship, flat curves
Interactions	Coplot	?	No obvious interaction, flat curves
Collinearity	GVIF & Pearson correlation coefficient	No	
Independence	ACF and plot of response against spatial variable	Yes	Crossed random effects (GLMM)

Appendix 4

Summary of the residuals investigation with the DHARMa package for the ZIP GLMM applied to the game count data. For each test, H0 = fitted model.

Assumptions	**DHARMa function**	**Test**	**Result**
Homogeneity Y	testResiduals	DHARMa nonparametric dispersion test via standard deviation of residuals fitted vs. simulated	$p > 0.05$
Uniformity	testResiduals	One-sample Kolmogorov-Smirnov test	
Outlier Y	testResiduals	DHARMa outlier test based on exact binomial test	
Zero-inflation Y	testZero Inflation	DHARMa zero-inflation test via comparison to expected zeros with simulation	
Temporal autocorrelation	testTemporal Autocorrelation	Durbin-Watson test	
Spatial autocorrelation	testSpatial Autocorrelation	DHARMa Moran's I test for spatial autocorrelation	

Appendix 5

Summary of the residuals investigation with the DHARMa package for the ZINB GLMM applied to the rhinoceros count data. For each test, H0 = fitted model. Significant results are depicted in bold.

Assumptions	**DHARMa function**	**Test**	**Result**
Homogeneity Y	testResiduals	DHARMa nonparametric dispersion test via standard deviation of residuals fitted vs. simulated	**p = 0.034**
Uniformity	testResiduals	One-sample Kolmogorov-Smirnov test	p > 0.05
Outlier Y	testResiduals	DHARMa outlier test based on exact binomial test	
Zero-inflation Y	testZero Inflation	DHARMa zero-inflation test via comparison to expected zeros with simulation	
Temporal autocorrelation	testTemporal Autocorrelation	Durbin-Watson test	
Spatial autocorrelation	testSpatial Autocorrelation	DHARMa Moran's I test for spatial autocorrelation	

Appendix 6

Akaike Information Criterion table for the final game count model depending on different lag effects of rainfall. Rainfall-1, -2, and -3 have cumulative rainfall values of the previous month(s), ranging from 1, 2, and 3 months prior to the rhinoceros observation, x *is the month of the observation.*

Model	**df**	**AIC**	**ΔAIC**
Rainfall-2 $\llbracket(x\rrbracket_{-1} + x_{-2})$	9	5974.740	0
Rainfall-3 $\llbracket(x\rrbracket_{-1} + x_{-2} + x_{-3})$	9	5974.740	0
Rainfall (x)	9	5981.512	6.8
Rainfall-1 $\llbracket x_{-1})$	9	5981.828	7.1

Appendix 7

Akaike Information Criterion table for the final rhinoceros count model depending on different lag effects of rainfall. Rainfall-1, -2, and -3 have cumulative rainfall values of the previous month(s), ranging from 1, 2, and 3 months prior to the rhinoceros observation, x *is the month of the observation.*

Model	**df**	**AIC**	**ΔAIC**
Rainfall-2 $\llbracket(x\rrbracket_{-1} + x_{-2})$	10	23129.44	0
Rainfall-3 $\llbracket(x\rrbracket_{-1} + x_{-2} + x_{-3})$	10	23132.85	3.4
Rainfall-1 $\llbracket(x\rrbracket_{-1})$	10	23134.01	4.6
Rainfall (x)	10	23136.96	7.5