

Consequences of White Rhinoceros (*Ceratotherium simum*) Poaching on Grassland Structure in Hluhluwe-iMfolozi Park in South Africa

*Konsekvenser av tjuvjakt på vitnoshörningen (*Ceratotherium simum*) på gräslandsstruktur i Hluhluwe-iMfolozi Park (HiP) i Sydafrika*

Emy Vu



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Emy Vu

Supervisor:	Joris Cromsigt, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Assistant supervisor:	Mariska te Beest, Utrecht University, Copernicus Institute of Sustainable Development - Environmental Sciences
Assistant supervisor:	Elizabeth le Roux, Nelson Mandela University, Department of Zoology
Examiner:	John P Ball, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
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Abstract

The megaherbivore white rhinoceros plays a vital role in African savannah ecosystem, where it affects the grassland through heavy grazing and creates a mosaic grassland varying in structure. Illegal removal of the white rhinoceros has dramatically increased, and led to a decrease of white rhinoceros' population density. My aim is to examine whether their illegal removal influences grassland structure, and whether this may affect habitat use of other species. The research was conducted in Hluhluwe-iMfolozi Park in South Africa, where I performed a correlative study on two scales, landscape and local. I quantified grassland structure, and the result showed that the white rhinoceros shaped grassland structure. The density of herbivores tended to decrease with higher altitude. No significance difference in grassland structure was found on a local scale, due to the lack of hotspots, i.e. middens and termite mounds, found along the transects. I conclude that there is variation in grassland biomass and distribution of dung of different herb's, and I also observed fewer hotspots in high poaching areas. In the future, it is crucial to get to the root of the illegal removal and to act towards a non-poaching environment, or else the white rhinoceros can go extinct.

Keywords: white rhinoceros, South Africa, Hluhluwe–iMfolozi Park, poaching, African savannah, herbivore, wildlife ecology, termite mound, *Macrotermes*

Introduction

A major cause for megaherbivore extinction has been proposed to be due to an increase in hunting pressure exerted by humans (Malhi et al. 2015). A second cause was rapid climate change (Malhi et al. 2015). The megaherbivore is characterized by a weight over 1000 kilograms as an adult and the consequences of this significant body size are the need for larger territories and food resources, but also a greater tolerance for less nutritious grass (Cromsigt et al. 2017). The last remaining African megaherbivores today are the white rhinoceros, black rhinoceros (*Diceros bicornis*), elephant (*Loxodonta spp.* and *Elephas spp.*), hippopotamus (*Hippopotamus amphibius*), and giraffe (*Giraffa camelopardalis*, Owen-Smith 1988). The white rhinoceros does survive non-human predators and create mosaic patches with regrowth on the grassland with higher biodiversity (Owen-Smith 1988). The loss of many megaherbivores resulted in a cascading effect on the ecosystem (Cromsigt et al. 2017). The few megaherbivores that exist today still face threats such as climate change and poaching (Aryal et al. 2017). Let us now consider the importance of white rhinoceros.

The megaherbivore white rhinoceros is an ecosystem engineer (Waldram et al. 2008) and a keystone species (Paine 1995) that is a crucial component to the South African savanna ecosystem (Owen-Smith 1988). Their ongoing grazing has an effect on the ecosystem, which changes fire dynamics (Cromsigt et al. 2017), and the megaherbivore is considered to be one key species of the big five (Caro & Riggio 2014), of major economic importance and popular for ecotourism (Lindsey et al. 2007). If they were to become extinct, there may be consequences such as more savanna fires and lower biodiversity on the grassland (Gosling 2014).

Moving on now to consider the threats that the white rhinoceros faces today. The white rhinoceros is now near threatened according to the International Union for Conservation of Nature (IUCN, Emslie 2012), and their biggest threat is the illegal poaching that is strongly on the rise. There is a demand from wealthy consumers who are willing to pay a large amount of money for the rhinoceros' horns, which are then used for medicine and drugs in Vietnam and China, and for dagger handles and ornaments in the Middle East and East Asia (Nowell 2012). The main drivers for poaching are traditional medicine trade on the Asian side aided by poverty on the South

African side (Cromsigt et al. 2017). Illegal removal has become a huge problem in protected areas around South Africa, such as Kruger National Park (Annecke & Masubelele 2016) and Hluhluwe-iMfolozi Park (HiP, Cromsigt et al. 2017).

Turning now to the effects of white rhinoceros on a local scale. Cromsigt & te Beest (2014) showed that there was higher grassland in areas with low density of white rhinoceros, and lower grassland in areas of high density of white rhinoceros (Cromsigt & te Beest 2014). An earlier study has shown that there are more likely to be shorter grass where there is high density of white rhinoceros, which leads to a less fire prone environment (Waldram et al. 2008). White rhinoceroses may have a bigger impact in certain hotspots where they use the landscape intensively, such as around termite mounds and white rhinoceros middens (Gosling 2014). Termites such as *Macrotermes* mix the soil layers, aiding nutrient turnover rate. This promotes plant growth and plant heterogeneity (Muvengwi et al. 2017). Consequently, this leads to more available nutrient-dense food resources, which may attract white rhinoceros to these localities (Gosling et al. 2016, Walker et al. 1987). In areas of high white rhinoceros' density, a clear pattern of intense grazing can be seen up to four to five meter surrounding termite mounds (Cromsigt & te Beest 2014). Thus, the grassland structures in immediate proximity to the termite mounds could arguably be viewed as being to a greater extent altered by the white rhinoceroses (Gosling 2014). What follows is an account of the variation in grassland structure created by white rhinoceros may influence mesograzers.

Large herbivores in HiP share the same habitat. They have different niches, which leads to different species having preferred different heights of grass and quality of grass. For instance, white rhinoceros prefer grassland, such as Guinea grass (*Panicum maximum*) during wet season or Red grass (*Themada triandra*) when there is less of the first mentioned grass. But during dry periods they can switch over to tall grassland at the hill slopes when it is needed. It has been suggested that the white rhinoceros graze one third of the grass biomass of all megaherbivores in HiP (Owen-Smith 1988). In the wet season, white rhinoceros do not overlap in diet a lot with the buffalo, zebra nor impala that prefer tall grass (Cromsigt et al. 2017). Having explained some white rhinoceros coexistence with other herbivores, I will now move on to discuss the hypotheses.

My study examines the white rhinoceros impact on the structure of the savanna grasslands in Hluhluwe-iMfolozi Park, South Africa. This protected area was chosen because it has one of the highest white rhinoceros' populations at present (Cromsigt et al. 2017). I tested the following hypotheses for the research project:

(I) On a landscape scale, the areas with high rates of illegal removal will have higher grass height than areas with less illegal removal.

(II) On a local scale, the areas with high rates of illegal removal will have higher grass height than areas with less illegal removal at white rhinoceros' hotspots (i.e. termite mounds and middens).

(III) The presence of white rhinoceros is beneficial for short grass grazers, and there are less short grass grazers at areas with high white rhinoceros removal.

Materials and Methods

Study site

The study area, Hluhluwe-iMfolozi Park, is located in north-eastern South Africa, within the KwaZulu-Natal Province and is fenced all around (Cromsigt et al. 2017). It is geographically situated at 28°00'–28°26' S, 31°43'–32°09' E and is 950 km² (Cromsigt et al. 2017). Annual rainfall range between 550–700 mm in the southern section of the park, iMfolozi and 700–1000 mm in northern section of the park, Hluhluwe (Balfour & Howison 2002). The wet season is from November to April, and the dry season is between May and October (Rutherford et al. 2006). The park's elevation varies from 60 to 580 meter (Davies et al. 2016). Maximum temperature is 32.6°C during January, while the mean temperature is only 25.3°C during July throughout the years 1959–1980 (Owen-Smith 1988).

Study design

I contrasted grassland structure between areas with high rates of illegal white rhinoceros removal and areas of low rates of white rhinoceros removal. I focused on two scales, i.e. at the landscape scale and at a more local scale, “hotspots” of intense white rhinoceros impact, such as termite mounds and white rhinoceros middens. The first scale included the sites with the transects that focused on the average landscape and the second scale was focusing on hotspots of white rhinoceros impact. I analyse both landscape scale and hotspot scale. Then I defined areas of illegal removal hotspots and coldspots, which is areas where there are less poaching. They are based on information facts received from the HiP's park conservation authority. They based this information of data on illegal removal locations that they mapped in GIS over the years. Also, I received the information that illegal removal risk is higher along the road crossing HiP's northern and southern parts, and areas closer to the fence. Therefore, I used both the distance to the road and fence as covariates in my models.

Landscape scale

I laid out 20 sites across high and low poaching areas in HiP, where the sites were grouped in four different blocks; two blocks in high poaching area and two blocks in low poaching area. Within each site, I walked three parallel 300 meter transects, each 150 meters apart. This resulted in a total of 60 transects, with 30 transects in high poaching areas and 30 transects in low poaching areas. ArcGIS was used to distribute transects in the park, to control for parameters such as vegetation density and distance to road. A digital elevation model (DEM) was used to avoid having transects located on steep slopes, because it is hard to walk there. The transects were located at minimum 50 meter from the closest small road. A larger road with more traffic divides the northern and southern sections of the park, and I laid the closest transects at least 300 meter from this road (Figure 1, Appendix Figure 8, ArcMAP™ Version 10.5.0.6491, Esri inc®).

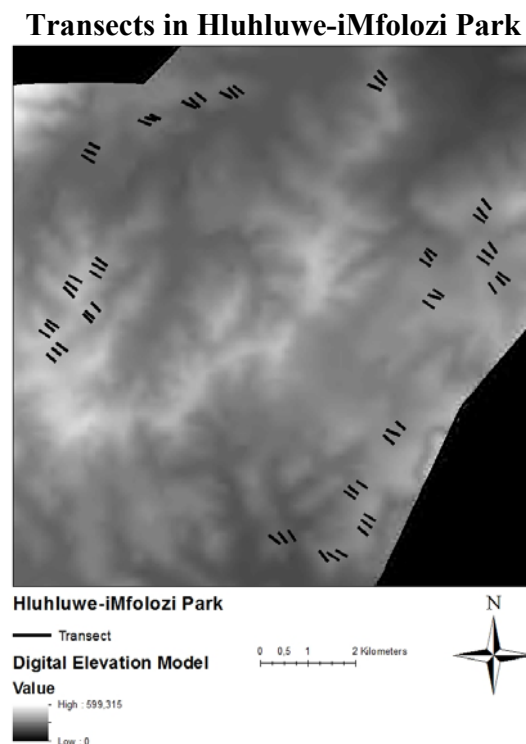


Figure 1. Map representing the transects (black lines) in HiP, with a DEM layer in the background with a low-lying area in white and areas of higher elevation in grey. There are four blocks, including 20 sites.

The location of areas with high and low poaching rates were informed by park management. Every two meters I took a disc pasture meter (DPM) measurement, noted vegetation type (lawn, bunch or bare soil), canopy presence (1/0), categorized tree height (0–40 centimeter, 41–85 centimeter, 86–

130 centimeter, 131 centimeter – upward) and recorded the presence and absence of dung of different herbivore species. The DPM measures grass biomass with the unit of kg ha^{-1} (Figure 2, Zambatis et al. 2006, Bransby & Tainton 1977). The geographic coordinates and elevation were noted every 50 meter of the transects with a GPS.



Figure 2. The DPM (disc pasture meter) consist of a metal pole with a movable disc. It measures the grass biomass under the disc that is dropped from the top to it reached the grass.

Hotspot scale

The second scale was at a local scale, which I took measurements at the white rhinoceros hotspot. This component of the study was performed at patch-scale where I expected white rhinoceros to have a disproportionately high impact; i.e., on termite mounds and white rhinoceros middens. I recorded the location of each hotspot and I placed transects leading away from the hotspots in all four compass directions pointing towards north, south, east and west. On each transect I measured every meter up to ten meter away from the center of the mound/midden with the DPM. Other parameters were noted such as vegetation type (lawn, bunch or bare soil), canopy presence (1/0), categorized tree height (0–40 centimeter, 41–85 centimeter, 86–130 centimeter, 131 centimeter –

upward) and the dung from selected species representing the grazer, mixed feeder and browser, which are the functional groups (Table 1, Figure 3).

Table 1. Species functional groups

Grazers	Mixed feeders	Browsers
white rhinoceros (<i>Ceratotherium simum</i>)	elephant (<i>Loxodonta spp.</i> and <i>Elephas spp.</i>)	black rhinoceros (<i>Diceros bicornis</i>)
buffalo (<i>Syncerus caffer</i>)	hare (<i>Lepus spp.</i>)	duiker (<i>Cephalophinae spp.</i>)
zebra (<i>Equus spp.</i>)	impala (<i>Aepyceros melampus</i>)	giraffe (<i>Giraffa camelopardalis</i>)
warthog (<i>Phacochoerus africanus</i>)	nyala (<i>Tragelaphus angasii</i>)	kudu (<i>Tragelaphus imberbis</i> and <i>Tragelaphus strepsiceros</i>)
wildebeest (<i>Connochaetes</i>)		



Figure 3. Hotspots (a) Middens (b) Termite mounds. Four transects were placed in different directions (north, south, east, and west) with measurements made on every meter away from the hotspot.

Data processing and analysis

To test whether the white rhinoceros increases short grass cover, I used linear mixed-effect models with the response variable being the log-transformed grass height in centimetres as measured by the DPM and the predictor variables were altitude and treatment (consisting of two levels: high and low poaching). Then I performed additional linear mixed-effect models to test if the distance to the road or distance to fence had any effect on grass height. For the hotspots, I used average DPM measurements per individual feature as response variable in a linear mixed-effect model, with the predictor variable treatment. Every hotspot had four DPM values per meter, because I measured in all points of the compass, which I took the mean of to get average DPM. In addition, I conducted linear mixed-effect models to test if distance to the main road and distance to fence had an effect on the average DPM measurement at hotspots. I analysed dung distribution data with generalized

linear mixed-effects with the response variable of the total number of dung piles counted per site and the predictor variables of treatment, altitude, and herbivore functional group, such as grazer, mixed feeder and browser. Second-order Akaike Information Criterion (AICc) and Akaike weights was used to simplify all the different models to decide the most suitable model. All statistical analyses were performed in R Studio version 1.0.143 (R Development Core Team 2016). ArcGIS was used to map all the transects, termite mounds and white rhinoceros middens. DPM height was modified to have graduated symbols with the DPM value, which gave all 20 sites a dot size according to their mean DPM height (Figure 1, Figure 3, ArcMAP™ Version 10.5.0.6491, Esri inc®).

Results

Landscape scale

The grass height varied between different sites (Figure 4).

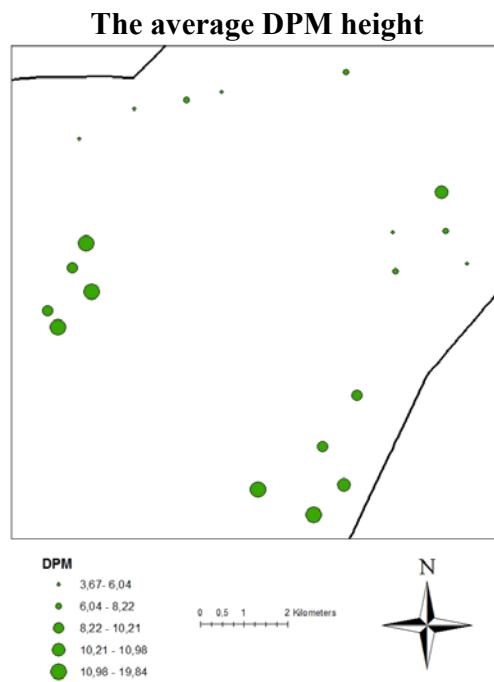


Figure 4. Map displaying the average DPM height (green circles) of the different sites in HiP. It is mostly higher DPM value in the right corner than further away from the road. The average DPM ranges from 3.67 cm to 19.84 cm.

Grass height

The model in which only the treatment effect had been retained was found to be the best fitted model with the AICc value of 19.357 and akaike weight value of 0.917 with the sample size of 20 sites (Table 2, Appendix Table 7, Appendix Figure 9).

Table 2. Linear mixed-effect models testing the effect of treatment and altitude on grass height at the landscape scale, ranked according to the AICc index. The best suited model is DPM~Treatment+(1|Block) with the AICc value of 19.357.

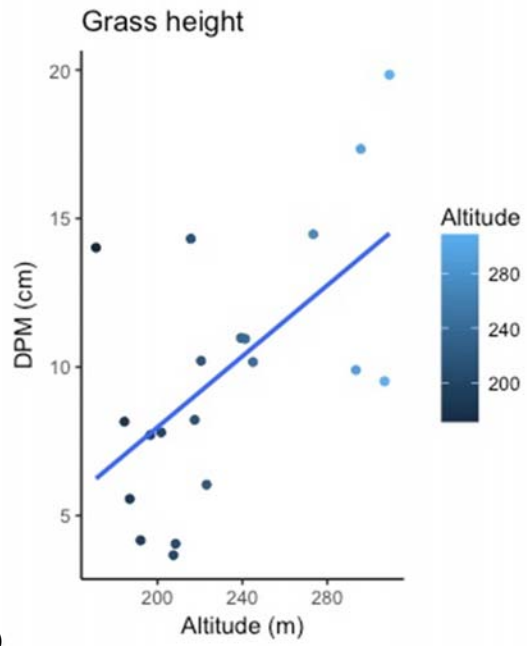
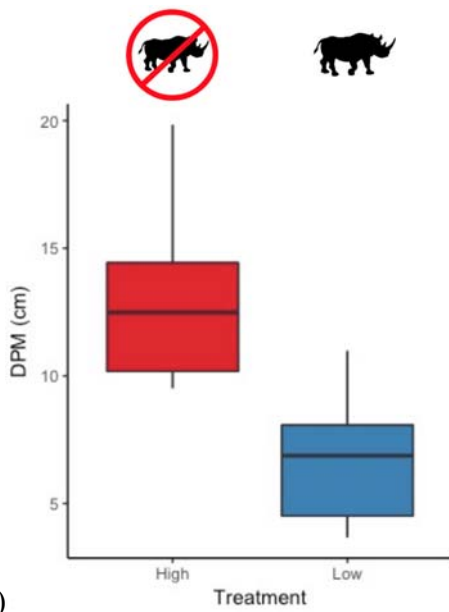
Model	AICc	Akaike weight
DPM~Treatment+(1 Block)	19.357	0.917
DPM~Treatment*Altitude+(1 Block)	25.544	0.042
DPM~1+(1 Block)	26.245	0.029
DPM~Altitude+(1 Block)	27.99	0.012

The average grass height measured by the DPM was significantly lower (p-value = 0.038, Table 3) in the low white rhinoceros removal than in the high white rhinoceros removal area with a sample size of 20. A correlation between DPM and altitude concluded that a rise in altitude corresponded to higher DPM height measurements (Figure 5). The effect of altitude was statistically tested and was non-significant (p-value = 0.131).

Table 3. Parameter estimates for treatment against DPM. In areas with low poaching rates average DPM were less than those in areas with high poaching rates.

Parameter	Estimate Value	Standard Error	p-value
(Intercept)	2.539	0.1	0
TreatmentLow	-0.705	0.142	0.038

Grass height



(a)

(b)

Figure 5. (a) DPM height in high (red) and low (blue) poaching areas in HiP. (b) DPM height increasing with the altitude from 170 meters up to approximately 300 meters above sea level.

Herbivore dung

I found dung of 13 different herbivore species on the transects, and divided them to the functional groups of grazers, mixed feeders and browsers with a sample size of 20 sites. The field technician and the guards were experts on different dung. AICc were used to select among models and showed that the best model was the one where altitude was retained. (Table 4).

Table 4. AICc index on the generalized linear mixed-effects models with herbivore dung data. Best suited model is $\text{Dung} \sim \text{Altitude} + (1|\text{Block})$ with a AICc value of 513.177.

Model	AICc	Akaike weight
$\text{Dung} \sim \text{Altitude} + (1 \text{Block})$	513.177	0.509
$\text{Dung} \sim \text{Treatment} + \text{Altitude} + (1 \text{Block})$	513.547	0.423
$\text{Dung} \sim \text{Treatment} + (1 \text{Block})$	518.514	0.035
$\text{Dung} \sim 1 + (1 \text{Block})$	518.606	0.034
$\text{Dung} \sim \text{FunctionalGroup} * \text{Treatment} + (1 \text{Block})$	772.75	0
$\text{Dung} \sim \text{FunctionalGroup} + (1 \text{Block})$	775.505	0
$\text{Dung} \sim \text{Specie} * \text{Treatment} + (1 \text{Block})$	1440.817	0
$\text{Dung} \sim \text{Specie} + (1 \text{Block})$	1491.447	0

The model included the response variable dung counts and predictor variables of treatment and altitude. Both parameters had p-values that demonstrate significance (Table 5).

Table 5. Overview of the generalized linear mixed-effects model with the response variable dung counts and predictor variable altitude, which gave a significant p-value.

Parameter	Estimate Value	Standard Error	Pr(> z)
(Intercept)	2.311	0.599	0.0001***
Altitude	0.006	0.002	0.004**

The dung counts on the transects showed that there is dung in low poaching areas compared to high poaching areas. The dung occurrence decreases more with the increasing altitude height (Figure 6, Appendix Figure 10).

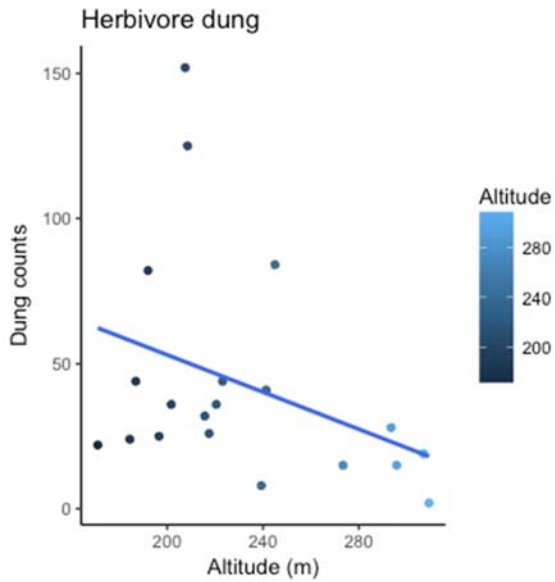


Figure 6. Dung counts measured every two meters in relation to altitude (p-value = 0.004).

In terms of the herbivore functional groups, i.e. browser, grazer and mixed feeder, grazer dung was most abundant, followed by mixed feeders and browsers (Figure 7).

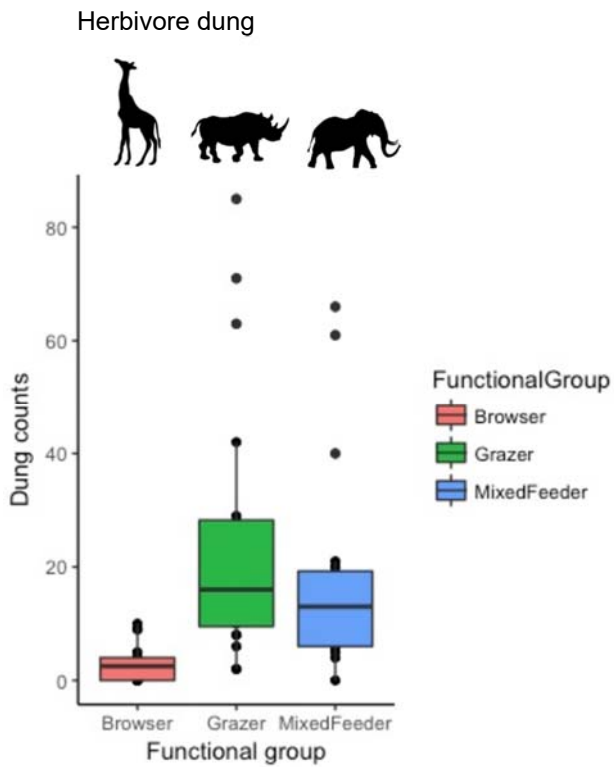


Figure 7. Dung counts measured at every two meters along the transect for each functional group, browser (red), grazer (green), and mixed feeder (blue). The dung counts is the highest for grazers, then mixed feeder, and lastly browsers. The grazers are white rhinoceros, buffalo, zebra, warthog, wildebeest, and mixed feeders are elephant, hare, impala and nyala. Lastly the browsers are black rhinoceros, duiker, giraffe, and kudu.

Hotspot scale

Models investigating the drivers of grass height on hotspots were based on twelve individual hotspots. There were five white rhinoceros middens and four termite mounds in low poaching, then there were one white rhinoceros midden and two termite mounds in high poaching. The models were ranked using AICc. Although it had marginally higher AICc value, the best fitting model was AverageDPM~1, random=~1|Block given its fewer parameters (Table 6, Appendix Table 8, Appendix Figure 11, Appendix Figure 12).

Table 6. AICc ranking of the linear mixed-effect models on hotspots, such as midden and termite mound. The model with the best fit is AverageDPM~Treatment,random=~1|Block.

Model	AICc	Akaike weight
AverageDPM~Treatment,random=~1 Block	291.2956	0.659
AverageDPM~1,random=~1 Block	292.7843	0.313
AverageDPM~DistanceToMiddle+Treatment,random=~1 Block	298.4066	0.019
AverageDPM~DistanceToMiddle,random=~1 Block	299.8541	0.009

Discussion

The aim of this study was to assess the importance of how white rhinoceros maintain grassland structure on the African savannah on a landscape and hotspot scale, to further understand their impact on the ecosystem. I found that at the landscape scale, there was a significant difference in grass height between areas of low illegal removal and high illegal removal, although a confounding effect of altitude was also detected. At the local scale (hotspots), the grass biomass did not show any significant difference between different treatments. Furthermore, the amount of dung from the selected herbivore functional groups was to a greater extent explained by altitude and not the difference in the rate of illegal removal.

What stands out in the results is that grass biomass tested against treatment yields a significant p-value, which indicates that the treatment in low poaching areas influences the grass height, which is affected by herbivores' feeding habits. The consequences of removing white rhinoceros, could lead to a domination of taller grass species. This could cause less biodiversity. The plot of DPM by treatment suggest that DPM is significantly higher in high poaching areas compared with low poaching areas; this supports the first hypothesis that short grass patches are more common in low poaching sections in HiP. My result both support and challenges previous research. Cromsigt and te Beest (2014), showed that in high density of white rhinoceros is correlated with short grazing patches compared to low density white rhinoceros' areas, which is in (Cromsigt & te Beest 2014). However, my results, differ from the findings of the van der Plas et al. (2016) study, that do not support my research. Instead van der Plas et al. (2016) did not find that the white rhinoceros have a big effect on the ecosystem, compared to other ungulate species (van der Plas et al. 2016). Closer inspection of the DPM in relation to the altitude indicates that DPM height increases at higher altitudes, which is confounding. However, altitude did not come out as the better model when running the AICc, or get a significant p-value. The hotspots, white rhinoceros midden and termite mound data showed no significant results, but this could be done to the small amount of data gathered and it showed a trend in the right direction. The future prospect is to have a bigger sample size and to do a power analysis. Gosling et al. (2012) showed that the termite mounds *Macrotermes* has high nutrient soil and high pressure grazing from herbivores (Gosling et al. 2012).

Results indicated that the diversity of other herbivores decreased with lower altitude. On the blocks that were chosen in which to perform the transects, there were largely more grazers, compared to mixed feeders, and lastly browsers. A possible explanation for this might be as Veldhuis et al. (2017) who state that grazers have a correlation towards grass patchiness, and browsers have a positive correlation towards woody vegetation (Veldhuis et al. 2017).

Had I measured the grass heights before and after the poaching incidents, it might have been possible to more reliably determine whether there was no difference in DPM between high and low poaching areas. I would have had a much stronger case. If I would have measured before poaching and after, then I would not have to take the other factors into consideration that can disturb the reliability of result. There is a difference in grass height in high and low poaching areas based on the difference in species and altitude, irrespective of poaching. I can not only by studying at poaching effect, exclude that all other factors in the environment do not affect the population of white rhinoceros.

Conclusions

My result support that there are a larger number of grazed patches in low poaching areas, and linear mixed effect model on DPM against treatment (high and low poaching) gave a significance p-value of 0.038. Although, this result is possibly being confounded by altitude and that I did not measure pre- and post poaching, but if I would measure it many of the disturbing factors would disappear. No significance was found when I tested if the hotspots have a white rhinoceros impact, although more replicates is needed.

Future research

There are still many unanswered questions about white rhinoceros in African savannas. An interesting idea would be to start identifying the different individuals to see pattern in their behaviour and understand their driving forces. If we invest more money in putting collars on focal individuals, it is possible to see territory pattern and see how they escape illegal removal areas and compare between the sexes. Identification could also happen through photographs, camera trap or observations in the fields, where we explore any difference between the individuals, for example the ear shape and pattern. This will make it easier to see how everyone acts when reported about

poaching in the park. Another research project is to focus on locating white rhinoceros middens and wallows in certain parts of the park, that is decided before, to further develop the hotspot hypothesis. An addition, other factors, I could add to my project could be to examine grass species composition in high and low poaching areas, and to see the long-term effect of these areas, and maybe investigate more abiotic factors and investigate the nutrients in the vegetation and dung in these areas. Another important idea is to see the effects of white rhinoceros by comparing different habitats, i.e. fire, rural and more urban areas and compare the biodiversity and investigate how the climate change will affect the park in the future. It is crucial to discover new ways to easily get out research information to the public and make it readable for those without a high education that live in these African rural areas. Illegal removal has been a long-term problem, and there is poverty in the country. If we understand the people that do poaching, it makes it easier to start solving problems. One strategy for decreasing the poaching is to have stricter laws and put more effort where the government and the people have better communications, as they did in Nepal and where the poaching decreased drastically (Aryal et al. 2017). In addition to problems with poaching the white rhinoceros are sensitive to habitat destruction and inbreeding, which are some factors that maybe decrease the population rate (Strien 2017). A good investment to continue working on is monitoring, so that it is possible to follow up on the population structure, and see the directions to further see patterns and draw helpful conclusions. It is important that government in Vietnam and China gets stricter against poaching, or else the white rhinoceros will go extinct within only 20 years (Di Minh et al. 2014). In overall more research needs to be done to have better arguments for reason why it is important to protect the white rhinoceros' population and to stop the poaching.

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Appendix 1

Supplementary to methods



Figure 8. Images of the four different areas (blocks) where the transects were placed in HiP, (a) A (b) B (c) C (d) D.

Appendix 2

Supplementary to results

Table 7. AICc ranking of the linear mixed-effect model on landscape scale, such as midden and termite mound. The model with the best fit is $DPM \sim 1, \text{random} = \sim 1 | \text{Block}$, which is the null hypothesis.

Model	AICc	Akaike weights
$DPM \sim 1, \text{random} = \sim 1 \text{Block}$	26.245	1
$DPM \sim \text{DistanceToFence}, \text{random} = \sim 1 \text{Block}$	45.641	0
$DPM \sim \text{DistanceToRoad}, \text{random} = \sim 1 \text{Block}$	47.988	0
$DPM \sim \text{DistanceToRoad} + \text{DistanceToFence}, \text{random} = \sim 1 \text{Block}$	66.839	0

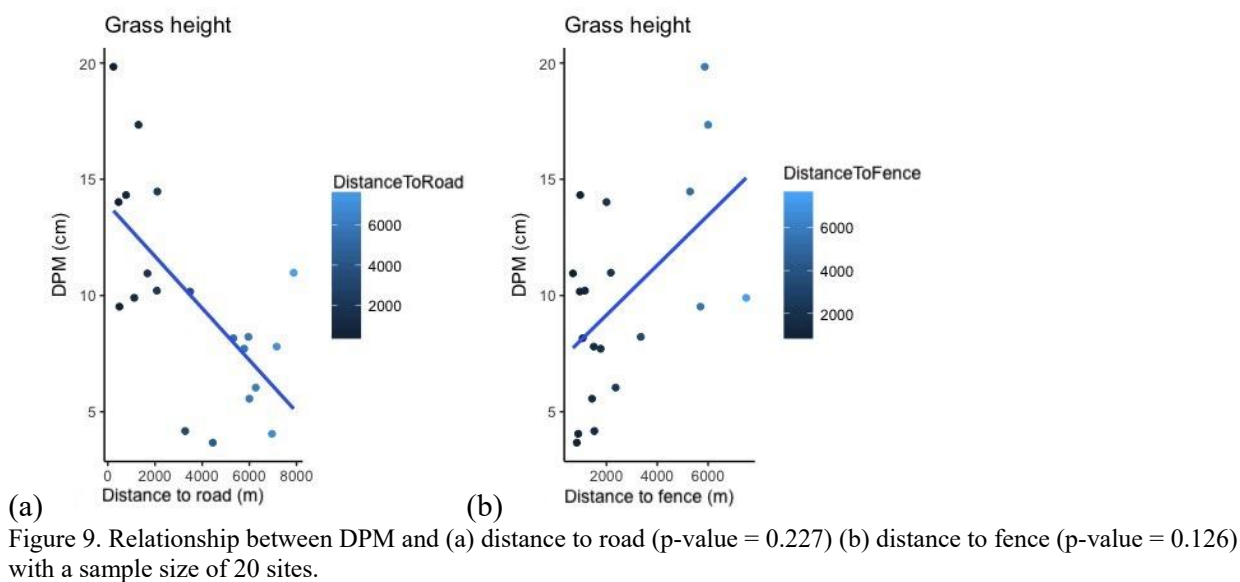


Figure 9. Relationship between DPM and (a) distance to road (p-value = 0.227) (b) distance to fence (p-value = 0.126) with a sample size of 20 sites.

Herbivore dung

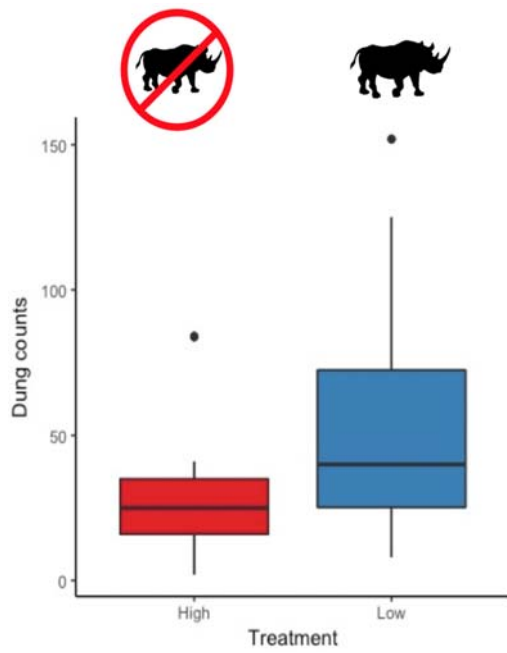
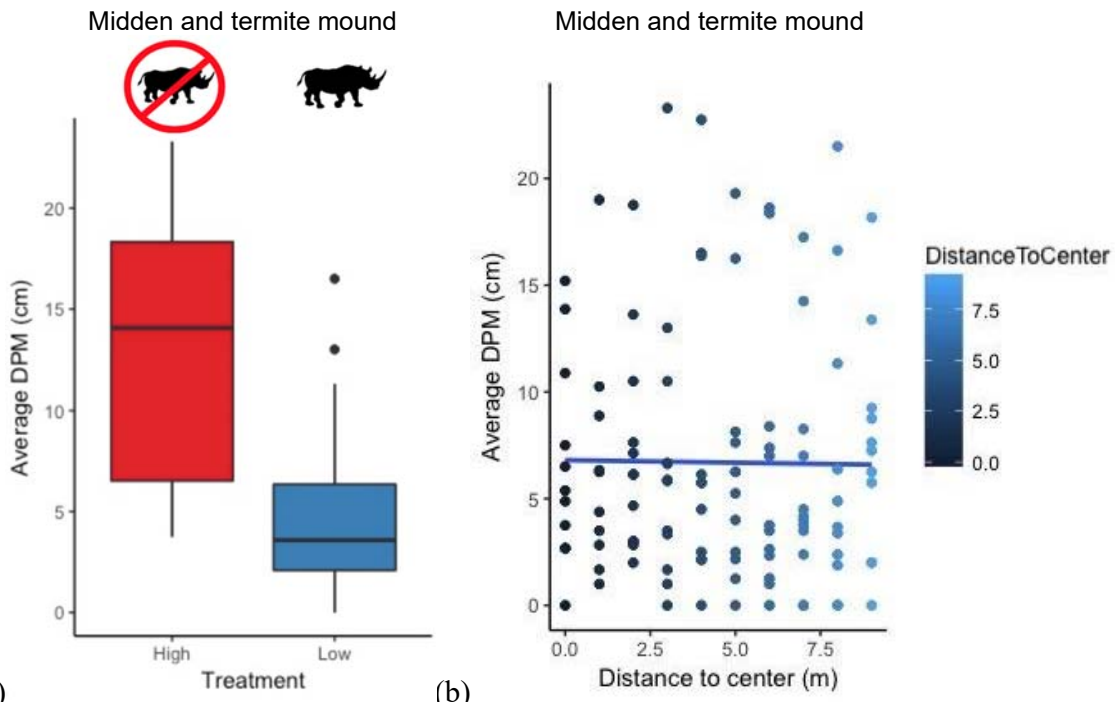


Figure 10. Dung counts measured every two meters (a) in relation to treatment of high (red) and low (blue) poaching (p-value = 0.041) with a sample size of 20 sites.



(a) (b) Figure 11. Relationship between average DPM and (a) treatment (p-value = 0.274) (b) distance to center (p-value = 0.483) with a sample size of twelve hotspots.

Table 8. AICc ranking by the linear mixed-effect model on hotspots, such as midden and termite mound. The model with the best fit is $\text{AverageDPM} \sim 1, \text{random} \sim 1 | \text{Block}$, which are the null hypothesis.

Model	AICc	Akaike weight
$\text{AverageDPM} \sim 1, \text{random} \sim 1 \text{Block}$	292.784	0.995
$\text{AverageDPM} \sim \text{DistanceToFence}, \text{random} \sim 1 \text{Block}$	303.401	0.005
$\text{AverageDPM} \sim \text{DistanceToRoad}, \text{random} \sim 1 \text{Block}$	307.898	0.001
$\text{AverageDPM} \sim \text{DistanceToRoad} + \text{DistanceToFence}, \text{random} \sim 1 \text{Block}$	315.301	0

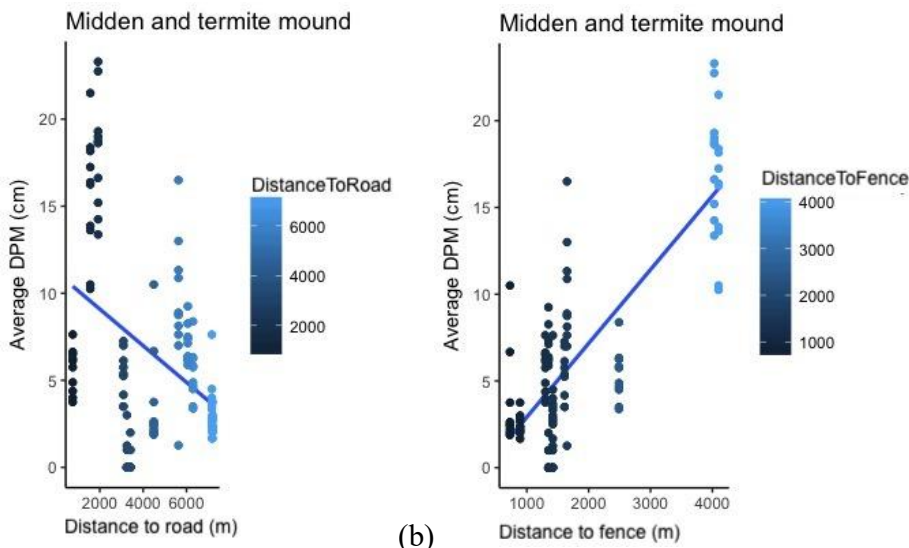


Figure 12. Relationship between average DPM and (a) distance to the road (p-value = 0.04) (b) distance to fence (p-value = 0.0004) with a sample size of twelve hotspots.

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