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Aktivitetsmönster hos stora rovdjur i ett inhägnat reservat i distriktet Laikipia, Kenya

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Uppsala 2016

MSc Animal Science

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Student report
Swedish University of Agricultural Sciences ***No. 644***
Department of Animal Environment and Health

ISSN 1652-280X

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Student report 644, Uppsala 2016

Advanced A2E, 45 ETCS, Degree Project in Animal Science, EX0719

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Keywords: Spotted hyena, African lion, activity patterns, movement ecology, conservation management, *Crocuta crocuta, Panthera leo*

Title of series, no: Studentarbete/Sveriges lantbruksuniversitet, Institutionen för husdjurens miljö och hälsa, nr. 644, ISSN 1652-280X

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Abstract

Large carnivores are sensitive to land-use changes and in African rangelands they have suffered seriously from an increased demand for land for agriculture and husbandry during the last decades. Mammalian carnivores are particularly exposed as they can also attack livestock, and are therefore frequently killed by farmers or wildlife managers. The conflict is a major cause of why most large carnivore populations are declining and is likely to increase with the rapid expansion of human populations. An improved knowledge about the activity patterns and behavior of large carnivores allow a better understanding of their requirements and further advances our understanding of carnivore–livestock interactions which is crucial for conflict mitigation and carnivore conservation. Although activity rhythms of lion and spotted hyena have been previously studied, the migratory behaviors of predators in fenced areas have not yet been thoroughly investigated. The general objective of this study was to investigate spatial and temporal movement patterns and behavior of two top predator species, the African lion (*Panthera leo*) and the spotted hyena (*Crocuta crocuta*), in a fenced conservation area with corridors that allowed animal crossings. I also investigated the impact of environmental variables on activity levels. The study was conducted in Ol Pejeta Conservancy, a private reserve located in Laikipia District, Kenya. Movement patterns were investigated by measuring activity at a water trough and at two wildlife corridors along the conservancy boundary where these animals can passage to other areas. Activity levels were also compared with the environmental variables moonlight and rainfall. I found that both species are nocturnal but with decreased activity around midnight. Lions and spotted hyenas showed very similar activity patterns. The corridors were frequently used by the predators and my results imply that they leave the conservancy for longer periods than a single night. Moonlight and rainfall had a positive effect on activity levels in spotted hyena but did not seem to be of high importance to lion activity. Differences in activity patterns between the two species could potentially result from intra-guild competition but I suggest that that the activity levels in the study were regulated by other factors such as prey activities or hunting techniques, rather than competition. Different hunting techniques may also explain the different results in weather data correlation between the two species. My results indicate that carnivore-livestock conflict in the Ol Pejeta area could be mitigated by confining livestock at night and during bad weather when predator activities are high.

Sammanfattning

Stora rovdjur är känsliga mot förändrad markanvändning och på Afrikas betesmarker har en ökad efterfrågan på mark för jordbruk och djurhållning medfört stora konsekvenser för områdets rovdjur. Särskilt utsatta är större rovdjur som ibland kan attackera boskap med följden att de blir dödade av bönder eller viltvårdare. Konflikten med lantbruk är den huvudsakliga orsaken till sjunkande populationer bland rovdjuren och denna kan antas öka med människans snabba populationstillväxt. En ökad kunskap om aktivitetsmönster hos stora rovdjur ger en bättre uppfattning om dessa arters behov samt förbättrar vår förståelse för interaktioner mellan rovdjur och boskap, vilket är en förutsättning för minska konflikten och skapa en framgångsrik rovdjursförvaltning. Tidigare studier har undersökt aktivitetsmönster hos både lejon och fläckig hyena, men kunskapen om rörelsebeteenden hos rovdjur i inhägnade områden är ännu mycket begränsad. Syftet med denna studie var att undersöka temporala och spatiala rörelsemönster samt beteende hos två topprovdjur, det afrikanska lejonet (*Panthera leo*) och den fläckiga hyenan (*Crocuta crocuta*), i ett inhägnat

reservat. Jag undersökte även hur miljömässiga variabler påverkade aktiviteten hos de båda arterna. Studien utfördes i Ol Pejeta Conservancy, ett privatägt reservat beläget i distriktet Laikipia i Kenya. Rörelsemönster undersöktes genom insamling av aktivitetsdata vid ett vattentråg samt vid två viltkorridorer längs reservatsgränsen där djuren kan röra sig mellan reservatet och omgivande områden. Jag undersökte också sambandet mellan aktivitet och miljömässiga variabler. Resultaten av denna studie visar att båda arter är huvudsakligen nattaktiva men med en minskad aktivitet vid midnatt. Lejon och fläckig hyena uppvisar likartade beteendemönster med få skiljaktigheter. Korridorerna användes kontinuerligt av båda arter och testresultaten indikerar även att rovdjuren lämnar reservatet över längre tidsperioder än enstaka nätter. Månljus och regn hade en positiv inverkan på den fläckiga hyenans aktivitetsnivåer men verkade vara av mindre betydelse för aktivitetsnivåerna hos lejon. Uppmätta skillnader i aktivitetsmönster mellan de två arterna kan möjligen härledas till konkurrensförhållandet mellan arterna, det är dock mer troligt att aktivitetsnivåerna i studien styrts av andra faktorer såsom aktivitet hos bytesdjur eller jaktteknik, snarare än konkurrens. Olika jaktteknik är också en möjlig förklaring till uppmätta skillnader i sambandet mellan aktivitet och miljömässiga variabler. Resultaten av studien indikerar att rovdjurskonflikten i Ol Pejeta-området kan minskas genom att boskapen hålls instängda nattetid och under dåligt väder då rovdjursaktiviteten är som högst.

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1. Introduction

1.1. Carnivore–livestock conflict

Resource competition between people and animals is one of the main threats to the survival of many endangered species in the world and is also a significant threat to local human populations. In Kenya, livestock contributes to over 12% to GDP (Gross Domestic Product) and is critical to many rural communities (Kabubo-Mariara 2009). Like most countries in the African continent, Kenya suffered from an extensive population growth during the last decades. In 2015, Kenya had an estimated population of 47.8 million with an average population density of 79.2 people per square kilometer of land (World Population Review 2016) with an annual growth of 2.6% (World Bank 2016). The encroachment on land has increased and the demand for land for agriculture and husbandry is constantly growing. As a result, wildlife has been reduced or even eliminated when their habitat is converted to cultivation. In African rangelands, carnivore-livestock conflict is particularly serious for mammalian carnivores, which can also prey on livestock, and are therefore frequently killed by farmers or wildlife managers (Woodroffe and Frank 2005). The conflict is a major cause of why most large carnivore populations are declining (Woodroffe and Ginsberg 1998, Hilton-Taylor 2000, Woodroffe 2000). These animals are considered threats to rural communities and their livestock and active persecution has contributed to the endangerment of many species and driven some of them to extinction (Woodroffe 2000, Woodroffe *et al.* 2005). A rapid expansion of human populations is challenging the carnivore-livestock coexistence and the conflict is inevitable and likely to increase. Many conservation areas in East Africa are fenced, either to prevent predation on livestock in human-populated areas, or to prevent poaching (Breitenmoser *et al.* 2005, Kiffner *et al.* 2013, Ol Pejeta Conservancy 2016). Fencing is also a way to restrain illegal livestock grazing and other unwanted vegetation damage (Kiffner *et al.* 2013, Ol Pejeta Conservancy 2016). Some areas are completely closed whereas others have corridors in the fences to allow animals to cross the fences towards selected areas, e.g. other conservancies. Also, the way the corridors are constructed can prevent rhinos or other threatened species to leave the conservation area.

1.2. Conservation status of lion and spotted hyena

Large carnivores are sensitive to land-use changes and have suffered seriously from anthropogenic and environmental developments that are rapidly reducing and fragmenting available habitats. Habitat loss and degradation also reduce the habitat available to populations of wildlife that are suitable prey for carnivores. Several carnivore species have become endangered and the African lion (*Panthera leo*) is currently classified as Vulnerable (VU) on the Red List of Threatened Species of the World Conservation Union (IUCN 2015a). In the past, the lion was one of the most widely distributed terrestrial mammals and ranged over most of Africa (Schaller 1972, Nowell and Jackson 1996). Lately, its abundance has decreased and current number of free-ranging African lions estimate between 23 000-39 000 lions for the whole continent (Chardonnet 2002, Bauer and van der Merwe 2004, IUCN 2015a). The spotted hyena (*Crocuta crocuta*) is the most abundant large carnivore in Africa but human–wildlife conflict is a major threat also to hyenas. Populations outside protected areas are continuously declining, mainly due to persecution and habitat loss (IUCN 2015b). The spotted hyena is today classified as Least Concern (LC) on the IUCN Red List, but is increasingly dependent on the continued existence of protected areas. As Africa’s largest carnivore, lion populations are of great ecological importance as structuring terrestrial communities as well as other predator populations (Krebs *et al.* 1995, Terborgh *et al.* 1999). Besides contributing to the maintenance of healthy ecosystems, lions are also crucial components of Africa's tourism industry (Nowell and Jackson 1996). Livestock attacks by large predators cause conflicts of interest between farmers and wildlife conservation and the need of scientific based knowledge and adaptive management strategies is critical. In areas used for pastoralism, development of conservation and management strategies for mammalian predators rely on understanding their spatial distribution as well as their activity patterns and behavior.

1.3. Activity patterns and expected results

Animals constantly move between different areas according to changing requirements and constraints. Why an individual moves from place to place vary both temporally and spatially but examples of important aspects motivating movements are food and water supply, competition, safety conditions, exploration, partner searching and other social needs (Barnard 2004). This study is focused on activity behavior of two top predator species, the African lion and the spotted hyena, in Ol Pejeta Conservancy, Laikipia District, Kenya. Activity patterns of top predators are adapted for efficient predation and result from both physiological rhythms and behavioral adaptations to environmental conditions (Daan 1981). Activity patterns may therefore vary considerably between species as well as between areas. Environmental variables that influence activity of terrestrial carnivores are for example light conditions, temperature, rainfall, wind conditions and vegetation (Beltran and Delibes 1994, Schmidt 1999, Funston *et al.* 2001, Lucherini *et al.* 2009). Also competitive limitations (Hayward and Slotow 2009), human activity and persecution (Bauer *et al.* 2003, Boydston *et al.* 2003, Bauer and De longh 2005) as well as prey activity patterns (Harmsen *et al.* 2011, Podolski *et al.* 2013, Heurich *et al.* 2014) are important. An essential factor affecting the variation in predator activity is food searching (e.g. Schmidt 1999). Cats hunt by using several senses but depend especially on their highly developed vision to capture prey (Sunquist and Sunquist 2002) and hunting success is expected to increase at night because of nocturnal hunters' superior night vision compared with their prey. Furthermore, darkness provides adequate concealment to enable hunting in open areas where predators at daytime are spotted from far distances. Therefore we would expect higher activity in both lions and spotted hyenas in Ol Pejeta during night hours. Coexistence of species that share similar niche has been suggested to be mediated by temporal partitioning (Kronfeld-Schor and Dayan 2003). Spotted hyena and lion share a large degree of dietary overlap (Hayward 2006) and in terms of avoiding lion encounters, which often ends with fatal outcome, other species may become active at other times (Hayward and Slotow 2009). This suggests that spotted hyena may show activity patterns different from lion.

Most protected areas are too small to support wide-ranging large carnivores and lion populations in fenced reserves are closer to their estimated carrying capacities than unfenced populations (Packer *et al.* 2013). In fenced areas that allow animal crossings, it is therefore possible that predators hunt outside these areas. Ol Pejeta Conservancy holds some of the highest predator densities in Kenya (Ol Pejeta Conservancy 2016). In addition, both lions and spotted hyenas are known to attack livestock within bomas (thornbush corrals) at night (Ogada *et al.* 2003, Woodroffe and Frank 2005, Kolowski and Holekamp 2006, Kissui 2008). A key factor responsible for low mammal populations outside protected areas is illegal hunting by local people (Caro 1999, Caro 2008, Kiffner *et al.* 2009) and persecution by humans is linked to the decline in several species of Africa's large predator guild (Ogada *et al.* 2003, Patterson *et al*. 2004). Ol Pejeta has wildlife protection squads patrolling the conservancy (Ol Pejeta Conservancy 2016) and hence lower persecution risk, why predators are expected to return to the conservancy after hunting. A range of environment-related parameters have been found to influence the hunting behavior of predator species (e.g. Beltran and Delibes 1994, Horning and Trillmich 1999, Funstol *et al.* 2001, Lang *et al.* 2005, Hammerschlag *et al.* 2006, Lucherini *et al.* 2009, Heurich *et al.* 2014). Rainfall and moonlight has been found to be two important environmental factors (Beltran and Delibes 1994, Funston *et al*. 2001). This suggests a relationship between activity and weather data. A strong relationship would suggest that these factors play an important role in activity levels at night. Hayward and Slotow (2009) suggest that because there are few competitive limitations on lion it is likely that they are active at times that optimize their hunting success, why we would expect a strong correlation between lion activity and weather data. Due to competitive limitations, spotted hyenas are expected to show a weaker correlation between weather data and activity.

1.4. Aim and objectives

The general objective of this study was to investigate spatial and temporal movement patterns and behavior of the African lion and the spotted hyena. More specifically, I investigated nocturnal patterns of activity and environmental factors driving activity patterns exhibited by large carnivores in a fenced conservation area. This study is considered to be important as the results will contribute to the understanding of the ecology of the African lion and the spotted hyena. Additionally, it advances our understanding of carnivore–livestock interactions which is crucial for conflict mitigation and carnivore conservation. Although activity rhythms of the lion and spotted hyena have been previously studied, the behaviors of predators in fenced areas have not yet been thoroughly investigated. Data were collected for two separate time intervals during 2014 and 2015. I used this data to test the following hypotheses:

i. Predators in Ol Pejeta are more active during night hours than day hours.
ii. Activity patterns differ between lion and spotted hyena.
iii. The main movement direction during evening is out and the main movement direction during morning is in.
iv. There is a relationship between weather/moon data and activity.

2. Material and methods

2.1 Study site

The study was conducted in Ol Pejeta Conservancy (0°00 N, 36°56 E). This is a 90,000-acre (360 km^2) private wildlife reserve located in Kenya's Laikipia District (fig. 1). The district majorly consists of wildlife habitat but large areas are used for pastoralism and commercial ranching, small-scale agriculture and tourism. Livestock production is the economic base of the Laikipia. Both commercial farmers and pastoralists use traditional livestock husbandry practices where stock are closely herded by day and kept in traditional bomas at night. The study site consists primarily of semi-arid bushed grasslands vegetation and receives low annual rainfall (600 to 800 millimeters). Most rainfall occurs during two wet seasons: in October–December and in late March–May. Because the study site is located at the equator, sunset and sunrise times vary insignificantly throughout the year, with hours of darkness occurring between 7 pm to 6 am (1900-0600 h). The conservancy holds several water troughs to provide water for livestock (fig. 2). These troughs are also used by wildlife. The conservancy is enclosed by an electrified fence but holds three wildlife corridors or “gaps” along the northern boundary of the conservancy and thus connecting it to the larger Laikipia–Samburu ecosystem (fig. 1). This allows all animals except the rhinoceros to enter or exit the conservancy. The corridors consist of a series of short fence-posts erected almost a meter above ground and spaced approximately 55 cm apart (fig. 3). In Ol Pejeta Conservancy, spotted hyena numbers are currently estimated at 100 individuals and the conservancy has a current population of 72 lions (Ol Pejeta Conservancy 2016).

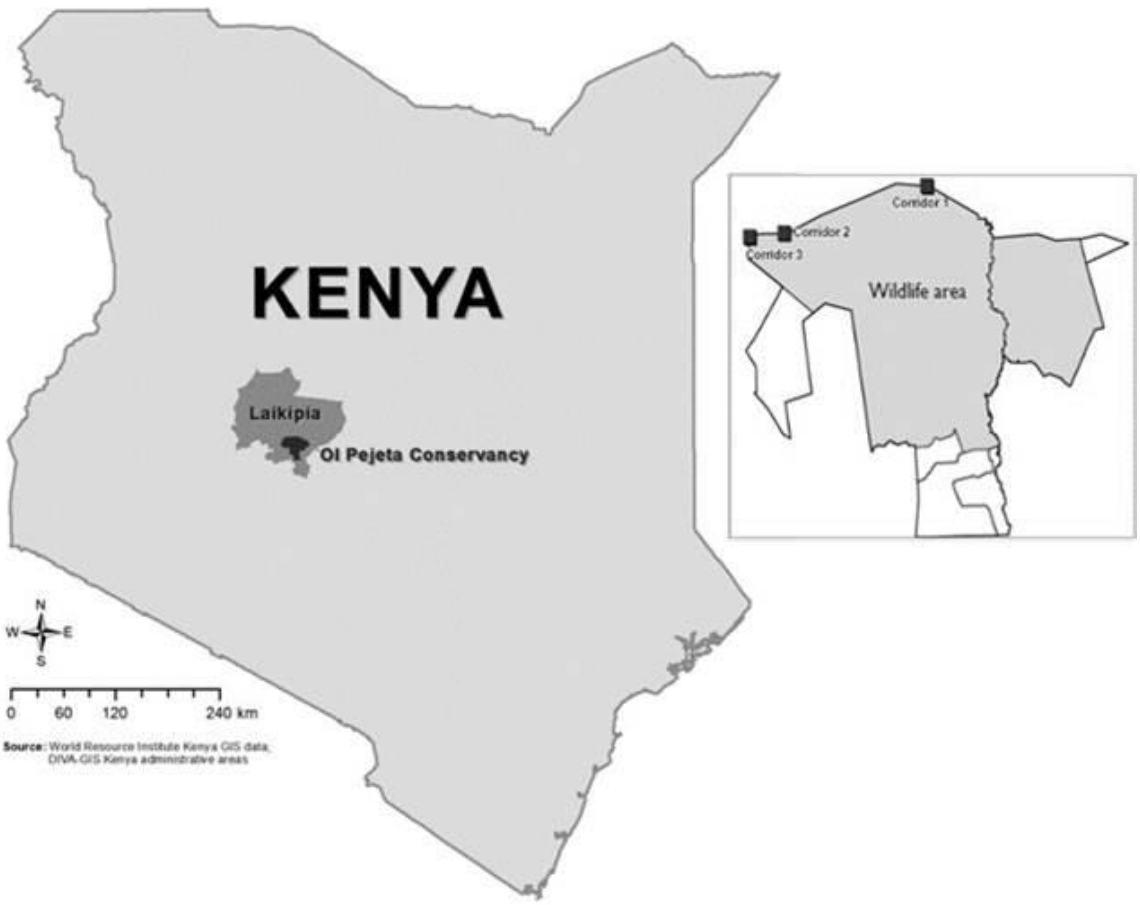

Figure 1. Area of study, Ol Pejeta Conservancy, within the context of Laikipia District and Kenya. The position of the three wildlife corridors are illustrated along the northern border of the conservancy. The water trough area is located approximately one kilometer south of corridor 2.

2.2 Data collection

Two different methods were used in this study. The methods include motion-activated infra-red camera traps that were set up by a water trough and direct observations that were conducted at the same site (fig. 2). Additionally, camera traps were mounted in two entry/exit corridors to record movements of predators in and out of the conservancy (fig. 3). Photographs of predators were taken using Reconyx HC600 Hyperfire motion-activated cameras. The detection range of the camera is up to 24 m (80 ft) at day but during darkness limited by the flash range to a maximum of 18 m (60 ft). The detection angle is 40.3°, field of view 42° and trigger speed 0.20 seconds. The cameras were mounted in a metal camera box fastened on a metal rod that was pushed into the ground. The boxes where placed at an average height of around 80 cm (31.5 inches) above the ground. I assume that the images provide a reliable index of activity of the occurred species in the study area. All data were collected during dry season. I assembled available local records on weather and moon data for Nanyuki which was assumed to be representative for the area.

Figure 2. Water trough area (Photo: Evelina Augustsson).

Figure 3. Corridor area (Photo: Evelina Augustsson).

Direct observations were conducted from a car 250 meters from a water trough during daytime from sunrise to sunset in February 2014 using binoculars. The water trough was located close to the Loirugurugu plains, approximately one kilometer south of corridor 2. Three students with two assistants collected data collectively but for different studies. In this paper I will only present collected data for the large predators. For each observation the date, time of day, weather, group size and behavior of all mammals and large birds at the study area were recorded. Direct observations with instantaneous and continuous recordings were collected for a total duration of ten days. During the instantaneous recordings different behavioral events were observed in 10 min intervals. Continuous recordings were made on one-hour intervals and all animals within the study area were concurrently plotted on a map. Additionally, behavioral events were recorded whenever predators were sighted from the car. The water trough was also monitored by five cameras for a 29-day trapping period during February-March 2014. The cameras were placed somewhat apart and aimed at different angles to obtain total coverage of the trough area. In this study, however, only data collected on predator behavior was used.

All three corridors are being camera monitored periodically. Corridor 1 was under reconstruction during the first duration of the data collection and therefore excluded from the study. Hence, I used collected data for corridor 2 and corridor 3 only in this study. I used images for two time intervals during 2014 and 2015. I used data for a total number of 71 days from December to February (2014-01-03 12 p.m. to 2014-02-15 12 p.m. and 2014-12-26 12 p.m. to 2015-01-23 12 p.m.). Five cameras were positioned and aimed at each corridor. The cameras were placed somewhat apart and aimed at different angles to obtain total coverage of the corridor.

2.3 Data analysis

Digital photographs were sorted using Microsoft Office Excel 2007. I summarized the total number of identifiable passages in photographs. Each identified animal per occasion was recorded as a passage where occasion was defined as a passing group. For photographs collected at the corridors and the water trough, for each passage a number of attributes were recorded: corridor number, year, month, day, time and species. For the corridor data, I also recorded direction of movement (in/out). For each variable, the alternative unknown (u) was available.

2.4 Statistical analysis

Descriptive statistical analyses were conducted in Microsoft Office Excel 2007 and Minitab 17 Statistical Software. The sample size for water trough was too small to test statistically, hence statistical analyses were conducted only on data from corridors. Activity was measured as number of passages. All analyses were conducted irrespective of year. Effects of temperature were not included for the reason that all data collection was conducted under similar conditions. Maximum daytime temperatures during the study period averaged 27°C (range 15–30°C) and minimum nighttime temperatures averaged 10°C (range 7–14°C). The effects of hours of darkness were not included as this number remained constant throughout the study period. Each day was measured as 24-hours and the division between dates was set at noon (1200 h). Data collected from midnight to noon was set to previous date. To investigate activity patterns, I divided each 24-h cycle into day (D) and night (N) where day lasted during hours 9-18 (0900-1859 h) and night during hours 19-8 (1900-0859 h). Nighttime was further divided into early night (EN) and late night (LN). EN stretched between hours 19-1 (1900-0159 h) and LN between hours 2-8 (0200-0859 h). The accepted level of significance was $P \leq 0.05$ for all tests.

A Student's t-test (two-tailed, unequal variances) was used to test for differences in in-passages and out-passages between early night (EN) and late night (LN) at the corridors. Analyses were conducted irrespective of corridor. Only data for night was used for the analysis and the sample mean for each group (EN and LN, n=213) was used. ”0-data” (no passages) was included in the analysis. The data with unknown direction was excluded for the analysis.

I used Pearson's correlation test to investigate the relationship between activity at the corridors and environmental data. Analyses were conducted irrespective of corridor. Rainfall was measured as mm per day. A moonlight index (moon index) was calculated from visible moon surface and hours of possible moonlight during dark hours. Hours of possible moonlight were obtained from moon position data (local time of moonrise and moonset). Dark hours were defined as hours 19-5 (1900-0559 h) for the whole study period.

3. Results

Direct observations by the water trough were conducted for ten days and the trough was camera monitored for 29 days. Additionally, movement data for the corridors were collected for a total of 71 days.

During direct observations at the water trough, I recorded two events of a single spotted hyena passing the water trough and two events of a flock holding 20 individuals of African wild dogs (*Lycaon pictus*) drinking. No instantaneous or continuous recordings were obtained for large predators. Camera monitoring at the trough showed a total of 13 passages of lion, 93 passages of spotted hyena, 1 passage of striped hyena (*Hyaena hyaena*), and 23 passages of African wild dog. I found a daily mean activity of 0.45 lion passages and 3.21 spotted hyena passages per day at the water trough (fig. 4).

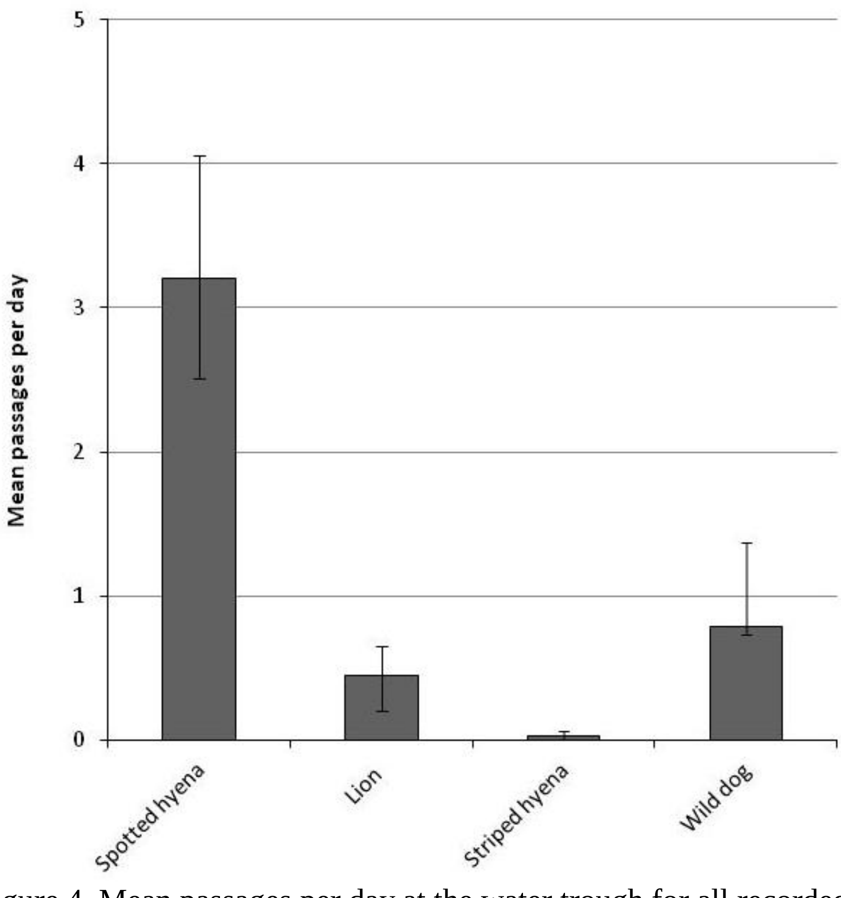

Figure 4. Mean passages per day at the water trough for all recorded species (± SE). Mean spotted hyena: 3.21, mean lion: 0.45.

At the corridors I recorded 94 passages of lion, 545 passages of spotted hyena, 33 passages of striped hyena, 10 passages of cheetah (*Acinonyx jubatus*), 9 passages of leopard (*Panthera pardus*), 54 passages of African wild dog, 3 passages of serval (*Felis serval*) and 1 potential passage of caracal (*Felis caracal*) (not confirmed). I found a daily mean activity of 1.32 lion passages and 7.68 spotted hyena passages per day at the corridors (fig. 5). My results showed generally less activity in corridor 3 than in corridor 2 for all recorded species.

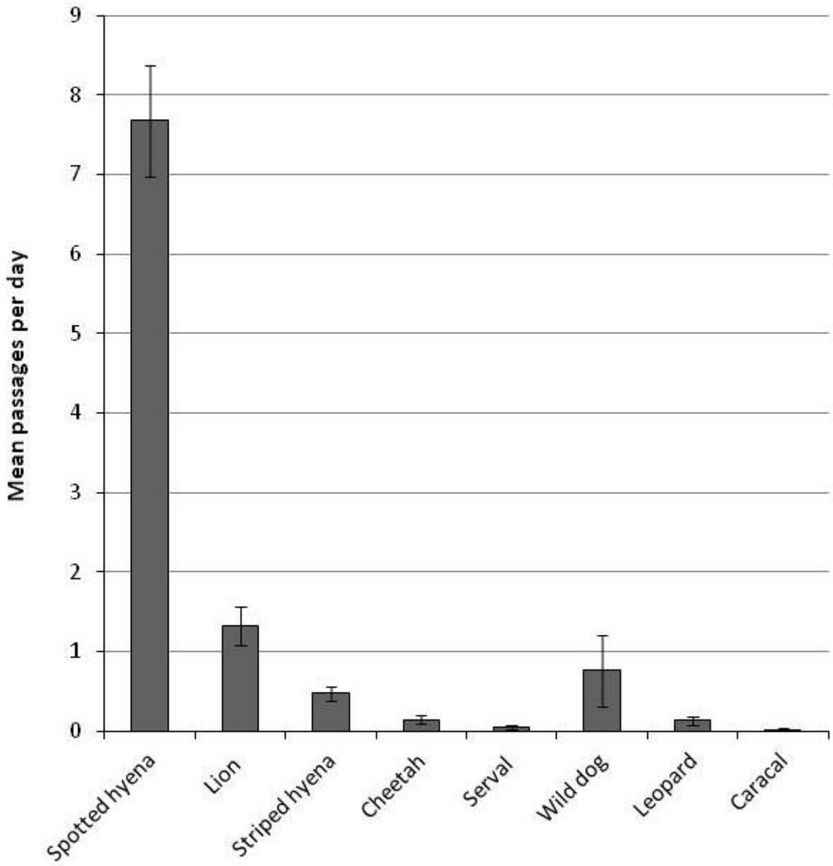

Figure 5. Mean passages per day at the corridors for all recorded species (± SE). Mean spotted hyena: 7.68, mean lion: 1.32.

3.1 Daily activity rhythms

Data from the water trough showed high activity for both lions and spotted hyenas during dark hours and peaks around hours 21-23 and 4-5 (fig. 6). Additionally, spotted hyenas showed another peak after midnight but this peak was not found in lions, however. I also found a dip in activity for both species around midnight.

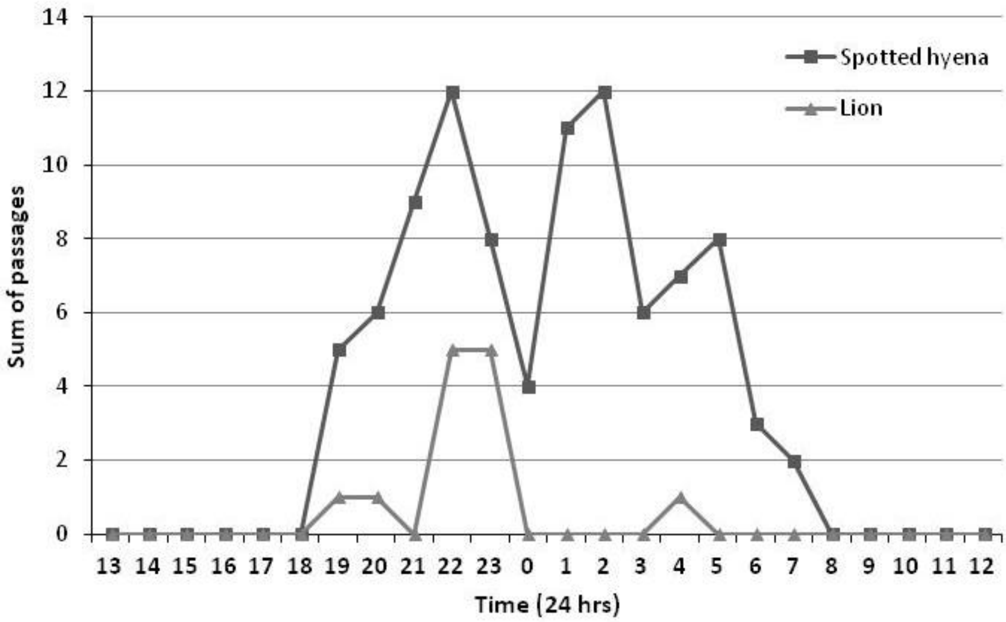

Figure 6. Activity at the water trough for lion and spotted hyena. Data is shown as sum of passages per hour.

At the corridors, in all collected species, 81% of all activity occurred during dark hours (hours 19-5) and 96% of all activity occurred during hours 19-8. I found high peaks in activity during hours 21-23 and 2-3 and a dip in activity during hour 0. In spotted hyenas, 83% of all recorded activity occurred during dark hours (hours 19-5) and 97% during hours 19-8 (fig. 7). Spotted hyenas showed peaks in activity during hours 22, 3 and 7, and dips during hours 0 and 5. In lions, 88% of all recorded activity occurred during dark hours (hours 19-5) and 97% during hours 19-8 (fig. 7). Lions showed peaks in activity during hours 21-23, 2 and 5, and dips during hours 0 and 3-4.

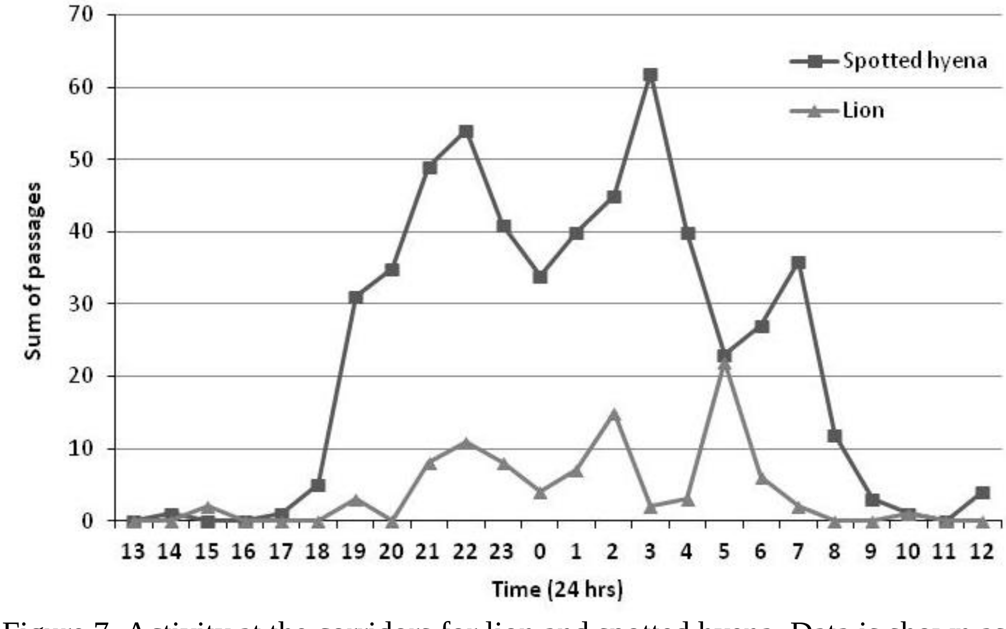

Figure 7. Activity at the corridors for lion and spotted hyena. Data is shown as sum of passages per hour.

Lions reduced their activity a few hours earlier than spotted hyenas both at the corridors and the water trough while spotted hyenas were still active a few hours following dark hours. At the corridors, spotted hyena showed a dip around hour 5 while lion instead showed an increase around the same time.

At the corridors, spotted hyena showed similar frequency of in- and out-passages both early and late night (fig. 8). For spotted hyena, the mean number of in-passages for early night was 1.69 and for late night 1.56. The mean number of out-passages for early night was 1.56 and for late night 1.25. The t-test failed to show any significant difference in in-passages between early night and late night ($t=0.31$, $p=0.758$, $df=137$; fig. 9), and I found no significant difference in out-passages between early night and late night for spotted hyena ($t=0.86$, $p=0.389$, $df=138$; fig. 9).

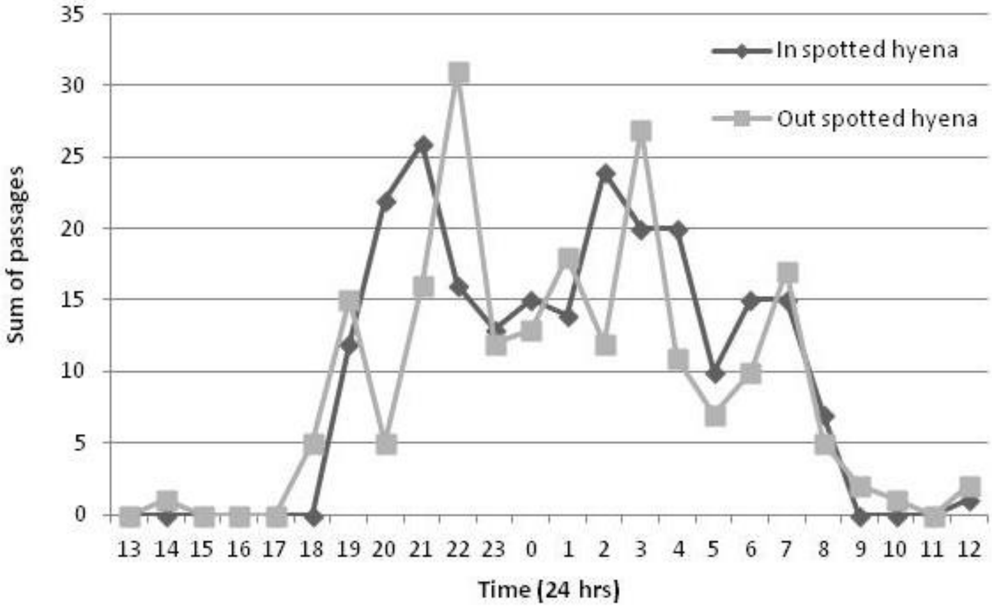

Figure 8. In- and out-passages per hour at the corridors for spotted hyena. Data is shown as sum per hour.

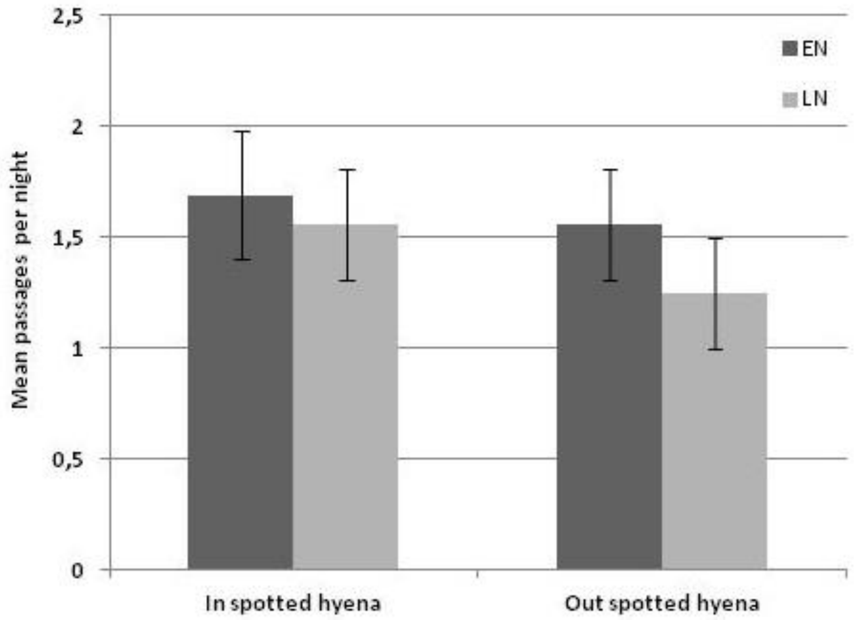

Figure 9. Mean number of in- and out-passages per night at the corridors for spotted hyena (± SE). Mean in EN: 1.69, mean in LN: 1.56. t=0.31, p=0.758, df=137. Mean out EN: 1.56, mean out LN: 1.25. t=0.86, p=0.389, df=138.

At the corridors, lion showed generally high out movement during hours 21-2 but a distinct peak in in-movement during hours 5-6 (fig. 10). The mean number of in-passages for early night was 0.15 and for late night there was a small increase to 0.44. The mean number of out-passages for early night was 0.25 and for late night 0.22. The t-test failed to show any significant difference in in-passages between early night and late night (t=-1.61, p=0.110, df=89; fig. 11), and I found no significant difference in out-passages between early night and late night for lion (t=0.20, p=0.840, df=136; fig. 11).

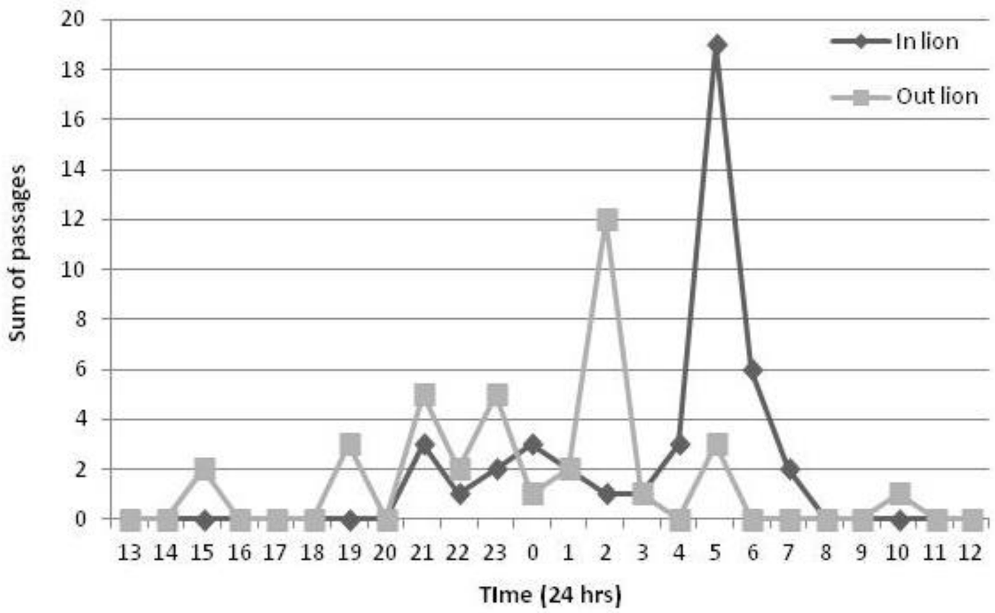

Figure 10. In- and out-passages per hour at the corridors for lion. Data is shown as sum per hour.

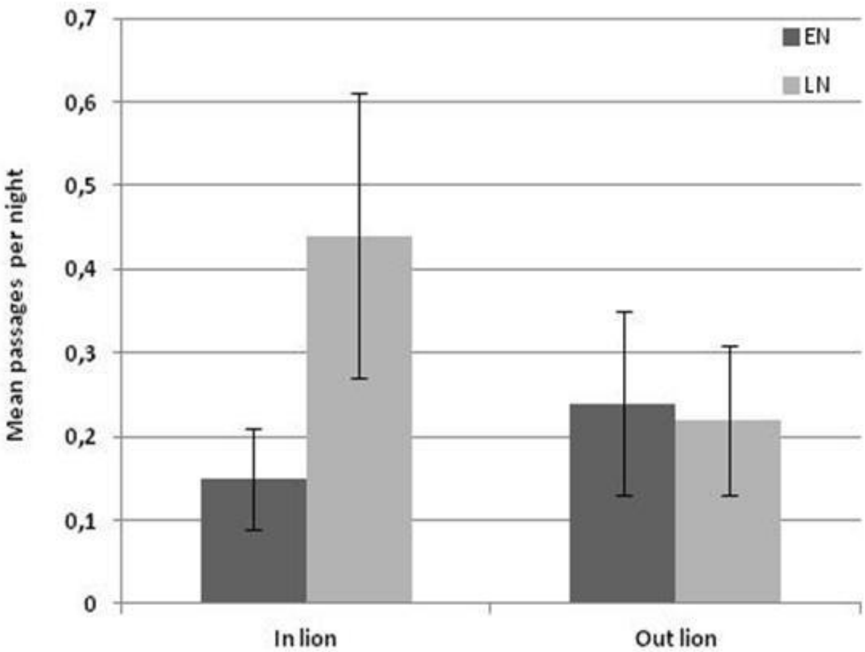

Figure 11. Mean number of in- and out-passages per night at the corridors for lion (± SE). Mean in EN: 0.15, mean in LN: 0.44. t=-1.61, p=0.110, df=89. Mean out EN: 0.25, mean out LN: 0.22. t=0.20, p=0.840, df=136.

3.2 Weather data correlation

Hours of possible moonlight during dark hours varied between 0-11 hours. Rainfall varied between 0-9 mm/day during the study period with an average of 1 mm/day. I found a positive correlation between moonlight (moon index) and activity in spotted hyena (r=0.259, p=0.029; fig. 12a). I also found a positive correlation between rainfall and activity in spotted hyena (r=0.411, p<0.001; fig. 12b).

My results showed no correlation between moonlight (moon index) and activity in lion (r=0.072, p=0.553; fig. 13a). I found a statistical tendency, however, towards a positive correlation between rainfall and activity in lion (r=0.225, p=0.059; fig. 13b).

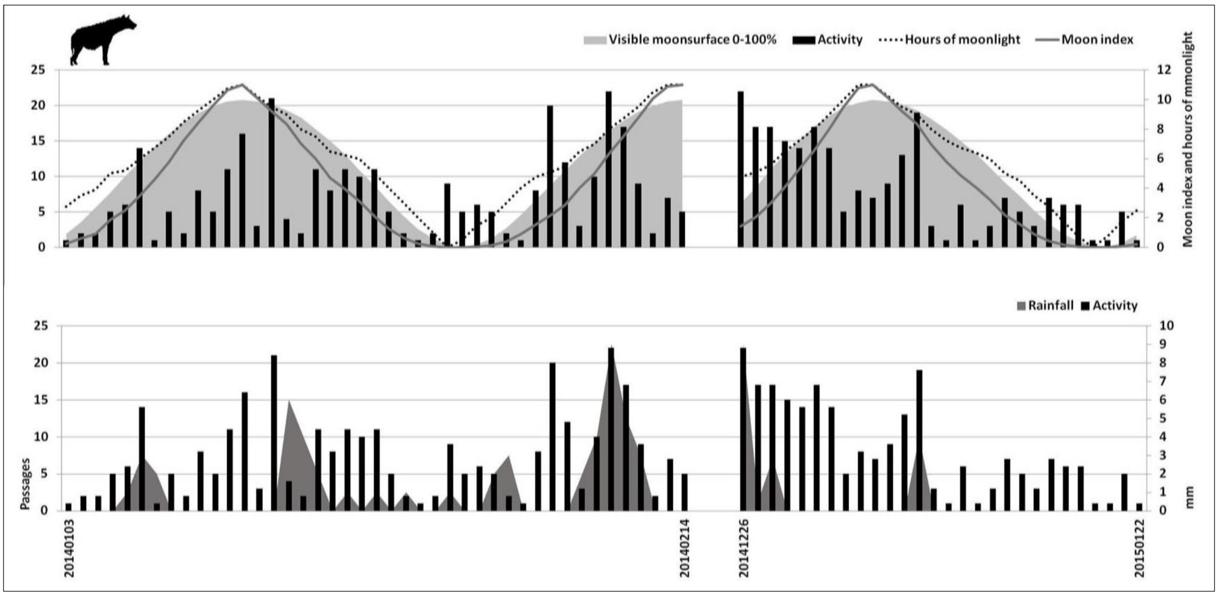

Figure 12 a.) Moonlight correlation and b.) rain correlation with spotted hyena activity at the corridors. Y-axis: total number of passages, x-axis: date, secondary y-axis: hours of moonlight (a) and mm rainfall (b).

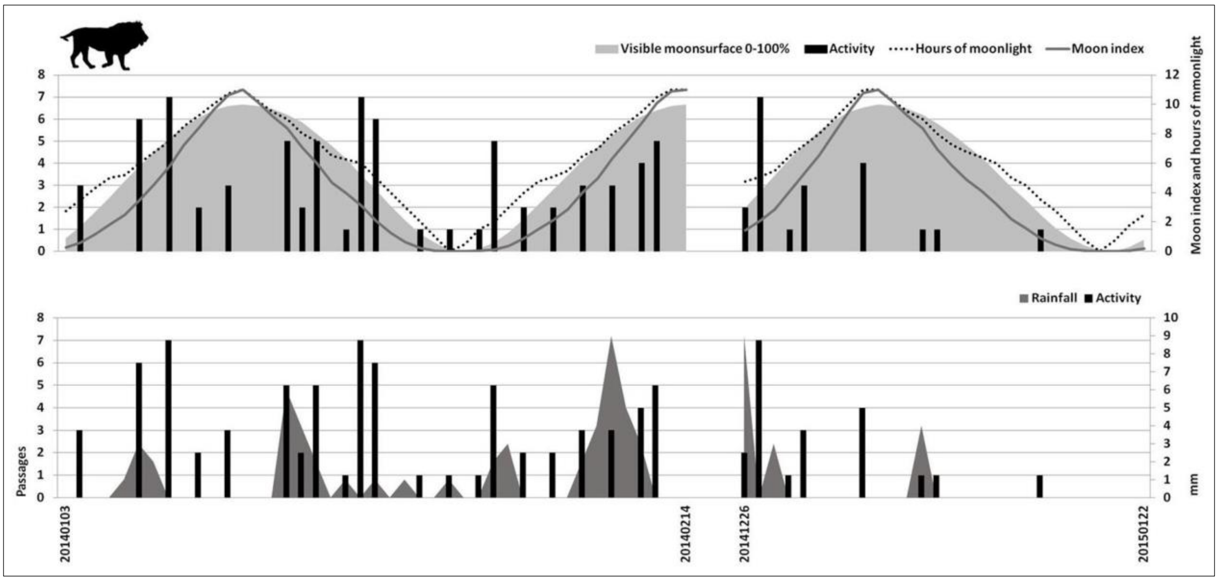

Figure 13a.) Moonlight correlation and b.) rain correlation with lion activity at the corridors. Y-axis: total number of passages, x-axis: date, secondary y-axis: hours of moonlight (a) and mm rainfall (b).

4. Discussion

This work investigated temporal movement patterns of lion and spotted hyena in a fenced conservation area. Another aim was to investigate how environmental variables impact on activity levels of these predators. My results showed that both species were nocturnal but with decreased activity around midnight. Lions and spotted hyenas showed very similar activity patterns. For spotted hyena I found no evidence that they migrate out of the conservancy in the evening or return in the morning why this hypothesis can be rejected. For lion I did not obtain enough data to neither strengthen nor reject this hypothesis. I found that the environmental variables tested had a positive effect on activity levels in spotted hyena but did not seem to be of high importance to lion activity. I collected data from a water trough and two wildlife corridors although obtained data volume from the water trough was too small to be tested statistically. The species composition differed between the corridors and the water trough. For example, I found a higher proportion of African wild dogs at the water trough. A low activity of wild dogs at the corridors compared to the trough, suggests that the conservancy is large enough to cater for these individuals' requirements. It is important to address, however, that the data quantity obtained from the water trough is very limited why this result should be interpreted with caution.

4.1 Daily activity rhythms

I confirmed that both lions and spotted hyenas in Ol Pejeta are mainly night active, as found in other studies (Elliott *et al.* 1977, Funston *et al.* 2001, Patterson *et al.* 2004, Fischhoff *et al.* 2007, Hayward and Hayward 2007, Hayward and Slotow 2009). Data from both the water trough and the corridors show the same patterns where both species exhibit high activity during dark hours but with a dip in activity around midnight. Similar patterns were found in Hayward and Slotow (2009) and also lions in Addo Elephant National Park, South Africa, showed crepuscular peaks around sunrise and sunset (Hayward and Hayward 2007). Hayward and Slotow (2009) suggest that nocturnal predators exhibit decreased activity at the darkest times of night due to visual limitations. If this hypothesis is true, predators should gain from brighter moonlight and we would obtain higher activity levels at brighter nights, e.g. nights with full moon. I found no such pattern for lions so this does not seem to be the case in my study. This hypothesis is also contrary to previous studies that found that the hunting success of lions was negatively influenced by moonlight (Van Orsdol 1984, Funston *et al.* 2001, Packer *et al.* 2011).

Lions and spotted hyenas in Ol Pejeta Conservancy show high proportion of overlapping activity patterns. A comparison between the hourly activity levels, however, shows that lions reduce their activity a few hours earlier than spotted hyenas. Additionally, spotted hyena showed a decrease in activity at the same time as lion showed an increase (hour 5). This could potentially reflect an incidence of temporal partitioning to minimize interference competition. Lions and spotted hyenas are dominant predators in Africa with similar diets (Hayward 2006) and it is possible that, to minimize the degree of competition, the spotted hyenas have adapted to the lions' activity patterns and are active at other times. It has been suggested that other species of Africa's large predator guild may become active in periods that limit their potential for interaction with lions (Hayward and Slotow 2009). In general however, both species showed similar activity levels which suggest that other factors are responsible for their daily activity rhythms. It is possible that the local predator densities are not high enough to motivate partition of activity times, which was suggested by Hayward and Hayward (2007), and at low densities, competitors can instead minimize chances of encountering through spatial partitioning of habitat. Why lions reduce their activity a few hours earlier than spotted hyenas could possibly be explained by different hunting techniques. Spotted hyenas are known to hunt successfully also in daylight and unlike lions, they rarely stalk and ambush their prey but rather sprint through the herd to scatter the prey, while looking for a weakened individual (Cooper 1990). Consequently, they are not likely depending on the camouflage of darkness to hunt successfully. Instead, spotted hyenas are thought to be nocturnal mainly because of their avoidance of high temperatures (Cooper 1990, Hayward and Hayward 2007). This could explain why the spotted hyenas are active also a few hours following dark hours.

Activity patterns may also alter over the year. Hayward and Hayward (2007) found that lions exhibited seasonal variations in activity patterns. Furthermore, the differences in activity between lions and spotted hyenas were suggested to be caused by temperature and by morphological limitations on hyenas that limited their activity during hot hours (Hayward and Hayward 2007). In turn, the level of influence on activity patterns caused by a parameter depends on the animal's ability to adapt to or cope with the given parameter. Spotted hyenas have, for example, been found to be sensitive towards high temperatures (Cooper 1990) why high temperatures could be expected to be more influential on their activity than on a species less sensitive. Consequently, weather parameters could be responsible for different activity rhythms between species.

Although environmental factors may affect predators directly, it may also act indirectly on the behavior of the predator. I suggest that the activity patterns of spotted hyenas and lions are influenced by feeding habits. Predator activity rhythms may also be depending on the activity of their prey. For instance, crepuscular activity peaks of the Eurasian lynx (*Lynx lynx*) have been shown to be due to prey activity patterns rather than light conditions (Heurich *et al.* 2014). Similarly, jaguars and pumas follow the nocturnal activity of their main prey (Harmsen *et al.* 2011) and black bears shift their activity patterns during salmon spawning run (Klinka and Reimchen 2009). For their prey, however, activity occasionally varied with moon phase (Harmsen *et al*. 2011). The spotted hyena is an opportunistic predator known to adapt to temporal variations in prey abundance and seasonally changing prey resources (Cooper *et al.* 1999, Holekamp *et al.* 1997, Hayward 2006). Consequently, this may influence their activity rhythm which further highlights the complexity of this context. However, neither prey availability nor prey activity was tested in my study. The study was conducted over a limited time range and all data was collected during dry season. For this reason, obtained data did not allow me to test for variations between seasons but it is possible that we would find different results during other times of the year.

I hypothesized that the predators migrate out of the conservancy in the evenings and return in the morning. This hypothesis was based on the assumption that the predators spend the majority of their time in the conservancy because of low persecution risk, but hunt outside due to higher prey availability. Both lions and spotted hyenas are known to attack livestock within bomas at night (Ogada *et al*. 2003, Kolowski and Holekamp 2006) why livestock held outside the conservancy could be a factor driving the activity of the predators studied. Depredation increases when natural prey decreases (Kolowski and Holekamp 2006) and for the time of my study, prey densities are generally low (Cooper *et al.* 1999). The t-test failed to show any significant difference in direction of movements between early night and late night for spotted hyena, hence this hypothesis can be rejected for spotted hyena. For lion I did not obtain sufficient data to neither reject nor strengthen this hypothesis. However, I found a pattern of high out-movement during hours 21-2 and a substantial peak in in-movement at hours 5-6. This suggests that my hypothesis could be true for lion which is further strengthened by the positive correlation between lion activity and rain, as livestock depredation frequency by predators has been found positively influenced by rain (Patterson *et al.* 2004, Woodroffe and Frank 2005, Kolowski and Holekamp 2006). The lack of differences in direction of movement between early and late night for spotted hyena suggests that the animals leave the conservancy for longer periods than one night. For example, hyenas can cover vast distances in a single night (Kolowski *et al.* 2007) and Hofer and East (1993) demonstrated that spotted hyenas in the Serengeti regularly undertake long extraterritorial forage trips to reach migratory prey. Furthermore, activity patterns are results of a range of selection forces why other movement driving factors than food dispersion may influence activity levels in lion and spotted hyena and hence, be responsible for my results. Such factors could be for example exploiting or partner searching (Barnard 2004). These activities are expected to require longer periods outside of the borders than a single night.

4.2 Weather data correlation

Moonlight does not seem to be a key requirement for lion activity in this study. This is contrary to my predictions and raises the question of what drives the lion activity in Ol Pejeta. Increased moonlight may enable predators to detect and catch prey more easily but good light conditions do at the same time increase the risk of being detected by prey. Lions use an ambush hunting technique and in bright moonlight they may be less likely to stalk or position themselves successfully before an attack. For this reason, I hypothesized a negative correlation between moonlight intensity and activity in lions. However, the influence of moonlight on lion activity varies considerably between study sites. For example, studies of nocturnal foraging in South Africa and Uganda have shown that lion hunting success increases on dark nights when the moon is absent or obscured by clouds (Van Orsdol 1984, Funston *et al*. 2001). Packer *et al.* (2011) similarly found that lions in Tanzania are less successful in obtaining wildlife prey during moonlit nights while Cozzi *et al.* (2012) found the nocturnal activity of lions and hyenas unaffected by moonlight and remained constant over the lunar cycle. These differences, however, could be explained as local adaptations. For example, the influence of moonlight on hunting success may alter due to other environmental related parameters such as vegetation cover and structure (Elliott *et al*. 1977, Funston *et al*. 2001). In areas with high vegetation cover the level of moonlight could be unimportant as the vegetation offers enough coverage even on moonlit nights. Occasionally, bushier habitat even allows lions to hunt during the day. Vegetation cover was not evaluated in my study and could possibly have influenced the results as the study area is rather bushy with few open grass plains. It is also important to address that my results of moonlight intensity correlation does not take cloud cover into account which we would expect to be of great importance as cloud cover reduces available moonlight. This leaves the correlation between activity and light conditions not to be fully tested in my study. The obtained data quantity is very limited, however, why this result should be interpreted with caution and it is also possible that there was no relationship between lion activity and moonlight because I did not obtain sufficient data. I found a positive correlation between moonlight and activity in spotted hyena. This is contrary to my predictions where I expected spotted hyena to show a weaker correlation than lion between weather/moon data and activity, due to competitive limitations, and suggests that spotted hyena activity rhythms are regulated by other factors than competition. The correlation with moonlight and activity levels has been found to alter between species using different hunting techniques (Cozzi *et al.* 2012). As described above, spotted hyenas do not depend on the camouflage of darkness to hunt successfully (Cooper 1990). This suggests that spotted hyenas would benefit from good light conditions which strengthen my results.

I found a positive correlation between rain and activity in spotted hyena and I found a tendency towards a positive correlation between rain and activity in lions. This is in accordance with other studies on terrestrial predators. Beltran and Delibes (1994) found that Iberian lynxes (*Lynx pardinus*) increased their diurnal movement rate during rain and Dietz (1984) found that maned wolves (*Chrysocyon brachyurus*) in Brazil showed greater activity during rainy and cloudy days than on sunny days. Also black bears have, although less active during rain, shown increased activity directly after rainfall (Garshelis and Pelton

1980). During drought, herbivores aggregate around few available water resources but during rainfall they are more scattered (Western 1975, Redfern *et al*. 2003). Consequently, finding prey requires higher activity during these conditions. Another potential explanation for this pattern could be that when prey is more difficult to find predators of Ol Pejeta switch to livestock hunting. This is further strengthened by several studies in Africa. Kolowski and Holekamp (2006) found that monthly livestock depredation frequency was correlated positively with rainfall, in a study on predators in Maasai Mara National Reserve. Other studies support that livestock depredation is positively influenced by rain (Patterson *et al*. 2004, Woodroffe and Frank 2005, Van Bommel *et al.* 2007, Kissui 2008). This trend is suggested to be driven by seasonal variation in local availability of natural prey. Kays and Patterson (2002) found that during droughts, lions in Tsavo spend most of their time near the few dependable water sources where prey was aggregated. Similarly, Valeix *et al*. (2010) found that lions in Zimbabwe selected for areas close to waterholes. This further suggests a negative relationship between rainfall and activity at the water trough. Unfortunately, I did not obtain sufficient data to evaluate this relationship in my study. However, there may be an alternative explanation to why predators attack livestock during rain. Both lions and spotted hyenas are known to attack livestock within bomas at night (Ogada *et al.* 2003, Patterson *et al*. 2004, Kolowski and Holekamp 2006) and it is expected that heavy rainfall causes noise, especially on tin roofs, which could make both livestock and herders inattentive and thus an easy prey. However, no studies have been found that confirm this hypothesis.

Activity patterns are results of a combination of several selection forces, and additionally, each variable is influenced by a range of underlying variables why the influence of each variable is difficult to predict. Understanding the relationships between ecological factors and temporal variation in predator activity at the conservancy borders allow us to better assess the risk of conflict with local people during different conditions. An improved knowledge about the activity patterns and behavior of the two large carnivores in this study allow a better understanding of their requirements and is therefore relevant to management efforts. The obtained results can help to predict predator movement patterns and thus contribute to modifications in local husbandry and guarding practices. My results indicate that livestock conflict in the Ol Pejeta area could be mitigated by confining livestock at night and during bad weather when predator activities are high.

In conclusion, both lions and spotted hyenas in Ol Pejeta are mainly night active as has been found in most other studies. Lions and spotted hyenas in Ol Pejeta Conservancy exhibit very similar activity patterns. The differences in activity between the two species could potentially result from intra-guild competition. However, it is more likely that the activity patterns in both species are regulated by other factors such as prey activities or hunting techniques. Hunting success is an essential factor affecting the variation in predator activity but movements could also be expected due to emigration and dispersal of subadults, immigration of new individuals as well as partner searching or exploiting. The numbers of lions and spotted hyenas in Ol Pejeta are fairly stable but my results suggest that the animals leave the conservancy not only to hunt but also for such activities that are expected to require longer periods outside of the borders than a single night. Environmental factors may act directly or indirectly on the behavior of the predator and different hunting techniques may explain the different results in weather/moon data correlation between the two species. For the study I have not evaluated attacks on livestock in the area but it is possible that both lions and spotted hyenas attack livestock outside the conservation area. My results further imply that predators in Ol Pejeta are more likely to attack livestock at night and during bad weather. Predator activity relationships vary widely between sites and must be evaluated locally. Although information on activity rhythms of the lion and spotted hyena has been gathered, additional research is needed to completely explain their activity patterns and relationship with environmental data.

Sources of error

There are several factors that could have influenced the observed data and affected the reliability of the results. Firstly, I assume that the images provide a reliable index of activity of the occurred species in the study area. It is possible that the activity at the corridors do not reflect the activity within the conservancy and thus providing misleading numbers. Secondly, motion-activated cameras can sometimes alternate animal behavior (Gibeau and McTavish 2009). Passing animal may get disrupted or scared by the camera flash and it is possible that the camera may change the animal's movement direction. It is also possible that the cameras failed to cover all passages or that I failed to identify animals when reading the photographs, in particular during nighttime when the flash range was sometimes very limited. In future research, other factors influencing activity, such as prey activity and prey abundance, have to be taken into consideration and when quantifying light availability, also taking into account cloud cover would be beneficial. On further studies on carnivore–livestock interactions and conflict mitigation, simultaneous studies of attacks on livestock would be informative as well as identification of photographed individuals to determine the number of active predators.

Acknowledgements

I would like to thank my supervisor Dr Jens Jung for his support and making this project possible. Field data was collected together with SLU students Henriette Sernert and Heidi Rautiainen. For the help of collecting field data, I would like to thank field assistants Caleb Ledama and Daniel Naurori. I also would like to thank the Swedish University of Agricultural Sciences (SLU) and the Swedish International Development Cooperation Agency (SIDA) for providing grants for this study as well as Ol Pejeta Conservancy for the permission to work in the area.

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APPENDIX A. Protocol for instantaneous recordings

INSTANTANIOUS

This form is used for instantaneous recordings. Behavioural events are recorded in 10 min intervals.

START TIME DATE VEGETATION OBSERVER

Time	Weather (S/C/SC)	Species	Group Size	Standing	Lying	Walking	Running	Sprint	Foraging	Vigilance	Social	Drinking	Comment

APPENDIX B. Protocol for continuous recordings

CONTINUOUS

This form is used for continuous recordings. Behavioural events are recorded on one hour intervals.

START TIME DATE VEGETATION OBSERVER

Species	7.00	7.00	7.00	8.00	8.00	8.00	9.00	9.00	9.00	10.00	10.00	10.00	Comment
	Drink	Jump	Sprint	Drink	Jump	Sprint	Drink	Jump	Sprint	Drink	Jump	Sprint	

APPENDIX C. Area map for hourly recordings

The water trough is visible as a black dot and the car was located 250 meters southeast of the trough.

MAP

This map is used on one hour intervals. Note position of animal groups (x), species and group size (#) within study area.

DATE OBSERVER:

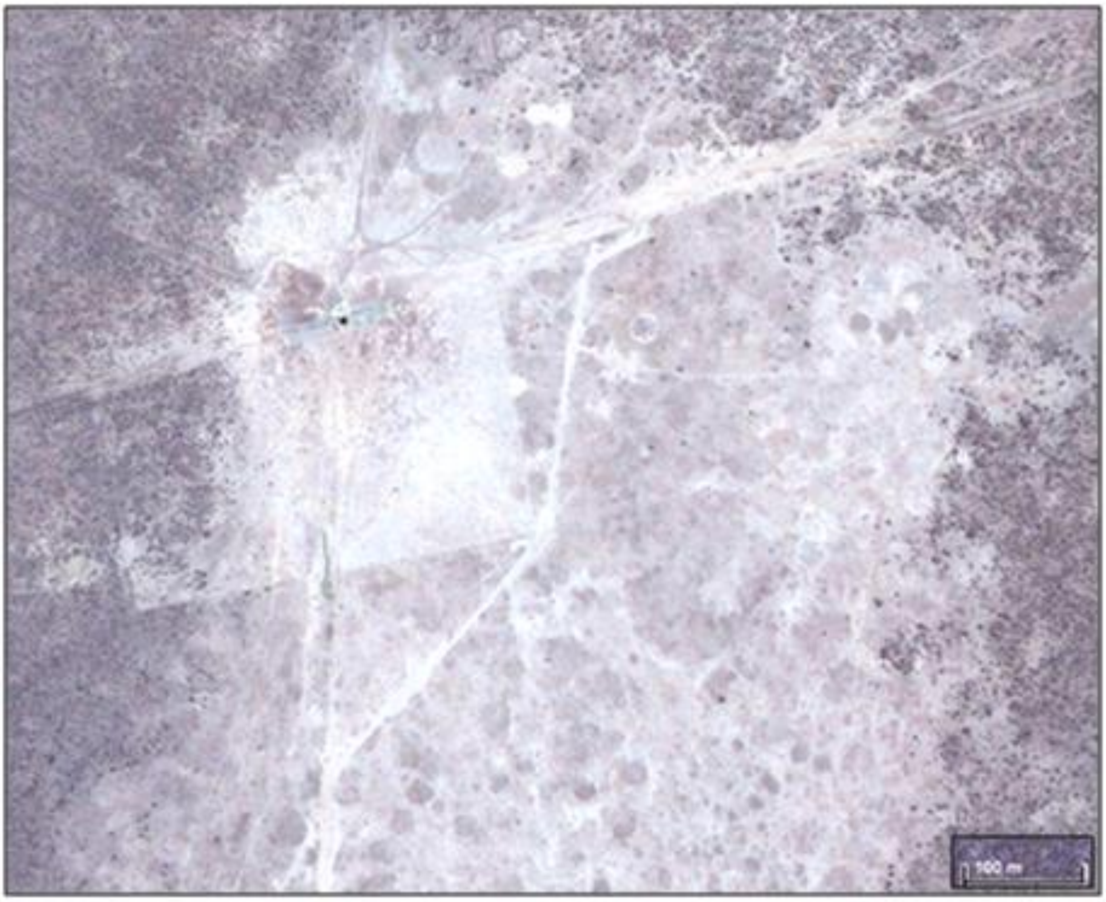
Time: ____________________

Weather (S/C/SC/R): ____________________

Comment: ____________________

____

____



APPENDIX D. Protocol for predator presence

PREDATOR PRESENCE (lion, hyena, cheetah, leopard, wild dog)

This form is used when predator is present. Record behaviour in predator and behaviour in prey in comment column (free text). Additionally, fill in map with predator location and movement over study area and take close-up pictures if possible.

DATE OBSERVER

Time	Weather (S/C/SC)	Location (Bush or Open area)	Species	Group Size	Standing	Lying	Walking	Running	Hunting	Social	Drinking	Comment

APPENDIX E. Ethogram for recorded behavior

BEHAVIOR	DEFINITION
Standing	Standing still (not grazing or being social etc)
Lying	Belly, side or back touching ground
Walking	Moving forward, not running or sprinting
Running	Any running except sprint
Sprint	Running away from potential predators (not collected for predators)
Foraging (herbivores)	Head down, eating on a bush
Foraging (predators)	Walking zigzag, stalking, hunting, eating
Vigilance	Looking around, moving ears, sudden jumping (not collected for predators)
Social behavior	Body contact (grooming, playing, fighting)
Drinking	Head down in the water

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