



Activity pattern of spotted hyena (*Crocuta crocuta*) in Ol Pejeta Conservancy (Kenya, Laikipia County)

How seasons, rain, and light influence the activity of a spotted hyena population in a fenced area

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Abstract

Spotted hyena (*Crocuta crocuta*) is the most abundant big predator in Africa. The rising human population is making their interaction with humans more and more common making studies about their behaviour vital for their conservation. This study investigated their activity pattern at the border of a fenced conservancy in Kenya (Laikipia County). Hyenas were photographed between 2017 and 2018 at the corridors that connect the conservancy with the surroundings. Their presence/absence was analysed in the relation to rainfall, calculated as the mm of water fallen each day and the average amount of mm fallen in the previous 7, 30, 60, and 90 days; biomass amount, calculated with a Modified Soil Adjusted Vegetation Index; and night brightness, calculated as an index including earth-moon distance, lunar illumination, and cloud coverage. Biomass didn't show any significant effect on the activity of hyenas ($p: 0.5991$), this was thought to be due to constraining effects that induced some hyenas to leave while others stayed inside the borders of the conservancy not resulting in a net positive nor negative effect. Night brightness, on the contrary, had a negative effect on hyenas presence. This result was explained by hyenas' hunting success during brighter nights and their relationship with other sympatric carnivores. Rainfall turned out to be a significant factor only if considered in the previous 7 days. With the increase in prey abundance inside the conservancy, hyenas didn't need to commute to other hunting grounds and were less active near the borders if there was more rain. However, studying the spotted hyena's behaviour in connection to environmental factors only, didn't give a complete picture of the complex inter- and intraspecific interactions that drive their activity. A larger dataset and more research are needed to obtain more complete and reliable results.

Keywords: Spotted hyenas, Crocuta crocuta, Eastern Africa, hunting success, rainfall, night brightness, activity pattern, seasons, MSAVI2

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Abbreviations

OPC	Ol Pejeta Conservancy
R1	mm of rain fell each day
R7	Mean mm of rain fell in the previous 7 days
R30	Mean mm of rain fell in the previous 30 days
R60	Mean mm of rain fell in the previous 60 days
R90	Mean mm of rain fell in the previous 90 days
MSAVI2	Modified Soil Adjusted Vegetation Index

1. Introduction

The Hyaenidae family used to have hundreds of species in the past. Today only 4 species are still alive -all of them occurring in Africa- making it one of the smallest clades in the order Carnivora. Brown hyenas (*Parahyaena brunnea*) are limited to South-Western Africa, Aardwolves (*Proteles cristatus*) are found in Eastern and Southern Africa while spotted hyenas (*Crocuta crocuta*) and striped hyenas (*Hyaena hyaena*) are found in the whole African continent (with the latter extending to Middle-East up to India) (Werdelin & Solounias 1991).

Spotted hyenas are the most abundant big carnivore in Africa (Smith & Holekamp 2023). Their great adaptability makes them able to thrive even in very densely populated areas where they can survive almost completely out of anthropogenic-originated food such as organic wastes (Yirga et al. 2012, 2013) or, when natural prey abundance is low, domestic animals (Abay et al. 2011). Sometimes spotted hyena's (*Crocuta crocuta*) population even increased with proximity to human settlements (Yirga et al. 2011). Their extremely adaptable behaviour might also explain this success in all its range (Wilkinson et al. 2024). They don't have any particular preference when it comes to prey and, apart from elephants, buffalos, and giraffes, they can take down any big herbivore. On top of that, their ability to hunt in packs, individually, or scavenge makes the spotted hyena (*Crocuta crocuta*) one of the most flexible and efficient predators in the African continent (Hayward 2006; Smith & Holekamp 2023). Another reason for hyenas' success is their activity pattern: hyenas are the most nocturnal of all the big African carnivores (Hayward & Slotow 2009), mainly to avoid high temperatures (Cooper, 1990), with the biggest of their activity comprised between 18 in the evening and 9 in the morning, but they can become even more nocturnal to avoid human presence (Kolowski et al. 2007). As a matter of fact, alongside lions and other hyenas (Green et al. 2018), humans are the biggest threat to hyenas' survival (Hayward & Slotow 2009).

In this picture of a growing population and increasing wildlife-human interactions -that may occur even on a nightly basis according to Raycraft (2024)- studying and understanding the behaviour of these animals may play a crucial role in the coexistence between humans and big carnivores.

1.1 Spotted hyena (*Crocuta crocuta*) threats

Despite its success, the hyenas' population is declining throughout the African continent (McFadden 2022. IUCN, 2024). Humans-hyenas direct or indirect interactions are at the base of the three biggest threats to hyenas' survival: poisoning accounts for 21.4% of hyenas' deaths, government lethal control for 21.3%, and persecution for 17.4 (even outside, or at the border, for protected areas) (Hayward & Slotow 2009; McFadden 2022). In this frame, retaliation against livestock depredation is the main reason why hyenas are killed. Alongside direct human activity, habitat loss is a major threat to hyenas' presence.

However, without considering humans, the biggest hyenas' natural competitors are hyenas themselves. In this species, intraspecific competition for food is fierce (Holekamp & Smale 1998; Pangle & Holekamp 2010; McCormick & Holekamp 2022) and each individual's access to food is determined by their social rank (Henschel & Skinner 1990; East 2001; Kolowski et al. 2007; Smith et al. 2008). Moreover, competition is extremely fierce with other sympatric predators as well. Hyenas-lions competition, for instance, can be brutal. Kleptoparasitism (Henschel & Skinner 1990; Périquet et al. 2015) and direct predation are very common interactions to the point that in some hyenas populations lions can be the first cause of mortality (Watts & Holekamp 2008). However, both populations seem to fluctuate positively with their prey abundance; thus, hyenas and lion population densities appear positively correlated with each other (Périquet et al., 2015).

1.2 *Crocuta crocuta*'s social structure

On the contrary to most big carnivores worldwide, spotted hyenas live in big groups, called clans. These clans are organized more similarly to the Cercopithecines ones (baboons and macaques) than to other mammalian carnivores (Holekamp et al. 2007; Watts & Holekamp 2008). They are defined as fission-fusion clans since foraging and other activities are carried on by multiple subgroups that can change composition multiple times even in a single day (Holekamp & Smale 1998; Boydston et al. 2003a; Kolowski et al. 2007; Belton et al. 2016; Green & Holekamp 2019). Being isolated (fission) gives an advantage when it comes to eat or avoiding kin-aggressive interactions. However, being together (fusion) is important to defend kills and reject other clans' intruders. Hyenas can use repetitive calls, called whoops, to gather individuals from their clan (East & Hofer 1991) in order to form bigger groups. If the receiver rank is lower than the whoop-producing hyena, it's more likely for it to start looking for the source of the call (Gersick et al. 2015).

The whole clan, on the other hand, can exceptionally reach the size of 120 individuals (Hayward & Slotow 2009; Green et al. 2018) with multiple generations represented by multiple individuals (Holekamp et al. 2007, 2012).

Females are mostly philopatric and, in each clan, are usually twice as abundant as males (Holekamp & Smale, 1998). Males, on the contrary, emigrate as soon as they reach sexual maturity to join another clan (Holekamp & Smale 1998; Hayward & Slotow 2009; Boydston et al. 2003). The social hierarchy is strictly matrilinear and every newborn acquires the rank right below its mother, while every male ends up at the bottom of the social pyramid as soon as they find a new clan to join, their rank is determined by the sequence they joined the clan with, following a queuing system (East 2001).

Competition inside clans is fierce and social ranking determines access to food (Smith & Holekamp 2019; Pangle & Holekamp 2010). When it comes to eating, high-ranking hyenas are the first to start devouring the carcass, followed by their offspring (Smith & Holekamp, 2019). Furthermore, low-ranking hyenas have to embark on longer journeys looking for food (Green & Holekamp, 2019. Kolowski et al., 2007. Boydston et al., 2003). They can travel up to 40km in a single night in search of food (Raycraft, 2024) and up to 90km in the migrations season (Avagar et al. 2014) exhibiting what Naciri et al. (2023) defined as long-distance commuting behaviour. Access to food eventually determines the reproduction rate of an individual, implying that high-rank hyenas reproduce at a higher pace than low-rank ones (Holekamp et al. 1996; Boydston et al. 2003a).

All these factors will determine easier access to food for high-rank offspring (Smith & Holekamp, 2019) that will thus grow faster and stronger, allowing matrilinear dynasties to establish in the clan.

Despite big differences in rank between individuals, all *Crocuta crocuta*'s live in the communal den, which is the clan's social heart (Boydston et al., 2003. Kolowski et al., 2007); where offspring find refuge (Holekamp et al. 1999) and where, periodically, adults return to nurse their young or simply rest (Smith & Holekamp, 2019. Kolowski et al., 2007).

1.3 *Crocuta crocuta*'s ecosystem services

Crocuta crocuta are capable of hunting up to 95% of their food (Holekamp & Dloniak 2010; Raycraft 2024) but, even if in small percentages, they integrate some scavenging into their diet (Périquet et al. 2015; Watts & Holekamp 2008). Also for this purpose, they evolved a powerful digestive system so powerful that can dissolve even bones leaving only inorganic materials in their droppings (Smith et Holekamp 2019) and bone-cracking jaws capable of cracking the toughest bones (Smith & Holekamp 2019). As opportunistic scavengers, hyenas prevent zoonosis

and diseases from developing in areas where they live in close contact with humans (Sonawane et al. 2021).

Top predators like hyenas, are essential for the health of ecosystems since they can trigger top-down processes capable of reshaping the communities they live in (Hayward & Slotow, 2009. Périquet et al., 2015), maintaining prey diversity and the structure of predator-prey trophic interactions (Sinclair et al. 2003) and even affect the environment and climate (Wilmers & Getz, 2005).



Figure 1. *Crocota crocuta* with a zebra leg at corridor 1. Source: camera trap pictures database from OPC Conservancy

1.4 Aim

Even though literature about hyenas is very abundant, few studies, if not any, focus on their activity pattern alongside environmental factors. Given its complex social life and its role as a predators most of the literature on hyenas' behaviour focuses on intraspecific and predator-prey relationships and, when the night activity is included, it's only considered as an hourly partitioned activity pattern.

This study investigates *Crocota crocuta*'s activity pattern and how it's affected by the changes in the environment they live in such changes in biomass, rainfall and night brightness. This approach could be crucial in a picture of changing climatic patterns and more unpredictable seasonal variations, highlighting an aspect of their life that's usually left behind.

Since hyenas are the most abundant predators in Africa this study might be a first step to a better understanding of their activity that might bring to an easier coexistence with this top predator.

1.4.1 Research questions

1. Is hyenas behaviour affected by season, when season is defined as rainfall per 1, 7, 30, 60, and 90 days and biomass abundance?
2. How does night brightness affects hyenas' activity pattern?

1.5 Hypothesis

Hyenas are not ambush predators, they rely on their stamina while chasing herds to identify a weak individual (Hayward, 2006. Cooper, 1990).

According to Wilkinson et al. (2024), hyenas' landscape use differs from wet to dry season. During the latter, they prefer rivers and avoid conservancy boundaries (when present) while in the wet season, they tend to avoid bodies of water. In this scenario is important to notice how the cameras are placed next to fences. On the other hand, during the dry season prey availability is more scarce, and thus hyenas have to travel longer distances to hunt (Green & Holekamp, 2019), even outside of the conservancy, which could balance the previous behaviour. In addition to that, hyenas' coursing hunting behaviour could be disadvantaged by tall grass during the wet season. These previous studies have allowed the formulation of the following hypotheses:

1. Night brightness will positively affect hyenas' hunting success and thus their nocturnal activity;
2. During the dry season hyenas will show reduced activity resulting in fewer camera registration;
3. Concurrently with the MSAVI2 index peaks a decrease in hyenas' activity will be seen.

1.6 Sustainable and ethical aspects

In the frame of a fast-growing population and cities' expansion, African wildlife is facing some of its biggest threats: human-wildlife conflict and habitat loss. Having a better understanding big mammals' activity patterns could help mitigate the threat posed by the overlap with human activity. That's why behavioural studies on wildlife play a crucial role in its conservation and, in the long term, could be a very effective tool to improve a peaceful coexistence with humans. Eastern Africa hosts some of the most famous and biggest national parks in the world and among them, OPC, despite its relatively smaller size, represents a sanctuary for wildlife in the area. For this reason, Ol Pejeta represents a perfect case study.

2. Methods

2.1 Study area

Ol Pejeta Conservancy is a 364 km² fenced conservancy in Laikipia county (Nanyuki, Kenya) (Ol Pejeta website, 2023). Previously a cattle ranch, in 2004 became a protected area (Ol Pejeta website, 2023) and since then has witnessed a steady increase in wildlife and tourists with an increase of the latter of 49% between 2021 and 2022 (Coulson et al. 2022).

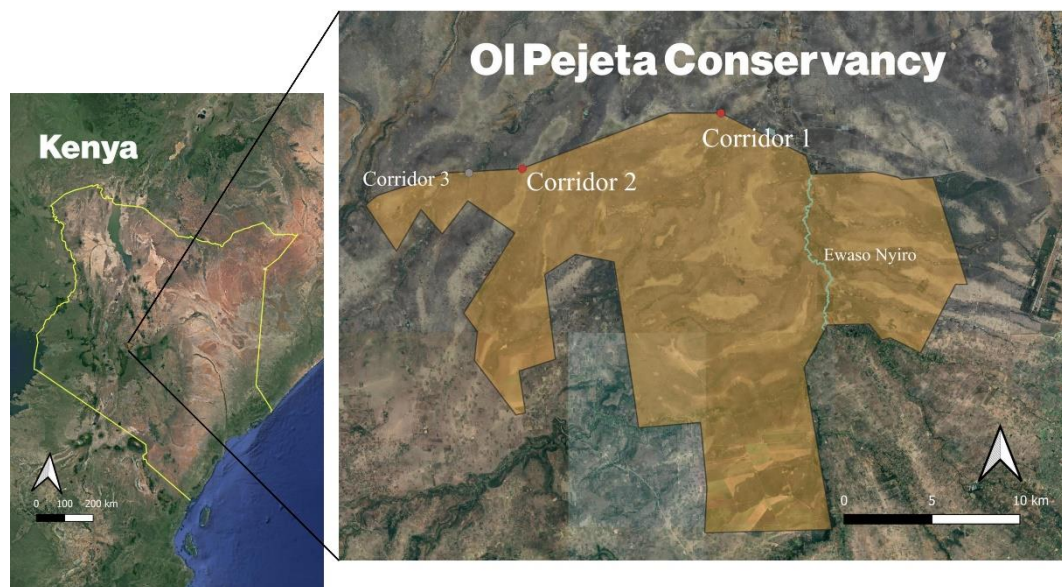


Figure 2. Ol Pejeta Conservancy. Credits: Tommaso Semprini Cesari

2.1.1 Corridors

The boundary, 150 km long (Coulson et al. 2022), is composed of an electric fence. However, in the north, the border with the Mutara Conservancy has three corridors that allow wildlife passage. The corridors are made of wooden pillars one meter tall and nearly 55cm separated from each other as a fence for rhinos. In front of the pillars and inside the conservancy lays an area of soil (fig. 3) and right outside the borders, there is a small rock barrier. Since corridor number three has been

closed for several months, only corridors 1 and 2 have been included in the study. Corridor 1 is the biggest (183 m wide) and has 6 cameras (Figure 4) while the smaller corridor 2 (34 m) has only 3 (Figure 5).



Figure 3. Corridor 1. Credits: Cara Heldmeier

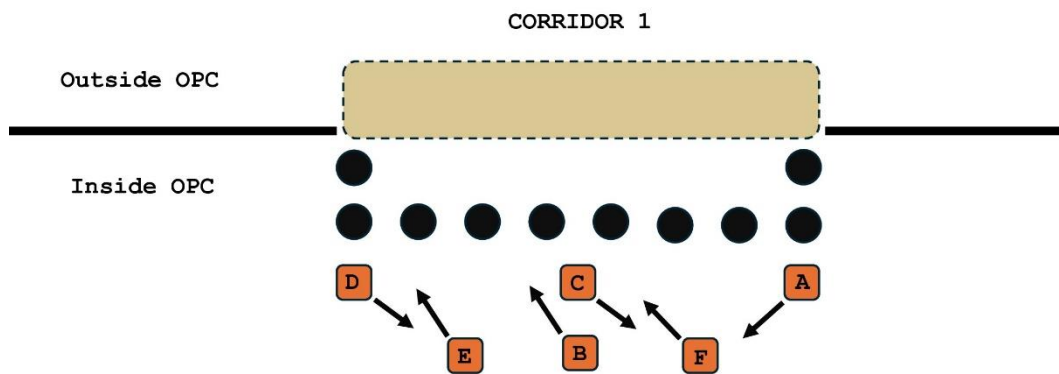


Figure 4. Corridor 1 and its 6 camera traps. Credits: Tommaso Semprini Cesari

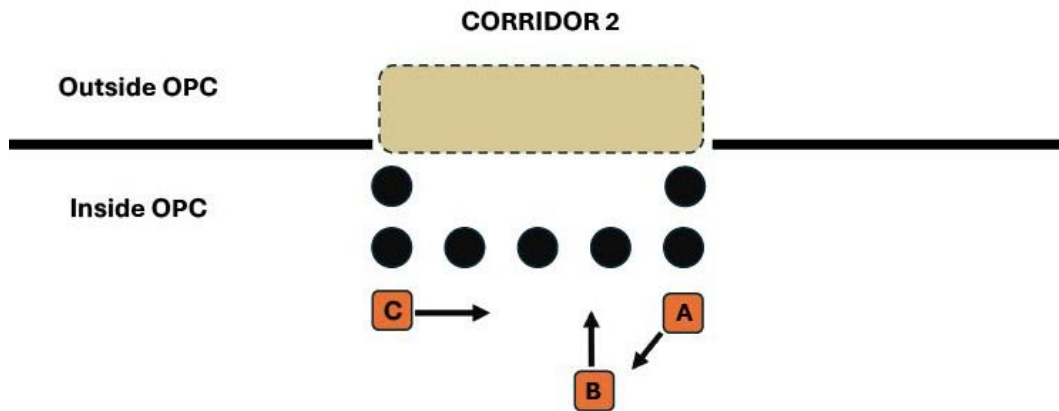


Figure 5. Corridor 2 and its three camera traps. Credits: Tommaso Semprini Cesari

2.1.2 OPC habitats

Inside OPC 4 main habitats are divided as follows (OPC website, 2023): Grasslands cover 24% of the territory, open bush areas 25%, dense bushes 49%, and riverine habitats 2%. According to Kavwele et al. (2017), dense bushes host the highest wildlife species diversity (calculated with the Shannon-Weiner index) while open grasslands have the lowest value.

Throughout the year, the rainfall pattern is bimodal with two rainy seasons during March-May and November-December periods when the arid landscape turns green. The mean annual rainfall is 739 mm (Kavwele et al. 2017); however, a prolonged drought that ended in 2022 (when 598 mm of rain fell) tested the limits of wildlife survival (Coulson et al. 2022). The temperature can occasionally drop to 1 °C in some moments of the year (Safari bookings) while the mean maximum temperature is 28°C and the minimum is 12°C (Kavwele et al., 2017)



Figure 6. Crocuta crocuta stands in OPC's grasslands in front of corridor 1. Source: camera trap pictures database from OPC Conservancy



Figure 7. OPC's dense bushes landscape. Credits: Tommaso Semprini Cesari



Figure 8. OPC's open bushes landscape. Credits: Tommaso Semprini Cesari

OPC is renowned as the last northern white rhino sanctuary in Africa but it also hosts consistent populations of big mammals. The herbivore density is 60,91 animals/Km² and there's one of the highest predator densities in Laikipia County (Coulson et al. 2022). In this frame, in OPC there are approximately 100 hyenas (Coulson et al. 2022).

2.2 Pictures and Cameras

The cameras used by the OPC were Reconyx HC600 Hyperfire which took a sequence of 5 (or 3 in the first months) pictures every time they were triggered. Each camera was placed in a metal box 80 cm above the ground with a 24m trigger distance during the day and 18m during the night. Once a week (every Friday) cameras' memory was emptied and the pictures were sorted by the animal they captured. A total of 67 972 pictures have been sorted with the camera traps software Camelot. Only pictures from 2017 and 2018 have been used since before and after these years most of the pictures have been lost. Pictures from gate 3 have not been

processed since the gate was closed for a significant amount of time. On top of that, 3056 pictures have been categorized as “wrong” since either they captured another species, they didn’t capture any animal at all or rangers were present in the pictures. The total amount of pictures considered in the analysis was thus 12 980. Pictures taken at least 15 minutes apart from each other were considered as two different photographic events.

Data were then grouped in Microsoft Excel where the number of hyenas per day was displayed next to each date, rainfall average, and light index. This allowed us to perform a statistical analysis using the number of hyenas observed each day as a response variable and the environmental data as predictors. The MSAVI2 index started 48 days later than the rest of the data, on the 16th of February.

2.3 Environmental data

2.3.1 Biomass

A modified soil adjusted vegetation index (Qi et al. 1994) has been calculated. This index type is useful for determining vegetation biomass dynamics without the

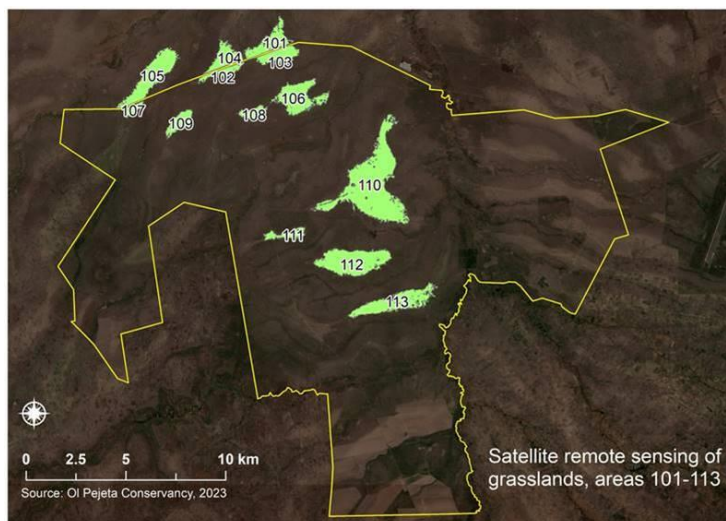


Figure 9. Areas used for measuring the MSAVI2 index

background influence of soil composition. To do that, satellite pictures from 13 areas inside and outside OPC (fig. 3) have been used. Since OPC’s vegetation cover changes drastically over the year, using vegetation dynamics is a good proxy to determine the amount of rainfall falling on the ground. Areas 107, 102, and 103 are the closest ones to the gates but, since

hyenas can travel very long distances to find food (Raycraft, 2024. Avgar et al., 2014. Naciri et al., 2023) all 13 areas have been used in the MSAVI calculation. Some days, especially during the rainy season, lack MSAVI values due to cloud coverage, making it impossible to see the ground from a satellite image. In these cases, the previous and successive values have been linked in continuity assuming a constant rainfall. This method is supported by the increase in the MSAVI (and thus in the vegetation) value during the absence of images.

2.3.2 Rainfall

10 weather stations inside OPC have collected rainfall data for analysis. For each day, rainfall has been calculated as the mean fallen rain (in mm) from the last 7, 30, 60, and 90 days (r7, r30, r60, and r90 respectively). And every single day (r1).

2.3.3 Light index

Night brightness has also been calculated through an index. The following factors have been used to create the index: distance index, moon illumination, and cloud coverage. The amount of time spent by the moon in the sky each night has been removed from the calculations since its strong correlation with moon illumination (correlation coefficient: 0.984). Distance index is the ratio between the moon-earth distance every night and the average moon-earth distance. Moon illumination is the proportion of the lunar circle illuminated each night. Cloud coverage stands for the percentage of the sky covered by clouds each night.

The light index has been created by the multiplication of these three factors mentioned above in order to have a value positively related to each of them.

2.3.4 Statistical analysis

The data (hyenas' appearances per day) have a Poisson distribution. The error follows the same distribution and on top of that, it shows overdispersion. That's why the statistical test (conducted with the coding language R) used was a GLM (Generalized Linear Model). In the first place, as predictors, the mean mm of rain fell in the previous 1, 7, 30, 60, and 90 days (respectively r1, r7, r30, r60 and r90), and then the MSAVI2 and Light Index have been integrated.

A principle component analysis (PCA) was used to determine the influence of each factor on the number of hyenas.

All the variables have been checked for correlations. In the presence of a strong correlation, one of the two variables has been omitted from the statistical analysis. The latter scenario was applied only with moon illumination and the amount of time spent in the sky by the moon each night: since they were two strongly correlated factors, only the moon illumination was included in the light index calculation.

3. Results

Over the 2017 and 2018 timespan, 634 days have been used in the analysis of which 150 pictures (23%) have shown no hyenas at all. The total number of individuals observed has been 5000, the day with the highest number of individuals (56) occurred on 31/08/2018.

During this time, the average number of hyenas passing in front of the camera was 7.886 per day (SE 0.346) with a median of 6 (SE 8.724) while the Standard Deviation was 8.724. Using a broader point of view, on average 204.2 hyenas per month triggered the traps (SE 24.0) with a median of 230.5 (SE 117.7). September 2018 showed the highest number of hyenas in a single month: 493. While July 2017 was the only month with 0 hyenas counted.

The mean value of rainfall was 2.002 mm per day (SE 0.187) with a standard deviation of 4.701. The median was 0 mm. The 12th of December 2018 has been the day with the most rainfall with a value of 37.220 mm.

Unfortunately, the number of days with working cameras each month wasn't constant throughout the years due to cameras malfunctioning and the loss of some pictures during the sorting process by the operators in OPC, and thus even before they were sent in Sweden, made the dataset even more uneven. The least number of days with active cameras was recorded between February and September 2017 and February and June 2018. This lack of data could have influenced negatively the quality of the study and thus the trustability of the results.

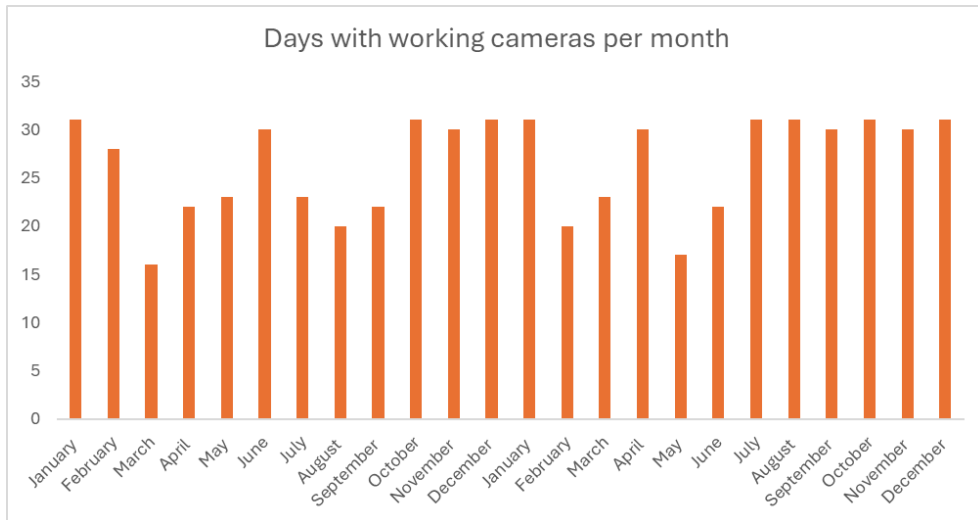


Figure 10. Number of days with functioning cameras per month

With 150 occurrences, days with no spotted hyenas were the most common. Days with 3 hyenas as the second most common (40 times during the two years) while days with 1, 5, or 6 hyenas occurred 32 times. To summarize, days with little hyenas per day were the most abundant which can suggest the tendency of spotted hyenas (*Crocuta crocuta*) to move in relatively smaller groups: groups bigger than

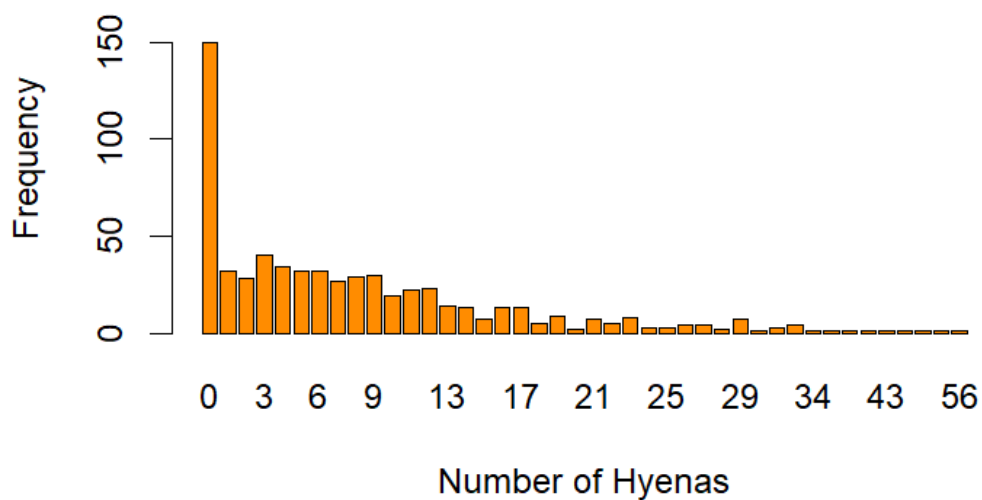


Figure 11.. Frequency of number of hyenas per day

10 individuals have been recorder only 4 times in two years with a maximum of 13 individuals.

The GLM was run looking for a correlation between the environmental factors (rain, night brightness and biomass) and the number of hyenas each day. When run with mean rainfall values, the GLM gave a significant p-value only for r7 (p-value: 0.0111). The other p-values are increasing the longer time span we considered. R30: 0.2417. R60: 0.4912. R90: 0.9239. Also, the amount of rain that fell in a single day (r1) proved to be not significant with a p-value of 0.5555.

Since its significance, r7 has been integrated into the next GLM alongside the MSAVI2 and the Light Index. In this second test, r7 appeared to be, once again, the most significant predictor (p-value: 3.2×10^{-6}) but this time also another predictor was significant: the light (p-value: 0.0479) with a slightly negative effect on the number of hyenas. At last, the MSAVI gave a result of 0.5991. All the above significant results proved to have a negative effect on the number of hyenas per day: -0.09656 (in the GLM with light and MSAVI) and -0.33741 for rainfall and light respectively.

Table 1. GLM results for rain. r1, r7, r30, r6 and r90 stand respectively for the rain fell each day and the mean mm of rain that fell in the previous 7, 30, 60 and 90 days

Factor	Estimate	Std. Error	t value	p value
(Intercept)	2.234664	0.175680	12.720	$<2 \times 10^{-16}$
r1	-0.007654	0.012978	-0.590	0.5555
r7	-0.065724	0.025810	-2.546	<u>0.0111</u>
r30	-0.039528	0.034112	-1.159	0.2470
r60	0.032596	0.044678	0.730	0.4659
r90	-0.010795	0.107078	-0.101	0.9197

Table 2. GLM results for 7 days rain, light and biomass

Factor	Estimate	Std. Error	t value	p value
(Intercept)	2.32652	0.16836	13.819	$<2 \times 10^{-16}$
r7	-0.09656	0.02053	-4.704	<u>3.2×10^{-6}</u>
light	-0.33741	0.17018	-1.983	<u>0.0479</u>
MSAVI2	0.19034	0.36190	0.526	0.5991

The distribution of observations is skewed to the left in the r1 and r7 graphs (fig. 12, 13) this distribution reflects the high number of days with little or no rain. Fig.

13 shows graphically the tendency shown by the Glm for r7 that the more rain fell the fewer hyenas there were, while from r30 to r90 the observations progressively shift to the right of the graph due to the lack of correlation between this factors and the number of hyenas per day (fig. 14, 15, 16). However, an evident pattern doesn't emerge from these scattered plots.

An even more random distribution is the one of the Biomass plot (fig. 17) which reflects the non-significant effect of this factor on the number of spotted hyenas observed.

Lastly, the night brightness plot (fig. 18) indicates the tendency of hyena observations to be less abundant in the presence of brighter lights.

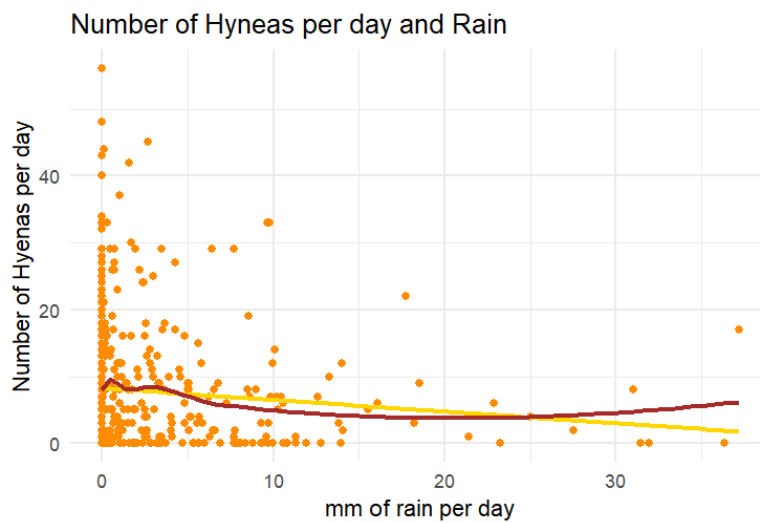


Figure 12. Number of hyenas per day and mm of rain per day. In yellow is the regression line, in brown is the trend line, p -value: 0.5555

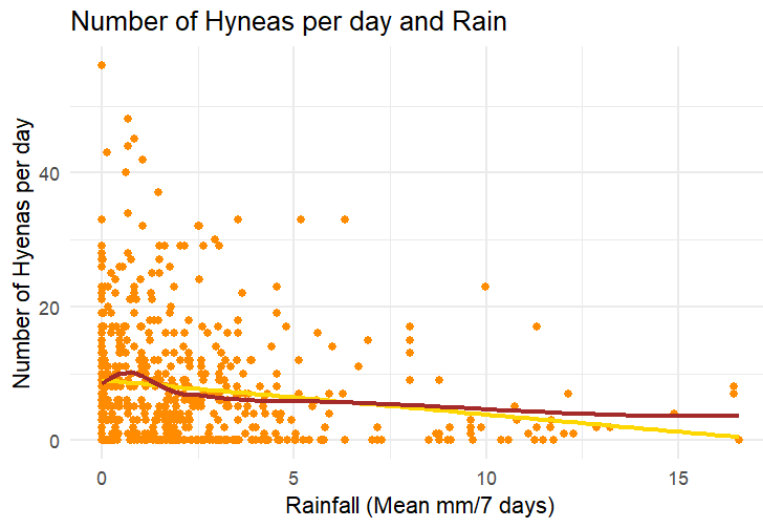


Figure 13. Number of hyenas per day and the mean value of mm of rain fell in the previous 7 days. In yellow is the regression line, in brown is the trend line. p -value: 0.0111

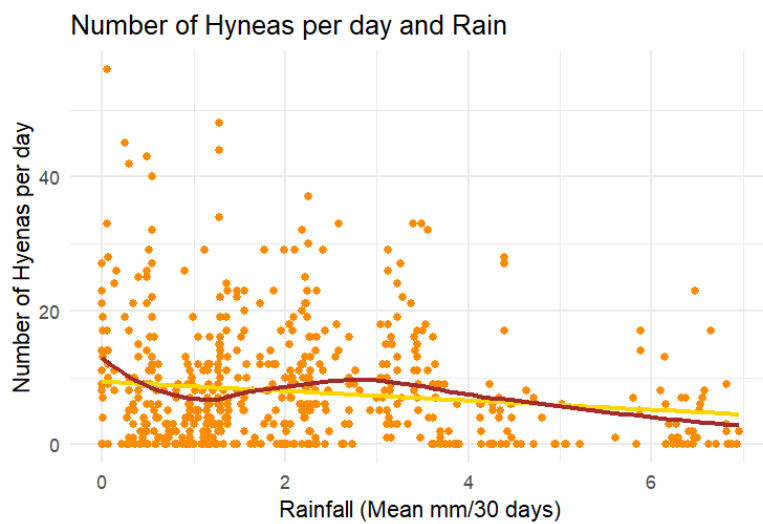


Figure 14. Number of hyenas per day and the mean value of mm of rain fell in the previous 30 days. In yellow is the regression line, in brown is the trend line. p -value: 0.2470

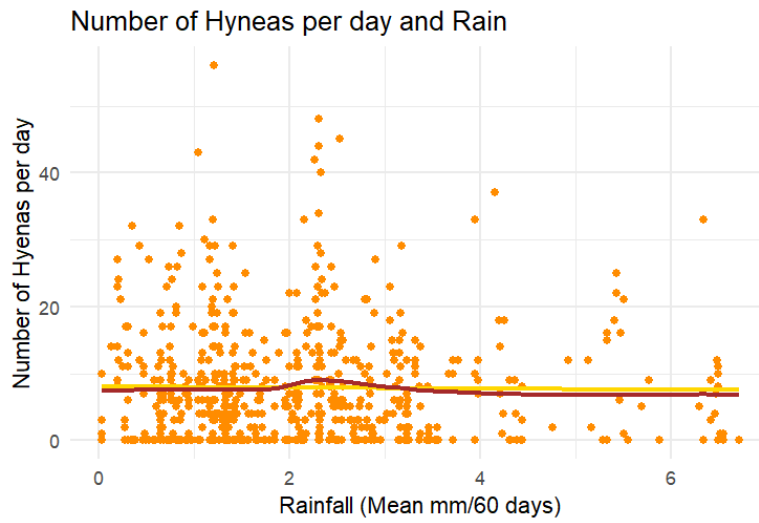


Figure 15. Number of hyenas per day and the mean value of mm of rain fell in the previous 60 days. In yellow is the regression line, in brown is the trend line. p -value: 0.4659

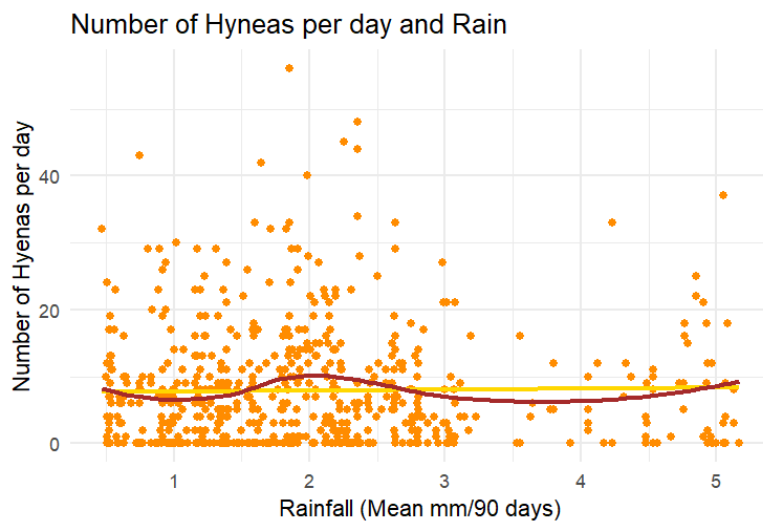


Figure 16. Number of hyenas per day and the mean value of mm of rain fell in the previous 90 days. In yellow is the regression line, in brown is the trend line. p -value: 0.9197

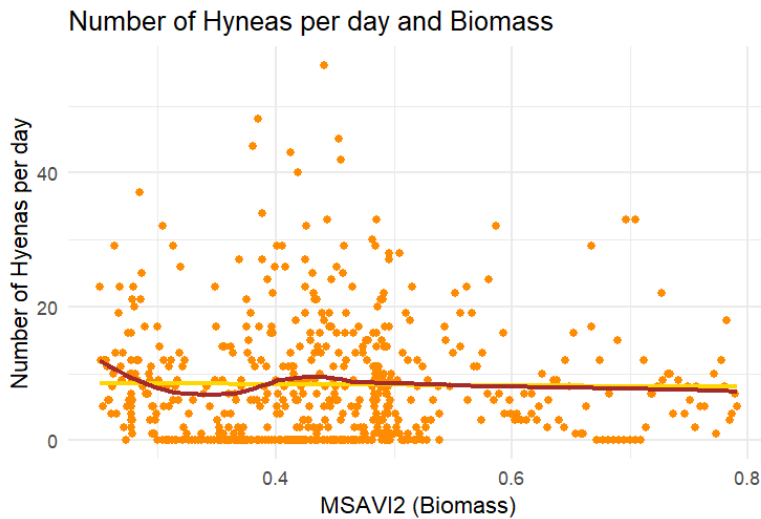


Figure 17. Number of hyenas per day and biomass. In yellow is the regression line, in brown is the trend line. p -value: 0.5991

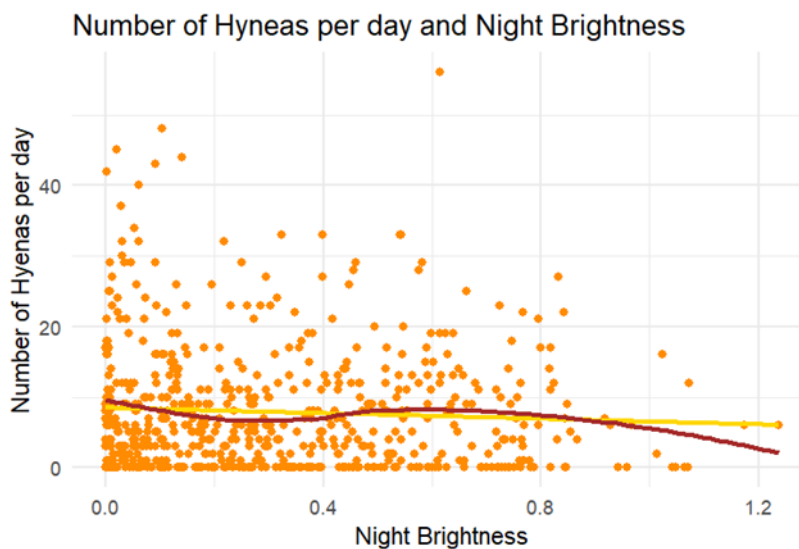


Figure 18. Number of hyenas per day and night brightness. In yellow is the regression line, in brown is the trend line. p -value: 0.0479

The principle component analysis (PCA) reflects what's shown in the GLM. Two Dimensions contribute to 99.9% of the total variance with Dimension1 only, accounting for 99%. In this context, $r7$ and light (night brightness) are considerably more influential than the amount of biomass, as shown by the GLM. In particular, $r7$ is strongly aligned with the first component axes proving that is the most influential factor of the dataset. The PCA has been used also to test whether there was a correlation between Rainfall and Light Index since the latter has cloud coverage as a variable, proving their uncorrelation.

However, the observations are clustered more on the left side of the graph showing that these factors alone are not enough to explain the observation of hyenas,

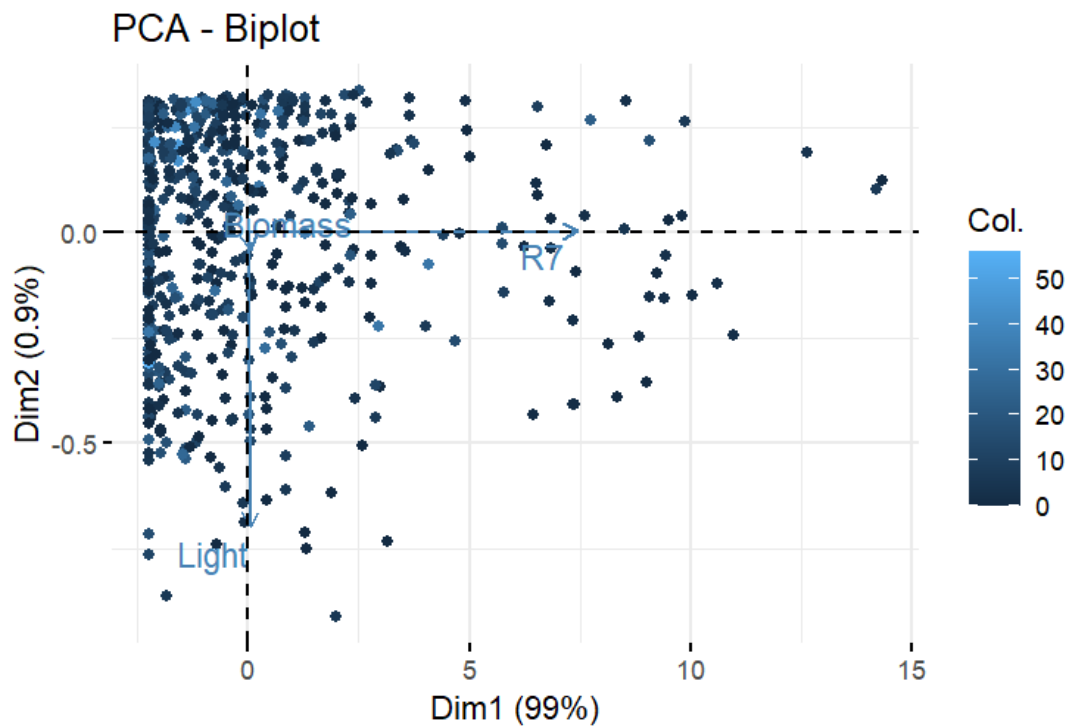


Figure 19. PCA biplot with Biomass, mean Rain fall in the previous 7 days and Night brightness. The blue color stands for the size of the hyenas group observed.

especially for bigger groups: groups of 20+ hyenas, in fact, are found only on the top-left side of the graph, far from the three arrows.

4. Discussion

The aim of the study was to understand how the environmental factors considered (night brightness, biomass and rainfall) effected hyenas activity pattern and why. The result obtained gave many hints but to properly interpret them, was necessary taking into account hyenas ethology and their social behaviour.

Hyenas have a long commuting behaviour when it comes to hunting (Naciri et al. 2023; Raycraft 2024; Avgar et al. 2014). However, when they are not hunting it's more likely to spot them in the proximity of the communal den, especially the higher rank individuals or females with lactating cubs (Boydston et al. 2003a), usually located in low prey density areas (Boydston et al. 2003b). This means, also considering that spotted hyenas tend to minimize the time spent in proximity of fences and approach them only if needed (Wilkinson et al. 2024), that activity next to the fence and the corridors might be interpreted as a proxy for hunting activity, especially outside of OPC. In this sense, the biggest exceptions might be dispersing males who leave their clan's territory looking for a new one to join (Holekamp & Smale 1998; Hayward & Slotow 2009; Boydston et al. 2003b).

4.1 Rainfall

It's unlikely that rainfall affects *Crocuta*'s behaviour directly since water is rarely a limiting factor (Holekamp & Smith 2019) and in extreme situations spotted hyenas can survive up to an entire week without drinking water (Holekamp & Dloniak 2010). Therefore, it makes more sense to focus on the indirect effects of rain: prey abundance.

OPC for most of the year appears as an arid bushland and grassland landscape. However, with the first rain during the two wet seasons (March-May and November-December), the vegetation immediately turns green attracting a wide array of big herbivores increasing significantly prey availability for OPC resident carnivores.

This study shows that an increase in rainfall during the past seven days has a slightly negative effect on hyenas' activity around the borders of OPC. This might be explained by the higher density of prey inside the conservancy. In addition to that hyenas tend to aggregate (fusion) more during periods of prey abundance while are more prone to forage alone (fission) during periods of prey scarcity (Smith et

al. 2008). This might reduce the likelihood that single, low-ranked, hyenas undertake a long journey in order to find food and instead join a bigger hunting party inside the conservancy.



Figure 20. *Crocota crocuta* crossing corridor 2 when flooded

This behaviour would have multiple advantages. A bigger hunting party would be capable of taking down bigger prey and most importantly would be able to defend the carcasses from other hyenas' clans or lions. In fact, cleptoparasitism is one of the most common interactions in the top predators' guild (Henschel & Skinner 1990; Périquet et al. 2015) and when facing lions, hyenas have to outnumber them by many individuals to maintain control of the carcass (Höner et al. 2002). Even though OPC hosts a thriving community of wildlife, it has also a strong presence of human activity and pastoralism inside its borders. Mogensen et al. (2011) found that lions -when exposed to anthropogenic disturbance- may become more nocturnal and thus overlap their activity pattern with hyenas, mostly active during the night (Boydston et al. 2003b; Kolowski et al. 2007; Cozzi et al. 2012; Sogbohossou et al. 2018; Horion et al. 2024). This circumstance might increase the need for hyenas to have bigger foraging groups even more during periods of high prey densities. This scenario breaks off when the rain falls for prolonged periods (high r30, 60, 90 values) and vegetation grows higher. Higher grass is less nutritious than fresh one (Cherney et al. 1993), and thus grasslands might concentrate less herbivorous lowering the prey density in hyenas' hunting grounds. In addition to that, higher grass gives an advantage to ambush predators (Orsdol 1984; Funston et al. 2001), e.g. lions and leopards, but might be detrimental to the coursing hunting technique of hyenas. This would increase the availability of carcasses that hyenas can exploit and scavenge, making the food source less dependent on prey density. Another effect of prolonged rainfall is the more widespread food and water availability for herbivores that will be less concentrated, leading to less efficient

hunts which usually match higher livestock depredation (Watts & Holekamp, 2008). This scenario can increase fission in hyena clans promoting a less targeted use of their territory. On top of that, rainfall data from 30 or more days before, will influence less directly the amount of vegetation available and thus rain alone would have a less significant impact on herbivores presence.

4.2 MSAVI2 (Biomass)

It is reasonable to think that *Crocuta crocuta*'s behaviour shows seasonal adaptations, especially when it comes to prey abundance (Boydston et al. 2003). However, this study's experimental design might not be the most suitable to detect it.

Even if it is strictly linked to rainfalls, the amount of biomass (calculated with the MSAVI2 index) hasn't significantly affected hyenas' activity. The amount of plant biomass is also an indicator of seasons, wet seasons have, in fact, a considerably higher amount of biomass available. Some aspects of hyenas' life cycle might show some seasonality, but in East Africa this is especially true during reproduction which usually peaks concurrently with the highest availability of food during the rainy season (Holekamp et al. 1999). During this period, nursing hyenas are less prone to leave the communal den (Boydston et al. 2003), and it is not rare that they would bring some parts of a carcass back to it (Skinner et al. 1986); factors that would determine a lower number of hyenas photographed by the camera traps. However, as Leirs et al. (2017) also found out, our data showed no significant difference in hyenas' activity during the year. This uniformity in their movement habits throughout the year might show a little pronounced reproductive seasonality in this population, which can be very variable in different areas (Holekamp et al. 1999) as well as an overall absence of the seasons' influence on hyenas' behaviour. In fact, even if an increase in biomass means an increase in prey availability it means also taller grass, which in East African savannas can reach up to 70 cm (Riginos & Young 2007). This could act as an obstruction to the coursing hunting strategy of hyenas which, standing around 80 cm at the shoulder (Swanson et al. 2013), might struggle more to chase and detect suitable prey while running, balancing out their higher food availability and resulting in no significant difference between the dry and the wet season. In addition to that, the increase in herbivores' abundance over longer periods affects hyenas in two different ways: if not involved in bigger hunting trips relatively close to the den, lower-rank hyenas have to travel longer distances looking for food (Green & Holekamp 2019) potentially triggering the camera traps more often; however, Wilkinson et al. (2024) found that inside fenced areas, or in protected areas in general according to Belton et al. (2016), spotted hyenas' ranges undergo an expansion from the wet to the dry season, a scenario that would see an increase in camera traps captures during this season as

well. Moreover, increased grazing pressure and anthropic disturbance - OPC was a cattle ranch and the presence of shepherds with cattle is still very substantial- can force hyenas to seek cover in more densely vegetated areas (Kolowski & Holekamp, 2009), in the inner part of OPC in this case, and thus far away from the corridors. All these contrasting scenarios may result in the overall hyena activity being uniformly detected across seasons.

4.3 Night Brightness

Previous studies tried to find a correlation between *Crocuta crocuta*'s activity and the moon finding no significant effect of the lunar cycle on their behaviour (Cozzi et al. 2012). The present study, however, doesn't take into account the lunar phases on their own but rather the brightness of nights and the results differ from the one from Cozzi et al. (2012). In OPC, spotted hyenas appear to be less active during brighter nights. Light will simultaneously give advantages to predators that rely on eyesight to detect their prey, like spotted hyenas, and prey that visually detect predators. Therefore, there is a trade-off and, for moonlight to increase hunting success, the prey's vulnerability must exceed the predators' advantage (Prugh & Golden 2014). Night brightness net effect can thus be seen as a trade-off of costs and benefits. In this context, habitat plays a crucial role, and, as the habitat cover increases light is less determinant in animals' behaviour. OPC offers a vast array of habitats and grasslands are very common so that hyenas shouldn't struggle to find a suitable hunting ground.

Green & Holekamp (2019) found that with the new moon, and thus with darker nights, hyenas tend to move at an average higher speed. This could imply not only faster but also longer journeys which could easily take hyenas outside of the OPC resulting in more camera trap observations during the darkest nights. This trend is even more evident in the presence of livestock (Green & Holekamp 2019) which in OPC can be very abundant. In this scenario, anthropic disturbance would play a crucial role in *Crocuta crocuta*'s behaviour but this is not the only factor worth considering. Lions are hyenas' biggest natural competitor and, as ambush predators, they rely on a different hunting technique making them significantly less efficient hunters during brighter nights (Mwampeta et al. 2023). This could influence spotted hyenas' behaviour since hungry lions could be more prone to kleptoparasitism forcing hyenas to hunt in bigger groups in order to protect their catch resulting in fewer hyenas commuting out of the OPC during the night.

4.4 Weak points and potential improvements

This experimental design shows multiple weak points. First of all, is the timespan considered. The original database included data from 2015 to 2019 but, due to the loss of numerous pictures through the years and the malfunctioning of the cameras only 2017 and 2018 were part of the study. On top of that, only two out of three corridors were considered in the analysis since corridor 3 has been closed for a prolonged time and the construction of a village nearby could have biased the data.

For all the above reasons, the sample size was not optimal, and increasing it would certainly give more reliable data.

Besides that, knowing the exact position of the communal dens and the number of clans that inhabit the area could give a more precise idea of the individual movements of hyenas and could help understand the reasons behind them. Unfortunately, these pieces of information were not available during the writing of the thesis. However, this kind of problem may be solved by installing camera traps not only at the OPC borders but inside the conservancy as well. Knowing how spotted hyenas behave inside their territory might be very helpful in understanding why they leave it. In addition to that, trying to have a clearer point of view on individuals' behaviours could be achieved by identifying single hyenas by their unique spots pattern or by installing a GPS collar on some individuals.

Understanding *Crocuta crocuta*'s behaviour could also be easier with a more complete picture of their ecology in OPC and more specifically their interaction with lions. A comparative study on the activity pattern of both these sympatric carnivores could be very interesting and maybe could highlight behaviours that, if considered each species on their own, wouldn't be visible.

Moreover, using environmental factors gives a very interesting insight into spotted hyenas' life and activity. Still, it doesn't take into account a multitude of complex social interactions that are behind their behaviour. Direct observations of them in their natural habitat could help understand the relationship between each other or with other animals and thus give a clearer idea of their activity.

5. Conclusions

Throughout the seasons, hyenas' activity has been influenced only by rainfall and, more specifically, by the rain fallen in the previous 7 days. This could be due to the increase in prey abundance inside the conservancy allowing *Crocuta crocuta* to avoid longer journeys looking for food. The non-significant results of biomass dynamic and rainfall per 1, 30, 60 and 90 days have been interpreted as a result of the weaker correlation between these measurements and prey abundance inside OPC.

Night brightness, on the other hand, showed a negative correlation with hyenas activity. This result is contrasting with the original hypothesis but can be explained by the stronger interspecific competition which could force hyenas to stay more inside the borders of OPC in order to protect their catches.

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Popular science summary

Spotted hyenas are the most abundant big carnivore in Africa and, as top predators, are of vital importance in maintaining healthy ecosystems. Africa fast-growing population and increasing wildlife-humans interactions, understating the activity patterns and behaviours of these animals is essential to prevent conflicts that might eventually threaten their existence.

The following study tries to understand what drives hyenas' activity along the borders of a fenced conservancy thanks to camera trapping, and which environmental factors are the most influential. These environmental factors are biomass, rainfall, and night brightness. The amount of biomass, and thus the amount of green vegetation, proved to have no effect on hyenas' activity. This result could be explained by the contrasting effects that the vegetation have on their behaviour: with an increase in vegetation some hyenas would stay in the proximity of their den while others would be more prone to leave the conservancy. On the contrary, night brightness influenced their activity and hyenas proved to be less active during brighter nights. That could be due to the higher chances of being detected by prey, scenario that would discourage hyenas to embark in big hunting trips. At the same time, lions are much less efficient hunters during these bright nights forcing spotted hyenas to form bigger groups to defend their prey from them. At last, rainfall proved to have a significant negative effect only if we consider the amount of rain fallen in the previous 7 days. This could be explained by the increase of prey availability inside the conservancy with the increasing rainfall that would keep more hyenas inside its borders. However, if rainfall keeps increasing, the prey population would be less concentrated and the higher vegetation could even be detrimental to the hunting success resulting in more hyenas leaving the fenced area and balancing the numbers of individuals inside and outside of it. That's why the amount of rain fallen every day, in the past 30, 60, and 90 days did not affect hyenas detection.

Having the cameras placed only at the Conservancy borders and using only environmental factors is not enough to give a complete picture of hyenas' lives. Having pictures that cover a longer timespan and placing camera traps inside the conservancy as well, closer to their dens, would result in a more accurate depiction of spotted hyenas' ecology and behaviour and the results would be much more reliable.

In conclusion, more time and more data are required to have a detailed and complete study of these animals.

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