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 (i) distance to the nearest waterhole, as waterholes can be considered prey hotspots in the study ecosystem, (ii) habitat type and vegetation characteristics, in particular visibility as it influences detection risk and shade for thermoregulation, (iii) location within the core territory of their main competitor/predator, the African lion (*Panthera leo*), where encounter risk would be higher, (iv) distance to the closest lion, and (iv) 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.

Key words: *Crocuta crocuta*, habitat, intraguild interactions, *Panthera leo*, shade, visibility

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), day time 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 2014a). 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 2014b 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. Whereas 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 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), and in areas with high 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. 1 500 km²) of Hwange National Park (14 600 km^2), 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 in 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 km^2 (Loveridge *et al.* 2016) and 9 individuals/100km^2 (Périquet 2014b) 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/km^2 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 3 collars and the others had 2, 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) and 200 mg Xylazine (Rompun; Bayer, Leverkusen, Germany, powder diluted at 200 mg/ml) or of 80 mg Zoletil (Virbac RSA, Halfway house, RSA, powder diluted at 100 mg/ml) and 4 mg Metedomidine (Zalopine, Wildlife Pharmaceuticals, Karino, RSA, 20 mg/ml). Drugs were then reversed with 16 mg of Yohimbine (Rx drug, Kyron Labs, Benrose, RSA, 6.25 mg/ml). 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 – April and the early dry season from May – 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 categorised 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 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 meter). 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. 25 m 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 and 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 on 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 Generalised 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. RSF 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: χ^2=8.9, df=3, p=0.03) with distance to lion having an overall significant effect on visibility ($F_{3,86}$=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: χ^2=66.4, df=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, Boydston *et al.*

2003b), 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.

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 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 for 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.

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 and 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 (2014b), 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 where 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.

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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 captions

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.

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.

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).

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.

Figure 1

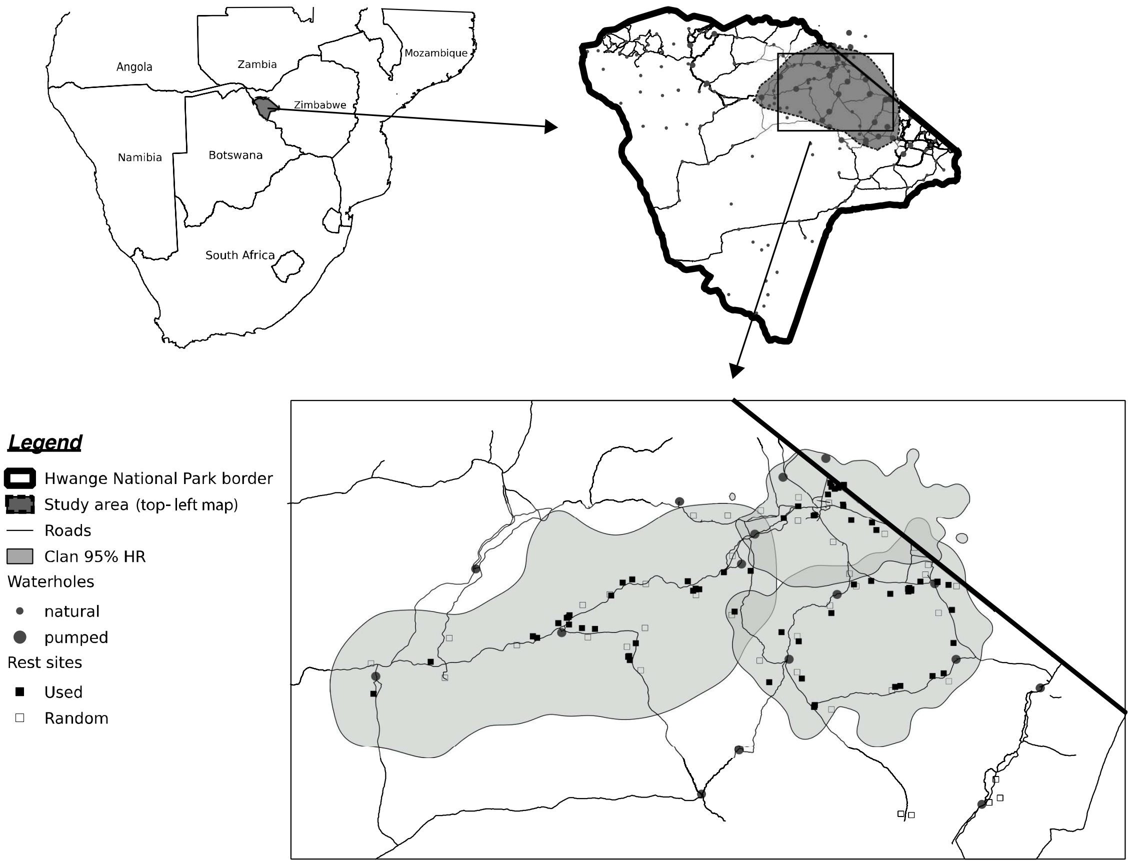

Angola
Zambia
Mozambique
Zimbabwe
Namibia
Botswana
South Africa
Legend
Hwange National Park border
Study area (top- left map)
Roads
Clan 95% HR
Waterholes
natural
pumped
Rest sites
Used
Random

Figure 2

a

b

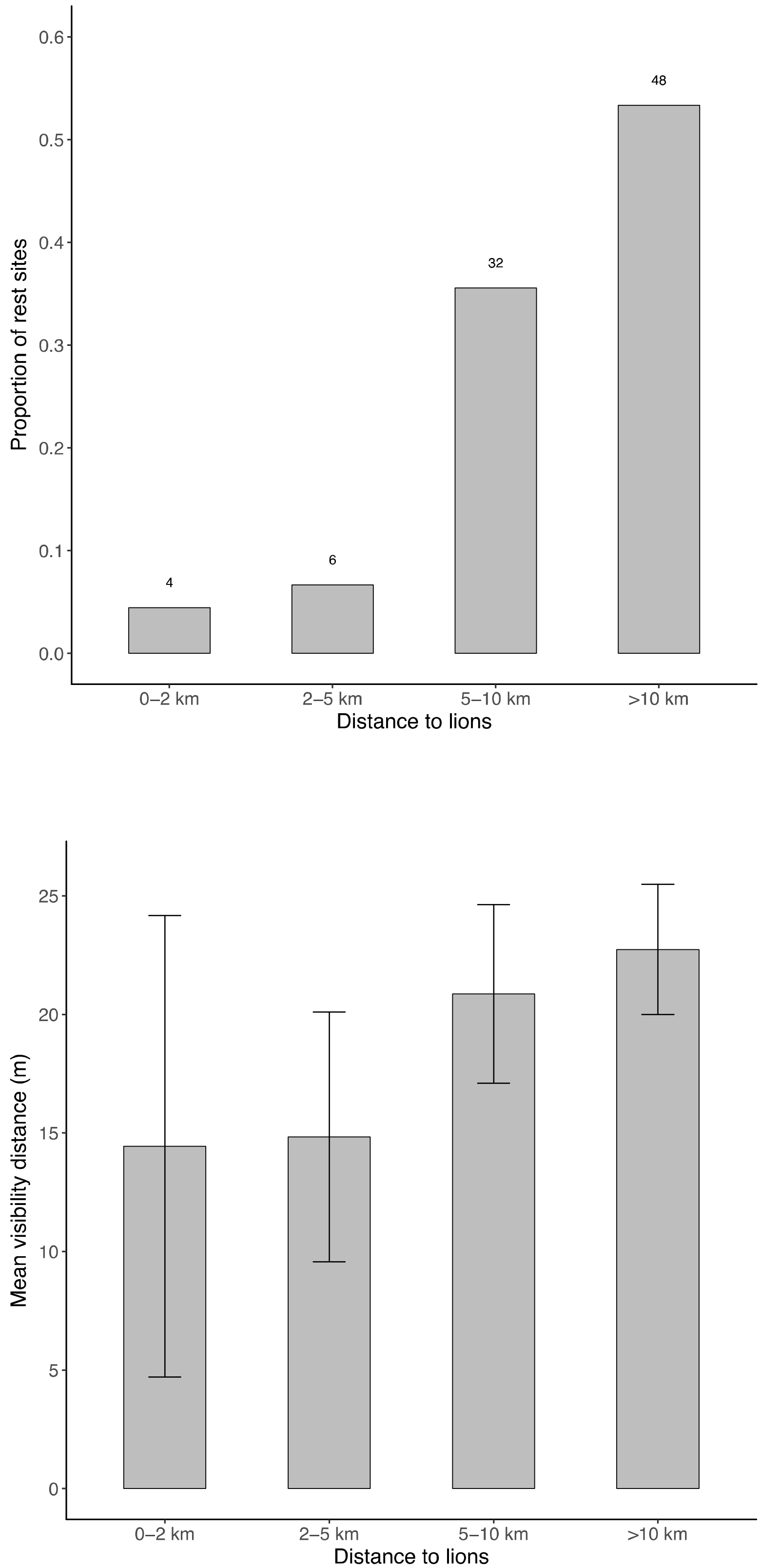

Proportion of rest sites
0.6
0.5
0.4
0.3
0.2
0.1
0.0
4
6
32
48
0–2 km
2–5 km
5–10 km
>10 km
Distance to lions
Mean visibility distance (m)
25
20
15
10
5
0
0–2 km
2–5 km
5–10 km
>10 km
Distance to lions

Figure 3

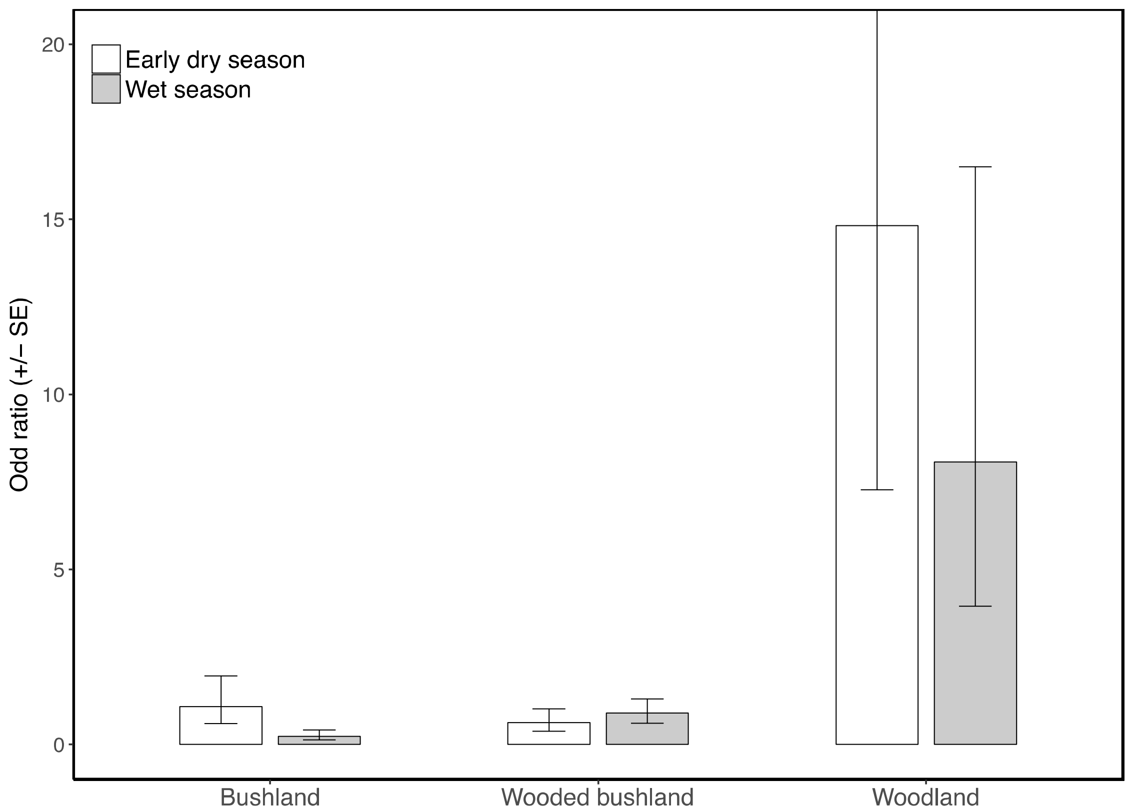
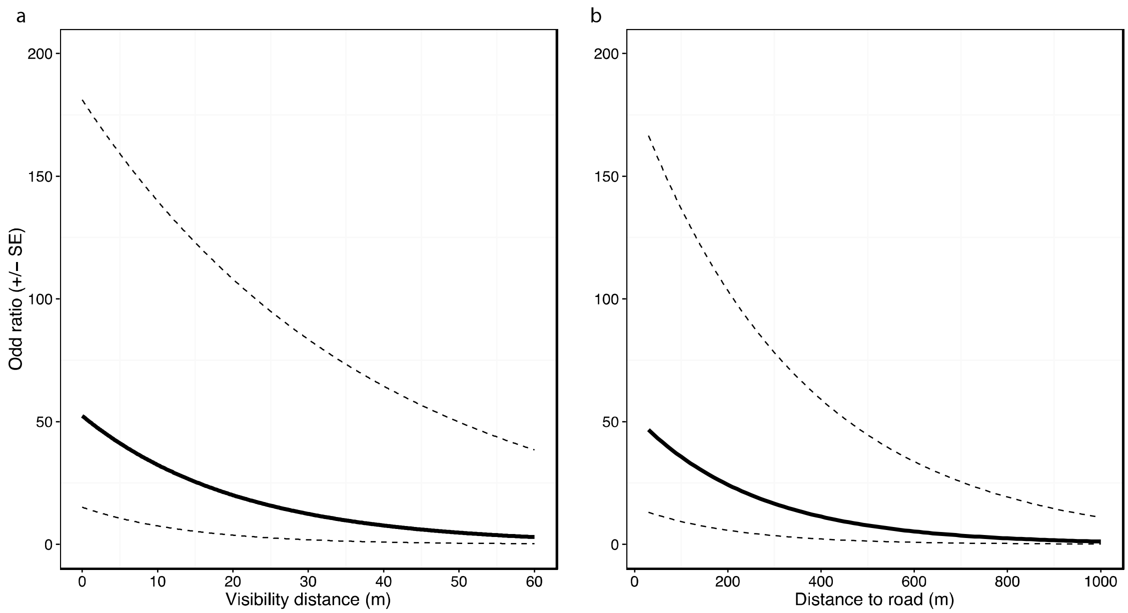
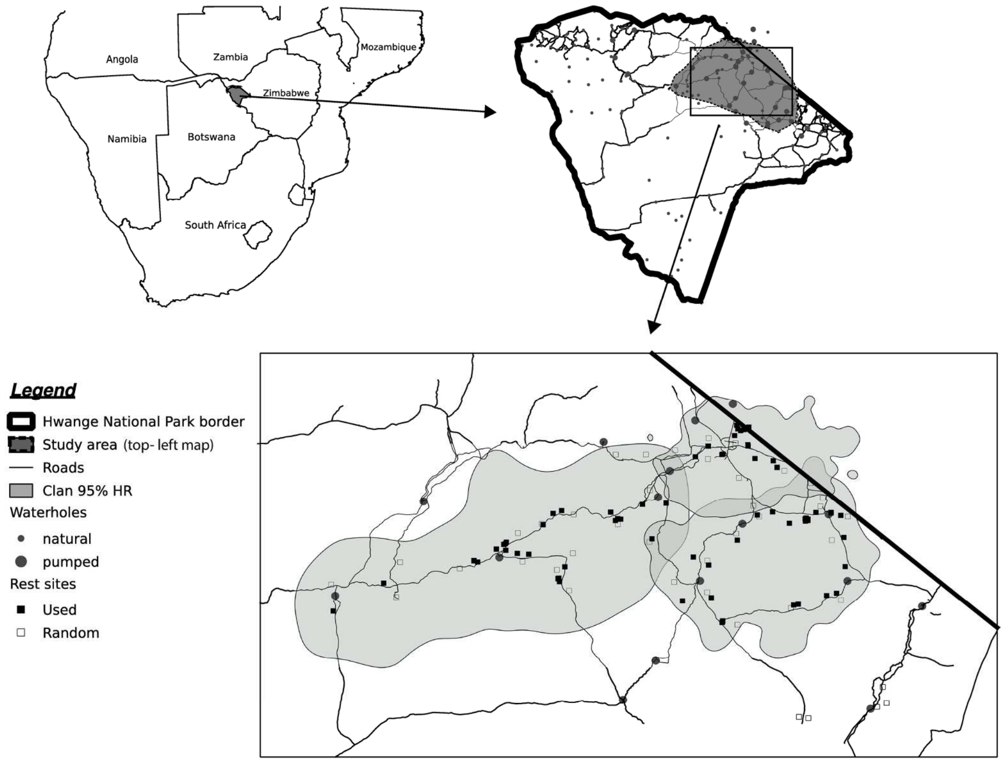

Early dry season
Wet season
Odd ratio (+/− SE)
20
15
10
5
0
Bushland
Wooded bushland
Woodland

Figure 4


a
b
Odd ratio (+/− SE)
200
150
100
50
0
0
10
20
30
40
50
60
Visibility distance (m)
200
150
100
50
0
0
200
400
600
800
1000
Distance to road (m)



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.

191x153mm (300 x 300 DPI)

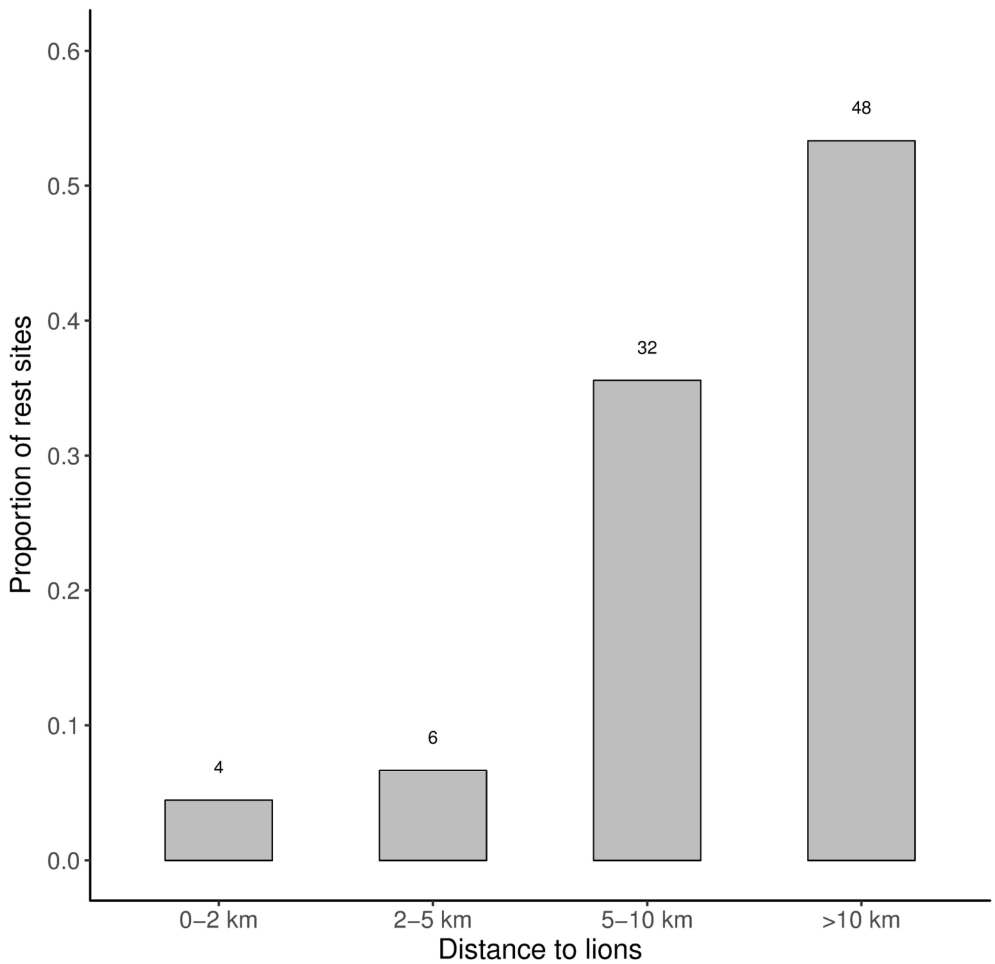


Figure 2
Distribution of a) rest sites and b) mean visibility distance in function of the closest distance to early morning lion locations. Numbers above bars represent sample size and error bars represent 95% confidence intervals.

177x178mm (300 x 300 DPI)

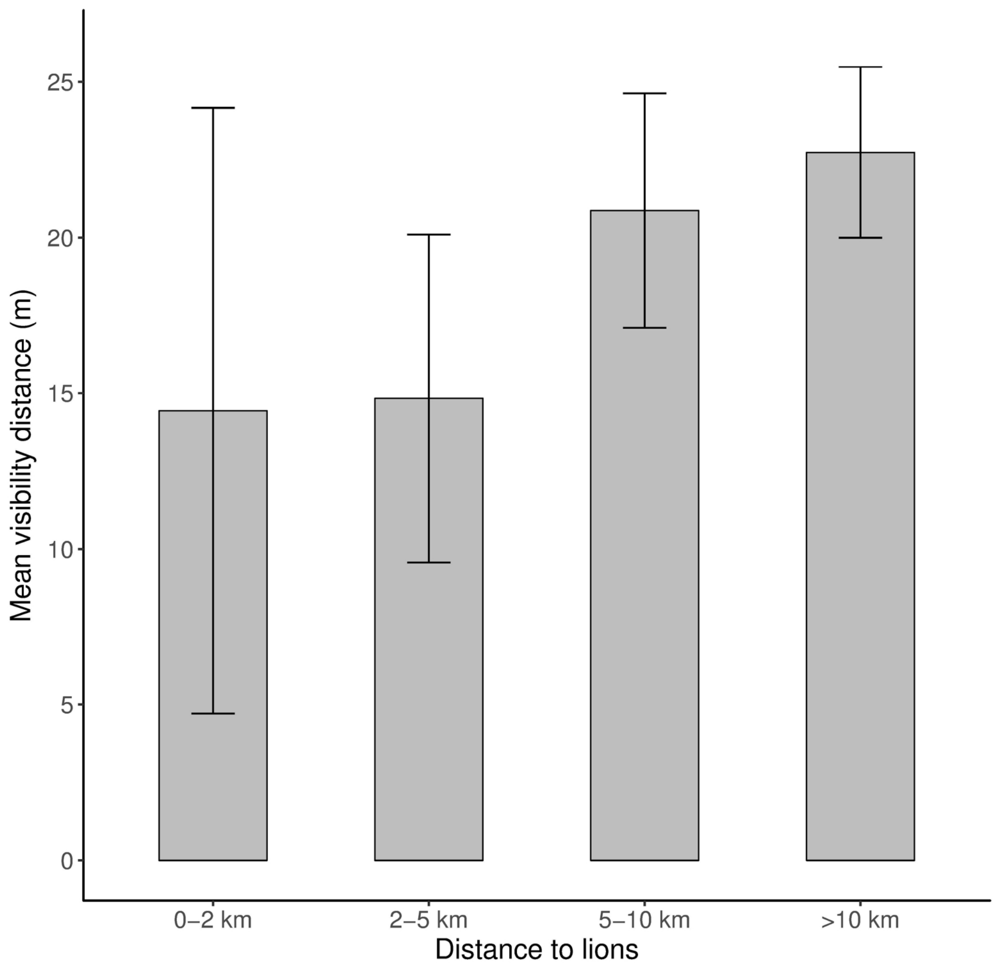


Figure 2
Distribution of a) rest sites and b) mean visibility distance in function of the closest distance to early morning lion locations. Numbers above bars represent sample size and error bars represent 95% confidence intervals.

177x178mm (300 x 300 DPI)

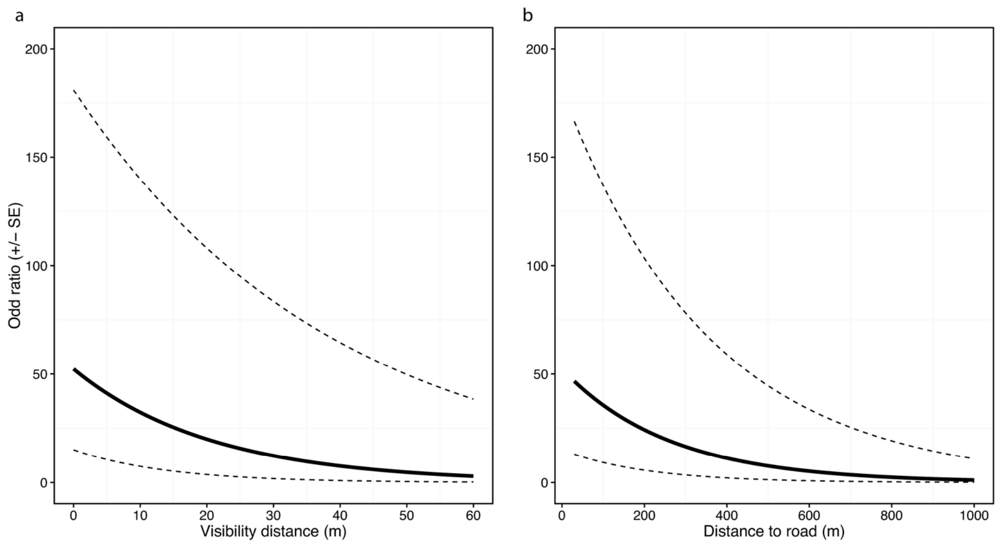


Figure 3‼ ┼ Effect of the interaction between habitat type and season on rest site selection by spotted hyaenas in Hwange National Park, Zimbabwe. The plot is truncated for extremely high values of standard errors for woodland in early dry season (upper CI reaches a maximum of 30.2).

172x93mm (300 x 300 DPI)

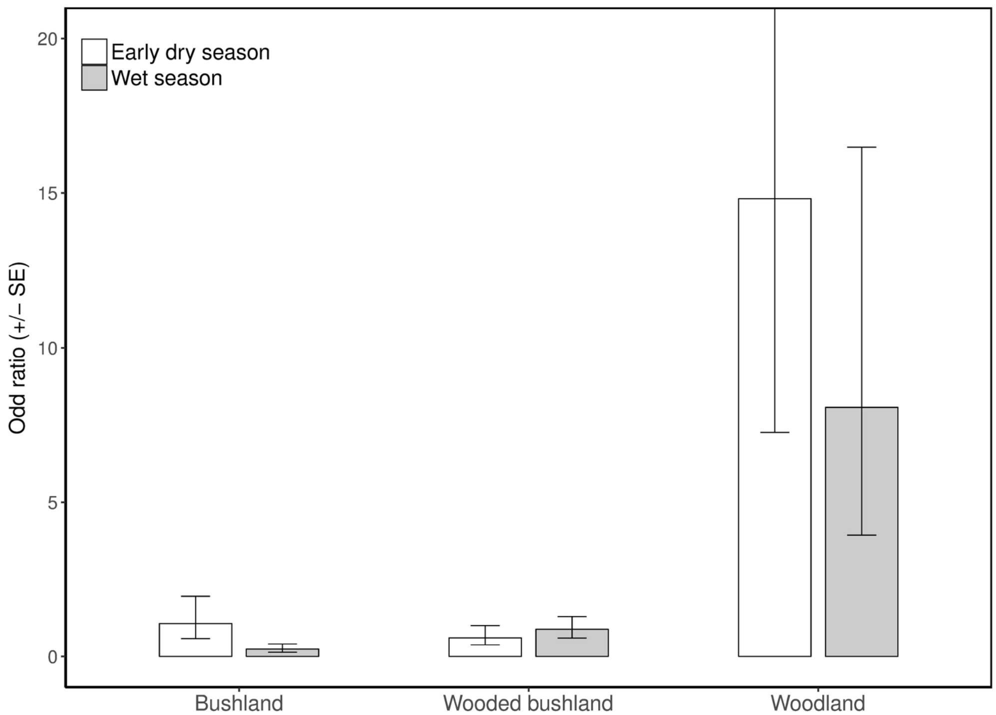


Figure 4‼ ┼ Effect of a) mean visibility distance and b) distance to the closest road on rest site selection by spotted hyaenas in Hwange National Park, Zimbabwe.

177x135mm (300 x 300 DPI)