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Assessing the activity pattern overlap among leopards (*Panthera pardus*), potential prey and competitors in a complex landscape in Tanzania

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Abstract

Studying activity patterns and temporal overlap among carnivores and their putative prey is difficult because of their secretive and elusive nature. With large carnivores declining worldwide, it is imperative for conservation planning that we understand how large carnivores interact with their prey and competitors. Camera trapping offers a promising avenue to address this issue. We investigated temporal overlap between male and female leopards, their known and putative prey as well as their competitor, the spotted hyenas, in the Udzungwa Mountains of Tanzania. Data consisted of 4297 independent events from a 30 min interval criterion from 164 camera trap sites we sampled. Leopards were captured by camera traps throughout the day, with male and female leopards showing significantly different activity patterns ($P < 0.001$) indicating sexual segregation in activity patterns, with male leopards being more nocturnal than female leopards. Leopards had significantly different activity patterns from that of the majority of their prey, with yellow baboons, that displayed peak activity during midday, that had the least overlap. Moreover, both male and female leopards had significantly different activity patterns from that of spotted hyenas ($P = <0.001$), with female leopards appearing to be inactive during hours with peak hyena activity. We conclude that systematic camera trapping is a useful tool to study activity patterns and temporal niche interactions between sympatric carnivores and, to a lesser extent, their prey.

Introduction

Studying interactions between carnivores and their prey can be extremely difficult due to their cryptic nature and low abundance (Carbone, Pettorelli & Stephens, 2010; Ripple *et al.*, 2014). Yet understanding how carnivores interact with their prey is key ecological knowledge needed for their conservation, because it can provide information on niche preferences (Ripple *et al.*, 2014). Foraging theory predicts that an apex predator should prefer prey of sufficient mass to be the most energy efficient, while also posing the least risk of injury to the predator (Stephens & Krebs, 1986). Additionally, for large carnivores that are not the apex of a carnivore intraguild, risk of kleptoparasitism is also a factor affecting prey preference and interactions (Macdonald, 1976; Balme *et al.*, 2017). Means of reducing kleptoparasitism between large carnivores could thus be through niche differentiation (Balme, Hunter & Slotow, 2007), caching prey so that it remains out of reach (Balme *et al.*, 2017), and temporal partitioning (Hayward & Slotow, 2009).

During the last decade, camera trapping has opened up the possibility to conduct systematic studies of activity patterns and temporal niche overlap between predators and prey. For example, recent studies have used this approach to demonstrate strong temporal overlaps between Sumatran tigers (*Panthera tigris sumatrae*) and their putative prey (O'Brien, Kinnaird & Wibisono, 2003; Linkie & Ridout, 2011), Sunda clouded leopard (*Neofelis diardii*) and some of their presumed prey species (Ross *et al.*, 2013), as well as prey species of puma (*Puma concolor*) and jaguar (*Panthera onca*) (Harmsen *et al.*, 2011;

Foster *et al.*, 2013). However, in the aforementioned studies camera traps were optimized for detection of the predator (i.e. logging roads). Thus, their results only reflect activity patterns of prey species on trails used frequently by predators, suggesting that camera traps are not optimal for studying predator–prey interactions. However, a recent camera trap study on sympatric felids on Borneo found evidence for both temporal and spatial partitioning (Hearn *et al.*, 2018). Combining telemetry and camera trapping to study interactions has been suggested as a potential method (Kays *et al.*, 2011), with the biggest challenge being capturing a sufficient number of individuals for telemetry collaring.

Leopards (*Panthera pardus*) have been found to exhibit more diurnal activity patterns in rainforests of Gabon (Henschel & Ray, 2003) and Thailand (Ngoprasert, Lynam & Gale, 2007), but more often exhibit cathemeral activity patterns in African savannah landscapes (Hayward & Slotow, 2009). A possible explanation for this has been to minimize kleptoparasitism and competition with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), which are absent in rainforests (Hayward & Kerley, 2008; Hayward & Slotow, 2009; Balme *et al.*, 2017).

Studying temporal overlap in activity patterns of carnivores and their prey could provide valuable insight into behavioural mitigations of competition. The obvious starting point for this type of study would be for a carnivore with prey specialization, with just one other competitor, as it reduces the number of influencing factors. Here, leopards are not ideal study subjects as they are true carnivore generalists, but if only one other large sympatric carnivore species occurs in a study area, there is still potential for studying temporal partitioning. Leopards are known to apply a range of strategies when hunting, but most frequently ambush their prey, often opportunistically (Hunter, Henschel & Ray 2013). As ambush is inherently a stationary behaviour that has most frequently been observed in medium dense habitat (Balme *et al.*, 2007), it is not very likely to be reflected in camera trap data, as camera trap placement is often biased towards trails to capture movement of leopards when patrolling their home range. As leopards do patrol their home ranges (Hunter *et al.*, 2013), it could be expected that they would do so when there is the least chance of overlapping with a potential competitor. In the Udzungwa Mountains in south-central Tanzania, leopards are the most abundant carnivore (Havmøller *et al.*, 2019) as no lions or African wild dogs (*Lycaon pictus*) are currently known to inhabit the landscape, but contrary to other African rainforest, spotted hyenas do occur in Udzungwa (Cavada *et al.*, 2019). This makes the Udzungwa Mountains a good model area to study the difference in temporal overlap between leopards, spotted hyenas and their prey, as there is no competition from other large carnivores, and this lowers the layers of complexity in the carnivore assemblage. Additionally, temporal partitioning between sexes of a carnivore species has rarely been studied. Female leopards in Namibia have recently been described to have a wider dietary niche than male leopards (Voigt *et al.*, 2018), especially with regard to smaller prey, yet temporal overlap between sexes in leopards has not been investigated.

We used data from camera trapping to investigate temporal overlap between male and female leopards, their presumed main competitor the spotted hyena, their putative prey species and two small carnivores, in the Udzungwa Mountains, Tanzania. We predict that male and female leopards show significant segregation in their use of the diel cycle to minimize intraspecific competition (Le Roux & Skinner, 1989), while spotted hyenas' activity pattern does not differ from those of both male and female leopards to maximize their opportunities to kleptoparasitize on either sex (Hayward & Slotow, 2009). We also predict that due to camera trap placement and predation avoidance, leopard activity patterns are significantly different to the majority of their prey (Ross *et al.*, 2013).

Materials and methods

Study area

The Udzungwa Mountains are located in south-central Tanzania (7°46′South, 36°43′East) and consist of a mosaic of large continuous blocks of Afrotropical rainforest and open Miombo woodland, ranging from 250 to 2600 m above sea level (Lovett, 1993; Rovero *et al.*, 2014a). The rainforest holds a remarkable richness of endemic vertebrate species, whereas the intervening dryer habitats harbour species that are more widespread in East Africa (Rovero & De Luca, 2007; Rovero *et al.*, 2014b; Cavada *et al.*, 2019). Due to this mosaic of different habitats, the Udzungwa Mountains have some of the highest mammalian species richness in East Africa. The total protected area of the Udzungwa Mountains National Park and bordering Kilombero Nature Reserve only encompasses 3335 km^2 (Rovero *et al.*, 2014a) out of the total 16 000 km^2 that defines the mountain range.

Data collection and statistical analyses

Camera trap data originated from a study on leopard density in the Udzungwa Mountains (Havmøller *et al.*, 2019) conducted during the dry seasons (June-December) of 2013 and 2014 (for map see Fig. 1). As sunset and sunrise only varied little over the course of the survey (maximum of up to 45 min between June and December; Table S1), we did not consider it useful to standardize our observations (Nouvellet *et al.*, 2012). Additionally, a recent study into diel activity patterns across latitudes and seasons concluded that transformation of time might not be necessary at latitudes below 20°, or in studies with a duration of less than a month (below 40° latitude) (Vazquez et al. 2019).

Leopards were sexed by presence/absence of external genitalia, overall body size and presence/absence of dewlap (Henschel & Ray, 2003). We only used camera trap data for species with ~100 independent events or more (Lashley *et al.*, 2018) that were either confirmed as prey in a DNA metabarcoding study on leopard diet in the same study area (Havmøller, 2016) or presumed to be prey (Table 1). Additionally, we investigated the temporal overlap of leopards and their only other competitor the spotted hyena.

Data were selected according to a criterion of 30 min intervals between photographic captures at the same camera trap site of the same species, to ensure data points were independent (Linkie & Ridout, 2011). The independent detection records for each target species are regarded as a random

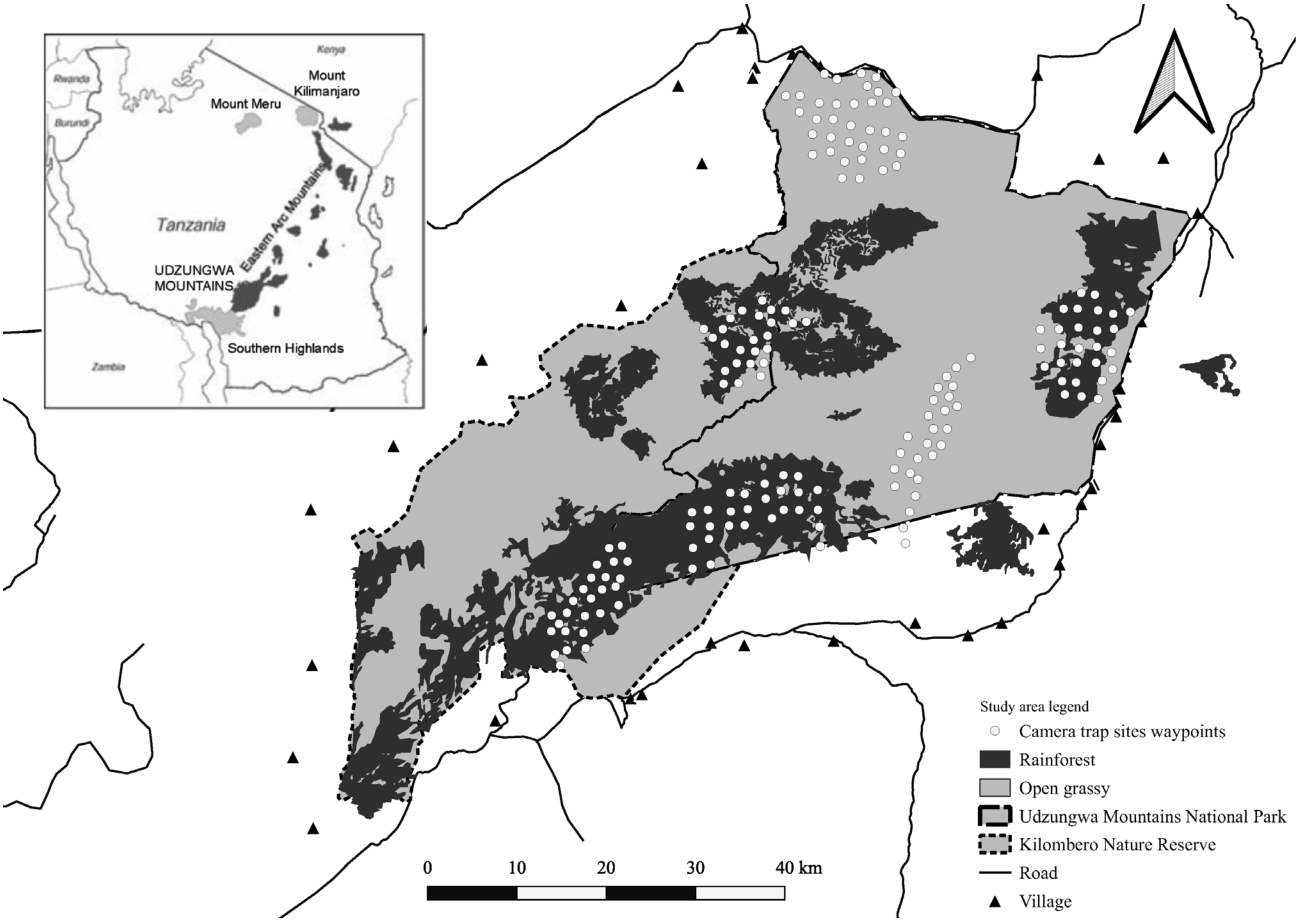


Figure 1 Map of the Udzungwa Mountains of Tanzania, with camera trap stations set to detect leopards and other mammals marked as white dots. The border of the Udzungwa Mountains National Park and Kilombero Nature Reserve is marked as a solid black line and a black-dotted line, respectively.

Table 1 List of species detected by camera traps with approximately 100 independent events including leopard, spotted hyena and putative leopard prey in the Udzungwa Mountains of Tanzania

	Scientific name	Common name	Independent events N
Artiodactyla	*Cephalophus harveyi*	Harveys' duiker	1135
	Neotragus moschatus	Suni	199
	Potamochoerus larvatus	Bushpig	241
	Syncerus caffer	African buffalo	77
	Tragelaphus scriptus	Bushbuck	321
	Madoqua kirkii	Ugogo dikdik	96
Carnivora	*Bdeogale crassicauda*	Bushy-tailed mongoose	411
	Crocuta crocuta	Spotted hyena	128
	Genetta maculata	Blotched genet	114
	Panthera pardus	Leopard	202
Primates	*Papio cynocephalus*	Yellow baboon	198
Rodentia	*Cricetomys gambianus*	Giant pouched rat	134
	Hystrix cristata	Crested porcupine	147

N is the number of independent events per species (minimum 30-minute intervals between events).

Table 2 Summary of Hermans–Rasson uniformity test to assess if a random activity pattern was exhibited over a circadian cycle for leopards, their prey species and a competitor, the spotted hyena derived from camera trapping in the Udzungwa Mountains, Tanzania

		Hermans–Rasson test		
Scientific name	Common name	N	*r*	*P*-value
Bdeogale crassicauda	Bushy-tailed mongoose	411	279.2	<0.001
Cephalophus harveyi	Harvey's duiker	1135	415.4	<0.001
Cricetomys gambianus	Giant pouched rat	134	86.2	<0.001
Crocuta crocuta	Spotted hyena	128	79.3	<0.001
Genetta maculata	Blotched genet	114	66.5	<0.001
Hystrix cristata	Crested porcupine	147	78.8	<0.001
Madoqua kirkii	Ugogo dikdik	96	27.8	<0.001
Neotragus moschatus	Suni	199	23.2	<0.001
Papio cynocephalus	Yellow baboon	198	147.3	<0.001
Panthera pardus	Leopard	202	14.3	<0.001
Potamochoerus larvatus	Bushpig	241	54.2	<0.001
Syncerus caffer	African buffalo	77	12.4	0.001
Tragelaphus scriptus	Bushbuck	321	10.1	0.005

N is the number of independent events per species (minimum 30-min intervals between events).

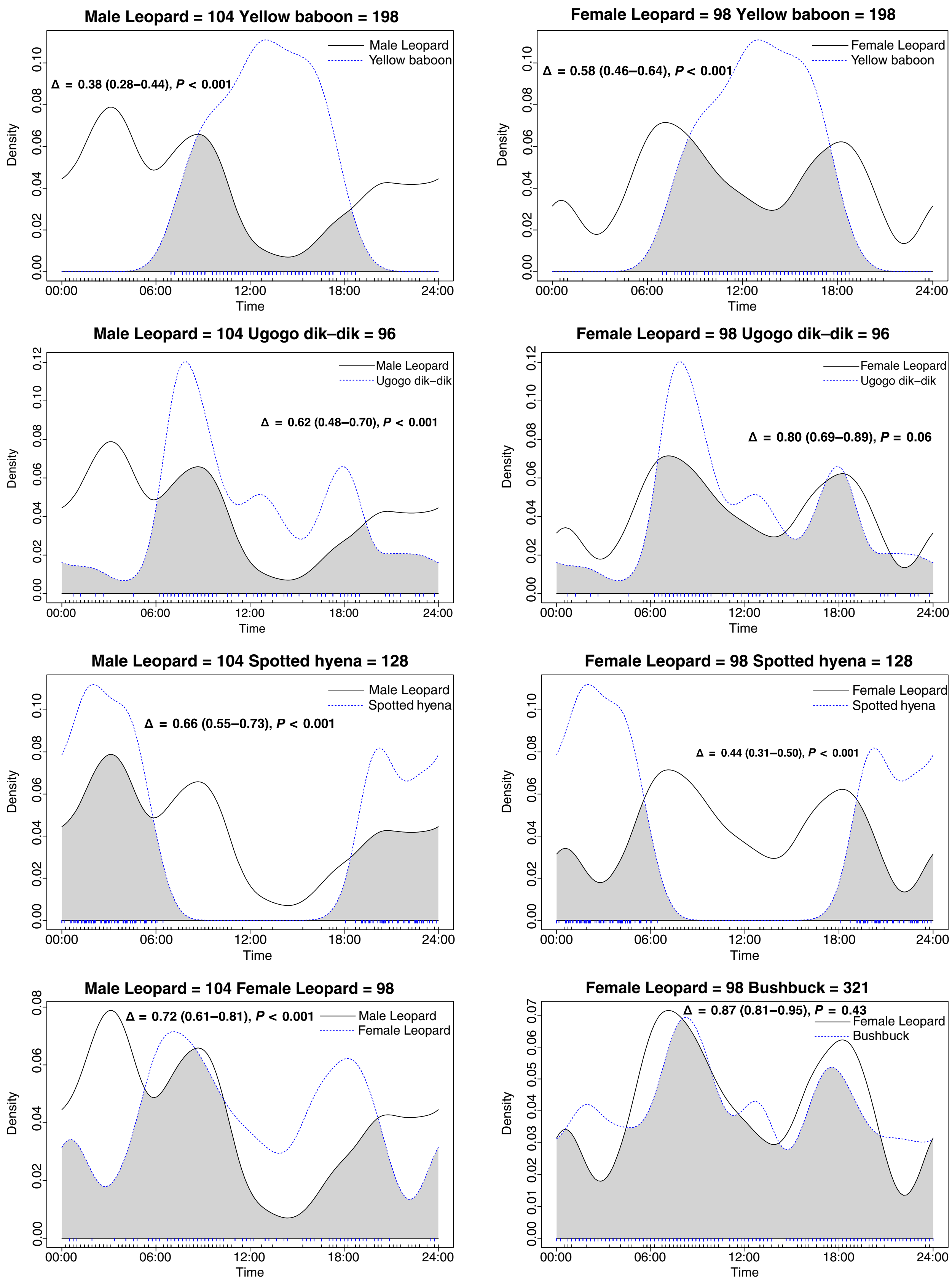
sample from the underlying circular continuous temporal distribution describing the probability of a photograph being taken within any particular interval of the day (Ridout & Linkie, 2009). A Hermans–Rasson test was performed for each species to assess if a random activity pattern was exhibited over a circadian cycle (Landler, Ruxton & Malkemper, 2019).

To quantify the extent of temporal overlap of leopards and their potential prey, as well as competitors, temporal activity patterns were first analysed by estimating the overlap. To complement the coefficient of overlap information concerning predator–prey daily activity, a Bootstrap test (Rowcliffe *et al.*, 2008) was conducted to compare the 24 h-distribution records of each species pair. All statistical analyses were performed in R-software v. 3.5.1 (R Development Core Team, 2014) using a published script (Zimmermann, Foresti & Rovero 2016). Kernel density estimation curves were produced using the R-package '*Overlap*' v.0.3.2 (Meredith & Ridout, 2014) to describe activity patterns for all species, where kernel density estimation is a non-parametric method for estimating the probability density function of a distribution of records (Linkie & Ridout, 2011). The probability density functions assume equal likelihood of recording a species at any time while active (Linkie & Ridout, 2011). The coefficient of overlap ($\boldsymbol{\Delta}$) can range from no estimated overlap ($\hat{\Delta} = 0$) to total overlap ($\hat{\Delta} = 1$). Overlap is defined as the area formed by the minimum values of the density function curves for the pairwise comparison of species' activity. When estimating $\boldsymbol{\Delta}$**,** the coefficient used was $\hat{\Delta}_4$ as all species investigated had over 75 records (Ridout & Linkie, 2009). Bootstrap percentile confidence intervals were calculated, based on 10 000 bootstrap samples. We used the function compareCkern() in the package '*Activity*' v.1.1 (Rowcliffe *et al.*, 2014) which provides a test of probability that two sets of circular observations come from the same distribution. We set the number of bootstrap iterations to 10 000.

Results

Surveys resulted in 5038 camera trap days recording a total of 4297 independent records based on a 30 min interval criterion from 164 camera trap stations (Fig. 1). All species had activity patterns that were significantly different from random according to the Hermans–Rasson test (Table 2). Female leopards exhibited a bimodal activity pattern with peaks primarily around sunrise (06:00) and to a lesser degree at sunset (18:00), while male leopards had activity peaks in the darker hours of the night (Fig. 2). This was also the case for all prey species; however, yellow baboon (*Papio cynocephalus*) exhibit a unimodal activity pattern with highest activity around midday (12:00) (Fig. 2). Leopards showed statistically different use of the diel cycle compared with the majority of their prey species, except for female leopards with Ugogo dikdik (*Madoqua kirkii*) and bushbuck (*Tragelaphus scriptus*) (Fig. 2; Table 3). Male leopards showed statistically different use of the diel

Figure 2 Overlap in activity pattern between male and female leopards to each other, their competitor the spotted hyena and three selected prey species from camera trap data. Coefficient of overlap ($\boldsymbol{\Delta}$), confidence intervals and p-values from a test of probability that two sets of circular observations come from the same distribution. The overlap between male and female leopards and yellow baboon represents the least mean overlap with any species investigated. Leopards had significantly different activity patterns compared with the majority of their prey, except for female leopards with Ugogo dikdik and bushbuck. Male and female leopards had significantly different activity patterns from each other and activity patterns of both sexes of leopard differed significantly from that of spotted hyena. Note, sunrise is circa 06:00 and sunset is at circa 18:00. Sunset and sunrise vary little over the year at this latitude and is not believed to have important effects on our study system. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]


Male Leopard = 104 Yellow baboon = 198
Male Leopard
Yellow baboon
Δ = 0.38 (0.28–0.44), P < 0.001
Female Leopard = 98 Yellow baboon = 198
Female Leopard
Yellow baboon
Δ = 0.58 (0.46–0.64), P < 0.001
Male Leopard = 104 Ugogo dik–dik = 96
Male Leopard
Ugogo dik–dik
Δ = 0.62 (0.48–0.70), P < 0.001
Female Leopard = 98 Ugogo dik–dik = 96
Female Leopard
Ugogo dik–dik
Δ = 0.80 (0.69–0.89), P = 0.06
Male Leopard = 104 Spotted hyena = 128
Male Leopard
Spotted hyena
Δ = 0.66 (0.55–0.73), P < 0.001
Female Leopard = 98 Spotted hyena = 128
Female Leopard
Spotted hyena
Δ = 0.44 (0.31–0.50), P < 0.001
Male Leopard = 104 Female Leopard = 98
Δ = 0.72 (0.61–0.81), P < 0.001
Male Leopard
Female Leopard
Female Leopard = 98 Bushbuck = 321
Δ = 0.87 (0.81–0.95), P = 0.43
Female Leopard
Bushbuck
Density
Time
00:00
06:00
12:00
18:00
24:00

cycle compared with all its prey species. Male and female leopards also showed statistically different use of the diel cycle from each other (Fig. 2), and both sexes showed statistically different use of the diel cycle compared with spotted hyena, with female leopards being much more diurnal and overlapping temporally as little as 44% (Fig. 2).

Discussion

We investigated the activity patterns and temporal overlap between leopards, their prey and spotted hyenas, the only competitor carnivore in the Udzungwa Mountains. Confirming our predictions, we found that male and female leopards in the Udzungwa Mountains have significantly different activity patterns, with males being much more nocturnal (Fig. 2). Contrary to our prediction, spotted hyena showed significantly different activity pattern than both leopard sexes, with female leopards having the least temporal overlap (44%; Fig. 2). Our results contrast the findings of Hayward & Slotow (2009), who found that only the subordinate carnivore species (African wild dog and cheetah [*Acinonyx jubatus*]) exhibited scramble competition avoidance in the form of temporal partitioning from dominant intraguild predators (lion, leopard and spotted hyena). However, the dominant predators did not exhibit temporal partitioning among sexes (Hayward & Slotow, 2009). However, these findings are not directly comparable to the study system, given the lack, or sporadic presence of, lion, cheetah and African wild dogs in Udzungwa (Cavada *et al.*, 2019). Sexual segregation in activity patterns for leopards has never previously been studied, while dietary segregation between male and female leopards has only recently been assessed in a population in Namibia, with females having a broader dietary niche, indicating specialization on smaller prey (Voigt *et al.*, 2018). If dietary specialization also occurs for leopards in Udzungwa, it is possible that differences in activity patterns are mainly related to competition avoidance between dominant male leopard and subordinate female leopards (Hayward & Slotow, 2009; Havmøller, 2016). While leopards in Udzungwa exhibit cathemeral behaviour and showed statistically different use of the diel cycle compared with the majority of their prey (Fig. 2; Table 3), we note that we placed camera traps on wildlife trails to maximize leopard detections. Our findings reflect activity pattern overlap among animals using these trails and indicate temporal avoidance for most prey species, which has also been found for Sunda clouded leopard (Ross *et al.*, 2013). Leopards have rarely been found to be active at the same time as their main prey species (Hayward & Slotow, 2009), and in our case, female leopard use of the diel cycle did differ for all prey species except for two species, bushbuck, often predated by leopards in Udzungwa, and Ugogo dikdik, an unconfirmed leopard prey in Udzungwa (Havmøller, 2016), but confirmed in other areas (Hayward *et al.*, 2006). Hunting behaviour is rarely captured by camera traps, and given that leopards have an eclectic diet, and apply a plethora of hunting strategies, including stalking, opportunistically divebombing prey from a tree and ground ambush, it is extremely difficult to determine whether temporal overlap between leopards and a specific prey species is direct evidence of leopards targeting them. In this context, the low temporal overlap between leopards and yellow baboon is noteworthy and represents the least mean overlap in activity patterns with any species investigated (38 and 52% for male and female leopards, respectively; Table 3; Fig. 2). The distinct unimodal activity patterns of the yellow baboon observed in this study (Fig. 2) seems to support the predator avoidance hypothesis (Edmunds, 1974). Direct observations of leopards hunting primates in rainforests are limited, but two strategies appear to be applied: flushing the arboreal primates out of exposed tree onto the ground (Kingdon 1977), and waiting in ambush in dense vegetation until the primates descend to low hanging branches (Jenny & Zuberbuhler, 2005; Henschel, Abernethy & White, 2005). Despite the lack of knowledge on how leopards hunt arboreal species, primates and other fully arboreal species constituted 45% of the biomass consumed by leopards in the rainforests of Udzungwa (Havmøller, 2016).

Our results that female leopards are relatively more diurnal as a likely result of kleptoparasitism avoidance from the sympatric spotted hyenas matches results from a study in South

Table 3 Coefficient of overlap (Δ, estimated overlap; lcl, lower confidence level; ucl, upper confidence level) for male and female leopards against prey species derived from camera trapping in the Udzungwa Mountains, Tanzania

			♂ leopards (N = 104)				♀ leopards (N = 98)			
Scientific name	Common name	N	Δ	lcl	ucl	*P*	Δ	lcl	ucl	*P*
Bdeogale crassicauda	Bushy-tailed mongoose	411	0.64	0.54	0.71	<0.001	0.42	0.29	0.47	<0.001
Cephalophus harveyi	Harvey's duiker	1135	0.5	0.39	0.57	<0.001	0.72	0.64	0.8	<0.001
Cricetomys gambianus	Giant pouched rat	134	0.62	0.52	0.7	<0.001	0.42	0.27	0.46	<0.001
Genetta maculata	Blotched genet	114	0.67	0.55	0.74	<0.001	0.47	0.33	0.53	<0.001
Hystrix cristata	Crested porcupine	147	0.67	0.58	0.76	<0.001	0.47	0.34	0.53	<0.001
Madoqua kirkii	Ugogo dikdik	96	0.62	0.48	0.7	<0.001	0.8	0.69	0.89	0.06
Neotragus moschatus	Suni	199	0.78	0.68	0.86	<0.001	0.78	0.7	0.88	<0.001
Papio cynocephalus	Yellow baboon	198	0.38	0.28	0.44	<0.001	0.58	0.46	0.64	<0.001
Potamochoerus larvatus	Bushpig	241	0.69	0.57	0.77	<0.001	0.69	0.58	0.78	<0.001
Syncerus caffer	African buffalo	77	0.78	0.66	0.88	0.01	0.72	0.6	0.83	<0.001
Tragelaphus scriptus	Bushbuck	321	0.78	0.71	0.87	<0.001	0.87	0.81	0.95	0.43

N, number of independent events; *P* is a test probability that two sets of circular observations come from the same distribution.

Africa (Balme *et al.*, 2017). Male leopards might be less vulnerable to kleptoparasitism, and records exist of male leopards intentionally predating upon spotted hyenas (Bailey, 1995). Consequently, the diurnal behaviour of female leopards also makes them more prone to anthropogenic disturbances, such as poaching and firewood collection, as these human activities are more pronounced during daylight hours. Physical distance to potential sources of disturbances has been found to be the single most influential factor affecting leopard densities in Udzungwa (Havmøller *et al.*, 2019). While not specifically looking into differences in activity of sexes, leopards in Thailand were found to become much more diurnal with decreased anthropogenic activity (Ngoprasert, Lynam & Gale, 2017).

In conclusion, this study provides insight into the behavioural ecology of leopards in a system where leopards exhibit intraspecific competition and interspecific competition only with the spotted hyena. While our camera trap placement was specifically aimed at targeting large carnivores, limiting the effectiveness to study predator–prey interactions (Kays *et al.*, 2011), camera trapping remains a valid method for studying temporal partitioning within and between large sympatric carnivores. We found, for the first time to our knowledge, evidence of sexual segregation in activity patterns between male and female leopards, and very clear interspecific segregation in activity patterns with their only competitor in the Udzungwas, the spotted hyenas. Future studies should investigate temporal interactions between leopards, co-predators and prey species in different habitats (e.g. rainforest and savannah). Our study also highlights the potential vulnerability of unhabituated female leopards to diurnal anthropogenic disturbances, which should be taken into consideration for protected areas expanding their tourism activities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Time of sunset, sunrise, daylength and maximum difference in daylength from the village of Ifakara close to the study site in the Udzungwa Mountains in Tanzania, during the study period (Annonymous 2019).