Title: Hunting success of lions affected by the moon's phase in a wooded habitat

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Abstract

Variation in moonlight affects foraging, hunting and vigilance behaviours in many nocturnal species. Here, we explore the effect of moonlight on the movement and hunting behaviour of African lions. Previous studies found bright moonlight is associated with reduced hunting success; however, those studies were largely undertaken in open habitats where predators are easily seen by prey species on moonlit nights. In this study we explored whether moonlight affected hunting behaviour and success in a largely wooded environment. Measures of short-term lion movements (distance moved, displacement, and path tortuosity) derived from GPS telemetry data were used as indicators of movement behaviour. Field observations of belly distension were used to assess recent food intake. Lions had greater belly distension (indicating feeding success) on dark nights. However, this change in feeding success was not reflected by lion movement patterns – there was no evidence that these changed across moon phases. There was no evidence that lions used more covered habitats on brighter nights to facilitate concealment.

Key words:

Moonlight; hunting success; movement ecology

Introduction

Nocturnal light varies substantially with the phases of the moon. And although moon light is not the only factor that affects how light any given night may be, the amount of moonlight affects a diverse range of taxa, and can affect reproduction, communication, foraging and predation (Kronfeld-Schor et al., 2013). Many species adjust foraging or vigilance behaviours, as the moon phase can affect predator-prey interactions, and therefore the ‘landscape of fear’ (Brown, Laundre, & Gurung, 1999) experienced by prey species. In some cases lighter nights are more dangerous as predators are more active, and in others it is the darkest nights when predators are hidden, that predation risk is highest. A meta-analysis of predation risk in relation to moonlight revealed divergent responses of nocturnal mammals to the moon’s cycle (Prugh & Golden, 2014). Prey species that use primarily visual signals showed increased activity with increased moonlight, whereas those using other sensory systems suppressed activity at these times (Prugh & Golden, 2014).

The hunting success and activity of nocturnal predators have also been shown to be affected by moon phase. The nocturnal activity of coursing predators, cheetahs (*Acinonyx jubatus*, Schreber) and wild dogs (*Lycaon pictus*, Temminck), was linked to the phase of the moon, with increased activity on lighter nights (Cozzi et al., 2012). Cheetahs’ nocturnal activities were related to the moon phase in the dry season, with an increase in time spent feeding on more illuminated nights (Broekhuis, Grünewälder, McNutt, & Macdonald, 2014). African wild dogs, which are principally diurnal, have also been seen to hunt on moonlit nights, and seem to be limited by light availability (Rasmussen & MacDonald, 2012). Wolves (*Canis lupus*, Linnaeus) were almost twice as successful when hunting on moonlit nights (Theuerkauf et al., 2003). Coursing predators are more successful at high levels of illumination (Cozzi et al., 2012), while ambush predators are at an advantage on darker nights that facilitate concealment (Funston, Mills, & Biggs, 2001; Orsdol, 1984).

Several studies have investigated the relationship between African lion (*Panthera leo,* Linnaeus) hunting behaviour and moon phase. As ambush predators, lions have an advantage when they are concealed, which may be facilitated by low moonlight. Packer et al. (2011) showed that food intake of lions was greater on moonless nights (according to belly size measures) and most attacks on humans occurred during the darkest nights of the moon cycle. Funston et al. (2001) showed a similar pattern for lions in Kruger National Park, with increased hunting success on moonless nights or when the moon was obscured by clouds, a result echoed in Queen Elizabeth National Park in Uganda (Orsdol, 1984). However, a more recent study by Cozzi et al. (2012) found no link between lion activity and the phase of the moon, although this study did not assess hunting behaviour.

Apex predators exert effects on other species in the ecosystem through direct predation (Grange et al., 2012), interference competition (Van Der Meer & Ens, 1997) and by modifying prey behaviour (Barnier et al., 2014; Creel, Christianson, & Winnie Jr., 2011). Lions have been shown to influence their prey in this way, through changes to vigilance behaviour (Periquet et al., 2010, 2012) and variation in spatial and temporal habitat use in relation to the risk of predation (Valeix, Fritz, et al., 2009; Valeix, Loveridge, et al., 2009). The phase of the moon is potentially an important aspect of this ‘landscape of fear’. Lion prey species avoided areas where lions were likely to be found and changed their behaviour in risky areas in relation to the moon in the Serengeti (Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017). This may only be the case when predators are present, as zebra and wildebeest increased their movements during brighter nights when lions were in close proximity, but showed no difference in movements through the lunar cycle when lions were more than a kilometre away (Traill, Martin, & Owen-Smith, 2016). Variation in hunting success over time is likely to affect the spatial and temporal distribution of prey species, which may in turn influence the wider ecosystem, or patterns of human-wildlife conflict.

The aim of this study was to test the effect of the moon phase on lion movement patterns and hunting success in a heavily wooded environment. Movement patterns can represent hunting behaviours, as well as habitat choices, for example, highly tortuous paths indicate searching and hunting behaviour (Benhamou, 1992). The vegetation in the study site, Hwange NP, is composed of woodland and bushland and with only 5% of the area being classified as open habitat (Rogers, 1993). It is far less open than either the Serengeti (Packer et al. 2011), Kruger (Funston et al. 2001) or Queen Elizabeth National Park (Orsdol, 1984). Dense vegetation may offset the potential negative impact of moonlight on lion hunting success. Lions may change their habitat preferences over the moon phase using more wooded areas on lighter nights. In addition, dense habitats could facilitate concealment of hunting lions on lighter nights, leading to more successful kills at these times of the moon's cycle, breaking the relationship between moon phase and hunting success. Some evidence of this has been seen in South Africa, as presence of moonlight is less important than vegetation structure in successful lion kill sites (Davies, Tambling, Kerley, & Asner, 2016).

Methods

Study Area

The study was carried out in Hwange National Park, Zimbabwe (HNP). HNP covers approximately 15,000 km^2 in the north west of Zimbabwe (19°00'S, 26°30'E). Altitude varies from 800 to 1100 m. The vegetation is primarily woodland and bushland savanna and vegetation communities are dominated by *Colophosperum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* and less than 5% of habitat is open (Rogers, 1993). HNP is a semi-arid ecosystem with a mean annual rainfall of 606 mm and highly variable annual rainfall (CV ≈ 30%) (Loveridge et al., 2009; Valeix, Fritz, et al., 2009).

Lion Movements

Movement data were collected by global positioning system (GPS) collars deployed on 63 individual lions (29 females and 34 males). The data were collected over 10 years between 2002 and 2013 by the Hwange Lion Research Project (Loveridge et al., 2009, 2016; Valeix et al., 2010). The study was undertaken in a study area of approximately 7000 km^2 (see Supplementary Material Figure S1 for map). Lions were fitted with global positioning system (GPS) collars with either UHF or satellite remote downloads (Televilt Positioning, Lindesberg, Sweden, 950 g; Africa Wildlife Tracking, Pretoria, South Africa, 1400 g). As far as possible one animal was collared in each pride and coalition in the study area. Lions were immobilised for handling and collaring by qualified field staff using standard protocols for the species (Fahlman et al., 2005). Study animals were located weekly to bimonthly from a 4 x 4 vehicle or microlight aircraft.

The GPS collars gave hourly co-ordinates for the individual's location throughout the daily cycle, or every nocturnal hour (according to the collar type). These locations were used to calculate total distance travelled, displacement distance, and path tortuosity. These parameters were used as they describe different aspects of lion movements (Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014). For example, a highly tortuous path may indicate search behaviour, as this is more efficient for random searching in resource areas (Benhamou, 1992). Lions were defined as sub-adult (less than four years old) or adult (over four years old), and for those study animals for which birth dates were not available ages were estimated from tooth-wear (Smuts, Anderson, & Austin, 1978).

A subset of lion data were selected from the complete GPS data to include the three nights surrounding the appropriate moon phase, i.e. one night before, the night of the moon phase, and one night afterwards. The data were also limited to nocturnal hours, from sunset to sunrise, on each of the three nights and to times when the moon had risen, i.e. between moon rise and moon set, during these night hours. Times for sunrise, sunset, moonrise and moonset for the study site were extracted using the R package "suncalc" (Agafonkin & Thieurmel, 2018). Some data were patchy due to missing location measurements, consequently the data from that period were discarded.

For each individual an hourly distance moved was calculated between every hourly GPS fix and the previous GPS fix, using Pythagoras' Theorem in R (Equation 1). Three different measurements were calculated from these hourly distances to represent movements; total path distance, displacement, and tortuosity.

$$Distance\ between\ coordinates = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

Equation 1

The total path distance travelled was calculated by summing the distances moved each hour during the three night period. This gave a measurement in meters for the total distance of the path travelled over the three nights i.e. the distances of the three paths (one from each night) were added together to give the total distance travelled during nocturnal hours over the moon phase period. Displacement was calculated as the direct distance (or displacement) from the first point of the first night of the moon phase (i.e. the hour after sunset (or moonrise if later) of Day 1) to the last point of the third night of that moon phase (i.e. hour before sunrise (or moon set if earlier) of Day 4) using Pythagoras theorem, as before. Tortuosity was calculated as a ratio of the total distance travelled and the displacement of the animal. This creates a tortuosity value of 1 for a straight line, and higher values indicate a more tortuous path. A very tortuous path is highly curved and meandering and is characteristic of search behaviour (Benhamou, 1992).

Belly Size

A belly size measure was used to indicate recent food intake, following the methods of Bertram (1975). A belly score of 1 indicates a distended stomach and recent food intake, a belly score of 3 is average, and 5 indicates very little food has been consumed recently. These belly sizes were recorded whenever lions were observed in the field from 2008 to 2013 along with other details including the time, the location and the identity of the animal. This method was also used in Packer's study of lion feeding behaviour and kill success (2011). Cubs were excluded from this data, as belly size measures are not accurate. A total of 1727 belly score observations were made between May 2008 and December 2013, from 275 lions (123 males and 152 females).

Habitat

Habitat variables were extracted from the MODIS Yearly Vegetation Continuous Fields satellite images (Hansen et al., 2003) and provided the percentage of tree cover to a resolution of 250m. A percentage of tree cover was extracted from the MODIS image for the relevant year for each lion GPS location, using the R package “raster” (Hijmans, 2018). These measurements were averaged over the three night period of the moon phase to provide an average tree cover experienced by the individual lion during this time. The range of tree cover values experienced by lions within three-night periods was low (with the majority of cases experiencing between 0 and 4% tree cover change, and one value experiencing a maximum of 30% tree cover change).

Season

Three seasons were recognised, these were the wet season (from November to February), early dry season (March to June) and late dry season (July to October). These seasons are a good proxy for the weather in this area, and therefore allow for changes in the visibility of the moon. For example, in the wet season cloud cover is greater, reducing the visibility of the moon. Season also affects vegetation cover, with denser vegetation present in the wet season, which may also have an effect on movements or hunting behaviour. Movements, hunting patterns and belly sizes might also be affected by season due to resource availability.

Moon Phase

Two variables were used to define the moon’s phase. The first was the phase of the moon according to the dates provided by National Aeronautics and Space Administration (NASA), and were defined as being either: New Moon, First Quarter or Full Moon (NASA, 2013). Last Quarter was not included as the first and last quarters of the moon’s phase have a similar illumination.

The second measure was the fraction of the moon which was illuminated on a given night; this data was sourced from the United States Naval Observatory (United States Naval Observatory, 2013). This data was used in the belly score analysis as a continuous measure.

Analysis

A linear mixed model was constructed for each movement parameter, with data for all lions included. We used model averaging for linear mixed models (Anderson, 2008), using R software (as described by (Grueber, Nakagawa, Laws, & Jamieson, 2011)). The method also allows for model uncertainty by creating an averaged model (Grueber et al., 2011). Moon phase, tree cover, and the interactions between moon phase and tree cover, season, sex, and age were included as fixed factors. Lion identity was included as a random factor. The *lmer* and *glmer* functions in the *lme4* package (Bates & Maechler, 2009) for R software were used to fit these models. Poisson error structures were used in the models analysing total path distance and displacement (rounded to the nearest metre) to reduce residual heterogeneity, and an observation-level random effect was used to reduce overdispersion in these models (Harrison, 2014). Tortuosity was log transformed to reduce residual heterogeneity, and *lmer* (Gaussian error structure) was used for the model.

Belly distension was used as a response in general linear mixed models (*lmer*). The same predictor variables were used (age, sex, season, tree cover) but moon illumination was included as a continuous predictor. The interaction between moon illumination and tree cover was also included, on the *a priori* expectation that tree cover might mitigate the effect of lunar illumination. The same model averaging procedure was used.

Results

Movements

There was no evidence that lion movement parameters were affected by the illumination of the moon (Figure 1), but age, season and tree cover were influential. Total distance travelled was higher for adults than sub-adults (Estimate = -0.226, Confidence intervals = - 0.365 to -0.086, Table 1). Total distance travelled was higher for males than females (Estimate = 0.296, Confidence intervals = 0.144 to 0.449, Table 1). Total distance travelled was also higher where average tree cover was higher (Estimate = 0.122, Confidence intervals = 0.026 to 0.218, Table 1). However, there was no evidence for an effect of the illumination of the moon (Figure 1, Table 1), or that the effect of moonlight depended on habitat (Table 1).

Similarly, displacement was also higher for males than females (Estimate = 0.272, Confidence intervals = 0.077 to 0.467, Table 2). Displacement increased with higher tree cover (Estimate = 0.299, Confidence intervals = 0.144 to 0.454, Table 2). There was no evidence for an effect of moon phase, or for an interaction between tree cover and moon phase (Table 2).

Tortuosity was lower in areas of higher tree cover (Estimate = -0.249, Confidence intervals = -0.296 to -0.065, Table 3). However, there was no relationship between tortuosity and the phase of the moon, or any interaction between tree cover and moon phase (Table 3).

Belly Size

Belly size scores were higher when moon illumination was greater (Estimate = 0.09, Confidence Intervals = 0.02 to 0.16, Table 4). There were no seasonal differences in belly scores. There was also no relationship between the tree cover and the belly score (Table 4).

Discussion

This study provides evidence that lion hunting success increases on darker nights, as seen in previous studies (Funston et al., 2001; Orsdol, 1984; Packer et al., 2011). We found no evidence that movement patterns of the studied lions changed with the moon phase, but they did appear to be affected by tree cover – lions moved further in less tortuous paths in wooded habitat. The effect of tree cover did not depend on moon phase.

Moon Illumination

The moon is not the only factor that affects the nocturnal level of darkness at ground level. Cloud cover, tree cover and other sources of light (both natural and artificial) can also affect the level of darkness. However, this study provides evidence for reduced hunting success on light nights, as there was a tendency to observe belly scores indicating lack of recent food intake on the lighter nights (close to full illumination) – otherwise there was no clear effect of moonlight on belly scores. This relationship between the moon and food intake is similar to that seen in other studies (Funston et al., 2001; Orsdol, 1984; Packer et al., 2011). However, lions in HNP may also hunt successfully on nights with intermediate moon illumination, rather than just the darkest nights, as belly scores indicating recent food intake were seen across a range of darker moon illuminations.

Movement measures were not influenced by the moon phase, a result which is similar to that of Cozzi et al. (2012) who found no link between lion movements and the moon phase. Lions in HNP do not seem to adjust their movements, or searching behaviours through the moon’s phase, but their movements do appear to be influenced by tree cover. In this study the habitat may be of importance, as in open areas (which make up only 5% of HNP (Rogers, 1993) and are prey-rich (Davidson et al., 2012)), a ‘sit and wait’ strategy may be altered to a stalking ambush technique on moonless nights. In contrast, in wooded habitats lions would not necessarily alter their behaviour between moonlit and moonless nights because cover to ambush prey is provided by vegetation. This follows similar principles to previous observations that lions hunt in the plains at night, and in forests during the day (Schaller, 1972), and that vegetation structure is key in successful kill sites (Davies et al., 2016). As HNP is a heavily wooded landscape, it may be that the illumination of the moon has an unimportant influence on how lions move in this area, whereas lions in more open areas (as in Funston et al. 2001 and Packer et al. 2011) have to adjust to the changing light levels from the moon. However, there is no interaction between moon phase and tree cover, which suggests that lions are not mitigating against the effects of full moon nights on their hunting success, as there is no evidence that they are using areas with greater tree cover on darker nights.

Lions in HNP do not change their movement patterns, but do appear to feed less on the most moonlit nights. Searching behaviour and general activity may remain high through the phases, as hunting is occurring throughout most of this time (as evidenced by belly scores indicating recent food intake throughout the other phases). This behaviour may also explain why some prey species react to the presence of lions rather than simply the phase of the moon, as the moon's phase is not an accurate signal of risk (Traill et al., 2016). During lighter nights there does not seem to be any change in searching effort, but lions could be performing other behaviours at this time (for example, patrolling territories) that rely less on remaining hidden from prey species. Predators may use different phases of the moon for different behaviours, that are more suited to the available light, for example, eagle owls (*Bubo* bubo, Linnaeus) hunt most on dark nights, but are more active on light nights and perform visual displays (Penteriani, Kuparinen, del Mar Delgado, Lourenco, & Campioni, 2011).

Tree cover

Distance travelled, and the displacement of the lions, increased in areas of higher average tree cover. Lions may be moving further when they are in areas of high tree cover, and moving only short distances in areas of low tree cover, because open areas are preferred to more covered areas. Tree cover could provide concealment for lions when hunting, but for this reason may be avoided by prey species. The teak woodland which makes up a large area of the study site is dystrophic (very unproductive) so very few prey individuals are located here, whereas there is a higher prey abundance in more open landscapes and lions in this area are known to prefer grassed bushland and areas close to waterholes (Davidson et al., 2012). A lower prey encounter rate, caused by lower prey densities and restricted visibility, might explain why lions seem to move greater distances and move a greater distance from the area when they are in areas of higher tree cover. Although there is also evidence that lions prefer to kill in denser habitats in HNP (Davidson et al., 2012). The different foraging techniques of lions may also influence their preference for open areas, as in prey-rich areas (open areas in HNP (Davidson et al., 2012)) a 'sit and wait' strategy is often used. This would lead to short distances being covered and less tortuous paths, as seen in our results. Tree cover may be more important than moon phase for lion movements in this area because of the concentration of prey animals in open areas.

Alternatively, it is possible that the average tree cover was simply likely to be higher when a greater distance or displacement took place, because areas of different habitat have been travelled through. Therefore, a low tree cover level was less likely to persist in our data when an animal had travelled a large distance, because large areas of low tree cover are rare, and lions are likely to enter areas with a higher tree cover and therefore increase the average tree cover experienced.

Lion traits

Displacement measurements, and the total path travelled, are higher for males than for females. This may be linked to home range size differences; male home ranges were found to be much larger than female home ranges in HNP (Loveridge et al., 2009). The difference in home range size, and males patrolling their territorial boundaries, could explain why males move further than females. This explanation potentially extends to the greater distances moved by adults compared to sub-adults, as sub-adults are likely to be with a pride and therefore have a smaller home range, like females, whereas lone adults with large home ranges will increase the average distance travelled of adult lions as a whole.

In conclusion, this study supports previous findings that lions are more successful at hunting on dark nights, and that the moon phase (rather than simply the presence or absence of the moon) affects lion hunting success. This study also shows that the moon is important to hunting success in a wooded area, as well as the more open areas where this relationship has been seen before (Funston et al., 2001; Packer et al., 2011), as moon illumination was correlated to belly size of lions. Some evidence of the moon affecting hunting success has been seen in African thicket, but the effect of the moon was small compared to other factors like the viewshed (the areas visible) around a kill site and the wind speed at the time of the hunt (Davies et al., 2016). These results suggests that even in wooded areas, the light of the moon, or lack thereof, is still important to lions. Moonlight is also known to affect jaguar behaviour, in secondary forests, with jaguars switching prey species across moon phases, tracking the changes to armadillo activity across the moon phase (Harmsen, Foster, Silver, Ostro, & Doncaster, 2011). Tree cover may not affect the effect of moon phase for large predators, and this may particularly be the case in HNP as fewer prey individuals are found in areas of high tree cover, meaning that there would be no advantage to switching activity to high tree cover areas during lighter nights of the moon to facilitate concealment for hunting. This may be another reason that prey species do not use areas of high tree cover, as these are high risk areas for predation.

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Tables

Parameter (Reference category)	**Estimate†**	**Confidence Intervals (95%)**		**Relative Importance ‡**
Age (Adult)	-0.226	-0.365	-0.086	1.00
Season Late Dry (Early Dry)	-0.015	-0.083	0.052	0.48
Season Wet (Early Dry)	0.031	-0.064	0.127	0.48
Sex (Female)	0.296	0.144	0.449	1.00
Tree Cover	0.122	0.026	0.218	1.00
Moon Phase Full Moon (First Quarter)	-0.019	-0.095	0.057	0.29
Moon Phase New Moon (First Quarter)	-0.003	0.054	0.047	0.29

Table 1 - Model averaged parameter estimates for factors affecting total distance travelled by lions at night. Only parameters included in the model set are reported. †Effect size has been standardized using R (see Grueber et al. 2011). ‡Relative importance is calculated according to the number of models that include the variable, and their weighting within the models.

Parameter (Reference category)	**Estimate†**	**Confidence Intervals (95%)**		**Relative Importance‡**
Age (Adult)	-0.055	-0.246	0.135	0.42
Season Late Dry (Early Dry)	-0.066	-0.232	0.010	0.50
Season Wet (Early Dry)	-0.002	-0.124	0.119	0.50
Sex (Female)	0.272	0.077	0.467	1.00
Tree Cover	0.299	0.144	0.454	1.00

Table 2 - Model averaged parameter estimates for factors affecting distance of displacement of lions at night. Only parameters included in the model set are reported. †Effect size has been standardized using R (see Grueber et al. 2011). ‡Relative importance is calculated according to the number of models that include the variable, and their weighting within the models.

Parameter (Reference category)	Estimate†	Confidence Intervals (95%)		Relative Importance‡
Age (Adult)	-0.082	-0.265	0.102	0.61
Season Late Dry (Early Dry)	0.023	-0.071	0.122	0.23
Season Wet (Early Dry)	0.015	-0.071	0.101	0.23
Sex (Female)	0.009	-0.060	0.077	0.20
Tree Cover	-0.181	-0.296	-0.065	1.00
Moon Phase Full Moon (First Quarter)	-0.050	-0.193	0.094	0.40
Moon Phase New Moon (First Quarter)	-0.029	-0.134	0.077	0.40

Table 3 - Model averaged parameter estimates for factors affecting tortuosity of path. Only parameters included in the model set are reported. †Effect size has been standardized using R (see Grueber et al. 2011). ‡Relative importance is calculated according to the number of models that include the variable, and their weighting within the models.

Parameter (Reference category)	Estimate†	Confidence Intervals (95%)		Relative Importance‡
Season Late Dry (Early Dry)	-0.032	-0.123	0.059	0.42
Season Wet (Early Dry)	-0.023	-0.103	0.056	0.42
Sex (Female)	0.059	-0.038	0.156	0.75
Tree Cover	-0.016	-0.079	0.047	0.71
Moon Illumination	0.092	0.023	0.160	1.00
Moon Illumination: Tree Cover	-0.106	-0.282	0.069	0.71

Table 4 - Model averaged parameter estimates for factors affecting lion belly scores over three night periods. Only parameters included in the model set are reported. †Effect size has been standardized using R (see Grueber et al. 2011). ‡Relative importance is calculated according to the number of models that include the variable, and their weighting within the models.

Figure legends

Figure 1 – (a) The total distance travelled by lions over three night periods; (b) the tortuosity of lion movement paths over three night periods; and (c) the displacement distance of lions over three night periods; during different phases of the moon. Dots indicate means across all lions, and bars show standard error.

Figure 2 – The mean moon illumination at belly scores of lions. Belly score of 1 indicates large belly and recent food intake, belly score of 5 indicates small belly and lack of recent food intake. Dots indicate means, and bars show standard error.