Drivers of diurnal rest site selection by spotted hyaenas

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Abstract

Rest sites are key locations to many animals but their selection has been poorly studied in large carnivores. We investigated seasonal diurnal rest site selection by spotted hyaenas (*Crocuta crocuta*) in Hwange National Park, Zimbabwe. We assessed the effects on hyaena diurnal rest site selection of (1) distance to the nearest waterhole, as waterholes can be considered prey hotspots in the study ecosystem, (2) habitat type and vegetation characteristics, in particular visibility as it influences detection risk and shade for thermoregulation, (3) location within the core territory of their main competitor/predator, the African lion (*Panthera leo*), where encounter risk would be higher, (4) distance to the closest lion and (5) distance to the nearest road as they can facilitate travelling by carnivores. We defined rest sites as midday locations of hyaenas equipped with GPS collars. Hyaenas preferred to rest in woodland areas with low visibility, close to roads and far from a lion. Distance to the nearest waterhole and location within lion core territory did not affect hyaena rest site selection. Overall, our study points to the combined importance of the structure of the vegetation (providing safety and shade), the availability of roads (to move through and exploit this bushed environment) and the avoidance of proximity to lions.

Introduction

Rest site availability is known to be influential in the distribution and density of animals, particularly to nocturnal mammals that need to spend daylight in safe refuges (Freire, 2011). Rest sites are used for various activities, such as sleeping sites (e.g. Anderson, 1998; Li *et al.*, 2015), refuges (Emsens *et al.*, 2013), daytime shelters (Kowalczyk, Zalewski & Jêdrzejewska, 2004; Mysłajek, Nowak & Jędrzejewska, 2012) and daytime rest burrows (Endries & Adler, 2005). Rest sites are places of rest and not linked to reproduction unlike den sites (see Ruggiero, Pearson & Henry, 1998; Ye *et al.*, 2007; Ross *et al.*, 2010; Périquet *et al.*, 2016 for den site characteristics). Rest sites are also key locations for many animals as they influence the risks of predation and/or parasitism (Emsens *et al.*, 2013; Li *et al.*, 2015), maintain social bonds or territories (Anderson, 1998; Endries & Adler, 2005) and maximize access to food or water resources (Li *et al.*, 2015). A variety of factors may shape rest site selection. For example, species such as the American mink (*Mustela vison*) using rest sites above ground select denser areas for cover (Zabala, Zuberogoitia & Martinez-Climent, 2007), while species such as the Eurasian badger (*Meles meles*) select rest sites underground, in hollow trees or under dense vegetation (Kowalczyk *et al.*, 2004). The location of rest sites is thus rarely random (Freire, 2011) and understanding the factors affecting rest site selection is needed for an in-depth knowledge of species ecological requirements and ultimately for species management and conservation.

While spotted hyaena (*Crocuta crocuta*, hyaena hereafter) is the most numerous large predator in African savannas, little is known on rest site selection for this keystone species due to its status of apex predator (Estes *et al.*, 2011) and their role in ecosystems (Trinkel, 2009; Périquet, 2014). Hyaenas are typically active at night (Kruuk, 1972), their social life is centred on a communal den where they often rest during the day, but they are also known to spend the day in other resting places far from dens (Kruuk, 1972; Hofer & East, 1993; Stratford & Stratford, 2011). Here, we used data from seven GPS radio-collared adult female hyaenas in Hwange National Park, Zimbabwe, to identify diurnal rest sites (excluding communal den

sites), study their characteristics, and assess their selection by hyaenas (using a Resource Selection Function – RSF – approach). Prey spatial distribution is known to influence habitat selection in many birds and mammals (Orians & Wittenberger, 1991; Lima, 1998; Edwards *et al.*, 2002; Spong, 2002), Thus, to hyaenas resting close to prey-rich areas is likely to maximize access to resources (Li *et al.*, 2015). In the semi-arid savanna of Hwange National Park, large herbivores tend to aggregate around waterholes (Valeix, 2011), which can be considered prey hotspots, and consequently the spatial ecology of predators is largely influenced by waterholes (see Valeix *et al.*, 2010 for lions, *Panthera leo*, Périquet, 2014 for hyaenas) even more so during the dry season. While hyaenas are nocturnal foragers (Kruuk, 1972) and consequently expected to visit waterhole areas at night, resting near waterhole areas will allow them to minimizing the costs of foraging trips and maximizing access to resources. We thus predicted that hyaenas would preferentially rest in the vicinity of waterholes, especially during the dry season. Additionally, rest sites may be selected based on the capacity of the vegetation to provide shade and safety (see Meia & Weber, 1993 for foxes, *Vulpes vulpes*, Neal & Cheeseman, 1996 for badgers, Jerosch *et al.*, 2010 for wildcats, *Felis silvestris silvestris*). Unlike the Eurasian badgers or foxes, which use burrows for thermal benefits (Meia & Weber, 1993; Kowalczyk *et al.*, 2004), hyaenas' use of burrows is centred on communal dens whose shelter is solely for cub nurturing and protection and hyaena day rest sites are above-ground rest sites (Kruuk, 1972; Hofer & East, 1993). We thus expected that hyaenas would select rest sites based on vegetation structure. Essentially, they would select woodland and wooded bushland, which provide shade for thermoregulation, and particularly in areas of low visibility to avoid being detected by competitors or predators. The selection for a given type of habitat might also be influenced by season, as during the wet season, shade will be readily available, while as the vegetation dries out and leaves start falling, denser canopy will be need to provide more shade. Although animals are known to avoid roads in areas where they are intensively used by humans (Whittington, St Clair & Mercer, 2005; Nellemann *et al.*, 2007), earlier studies on hyaenas (Kruuk, 1972) indicated they have a strong tendency to follow roads in ecosystems where roads are not busy, and particularly in bushed ecosystems. Because Hwange National Park is a wooded savanna with a very low road traffic, we therefore expected hyaenas to select rest sites close to roads.

Finally, with lions being their main competitor, and potentially dangerous for hyaenas through intraguild-predation (Périquet, Fritz & Revilla, 2015), their presence is likely to affect hyaena spatial behaviour (see also du Preez *et al.*, 2015 for a similar effect in leopards, *Panthera pardus*). Even though the two predators are not very active during the day, and hence the risk of encounter is low, resting near lions would increase the probability of encounter when both predators start moving again in the late afternoon. We thus tested whether hyaenas select rest sites outside lion core territories to minimize the probability of encounters with them (long-term risk of encountering a lion). We also expected hyaenas to avoid resting in areas where lions had been recently (short-term risk of

encountering a lion). We further expected hyaenas to rest in denser vegetation when the risk of encountering lions was high.

Materials and methods

Study area

This study was conducted in the Main Camp area (c.a. 1500 km²) of Hwange National Park (14 600 km²), located in north-western Zimbabwe (19°00′S, 26°30′E). Main Camp area is characterized by Kalahari sandy soils (Rogers, 1993). The vegetation is primarily woodland and bushland savanna, interspersed with small patches of grassland. The Hwange ecosystem is a semi-arid area with a mean annual rainfall of 600 mm over the past century (coefficient of variation=25%) and a wet season that stretches from October to April (Chamaillé-Jammes, Fritz & Murindagomo, 2006). October is the hottest month with a mean daily temperature of 33.2°C, whereas July is the coldest month with a mean daily temperature of 4.1°C. During the early dry season (May to August), frost is an occasional event. Availability of water to animals is primarily from rainwater collected in natural depressions that dry up as the dry season progresses, as well as perennial artificial waterholes sustained by diesel, solar and wind powered water pumps. Lion and hyaena densities in the study area are estimated to be approximately 4.3 individuals/100 km² (Loveridge *et al.*, 2016) and 9 individuals/100 km² (Périquet, 2014) respectively. Wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*) and leopards are also present in the study area. The most common resident prey species for hyaenas with densities above 1 individual/km² are impala (*Aepyceros melampus),* steenbok (*Raphicerus campestris*), greater kudu (*Tragelaphus strepsiceros),* buffalo (*Syncerus caffer)* and plains zebra (*Equus quagga*) (Chamaillé-Jammes *et al.*, 2009).

Hyaena GPS data and random locations

From July 2009 to October 2013, seven adult female hyaenas belonging to three different clans (one clan was equipped with three collars and the others had two, estimated number of individuals per clan was 11, 16 and 26) were fitted with GPS collars (African Wildlife Tracking, UHF 407, GPS/VHF). Dominant females were targeted for collaring due to hyaenas matriarchal hierarchy and in order to limit behavioural variations between individuals. Hyaenas were immobilized from a distance of 15 to 20 m by a professional team either with a standard mix of 500 mg Ketamine (Kyron laboratories Pvt. Ltd, Ben- rose, RSA, powder diluted at 250 mg ml^{-1}) and 200 mg Xylazine (Rompun; Bayer, Leverkusen, Germany, powder diluted at 200 mg ml^{-1}) or of 80 mg Zoletil (Virbac RSA, Halfway house, RSA, powder diluted at 100 mg ml^{-1}) and 4 mg Metedomidine (Zalopine, Wildlife Pharmaceuticals, Karino, RSA, 20 mg ml^{-1}). Drugs were then reversed with 16 mg of Yohimbine (Rx drug, Kyron Labs, Benrose, RSA, 6.25 mg ml^{-1}). Full recovery was ensured by staying with the animal until it would walk away normally. Permits were provided by the Zimbabwe Parks and Wildlife Management

Authority and relevant animal care protocols were followed during capture and collaring of carnivores (Wildlife Drugs Sub-committee of the Drugs Control Council of Zimbabwe and Zimbabwe Veterinary Association). Collars were replaced or removed within the framework of long-term monitoring protocols. Collars were programmed to take hourly fixes at night between 6 PM to 8 AM and three locations during the day at 8 AM, 12 PM and 4 PM. We defined diurnal rest sites as (and collected data from) midday locations of days when the net displacement between the 8 AM and 4 PM fixes was less than 50 m. Due to logistical reasons, we only studied rest sites within 2 km of a road, in two seasons (the wet season from January to April and the early dry season from May to July of the year 2014). Ninety diurnal rest sites were visited on foot. To assess diurnal rest site selection, we compared their characteristics to random locations generated within hyaena clan territories. Clan territories were defined as 95% isopleths of location-based kernels using all the GPS locations of the

collared individuals belonging to a given clan and using the reference smoothing factor h_{ref} as recommended by Hemson *et al.* (2005). We generated random locations within each clan territory and visited 69 of them (16, 21 and 32 locations per clan respectively) selected at random and all located within 2 km of a road (Fig. 1).

Environmental characteristics

Habitat type at each site (rest or random) was categorized as grassland, bushland, wooded bushland or woodland following definitions by Davidson *et al.* (2012). The visibility at each site was assessed using a 50 cm × 50 cm white board attached to a pole and set at 10–60 cm corresponding to the height of a resting hyaena. One person (observer) crouched at the rest site simulating a resting hyaena while a second person walked away from the site, holding the visibility board behind at 10–60 cm in each of the four cardinal directions. The board was always held
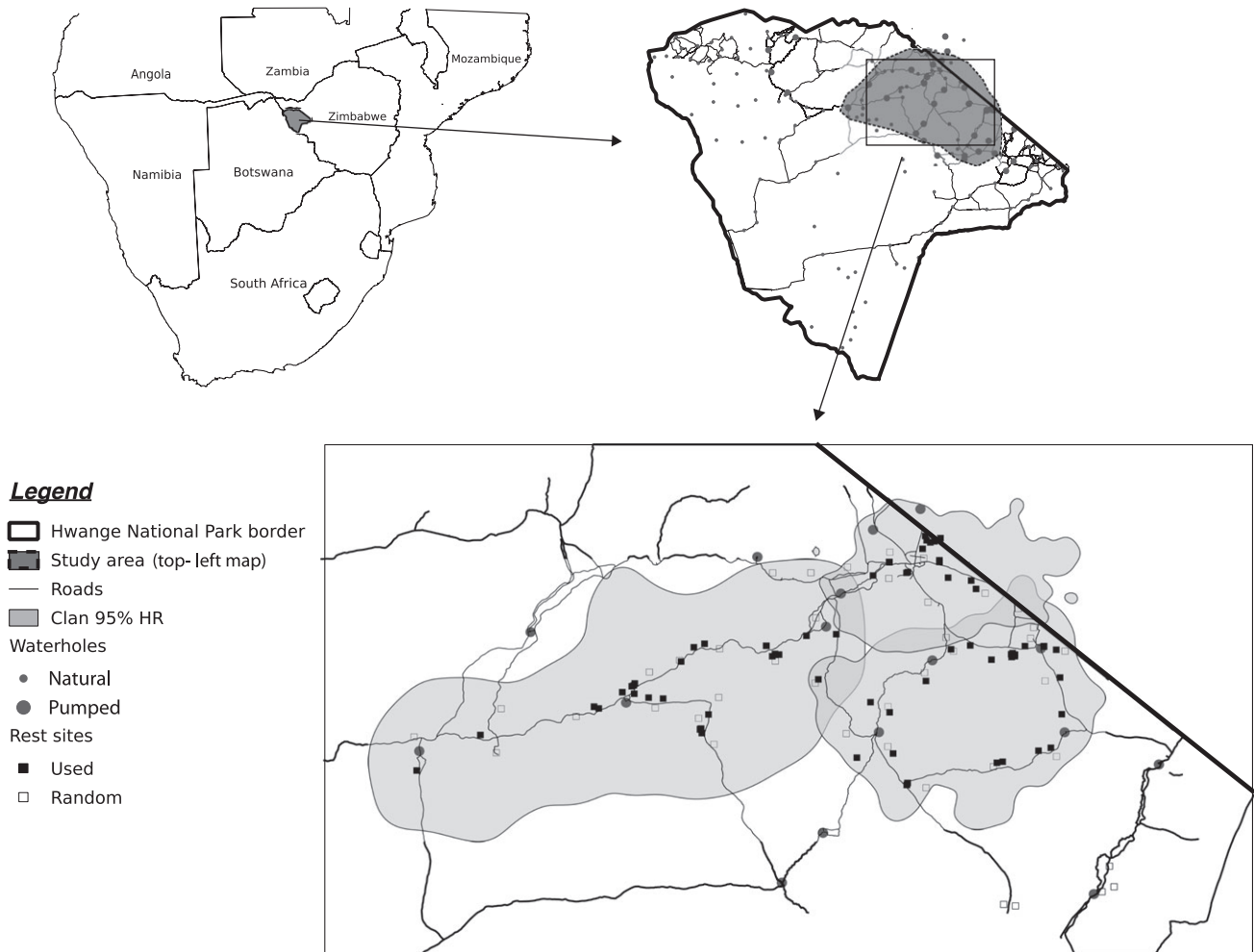

Figure 1 Map of the study area in the Main Camp area of Hwange National Park, Zimbabwe. Used rest sites are represented as black squares, while random locations are empty squares. The dotted polygon on the top left map showed the area where lion movement were intensively monitored.

perpendicular to the direction walked so that the observer could potentially see the entire board. The distance at which the board could no longer be seen was measured using the number of steps from the observer (each step was calibrated to be one metre). The distances in each cardinal direction were then averaged to give a mean visibility measure at each site. Distances to the closest waterhole and to the closest road were extracted in QGIS from existing GIS layers. Average distance between waterholes was 6.4 ± 3.1 km (1.7–12.9 km).

Shade Availability

Shade availability at each diurnal rest site was assessed along 25 m line transects from the central point (i.e. rest site) in all the cardinal and ordinal directions. Twenty-five metres was considered a sensible radius to describe microhabitat characteristics around the rest site. An observer walking along these eight transects estimated shade scores for every 5 m by assessing the percentage of canopy/bush cover within a radius of 3 m. Because we did not measure the actual shade on the ground, this measure of shade was independent of the time of day at which it was estimated. A shade scoring system with 0 (representing not more than 20% canopy/bush cover), 0.5 (having 25–50% of canopy/bush cover) and 1 (more than 50% canopy/bush cover) was used. The 40 shade scores (for each site) were then averaged to produce an average shade score for that site. Shade availability was not determined for the random sites and thus was not included in rest site selection analysis.

Lion data

During the course of the study, 43 lions were equipped with GPS collars (see Benhamou *et al.*, 2014; and Périquet *et al.*, 2016 for temporal overlap between hyaena and lion GPS data), 35 (11 females and 24 males) of which had overlapping territories with hyaenas. Collars were set up to record hourly position between 6 PM and 8 AM. At least one individual per pride was collared in the study area and since individuals from the same pride spend most of their time together, their locations reflect those of the entire pride (Valeix *et al.*, 2009). We selected all lion GPS data in the year preceding our first rest site sampled, up to the time the latest rest site was used, and we built lion Movement based Kernels Density Estimator (MKDE) for GPS data from each collared lion. MKDE were built using the R software version 3.2.2 (R Core Team 2016) using the 'BRB.D' function from the package 'adehabitatHR' (Calenge, 2006). A given site (diurnal rest site or random) was considered as located within a lion core territory if it was located at least within one lion 50% isopleth. This is considered as a proxy of the long-term risk of encountering a lion.

In addition, we computed the distances of lions equipped with GPS collars to each hyaena rest site located in the study area during morning hours (between 5 and 8 AM, four locations per lion). The shortest distance was then used as a proxy of the short-term risk of encountering a lion at a given rest site (distance to lion hereafter). We divided distances to lion into four classes: 0–2 km, 2-5 km, 5–10 km and >10 km for the subsequent analyses.

Statistical analyses

All analyses were conducted in R (R Core Team 2016). Data exploration was conducted based on the guidelines described in Zuur, Ieno & Elphick (2010). Model assumptions were confirmed by plotting residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model (Zuur & Ieno, 2016).

We preliminarily investigated the link between mean shade and habitat type (89 locations) and mean visibility distance and habitat type (159 locations) using linear models. Grassland was not included in any analysis involving habitat type as only one rest site was in grassland. Mean visibility distance was log-transformed to meet model assumptions.

We used a Fisher exact test to compare the distribution of the rest sites depending on the distance to lion to a uniform distribution (equal number of rest sites in each category of distance to lion). We further used a Linear Mixed effects Model (LMM) to test the effect of distance to lion (four categories) on the visibility at rest sites. We included clan as a random effect and visibility was log-transformed to meet model assumptions.

We used logistic regressions to develop resource selection functions (RSF) with the dependent variable being 1 for diurnal rest sites used by hyaenas and 0 for random sites. We used a Generalized Linear Mixed effect Model (GLMM) with a binomial distribution, logit link function, and clan identity included as a random effect to study the effects of different parameters on the probability of a site being selected as a rest site by hyaenas. We included vegetation type, mean visibility distance, distance to the closest artificial water, distance to the closest road and location within at least one lion core territory as simple main effects. We also included the following interactions: season × vegetation type, season × distance to water and mean visibility × location within lion core territory. We found no evidence of collinearity between the variables included in the model. RSFs were conducted using the package 'lme4' (Bates *et al.*, 2015). We tested the goodness of fit of our model using a Likelihood Ratio Test (LRT) comparing each model to a null model with the same random effect structure (when applicable) and including only the intercept.

Results

Diurnal rest site description

We visited a total of 90 diurnal rest sites used by hyaenas, including 45 during the wet and 45 during the early dry season (Fig. 1). The number of rest sites investigated per clan was 29, 30 and 31. Rest sites were mostly located in wooded bushlands (45.6%, *n* = 41) and woodlands (36.7%, *n* = 33). Fifteen (16.7%) rest sites were in bushlands and only one (1.1%) in grassland. The average shade score within a 25 m radius of rest sites was 0.56 ± 0.16 (range: 0.03–0.84). LRT showed that habitat type had a significant effect on the mean shade (*F* statistic=8.0, *P* < 0.001) at rest sites. The mean shade was significantly higher in woodlands (0.64 ± 0.12), than bushlands (0.54 ± 0.13, *t* = −2.3, *P* = 0.03) and wooded bushlands (0.50 ± 0.17, *t* = −4.2,

$P < 0.001$), with no significant difference in shade between the two latter habitats. The only rest site located in grassland had a shade score of 0.2. On average, rest sites were located 3.3 ± 1.7 km (range: 0.7–7.7 km) from a waterhole and 331 ± 216 m (37–991 m) from a road. The mean visibility distance around rest sites was 21.2 ± 9.7 m (8.8–60 m). Habitat type had no significant effect on mean visibility distance (LRT F statistic=2.5, $P = 0.07$).

Half of the rest sites (51.1%, $n = 46$) were located within at least one lion core territory. Rest site distribution in terms of distance to lion was not uniform (Fisher's exact test $P < 0.001$) and 89% ($n = 80$) rest sites were located more than 5 km away from any early morning lion location (Fig. 2a), with only 4.4% ($n = 4$) within 1 km of a lion location (Fig. 2a). The LMM including distance to lion as a fixed effect was significantly better than the null model at explaining visibility at rest sites (LRT: $\chi^2=8.9$, d.f.=3, $P = 0.03$) with distance to lion having an overall significant effect on visibility at rest sites ($F_{3,86}=3.0$, $P = 0.04$). However, the only significant difference was between the 0–2 km and >10 km classes ($t = 2.1$, $P = 0.04$, Fig. 2b).

Diurnal rest site selection

The model built was significantly better than the null model at explaining pattern of diurnal rest site selection by hyaenas (LRT: $\chi^2=66.4$, d.f.=11, $P < 0.001$). We found that visibility, distance to the closest road, habitat type and its interaction with season influenced the probability of a site being selected by hyaena to rest during the day. The location within a lion core territory did not affect the probability of selection (Table 1). Overall, hyaenas were more likely to select for sites located in woodland compared to bushlands and other vegetation types (Table 1, Fig. 3), and the probability of selection of a site in bushlands was lower during the wet compared to the early dry season (Table 1, Fig. 3). Hyaenas had a higher probability of using sites with low mean visibility distance and close to a road (Table 1, Fig. 4) to rest during the day.

Discussion

Our results revealed an effect of the short-term risk of encountering a lion (i.e. lion presence during the last hours of the preceding night) on hyaena rest site location and of the vegetation characteristics of these rest sites. Our study further showed that the probability of a site being selected as a diurnal rest site by hyaenas was influenced by visibility, habitat type and its interaction with season, and distance to the closest road. Contrary to our predictions, we found no effect of the long-term risk of encountering a lion (i.e. within a lion core territory) or of the distance to water on the patterns of rest site selection. Even though previous studies showed different movement patterns between sexes (Boydston *et al.*, 2003a,b), we believe that competition for rest sites is unlikely to occur as Hwange National Park is densely wooded (providing many shade and concealment opportunities) and therefore do not expect any difference in terms of rest site selection nor response to lion presence between sexes.
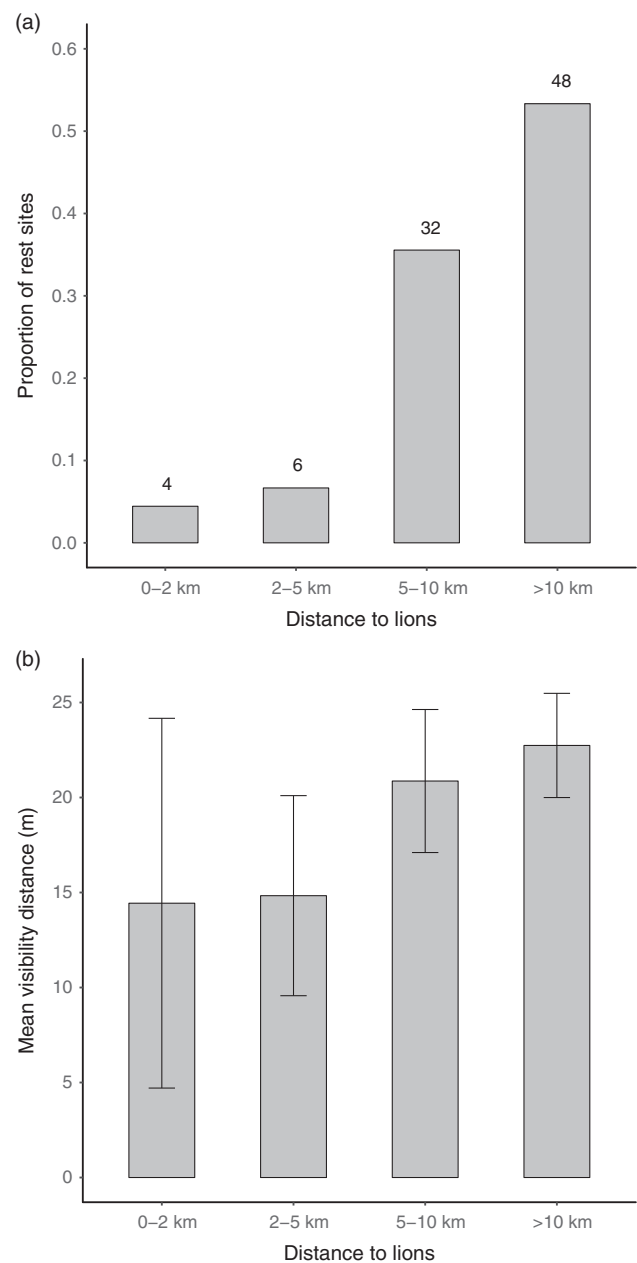

Figure 2 Distribution of (a) rest sites and (b) mean visibility distance in function of the closest distance to early morning lion locations. Numbers above bars represent sample size and error bars represent 95% confidence intervals.

Several studies have already highlighted the important role of vegetation characteristics in rest site selection by various mammals (Zabala *et al.*, 2007; Carter *et al.*, 2010; Jerosch *et al.*, 2010; Stratford & Stratford, 2011; Mysłajek *et al.*, 2012). We found that rest sites were mostly situated in wooded bushlands and woodlands (82.3% of the study rest sites were in these habitat types) and that hyaenas particularly selected for woodlands. This is consistent with the fact that

Table 1 Parameter estimates for diurnal rest site selection by spotted hyaenas in Hwange National Park, Zimbabwe. Parameters having a significant effect are represented in italic lettering

Variable	Estimate	Std. Error	Z value	Pr(>|z|)
Bushland (Intercept)	4.03	1.27	3.18	0.001
Woodland	2.67	0.96	2.79	0.005
Wooded bushland	−0.59	0.82	−0.73	0.47
Mean visibility	−0.05	0.02	−2.32	0.02
Distance to water	−0.32	0.21	−1.52	0.13
Distance to road	−0.004	0.001	−3.69	0.0002
Lion core territory	1.35	1.02	1.33	0.18
Bushland × wet season	−3.39	1.35	−2.51	0.01
Woodland × wet season	1.00	1.26	0.80	0.43
Wooded bushland × wet season	2.04	1.07	1.91	0.06
Distance to water × wet season	0.49	0.26	1.91	0.05
Visibility × lion core territory	−0.05	0.04	−1.34	0.17
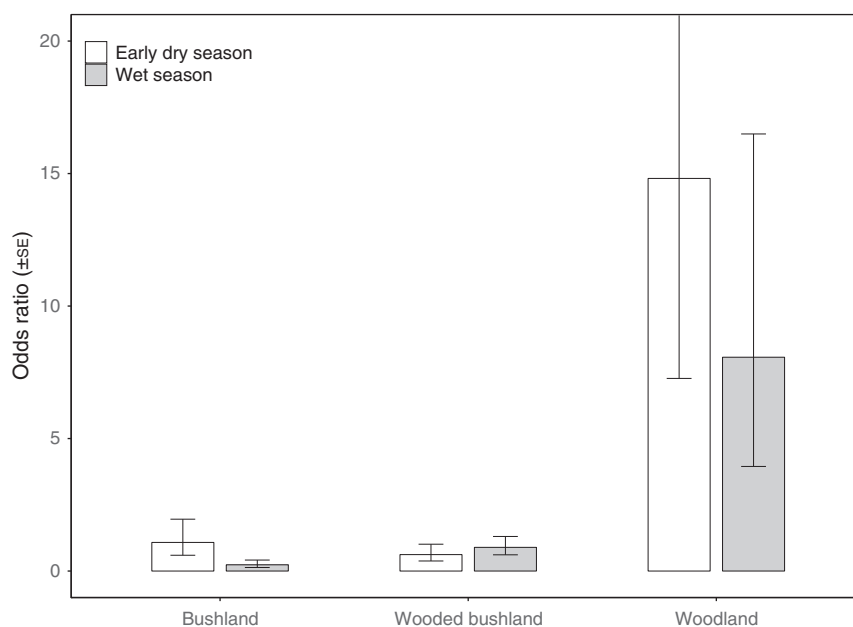
Figure 3 Effect of the interaction between habitat type and season on rest site selection by spotted hyaenas in Hwange National Park, Zimbabwe. The plot is truncated for extremely high values of standard errors for woodland in early dry season (upper CI reaches a maximum of 30.2).

woodlands are the habitat type that provides the most shade needed for thermoregulation. Indeed, diurnal temperature often exceeds body temperature and selection for shade is an important behavioural adjustment of large mammals in hot ecosystems such as African savannas (see Mole *et al.*, 2016 for an example on African elephants *Loxodonta africana*, Trethowan *et al.*, 2017 for lions). Similar patterns have been observed in the Ongava game reserve (Namibia) where hyaenas have been showed to avoid sites such as hilltops which expose them to weather elements (Stratford & Stratford, 2011). Hyaenas selected sites with lower visibility, probably to enhance concealment for safety reasons, as observed in wild dogs (van der Meer *et al.*, 2013).

While we had expected distance to water to be a determinant of hyaena rest site selection, our findings did not support that expectation. It should be noted, however, that the study was carried out during the first half of the year when surface water is widely available, likely reducing the importance of waterholes. Hence, there is a need to study the influence of distance to water during the driest months of the year as we would expect a stronger effect due to the impact of waterholes on prey distribution and the need for water (for drinking and thermoregulation purposes) would be greater. However, hyaenas might not prefer to rest close to waterholes in order to avoid being detected by prey in the vicinity where they may hunt in the evening.
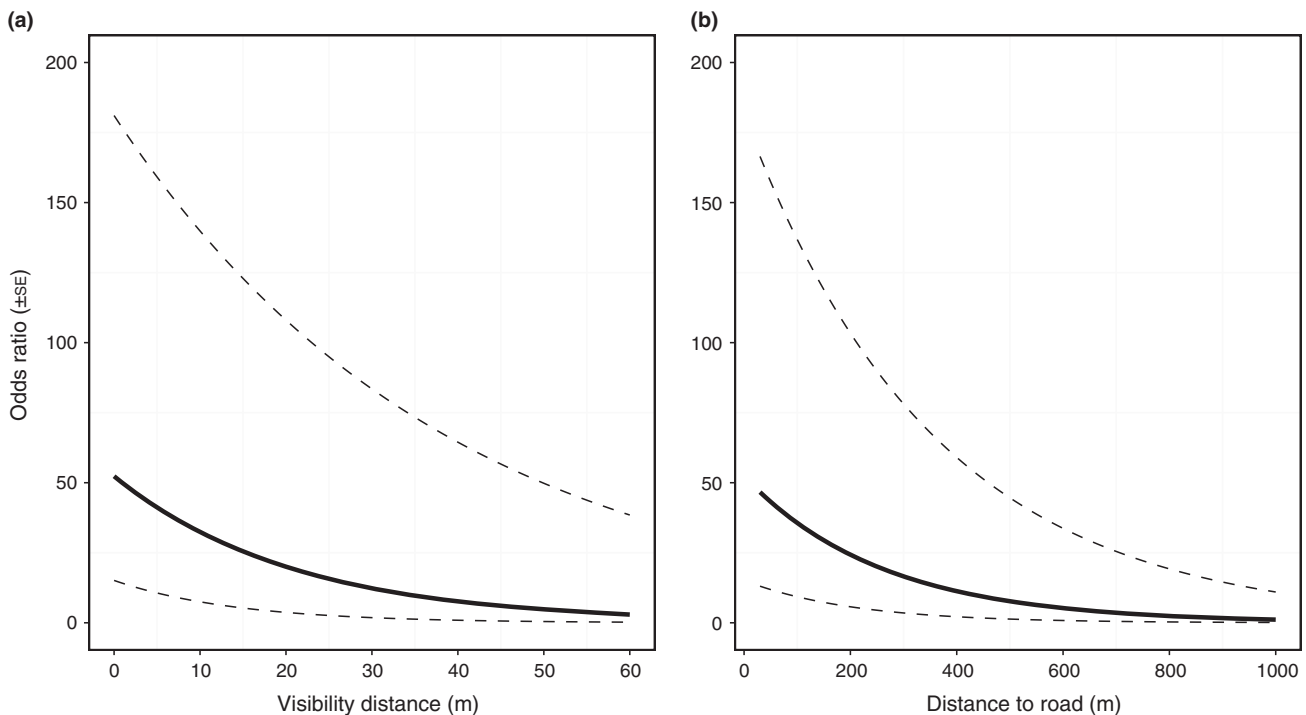
(a)

(b)

Figure 4 Effect of (a) mean visibility distance and (b) distance to the closest road on rest site selection by spotted hyaenas in Hwange National Park, Zimbabwe.

Results from this study suggest that hyaenas prefer to rest close to roads although our findings might only apply to rest sites within 2 km of the roads. While roads are known to have several negative effects on animal ecology (mortality due to vehicle collisions, noise disturbance, altered movement patterns, Trombulak & Frisell, 2000), some studies have suggested that they also allow animals to move faster and more easily (e.g. Whittington *et al.*, 2005 for wolves, *Canis lupus*). Hence, it is not surprising that a cursorial predator such as the hyaena rests near roads. Our result contrasts with observations from Stratford & Stratford (2011) who found that hyaenas avoided using existing road networks and those frequently used by vehicles, with the exception of cleared paths in rarely frequented areas. Our study was carried out in a period characterized by very low tourism intensity, and thus unlikely to significantly disturb hyaenas resting near roads. Additionally, roads in Hwange National Park often follow vlei lines, which are characterized by rich grasslands, attractive for grazing prey species. Rest site proximity to roads could thus be linked to prey richness in these areas.

The presence or absence of lions in an area was expected to have a strong influence on rest site selection by hyaenas. However, our results revealed that hyaenas did not avoid sites located within lion core territory. These findings are consistent with the fact that most hyaena den sites were also located within lion core territory and that the long-term risk of encountering a lion did not affect their den selection (Périquet *et al.*, 2016). Our results suggest that the short-term rather than the long-term risk of encountering a lion affected hyaena rest site

selection. This reactive rather than predictive response to lion presence has also been highlighted by Périquet (2014), suggesting that interactions between hyaenas and lions are complex and dynamic. A similar observation was made on the reaction from cheetahs and leopards to lions (Broekhuis *et al.*, 2013; du Preez, 2014). We found that many of the rest sites were located in areas with no lions in the vicinity in the early morning and for the few rest sites used where lions were close by in the morning, vegetation density was high, providing cover and concealment to hyaenas. In conclusion, our study showed that hyaena diurnal rest site selection is mostly driven by habitat features (visibility, distance to road and habitat type linked to shade availability) with a negative effect of the short-term risk of encountering a lion, but neither the abundance of their prey (proxy: distance to waterhole) nor the long-term risk of encountering a lion had an effect. We encourage future studies using similar methods to identify the factors influencing rest site selection in spotted hyaenas at different locations and in other species.

Acknowledgements

References

Anderson, J. R. (1998). Sleep, sleeping sites and sleep-related activities: awakening to their significance. *Am. J. Primatol.* **46**, 63–75.

Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Softw.* **67**, 1–48.

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W. & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Anim. Behav.* **90**, 171–180.

Boydston, E. E., Kapheim, K., Szykman, M. & Holekamp, K. E. (2003a). Individual variation in space use by female spotted hyenas. *J. Mammal.* **84**, 1006–1018.

Boydston, E. E., Kapheim, K., Watts, H. E., Szykman, M. & Holekamp, K. E. (2003b). Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* **6**, 207–219.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W. & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *J. Anim. Ecol.* **82**, 1098–1105.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516–519.

Carter, N. H., Brown, D. G., Etter, D. R. & Visser, L. G. (2010). American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. *Ursus* **21**, 57–71.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2006). Spatial patterns of the NDVI-rainfall relationship at the seasonal and interannual time-scales in an African savanna. *Int. J. Remote Sens.* **27**, 5185–5200.

Chamaillé-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F. & Fritz, H. (2009). Seasonal density estimates of common large herbivores in Hwange National Park Zimbabwe. *Afr. J. Ecol.* **47**, 804–808.

Davidson, Z., Valeix, M., Loveridge, A. J., Hunt, J. E., Johnson, P. J., Madzikanda, H. & Macdonald, D. W. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *J. Mammal.* **93**, 677–685.

Edwards, G. P., De Preu, N., Crealy, I. V. & Shakeshaft, B. J. (2002). Habitat selection by feral cats and dingoes in a semi-arid woodland environment in central Australia. *Austral Ecol.* **27**, 26–31.

Emsens, W., Suselbeek, L., Hirsh, B. T., Kays, R., Winkelhagen, A. J. S. & Jansen, P. A. (2013). Effects of food availability on space and refuge use by a neotropical scatterhoarding rodent. *Biotropica* **45**, 88–93.

Endries, M. J. & Adler, G. H. (2005). Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), in Panama. *J. Zool.* **265**, 147–155.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D. & Jackson, J. B. (2011). Trophic downgrading of planet earth. *Science* **333**, 301–306.

Freire, S. I. M. (2011) *Day resting site use and fidelity of Alpine otters (Lutra lutra) on southeast Austria*. PhD Thesis, University of Lisbon.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. & MacDonald, D. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol.* **74**, 455–463.

Hofer, H. & East, M. L. (1993). The commuting system of the Serengeti spotted hyenas: how a predator copes with migrating prey. III Attendance and maternal care. *Anim. Behav.* **46**, 575–589.

Jerosch, S., Go¨tz, M., Klar, N. and Mechthild, R. (2010) Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): implications for its conservation *J. Nat. Conserv.*, **18**, 45–54.

Kowalczyk, R., Zalewski, A. & Jêdrzejewska, B. (2004). Seasonal and spatial pattern of shelter use by badgers *Meles meles* in Bialowieza Primeval Forest (Poland). *Acta Theriol.* **49**, 75–92.

Kruuk, H. (1972). *The spotted hyena: a study of predation and social behavior*. Chicago: University of Chicago Press.

Li, D., Zhou, Q., Tang, X., Huang, H. & Huang, C. (2015). Sleeping site use of the white-headed langur *Trachypithecus leucocephalus*: the role of predation risk, territorial defense, and proximity to feeding sites. *Curr. Zool.* **57**, 260–268.

Lima, S. L. (1998). Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.* **27**, 215–290.

Loveridge, A. J., Valeix, M., Chapron, G., Davidson, Z., Mtare, G. & Macdonald, D. W. (2016). Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. *Biol. Conserv.* **204**, 247–254.

van der Meer, E., Mpofu, J., Rasmussen, G. S. A. & Fritz, H. (2013). Characteristics of African wild dog natal dens selected under different interspecific predation pressures. *Mamm. Biol.* **78**, 336–343.

Meia, J. S. & Weber, J. M. (1993). Choice of resting sites by female foxes *Vulpes vulpes* in a mountaneous habitat. *Acta Theriol.* **38**, 81–91.

Mole, M. A., DÁraujo, S. R., vanAarde, R. J., Mitchell, D. and Fuller, A. (2016) Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. *Conserv. Physiol.* **4**, 1–11.

Mysłajek, R. W., Nowak, S. & Jędrzejewska, B. (2012). Distribution, characteristics and use of shelters by the Eurasian

badger *Meles meles* along an altitudinal gradient in the Western Carpathians S Poland. *Folia Zool.* **61**, 152–160.

Neal, E. and Cheeseman, C. (1996) *Badgers*. London: Poyser.

Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B. P., Martin, J. & Ordiz, A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biol. Conserv.* **138**, 157–165.

Orians, G. H. & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat selection. *Am. Nat.* **137**, 29–49.

Périquet, S. (2014) *Sharing the top: How do Spotted hyaenas cope with Lions? Apex predator coexistence in a wooded savanna*. PhD Thesis, Université Claude Bernard Lyon 1.

Périquet, S., Fritz, H. & Revilla, E. (2015). The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biol. Rev.* **90**, 1197–1214.

Périquet, S., Mapendere, C., Revilla, E., Banda, J., Macdonald, D. W., Loveridge, A. J. & Fritz, H. (2016). A potential role for interference competition with lions in den selection and attendance by spotted hyaenas. *Mamm. Biol.* **81**, 227–234.

du Preez, B. D. (2014) *The impact of intraguild competition with lion Panthera leo on leopard Panthera pardus behavioural ecology*. PhD Thesis, University of Oxford, UK.

du Preez, B., Hart, T., Loveridge, A. J. & Macdonald, D. W. (2015). Impact of risk on animal behaviour and habitat transition probabilities *Anim. Behav*. **100**, 22–37.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rogers, C. M. L. (1993). *A woody vegetation survey of Hwange National Park*. Harare, Zimbabwe: Department of National Parks and Wildlife Management Authority.

Ross, S., Kamnitzer, R., Munkhtsog, B. & Harris, S. (2010). Den-site selection is critical for Pallas's cats (*Otocolobus manul*) *Can. J. Zool.* **88**, 905–913.

Ruggiero, L. F., Pearson, D. E. & Henry, S. E. (1998). Characteristics of American marten den sites in Wyoming. *J. Wildl. Manage.* **62**, 663–673.

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behav. Ecol. Sociobiol.* **52**, 303–307.

Stratford, K. J. & Stratford, S. M. (2011). Fine-scale movements and use of space by spotted hyaena (*Crocuta crocuta*) on Ongava Game Reserve Namibia. *Afr. J. Ecol.* **49**, 343–352.

Trethowan, P., Fuller, A., Haw, A., Hart, T., Markham, A., Loveridge, A. J., Hetem, R., Preez, B. & Macdonald, D. W. (2017). Getting to the core: internal body temperatures help reveal the ecological function and thermal implications of the lions' mane. *Ecol. Evol.* **7**, 253–262.

Trinkel, M. (2009). A keystone predator at risk? Density and distribution of the spotted hyena (*Crocuta crocuta*) in the Etosha National Park, Namibia. *Can. J. Zool.* **87**, 941–947.

Trombulak, S. C. & Frisell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* **14**, 18–30.

Valeix, M. (2011). Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park Zimbabwe. *J. Trop. Ecol.* **27**, 163–170.

Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**, 23–30.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D. W. (2010). How key habitat features influences large terrestrial carnivore movements: waterholes and African lions in a semi arid savanna of north-western Zimbabwe. *Landscape Ecol.* **25**, 337–351.

Whittington, J., St Clair, C. C. & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecol. Appl.* **15**, 543–553.

Ye, X., Yong, Y., Yu, C. & Zhang, Z. (2007). Den selection by the giant panda in Foping Nature Reserve China. *J. Nat. His.* **41**, 2529–2536.

Zabala, J., Zuberogoitia, L. & Martinez-Climent, J. A. (2007). Winter habitat preferences of feral American mink *Mustela vison* in Biscay Northern Iberian Peninsula. *Acta Theriol.* **52**, 27–36.

Zuur, A. F. & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.* **7**, 636–645.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14.