Movement patterns of lions (*Panthera leo*) in an East African conservancy -Avoiding conflict

Rörelsemönster hos lejon (Panthera leo) i ett östafrikanskt reservat -Att undvika konflikt

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Abstract

The conflict between wildlife, particularly predators, and humans is one of the main reasons for the rapid decline of predator populations. In Kenya, lions (*Panthera leo*) are a major threat to livestock and humans living around the wildlife conservancies. Ol Pejeta, in Laikipia County, is such a conservancy where three wildlife corridors allows the animals to move freely between the conservancy and adjacent areas. Knowledge about when, and why, the lions move in and out of Ol Pejeta could help understanding how to better manage the population and give information to people living in the area of when the risk of lion depredation might be higher. To investigate the activity patterns of the lions in Ol Pejeta, I compared the passages at the corridors with environmental data such as rain period and moon phase. I also looked at how the lions distributed their activity during the day to see at what time they were most active. Finally I compared the number of passages with gender distribution to see if there was a difference between males and females. The results showed that there was no difference in activity between moon phases but a high significance between rain periods where there was a higher activity during the driest period. I also found that the lions were active right after sunset all the way to sunrise with a peak between 19.00 pm to 20.00 pm, and all passages out of the conservancy occurred during nighttime. There was no difference in passages between males and females. Due to these results, I suggest that the reason for the activity outside the conservancy is due to hunting and that the lions might be hunting for different types of prey during different times of the month which could further help farmers in the area, and the monitoring unit at Ol Pejeta, to know when there might be a higher risk for depredation.

Sammanfattning

Konflikten mellan vilda djur, särskilt predatorer, och människor är en av de huvudsakliga anledningarna till den hastiga minskningen av rovdjurspopulationer. I Kenya är lejon (*Panthera leo*) ett stort hot emot boskap och människor som bor i närheten av naturreservat. Ol Pejeta, i Laikipias län, är ett sådant naturreservat där tre korridorer tillåter djuren att röra sig fritt emellan Ol Pejeta och kringliggande områden. Kunskap om när, och varför, lejonen rör sig in och ut ur Ol Pejeta skulle kunna öka förståelsen kring hur man bättre kan hantera populationen och ge information till människor som lever i området om när det kan vara större risk för lejonpredation. För att undersöka lejonens aktivitetsmönster så jämförde jag antalet passager vid korridorerna med miljödata så som regnperiod och månfas. Jag undersökte också hur lejonen distribuerade sin aktivitet under dagen för att se under vilken tid på dygnet de var som mest aktiva. Slutligen så jämförde jag antalet passager med könsfördelning för att se om det fanns en skillnad mellan honor och hanar. Resultaten visade att det inte fanns någon skillnad mellan aktivitet och månfas men det fanns en stor skillnad mellan regnperioder där den högsta aktiviteten skedde under den torraste perioden. Jag fann också att lejonen var aktiva direkt efter solnedgång, ända fram till soluppgång, med en topp runt klockan 21.00, och alla passager ut ur reservatet skedde under natten. Det fanns ingen skillnad mellan passager och kön. På grund av dessa resultat

så föreslår jag att anledningen till lejonens aktivitet utanför resrevatet är på grund av jakt och att lejonen skulle kunna jaga olika typer av byten vid olika tider på månaden vilket skulle kunna hjälpa människorna som bor i området, och övervakningsenheten på Ol Pejeta, att veta när risken för predation kan vara särskilt hög.

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1.0 Introduction

Large predators can work as an important tool in conservation management as they can increase species richness, promote resources for other trophic levels and increase ecosystem productivity (Sergio *et al*. 2008). To improve the protection of such animals, and facilitate the farmers and local people in conflict with them, understanding their movement patterns, why and when they move, can play an essential role in management.

It is known that all carnivores adapt their home range size after metabolic needs and body size and that there is a positive correlation between these two (Gittleman & Harvey, 1981). The estimation of the actual size of the lion's (*Panthera leo*) home range seem to vary between researchers. According to Gittleman & Harvey (1981) the home range size of lions is about 240 km^2 whereas Woodroffe and Ginsberg (1998) argue that it is closer to 120 km^2 (although this number refers to the mean area used by adult females). Knowledge about the circumstances under which large predators move in different areas is important for the ongoing conflict between wildlife and livestock owners. Livestock attacks by predators are common and often result in fear and persecution of these predators (Michalski *et al*. 2006). This conflict is the main reason for the large decline in predator populations (Patterson *et al*. 2004) and mitigation, and understanding of depredation on livestock is important for facilitating coexistence in these areas.

1.1 Predator- prey interactions and hunting behaviour

When analyzing the movement patterns of predators it is important to consider the movement patterns of their prey. Prey animals alter their behaviour and habitat preference in relation to the behaviour of the predator, if the predator is absent then the prey is more likely to be active and vice versa (Fishhoff *et al.* 2007). Since lions are mostly nocturnal, the moon phase can also be an important factor in their predation success (Orsdol, 1984; Packer *et al*. 2011) in the sense that moon phases closer to the full moon will generate more moonlight and vice versa (given that cloudiness does not affect). Herbivorous prey often avoid the moonlight since they are more easily detected during these circumstances, which means that they decrease their activity (Griffin *et al*. 2005). During periods with more moonlight, the lions' hunting success decreases which is probably also due to the fact that the lions become more visible to their prey (Orsdol, 1984; Packer *et al*. 2011).

The expansion of human settlements have caused a drastic decline in the lion populations, and may also cause problems when adjacent to national reserves (Patterson *et al*. 2004). In these scenarios, the lions get closer to the people and theirby their livestock, making the risk of depredation and interactions between lions and humans increase (Patterson *et al*. 2004). Depredation in these areas is inevitable as a lot of native wildlife has been replaced in favor of livestock (Patterson *et al*. 2004). Depredation on cattle is especially common for lions and hyenas as prey selection is positively correlated to body size, and smaller predators such as cheetahs select for smaller prey like sheep and goats (Patterson *et al*. 2004). Another factor affecting prey availability are the wet seasons. During this time, many migratory animals spend more time in the plains (large open areas) than during dry periods as there is moore vegetation around and they can graze over larger regions (Grant *et al*. 2005). Even though not all herbivores on the savannah are migratory, this could mean that depredation on livestock is higher during dry periods when there might be fewer animal species on the plains. Drought, rain, human activities and other aspects are consequently important to take into account when planning for management as climatic factors vary greatly between areas and can affect prey availability (Patterson *et al*. 2004).

Hunting by lions is mainly done by the young females (Scheel & Packer, 1991) and due to this fact it would make sense to assume that most of the predation activity outside the conservancy is done by females. This could also mean that females are the ones spending most time in the adjacent areas over all, should the behaviour be due to hunting. As lions are, to a large extent, nocturnal they mostly hunt by night, actively stalking their prey, when the darkness shields them and allows them to hunt in open areas (Fishhoff *et al*. 2007). When they do hunt during the day, they do so in bushy areas where the vegetation can conceal them (Elliot *et al*. 1977). Grant *et al*. (2005) found that lions within Serengeti national park, Tanzania, selected areas where prey were easier to catch rather than areas where prey densities were highest. I think that this might suggest that unmonitored livestock may face a greater risk of being attacked as livestock has proven to be an easy target for lions (Kolowski & Holekamp, 2006). When lions hunt on the Serengeti plains, Grant *et al*. (2005) found that erosion embankments, like river banks and animal paths, and also proximity to water was important for the lions. The importance of water is not only dependent on water as a resource, but also the fact that prey species dwell around water holes and that vegetation around these areas can cover the lions and minimize detection (Grant *et al*. 2005).

1.2 Social behaviour and competition

Mosser & Packer (2009) states that lion prides usually consists of about 1-21 adult females, their offspring and a temporary group of 1-9 adult males. They further claim that the pride is a stable social unit, although there is a fission-fusion composition where some individuals form smaller subgroups and where males will not stay permanently as they leave the pride at three to four years of age. The sizes of these subgroups can play a big role in intergroup competition when there are limiting resources (Mosser & Packer, 2009). They also found that female lions are more likely to move further away from the territory center when the group is small (2-3 adult females). This could be due to a decrease in female reproductive success and an increase in female mortality when the larger groups have an advantage in intergroup competition (Mosser & Packer, 2009; Spong, 2002). The lion population in the study area currently consists of 72 lions, with five known prides (Ol

Pejeta conservancy, 2016), and it is possible that there are several subgroups with high competition. Some of the individuals may need to move further away from the territory center in order to feed or mate.

The aim of this study is to understand the underlying behaviors of the activity outside the conservancy and under which circumstances the lions leave the area. Attacks on livestock occur all over the conservancy but especially outside the borders as livestock usually are less guarded there (Personal message: Dr Jens Jung, Uppsala University, 5-6-2017). Wheather livestock occur in enclosures or not have proven not to be of importance, however, unguarded livestock has a higher risk of being attacked compared to unguarded livestock (Ogada *et al*., 2003). The primary questions, considering previous research and knowledge about lion behaviour are:

I. Do the lions move in and out of the conservancy more during nighttime?
II. Is there a difference in activity between different moon phases?
III. Does female lions move in and out of the conservancy more than male lions?

2.0 Method

2.1 Study area

The study took place in Ol Pejeta conservancy, in Laikipia County, Kenya. The size of the area is 360 km2 (Ol Pejeta Conservancy, 2016), it primarily consists of open bushland (fig. 1) and has two rain seasons per year. The first one ranges from late April to early June and the second one ranges from October to December.

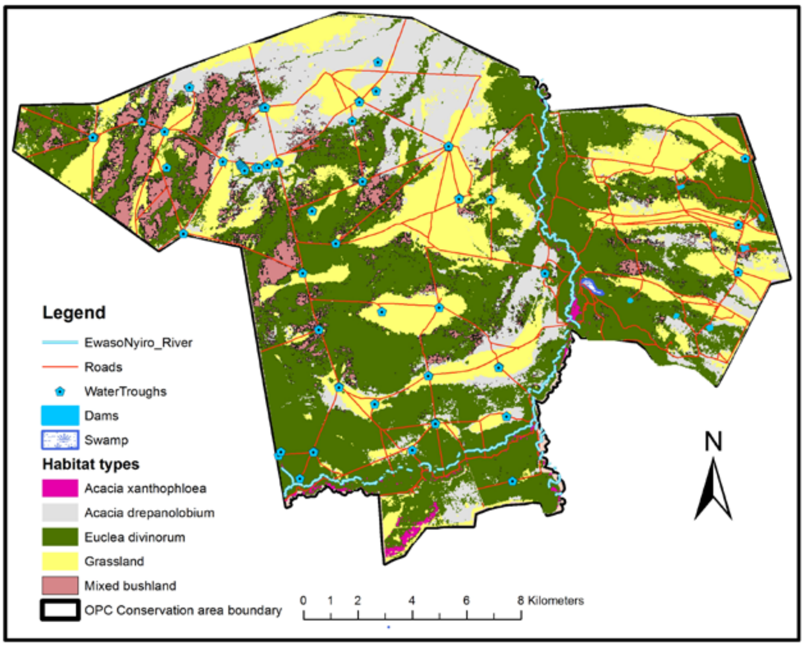

Figure 1. Map over Ol Pejeta conservancy with habitat types. Courtesy of Ol Pejeta conservancy

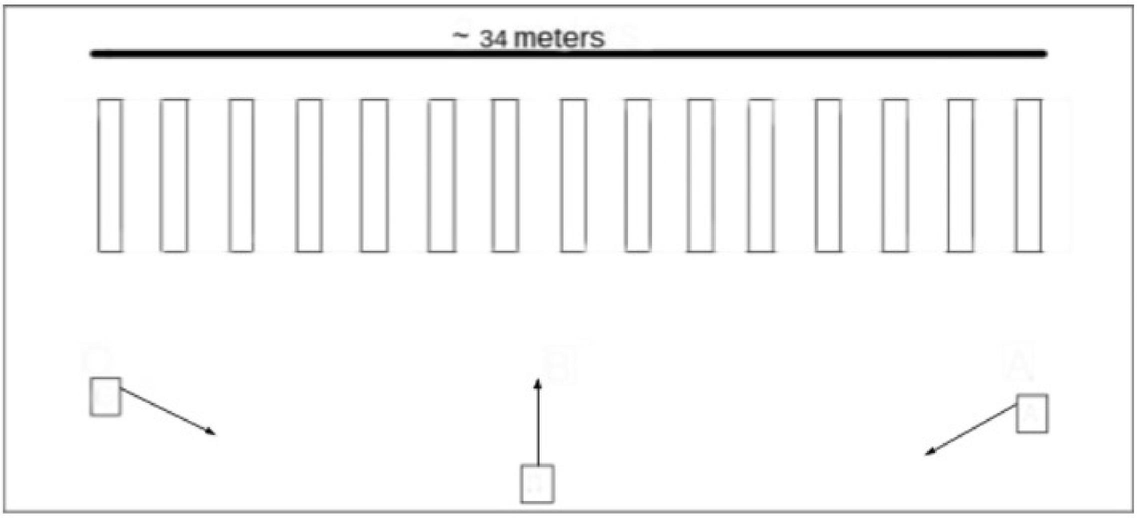

Figure 2. The position of the cameras in relation to the corridors

The reserve has three openings, so called corridors, all facing north in the conservancy in the otherwise electrical fenced area. The corridors consists of wooden pillars that reaches about one meter above the ground with 55 cm between them. The length of the corridors differ, corridor one is about 183 meters long and corridor two and three is about 34 meters long. Each corridor has three cameras located along it, one on each end facing into the conservancy and one more centered facing out of the conservancy, to maximize detection of animal movement (fig. 2). Because of the lack of carnivore activity in corridor 1, this corridor was excluded from the study. Even though Ol Pejeta mainly consists of wildlife habitats, large areas are used for ranching and tourism why a lot of livestock also inhabits the conservancy. A lot of the livestock husbandry inside Ol Pejeta is traditional where the animals are guarded during the day and is kept in bomas during the night. This can make it harder for predators to attack the livestock inside the conservancy compared to outside.

2.2 Data collection and sorting

Using Reconyx HC600 Hyperfire motion-activated cameras, animals were photographed whenever they passed the cameras. Each picture was taken with about two second’s interval, dividing the pictures into sequences of three or five. This means that, for example, between picture one and five, within the same sequence, there was about ten seconds. The same individual could therefore be shown through many sequences, depending on how long it stayed or moved in front of the camera. However, the interval between pictures differed slightly between cameras as a result of installation, as did the number of pictures within each sequence. The silent period was set between 0-5 seconds depending on the camera which means that it took zero to five seconds for the camera to restart a sequence, in case there were more than one animal passing by. Each picture showed corridor number, camera number, date, time of day, sequence (1-5/5 or 1-3/3), temperature and moon phase. The detection range of the cameras was different depending on if it was night or day, with about 24 meters during day and 18 meters during night, using a flash. The camera's batteries were supposed to be collected every Friday while the memory cards were uploaded to a computer. This was to make sure that the batteries were changed with an even interval to make sure that the quality of the pictures were constant throughout the study period. However, there were a few instances where the batteries were not changed every week, for example during the Christmas holidays when they were first changed after two weeks. Considering the slight inconsistency in battery change, the pictures that had been taken on Thursdays, the day before the supposed battery change, had to be overlooked. This was to make sure that the quality of all pictures stayed the same. Once collected from the cameras, the pictures were roughly sorted into different species folders by personnel on sight. The folders included: aardvarks, baboons, birds, buffalos, cheetahs, elands, elephants, giraffes, Grant’s gazelle, human activity (including humans, vehicles, dogs, cattle etc.), impalas, interesting pictures (such as fights or other interactions between species), lions, jackals, leopards, rare species, spotted hyenas, striped hyenas, Thomson's gazelle, unknown (including pictures showing only eyes), warthogs, wild dogs, and zebras. The sorted images were then uploaded to Dropbox into folders sorted by date. However, only the species relevant for the study was uploaded. Each Dropbox folder contained pictures taken during one week. These folders were in turn divided into corridor, camera and finally species, to facilitate the processing of the pictures.

Using the information from the pictures on Dropbox, each individual lion was recorded as a passage using Google Sheets. Each passage was given information from the picture about the image number, corridor number, camera number, date, sex of the individual, age class of the individual (cub, sub adult, adult), whether the individual was going in, out or along the corridor, group size, group ID, moon phase (1-3), the time of rise and set of the moon and temperature for that specific date (min, max and mean).

A group was defined as more than one animal passing the cameras within five minutes after the previous individual had passed. In this case each animal was given a separate passage number but the same group ID. To estimate whether the animal was going in, out or along the corridor, the angle and the positioning of the camera was used (fig. 3).

Figure 3. This lion is walking in to the conservancy based on the position and the angle of the camera

Each camera was installed with a 45 degree angle. This way, the direction that the lion walked in could be used to assess where it was going. Using the website Weatherunderground.com, historical moon phase data could be obtained for all of the dates included in the study. The moon was divided into three phases by categorizing the illuminated percentage. Phase 1 was defined as 0-33 %, phase 2 as 34-66 % and phase 3 as 67-100 %. If a variable was unknown, for example sex or age, this was noted in the Google Sheet. Information was also added for each day where there was no passage at all in order to calculate the average number of passages for moon phase and month. In this case only the date, moon phase (1-3 and percent) and temperature was added as these variables were still needed in the analysis. On dates that lacked pictures due to low camera performance I noted N/A in the Google Sheet to clarify that there were pictures lacking due to technical difficulties. In addition to the information from the cameras and the historical moon phase data, historical rain data was obtained from two weather stations at Ol Pejeta. This rain data was then categorized into the amount of rain that had fallen 7, 30 and 90 days before, on every date. These three variables were divided into three new categories, 1, 2 and 3, by sorting the data from the smallest to the highest value and dividing it into three equally large parts. This was done so that it would be easier to analyze the relationship between number of passages and amount of rain. Category 1 had the least amount of rain, category 2 had an intermediate amount and category 3 had the largest amount of rain. This variable will from hereon be called rainfall. This study was conducted using 12 months of data, from June 1 2015 until May 31 2016.

2.3 Statistical analysis

I conducted descriptive statistical analyses using Microsoft Office Excel 2013 and Minitab 17 statistical software. All analyses were made irrespective of year and corridor. $P \leq 0.05$ was the accepted value of significance for all tests. Activity was analyzed as number of passages, where one passage corresponded to one individual. An Anova was used to calculate any differences between passages and grouped variables such as rain period, moon phase and gender. A two sample t-test was used to see where the difference was between each group when the result was significant. Some variables, such as temperature, were excluded from the analysis of this study as they did not relate to the concerned questions, although they were still put in in order to be potentially used for future studies.

3.0 Results

A total of 479 passages were recorded during a twelve month period. When comparing passages per day for moon phase 1-3, independent of year and corridor, there was no significant difference ($p=0.752$) (fig. 4).

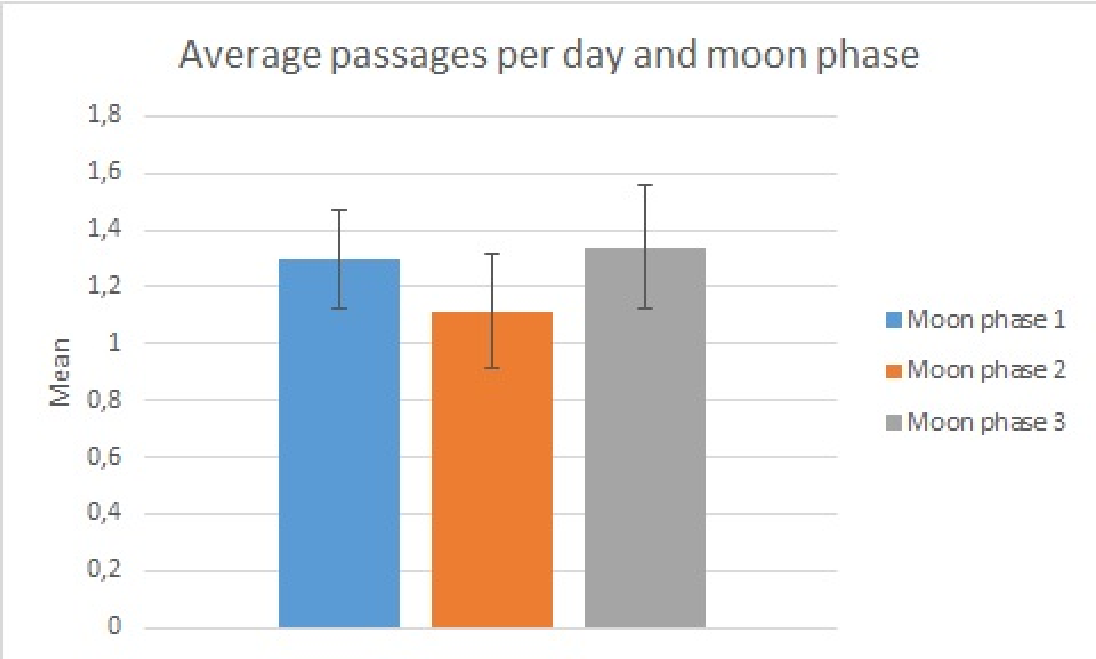

Figure 4. The mean number ± SE of passages per day and moon phase

There was a statistical tendency when comparing passages per month (p=0.08), although there was a relatively high variation in passages between months. When looking at the number of in and out passages per moon phase (fig. 5) there was no significant difference between out passages (p=0.0) and in passages (p=0.84) between the moon phases.

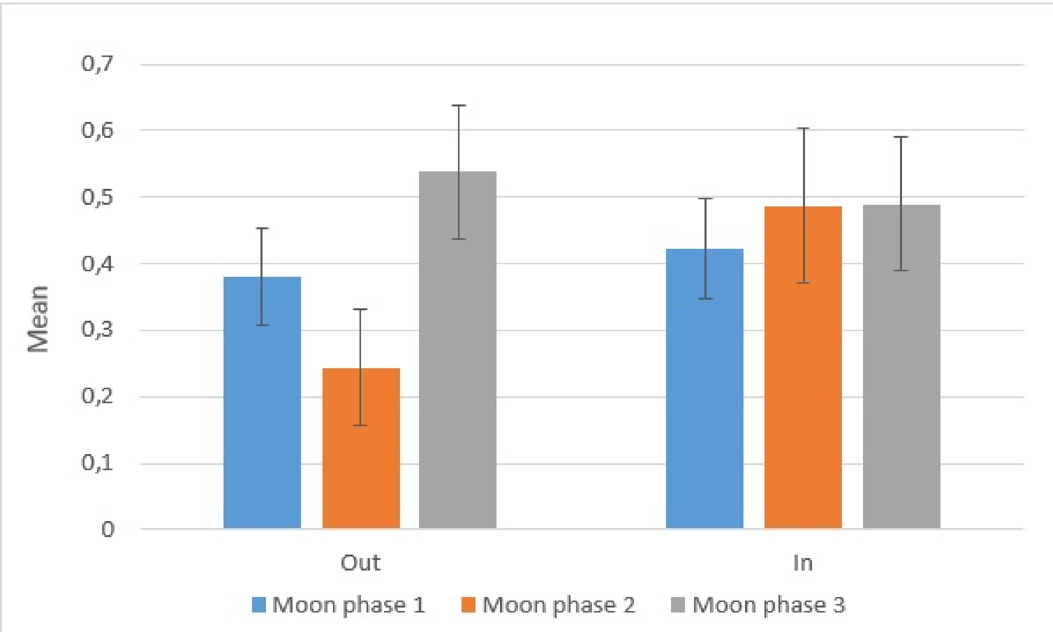

Figure 5. The mean number ± SE of in and out passages per day and moon phase

When dividing the passages per month by sex, there was no significant difference in activity between males and females (fig. 6). The number of unknown individuals is regrettably quite high. There was a significant difference between the distribution of sex ($p=0.04$), however not between males and females but between males/unknown ($t = 2.49$, $p = 0.02$, $df = 11$) and females/unknown ($t = 2.71$, $p = 0.02$, $df = 11$).

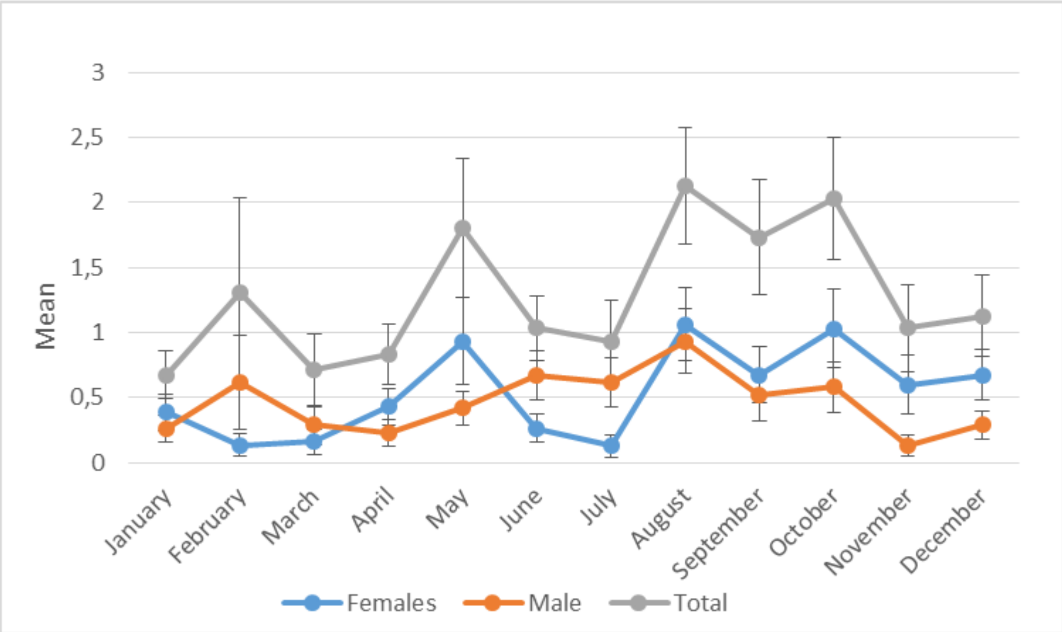

Figure 6. The mean number ±SE of passages per day and sex.

Looking at the sum of passages for each hour, there is a clear nocturnal pattern (fig. 7). Based on my own observations in Ol Pejeta, it is completely dark from 19.00 pm to 07.00 am. Considering the hours of darkness, over 94 % of all the passages occurred during the dark hours.

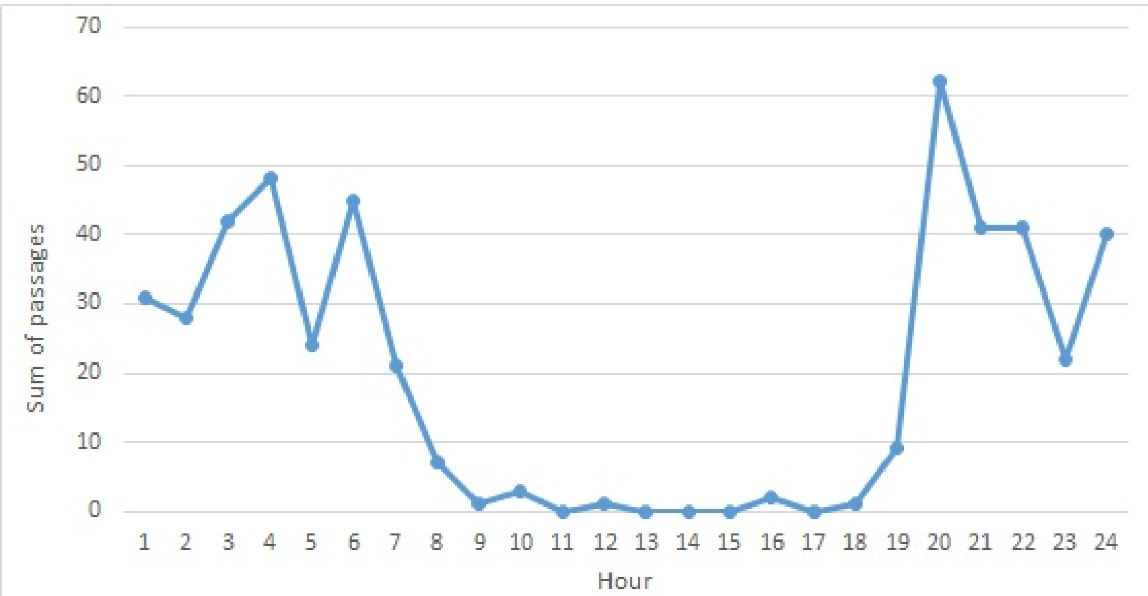

Figure 7. The sum of passages per hour

Also, looking at the number of in and out passages per hour there is a clear pattern showing that there were almost no passages at all during daytime and the few that did occur all happened during the day (p=<0.05) (fig. 8).

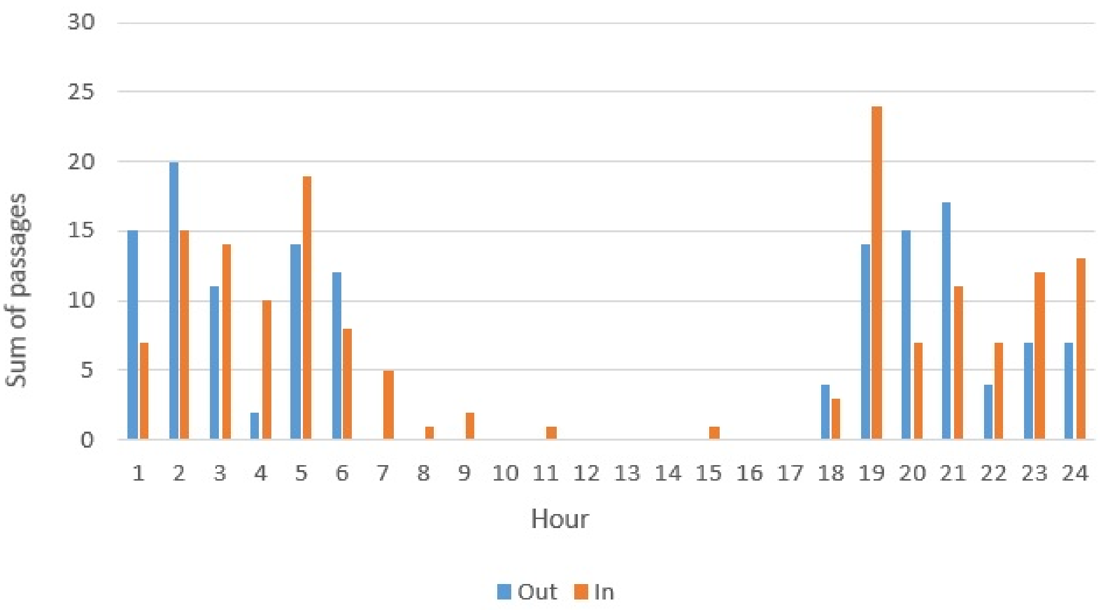

Figure 8. The sum of in and out passages per hour

As moon phase and month did not have any significant impact on the number of passages, I compared passages to rainfall categories which proved to be highly significant when looking at rainfall that had fallen 90 days before (p=0.004). There was a clear pattern between period 1 in relation to 2 and 3 (where 1 had the lowest amount of rain and three had the highest amount) (fig. 9), showing that there was a higher activity during rain period 1. There was no significant result when comparing passages to rainfall that had fallen 7 or 30 days before.

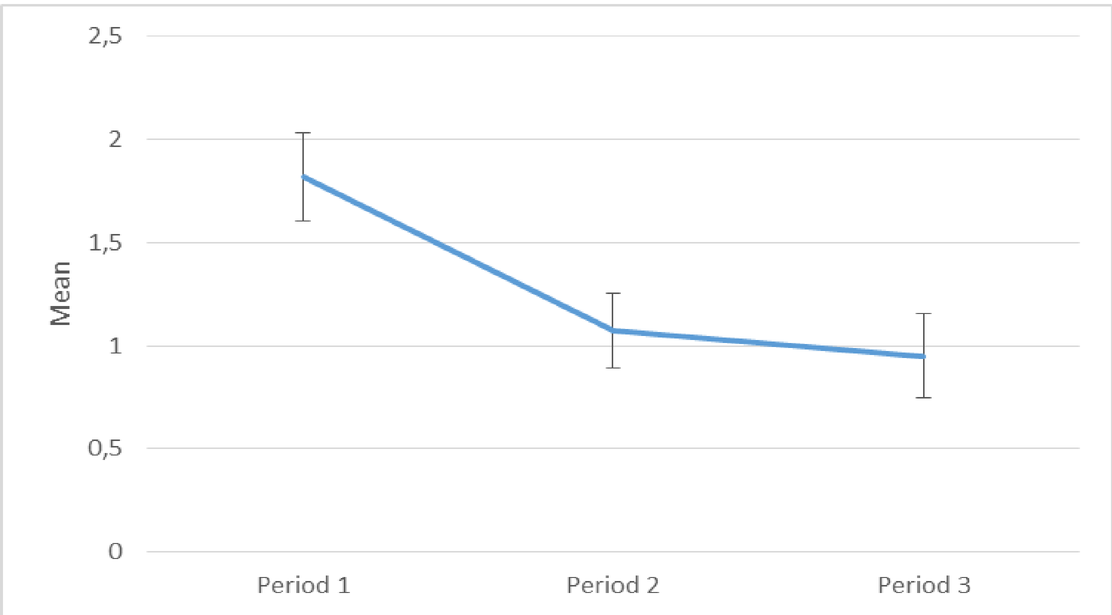

Figure 9. Mean number and ±SE of passages per day and rain period. The Y-axis shows the mean number of passages where rain period 1 has the highest amount of activity

4. Discussion

The aim of this study was to investigate the activity patterns of lions in Ol Pejeta conservancy and when they move in and out of the area. To know *why* the lions move back and forth out of the conservancy is a problematic question to answer as it requires to include many factors and observe the lions for a long period of time. This particular study was conducted using data from one year but the final sample size was still relatively small and not always leading to clear results.

4.1. Activity patterns

Looking at the impact of moon phase on activity, there were no significant results whatsoever. There was no difference in frequency of passages in relation to moon phase (p=0.752) which was a bit surprising considering previous research (Orsdol, 1984; Packer *et al*. 2011). But again, you have to take the size of the sample into consideration and should the sample have been bigger, a more differential result could perhaps have been obtained. Passages in (p=0.84) and out (p=0.10) of the conservancy in relation to moon phase showed no significanse either. As native prey species decrease their activity during nights with a lot of moonlight (moon phase 3) (Griffin *et al*. 2005), I would have expected the lions to leave the area more during these times to hunt for livestock outside of the conservancy. I think this is another result affected by the sample size, if I would have had more data I believe that there would have been a higher amount of out passages during moon phase 3. When it comes to daily activity patterns, it was clear that the lions are more active during the night than during the day. This is not surprising as lions are nocturnal (Fishhoff *et al*. 2007). But how they generally distribute their active time can still be of interest. Looking at the lions in Ol Pejeta, they were most active just after sunset (between 19.00 pm – 20.00 pm) where the sum of passages per hour showed a steep incline and then declined again around 6.00 am, suggesting that these lions, generally, are very active right after sunset all the way to sunrise.There where also no out passages at all during daytime ($p=<0.05$) and this could be important information to people living in the area and especially for herders guarding livestock. To know during what hours the lions are most active, not just that they are nocturnal, is an important asset. This could not only decrease the amount of depredation but also decrease overall human-lion encounters. Habitat type is also important to consider when looking at the daily activity patterns of lions as it has been shown that they generally inhabit more open landscape during night which in turn makes some of their prey species, such as zebras, spend more time in bushy landscape during these peiods (Fishhoff *et al*. 2007). This could support the hypothesis that the lions in Ol Pejeta hunt outside of the reserve at night, as this area is more open than the landscape inside the reserve. However, it is important to remember that these activity patterns are not saying anything about the lions' activity outside or inside the conservancy, it simply shows when the lions move across the border. But by combining the information at hand one can stipulate what the reason for them to leave the conservancy might be. To know for sure what lies behind the activity outside of the conservancy, it would be necessary to observe the lions once they have exited the area, perhaps by using GPS-collars or by direct observations.

When combining the monthly activity with rainfall during the previous 90 days there was a lot more activity during category 1 (p=0.004), i.e. the driest period, and the fact that there is a high activity during this time is interesting as it could be due to hunting efforts on livestock. Many studies have shown that depredation by lions on livestock increases during rainy periods, as native prey become more nourished and consequently more alert and harder to catch (Patterson *et al*. 2004; Frank, 2010). But in constrast, other studies have shown that lions are more likely to attack livestock during dry periods as native prey migrate further to find water, leaving the non-migratory predators with less prey options (Karani, 1994). During dry periods, native prey species often decline due to poor health (Hayward & Kerley, 2005) which may also force the lions to hunt for alternative prey species such as livestock. This may very well be the case outside Ol Pejeta as there are a lot of alternative prey around. However, as there are water troughs all over Ol Pejeta it is unlikely that lack of water would cause native prey to migrate outside the conservancy to drink. I think a more reasonable explanation would be that during dry seasons there is less vegetation in the area and herbivores might have to migrate further to find food. They are not however limited by drinking water and may still return to the conservancy to drink. This could mean that even during dry periods, the native prey are only limited by vegetation but might be more energetic and healthy compared to if they did not have access to water, still making them hard to catch. This could suggest that the lions instead hunt for livestock outside of the conservancy during rain category 1 if native prey are more scattered. Another reason for lions to select for livestock during dry periods may be their weight. It has been shown that lions select prey species that ranges from 190-550 kilos (Hayward & Kerley, 2005) with the most preferred weight around 350 kilos. Livestock in Kenya weighs about 400-500 kilos depending on the species and are consequently larger than for example zebras that weigh about 200-300 kilos (Joubert, 1974). Should the native prey loose a lot of weight during periods with lack of resources (such as dry periods) the lions might select for larger prey types as livestock. Even though livestock would most probably also loose weight during these circumstances, the lions still need to maximize their energy intake and therefore might select livestock instead (Hayward & Kerley, 2005). There was no significant difference when comparing number of passages to rainfall during the previous 7 and 30 days. My theory is that this might be because of the fact that the data values were so low (close to zero) and similar to each other in these groups, there were also a lot more values of zero overall as these groups did not measure rainfall as far back in time.

The distribution of males and females in this study proved not to be different. There was only a significant difference between unknown individuals and males (p=0.02) and females (p=0.02) respectively. The number of unkown individuals, when analyzing sex as a factor, was regrettably quite high. This was due to dark pictures where the sex could not be determined, pictures with bad quality and the amount of young individuals. It was impossible to determine the sex of cubs and sub-adults and this contributed to the high amount of unknown individuals. Even though there was no difference in the number of passages between the sexes there was however a difference in activity patterns between males and females, especially between June and July, where the males' activity increased and the females decreased. The overall pattern seems to be that males and females do not walk together but rather avoid each other. This might be because they simply belong to different prides and do not interact with one another. Allthough, as some pictures showed females with cubs, I think it might be possible that females avoid males as they might risk infanticide (Mosser & Packer, 2009). The timeframe of passages out of the conservancy combined with the fact that most passages occurred during the dry period could indicate that hunting efforts on livestock are behind this behaviour, although this cannot be concluded with certainty as none of the lions were traced but merely observed leaving and entering the reserve. This hypothesis could perhaps have been answered better if there where more clear results concerning activity related to moon phase. I think that it could have been more supported if the lions would prove to be more active leaving the reserve during moon phase 3. For future studies I would suggest to gather data for a longer time period to test this further.

4.2. Decreasing conflict

As depredation is a major cause of conflict, and one of the reasons to why the lion population is declining, understanding when risk for depredation on livestock may be particularly high would be a valuable asset. As native prey species reduce their activity levels during moonlit nights (moon phase 3) (Penteriani *et al*. 2011), it is reasonable to assume that the lions increase their activity levels as they need to search for prey more actively (Panteriani *et al*. 2011). However, foraging is always costly in terms of energy (Kacelnik & Houston, 1984) and it seems counter intuitive that generalist predators would spend large amounts of energy on searching for species that are hard to find when they could adapt their behaviour to hunt for other available prey - such as livestock. This can further be supported by the fact that all cats hunt by visual and auditory cues and react to movement which makes them more likely to hunt active prey (Harmsen *et al*. 2010). If native prey additionally were more active during dark periods, this should aid the lions as they are more concealed by the dark which further helps them stalking their prey (Orsdol, 1984; Packer *et al*. 2011). This is important to consider when it comes to depredation on livestock.

Depredation is a common phenomenon and is virtually impossible to escape when human settlements are surrounding the protected areas where the large carnivores live (Ogada et *al*., 2003; Patterson *et al*. 2004; Kissui, 2008). Attacks occur when native prey, for any reason, is inaccessible (Patterson *et al*. 2004) and could hence increase when the lions cannot find suitable native prey. Many livestock settlements are constructed to contain the livestock, not to keep the predators out, because it is thought to be the herders' job to defend and protect the livestock (Patterson *et al*. 2004), making the killing a fairly easy task for the lions. Livestock often occur in large numbers and are suitable targets for many predators, independent on whether they are free ranging or enclosed (Kolowski & Holekamp, 2006). As livestock can be seen as alternative prey to lions, in relation to one of their main prey species zebra (Hayward & Kerley, 2005), it would be interesting to particularly investigate depredation during all moon phases. The fact that the lions in this study did not show any difference in activity between the moon phases could perhaps mean that they simply hunt different types of prey during different times of the month. For example, they could be hunting native prey during moon phase 1, and livestock during moon phase 3, and perhaps livestock would be extra vaulnerable during this time if the landscape is very dry. This switching behavior could explain the similarities in activity between the moon phases. To prove this would require further studies where one could trace the lion's whereabouts outside the conservancy and compare livestock attacks by lions with moon phases during the attacks. As there are a lot of livestock inside Ol Pejeta, it might seem strange that they would exit the area to hunt outside the reserve. However, high levels of human activity and the presence of watch dogs have proven to decrease lion depredation on livestock (Ogada *et al*., 2003) and as mentioned earlier, the livestock inside Ol Pejeta is more guarded and therefore not as accessible to the lions. I therefore think it is possible that they hunt for livestock outside the reserve when they need to, and then return to Ol Pejeta where they are more shielded by the vegetation and has access to water.

To further avoid conflict, it can also be important to consider the amount of available ungulates and other prey types within the conservancy and adjacent ranches. Polisar *et al*. (2003) found that the access to ungulates around ranches reduced the risk of depredation on livestock. Furthermore, it could favor herders to more carefully choose where they keep their livestock during different periods of the rearing. As lions, and many other predators, use tall grass and bushes during the day to stalk and hide from their prey, keeping maternity pastures away from these habitats and onto open plains could decrease the risk of depredation (Polisar *et al*. 2003). Using the knowledge of what habitat types lions use during different times of the day (Polisar *et al*. 2003; Fishhoff *et al*., 2007), it may be beneficial to keep livestock on open plains during daytime and in more bushy landscape during nighttime.

The findings in this study could shed light on when and why the lions move out of Ol Pejeta and also when there might be higher risk for human/lion interactions. The results can be used to inform farmers in the area of when they need to be extra careful in looking after their livestock, but also when they might use less resources to protect them. As Kolowski & Holekamp (2006) found that depredation on free ranging livestock is just as common as depredation on enclosed livestock, the time consuming work of gathering the animals and keeping them in an enclosure may not be necessary. This would limit the workload for the herders and could perhaps also increase the growth of the animals as they would get access to more resources when they are free ranging. Instead, it could be more effective to apply more manpower during the periods of increased risk in form of more herders protecting the livestock (Ogada *et al*., 2003). Not keeping the livestock in enclosures could also have a positive economic effect as many enclosures are destroyed when lions frighten their prey, causing them to panic and break the enclosure (Kissui, 2008). It also gives the monitoring unit of Ol Pejeta a better understanding of when to monitor the lions as they might be more at risk for poaching during certain periods.

4.3 Economic and ecological impact

Even though depredation on livestock is a big problem, the economic loss for the herders is often negligible as livestock has been reported to only comprise a small part of the lions' diet, about 5.8 % (Patterson *et al*. 2004). Disease and parasites are much larger contributors to livestock deaths according to Patterson *et al*. (2004) who conducted their study on ranches neighbouring Tsavo National Park in Kenya. They further state that making sure to keep your livestock healthy could therefore make up for potential losses from depredation.

There are more reasons as to why large predators need to be protected, both for the sake of biodiversity and for the sake of the impact on humans. As apex predators, such as lions, are at the top of the food chain, they control a lot of the other trophic levels, ranging from herbivores to primary producers. The decline or loss of these apex predators could result in trophic cascades or mesopredator release (Ripple *et al*. 2014). A trophic cascade is characterized as the indirect effect that predators have on plants, mediated by herbivores (Schmitz *et al*. 2004). In this particular case, if lions were to decrease drastically or go extinct, their prey would increase as a result of less predation which would cause a higher grazing pressure on the plants. Plants as primary producers do not only have a vital role for herbivores as food but also for insects and birds that may use plant structures for nests, coverage and burrows. This however is, in my opinion, not likely to happen any time soon as lions do not only have one prey and their prey do not only have one predator. The more complex the ecosystem, the less likely a trophic cascade is (Pace *et al*. 1999) because the interaction between the different levels are not as strong. Even so, as more and more predator species are declining due to conflict with humans, it is important to consider potential trophic changes if the ecosystem becomes less diverse.

Another aspect of suppressing large predators is the mesopredator release hypothesis. When apex predators decline, they can leave room for smaller predators as the competition, and potential killing of the smaller predators, decreases (Ripple *et al*. 2014). In Africa, lions and leopards can suppress mesopredators when they live in sympatry. One example of such a mesopredator is the baboon that can cause great damage to livestock and agriculture if they get the chance to increase (Ripple *et al*. 2014). The reason for this is that baboons utilize a lot of the same food as humans and can often raid crop fields which can devastate an entire harvest (Ripple *et al*. 2014). Livestock in Kenya are not only preyed upon by lions and should the lions decrease, it could result in less competition for the other predators. This information may seem inconsequential in the context of this study but I think it is important to mention the ecological role of lions as this is the main reason to why it is so important to protect them. Evidently, the loss of one enemy can result in a new one. To poach large predators may not have the desired effect and could surely be avoided with better knowledge of the behaviour of these animals.

4.4 Future research and sources of error

One of the issues with this study was that many of the pictures that were analyzed were taken the year before the study began. This meant that the settings of the cameras could not be changed in favor of this study and as a result of installation (made long before this study started), the silent period and the number of pictures in each sequence differed slightly between the cameras. The preferable scenario would of course be to have the same settings, even though the characteristics of the different settings were known in this case. It would also have been advantageous to have the silent period set to zero, something that was changed during our visit in favor of future studies. This puts the sequences more closely together and you do not risk missing an animal passing due to a long silent period. The number of pictures per sequence is also important. With a higher number of pictures per sequence it is easier to analyze in what direction the lion is moving. Having the batteries changed with an even interval is another important factor. This is to insure that the pictures share the same quality and that the performance of the camera, due to low batteries, do not affect the camera's ability to take pictures. As the changing of the batteries was done by personnel in Kenya as the study continued in Sweden, it was difficult to know exactly when they were changed, even if the agreement was once a week. As mentioned earlier, the batteries were not changed for two weeks during the holidays due to the personnel having time off and this should, in the largest degree possible, be avoided. The reason for this is that it is imperative to know when there are no passages due to no activity and when there are no passages due to low camera performance.

For future studies I think it would be important to look at the composition of the lion prides. There are five known prides in Ol Pejeta at the moment but when looking at the pictures, it is impossible to distinguish between them. As the number of lions within a pride can have an effect on the lions’ behaviour (Mosser & Packer, 2009), it would be interesting to observe each pride separately, especially since there might be “problem individuals” when it comes to depredation on livestock. As mentioned earlier, in order to say anything about the lions’ activity outside the conservancy, you would have to observe them once they have left the area. By keeping track of the different prides and observing them with, for example, GPS-collars, I think the question as to what they are doing outside the conservancy could be better answered.

Conclusions

I. Do the lions move in and out of the conservancy more during nighttime?

Yes. There is clearly a higher activity during nighttime as 94 % of all the passages occurred during this time. Furthermore, all the passages out of the conservancy occurred during night ($p=<0.05$).

II. Is there a difference in activity between different moon phases?

No. The different moon phases showed no impact on activity ($p=0.752$) and there was no difference between in ($p=0.84$) and out ($p=0.10$) passages during different moon phases.

III. Does female lions move in and out of the conservancy more than male lions?

No. There is no difference in activity beween the two sexes, only between unknown individuals and males ($p=0.02$) and females ($p=0.02$) respectively. Although male and female lions seem to be avoiding each other as their movement patterns are very different.

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