Original Investigation

A potential role for interference competition with lions in den selection and attendance by spotted hyaenas

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ABSTRACT

Inter-specific killing is common among carnivore species and is likely to be a major driver of their spatial ecology and habitat selection. Here, we test how selection of, attendance at, and proximity to dens by spotted hyaenas may be influenced by the risk of predation by lions. We studied 57 dens in the semi-arid savanna of Hwange National Park, Zimbabwe. Hyaenas did not appear to avoid denning in lion home ranges or their cores, but den selection correlated with environmental proxies of predation risk. Hyaenas preferred dens far from waterholes, which were intensively used by lions, and with numerous entrances presumably providing many escape options for cubs. Den attendance did not appear to be influenced by proxies of predation risk. However, as the risk of predation risk by lions (frequency and proximity of their presence in the vicinity of a den) increased during a given week, the likelihood of a hyaena visiting that den during this same week decreased (regardless of its current state, used or unused). This effect seemed to be stronger when lions were closer to the den. In addition, hyaenas appeared to adjust their patterns of den attendance according to recent (up to a month) lion presence in the vicinity of the den. They avoided using dens in a given week as the presence of lions during the preceding weeks increased. Hyaenas appeared to select their dens based on proxies of predation risk but may have also selected them depending on their knowledge of lion presence (current or past) in the area. Hyaena denning behaviour is therefore very dynamic and appears to be driven, at least in part, by the presence of their main competitor.

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Introduction

Interactions among species regulate natural populations and shape community structure. Inter-specific killing is an extreme case of interference competition among carnivores (Donadio and Buskirk, 2006; Polis et al., 1989) and has been shown to occur amongst a wide range of species (Palomares and Caro, 1999). Predation by other carnivores is one of the main causes of juvenile mortality in some species (see Laurenson et al., 1995; Mills and Biggs, 1993 for wild dogs; Mills and Mills, 2013 for cheetahs) and

might thus impact on population dynamics and recruitment. The protection of young animals may be the reason for many species to use dens (Carter et al., 2011; Tannerfeldt et al., 2002; Theuerkauf et al., 2003). In studies of predator avoidance, some suggested that individuals may use long term knowledge of their predators' space use (Fuller and Keith, 1981), but recent work suggests that their response can be reactive rather that predictive (Broekhuis et al., 2013).

Several studies have shown that dens may be selected based on environmental features such as thermal insulation (Kaneko et al., 2010), soil type (Way et al., 2001) forest composition (Norris et al., 2002) and distance to water (Henner et al., 2004). Less is known about how predation risk influences den selection and use. It has been suggested that some species select dens as a function of predation risk. For instance, Carter et al. (2011) argue that red fox (*Vulpes vulpes*) breeding dens have more entrances than do non

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breeding dens in order to protect the pups from predation. However, there seems to be no existing knowledge on how species use their dens based on the previous whereabouts of their competitors and/or intraguild predators.

Dens play an essential role in spotted hyaena (*Crocuta crocuta*) ecology (Kruuk, 1972). Hyaena cubs are born and raised in such dens, depending on them for safety and survival during the first year of their life (Hofer and East, 1993). Despite this, most cub mortality at dens is due to lions, *Panthera leo* (Kruuk, 1972; Mills, 1990; Watts and Holekamp, 2009). Spotted hyaenas (hyaenas hereafter) are large predators (~60 kg) that live in groups called clans (Kruuk, 1972) and together with lions, they are the largest and most numerous predators in Africa. All adult females in a hyaena clan raise their litters together in a communal den. A clan usually uses one communal den at a given time but hyaenas move their cubs from time to time to other locations creating a new communal den (Boydston et al., 2006; Kruuk, 1972). Hyaenas do not excavate their own dens, but rather use holes dug by aardvarks, warthogs or porcupines and can only enter the dens narrow tunnels (Kruuk, 1972). Dens usually have several entrances allowing cubs to gain fast access in the presence of danger. Consistent den use in hyaenas is mostly determined by the reproductive condition of females. If a female has dependent cubs, she will visit the den to nurse them at regular intervals for at least a year (Kruuk, 1972). However, several studies have shown that dens are also central places in the social life of a clan (Cooper, 1993; Hofer and East, 1993; Kruuk, 1972; Mills, 1990) and that all clan members spend extended periods there. Thus, it is common for at least one adult member of the clan to be present at the den. However, when lions approach, adult hyaenas usually run away, most likely to lure the lions away (Cooper, 1993; East et al., 1989) while cubs remain hidden inside the den. Cubs remaining outside the den are frequently killed (Cooper, 1993). It is therefore crucial for hyaenas to find and use dens that are safe from lions.

This work is one of the first studies on the ecology of spotted hyaenas in a wooded savanna. In this habitat, such as Hwange National Park, Zimbabwe, very little is known about den sites themselves. Finding dens in densely wooded areas is difficult, as is behavioral monitoring, but recent developments in radio-telemetry allow for long-term tracking of animal movement and space use. We expected that hyaenas would select dens in areas with a low probability of lion presence and that provided protection from intraguild predators, using specific dens when lions were not present in the area. In particular, we predicted that (1) hyaena dens would be located outside of lion core home ranges (HRs) and that they should avoid denning close to waterholes as these are areas of high lion activity (Valeix et al., 2009b). We also expected that (2) hyaenas should select for dens with several entrances and in dense vegetation. Finally, we predicted (3) that the presence of lions in the vicinity of a den for a given period should decrease the likelihood of the den being visited during the same period by hyaenas and that hyaenas may also respond to past lion presence around a den.

Material and methods

Study area

Hwange National Park (HNP) covers an area of approximately 14,600 km^2 in north-western Zimbabwe (19°00′ S, 26°30′ E). The study area (≈1500 km^2) is located in the northern part of HNP without any significant relief and is characterized by Kalahari sandy soils. The vegetation is primarily woodland and bushland savannah, interspersed with small patches of grassland (Rogers, 1993). HNP is semi-arid with a wet season from November to April and a dry season from May to October. The long-term mean annual precipitation is 600 mm. The availability of water to animals is primarily from rainwater collected in natural depressions. However, most of these do not hold water during the dry season, when water is artificially supplied in about 50 waterholes spread throughout the study area. In the study area, the average hyaena density between 2009 and 2012 was 9.2 hyaenas/100 km^2 and lion density was 3.5 lions/100 km^2 (Andrew J. Loveridge, pers. com).

Movement data and predation risk by lions

During the course of this study, from July 2009 to August 2012, eight adult female spotted hyaenas belonging to four different clans were equipped with GPS radio-collars (African Wildlife Tracking, UHF 407, GPS collar with UHF download and VHF transmitter). There was no evidence that these individuals had dependent cubs at the time of capture. Nevertheless, we expect them to recurrently visit dens used by the cubs of the same clan as well as other dens. Collars were set up to take hourly GPS from 18:00 to 6:00 when hyaenas are most active (Kolowski et al., 2007) and the risk of encountering lions is high. Collar accuracy was about 16 m in wooded areas, estimated from stationary collars positioned for the purpose. We defined HRs and cores using 95% and 50% Kernel isopleths respectively using the reference smoothing factor h_{ref} as recommended by Hemson et al. (2005). HR estimation was calculated for the whole hyaena dataset (individuals were monitored for at least 3 consecutive months). As individuals were often not seen for extended periods of time (up to four months), their reproductive status could not be assessed.

During the study, 17 lions (10 males and seven females) from different social groups were fitted with GPS radio-collars. GPS collars were programmed to take hourly fixes during the night from 18:00 to 07:00. At least one individual per pride and coalition was collared in the study area and since individuals from the same pride/coalition spend most of their time together their locations reflect the ones of the entire pride/coalition (Valeix et al., 2009b). We thus monitored 10 coalitions and seven prides, for at least several consecutive months. As lions are territorial, there is very little chance of lion presence not being accounted for in our analysis. Temporal overlap between lion and hyaena GPS data is shown in Fig. 1.

Hyaenas were immobilized by a professional team (see Périquet, 2014 for details). Details on lion immobilization and collaring are provided in Loveridge et al. (2007). Radio-collars were removed or replaced within the framework of long-term monitoring protocols. 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, Wildlife Group, and licenses to acquire, possess and administer game capture drugs/dangerous drugs), and permissions were provided by the appropriate agency (Zimbabwe Parks and Wildlife Management Authority).

We defined two levels of predation risk: the long-term risk of encountering lions and the actual presence of lions in the vicinity of a den. We first defined a long-term risk of encountering lions using all lion GPS data over our study period, as in HNP, hyaena and lion HRs do not vary in size nor shape seasonally (Loveridge et al., 2009; Périquet, 2014). We calculated a HR for each lion (95% Kernel isopleths) using its total dataset. Each site was then coded as 1 (or 0) if it was located (or not) within at least one lion HR. We repeated this procedure for HR cores (50% Kernel isopleths). The analysis was conducted for male and female lions separately. As all dens and controls (but one) were located within at least one lion HR, we focused our analysis on HR cores.

We then quantified the presence of lions in the vicinity of a den at different spatio-temporal scales, representing the actual risk of encountering lions nearby the den. We defined ring buffers of 3 km,
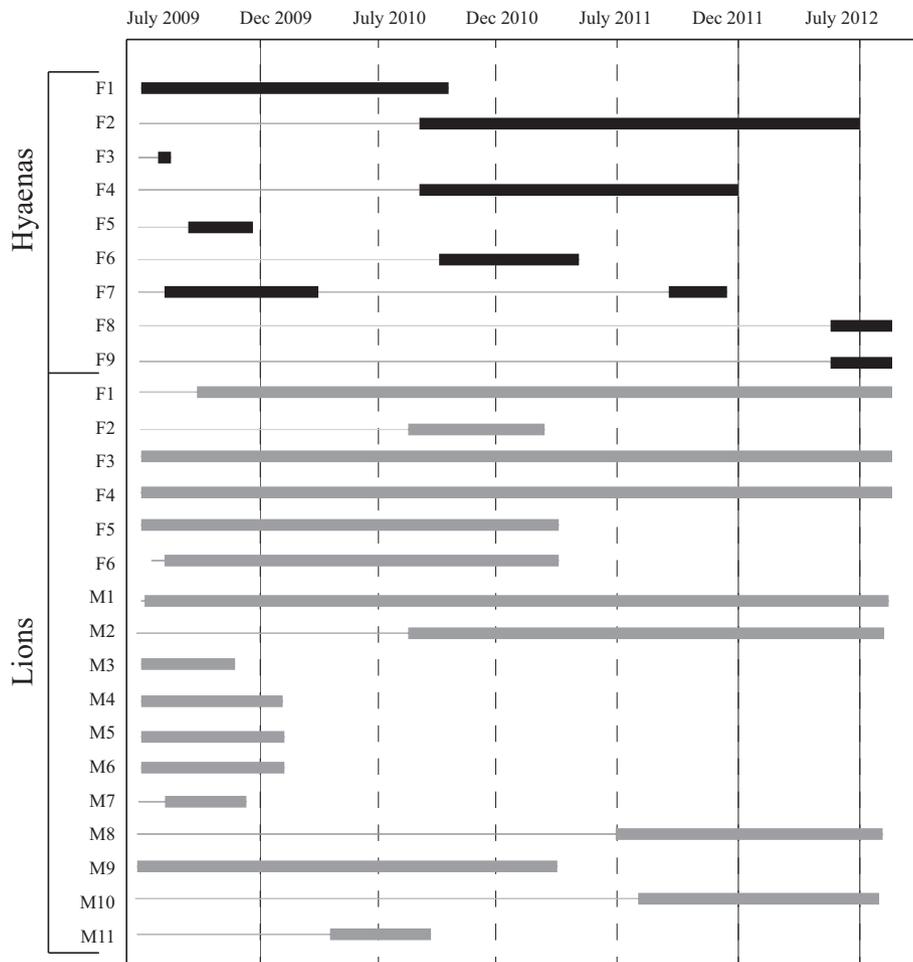
Fig. 1. Gant chart of temporal overlap between hyaenas (black) and lions (grey) GPS data between July 2009 and August 2012.

1.5 km, 1 km and 500 m around dens and calculated the number of days per seven days period i.e. week, when lions were found within the buffer. For each week, we also quantified the presence of lions at four temporal levels: during the week of interest as well as during each of the four weeks preceding the week of interest.

Den selection

Clusters of locations from hyaena GPS data (areas where hyaenas spent at least three consecutive hours at night within a 50 m radius circle) were visited on foot to search for dens, i.e. holes in the sand where signs of hyaena presence, such as tracks, scats, urine, pieces of bones or regurgitated pellets were found. Potential den sites were visited as soon as possible after cluster detection, and due to logistic constraints, no investigation was made after the rainy season started. Out of 281 clusters detected, we visited 263 and found 32 dens. We added 25 dens detected by other means (during routine field work, information given by other scientists, game rangers, etc.) to this data set, making up to 57 dens actually used by hyaenas. All dens were too small for adults to enter, thus could not be considered as adult resting sites. Areas around dens were most often showing signs of intensive use by several adult hyaenas (trampled vegetation, lying places, etc.) therefore all dens were considered as communal dens.

As hyaenas do not excavate their own dens, we defined the 51 additional holes encountered ad hoc during walks to investigate GPS clusters or during other activities as control holes. All control holes fell within hyaena territories and were at least the size of a springhare (*Pedetes capensis*) burrow in which small cubs can crawl

and thus has the potential to be used as dens by hyaenas. For each den and control hole, we recorded the number of entrances, distance to the nearest waterhole and visibility. The visibility at each den 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 standing hyaena. One person stood at the den/hole holding the visibility board while a second person walked away from it in each of the four cardinal directions. The distance at which the board could no longer be seen was measured using a handheld GPS device (Garmin GPSmap 60CSx; Garmin, Olathe, Kansas, USA) with an accuracy of about 4 m. The distances in each cardinal direction were then averaged to give a mean visibility measure at each site.

We used generalized linear models with a binomial error structure and logit-link function to predict the probability of a hole being selected as a den or not (1, actual dens; 0, control holes) by hyaenas as a function of its number of entrances, visibility distance, distance to the nearest waterhole and the interaction between these two last variables. We selected the best supported models based on the Akaike Information Criterion with a correction for small sample size (AICc, Burnham and Anderson, 2002). We followed Richards et al. (2011) recommendation and used model averaging to calculate estimates based the set of models within ΔAICc<6 but removing from the set models that are a more complex version of models with a lower AICc.

Den use

For dens discovered using GPS data (*n* = 32), we used the following criteria to define periods of potential den use. Each den was
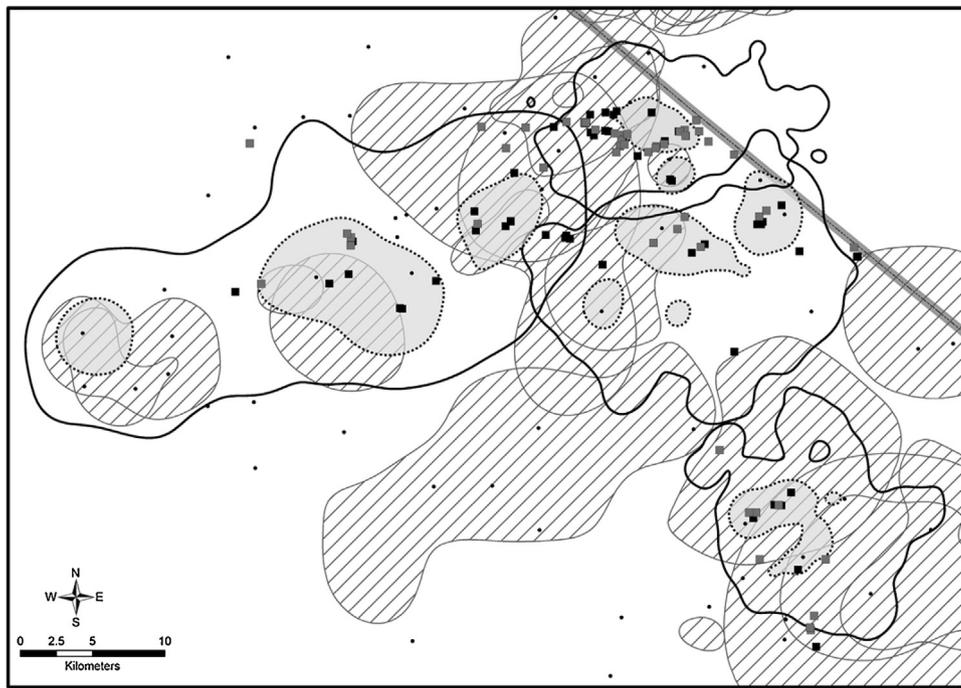
Fig. 2. Locations of dens (black squares) and control holes (grey squares). Thick black lines represent hyaena clans 95% kernels contour HR and greyed areas represent clan cores (50% Kernels). Hashed areas signify cores of individual lion 95% HR. HNP lies Southeast of the thick grey line and small black dots represent waterholes.

Table 1
Models for den selection based on proxies of predation risk by lions. Best models used for model averaging are shown in bold with the corresponding results for the Hosmer–Lemeshow goodness of fit test. ωAICc represent the AICc weight of each model within the complete set of 11 models.

Model	K	AICc	∆AICc	ωAICc	Hosmer–Lemeshow test
DWT + NB ENT	**3.0**	**146.7**	**0.0**	**0.34**	$X^2 = 3.74$ $p = 0.88$
NB ENT	**2.0**	**147.0**	**0.3**	**0.29**	$X^2 = 0.01$ $p = 1$
DWT + VISIB + NB ENT	4	148.8	2.1	0.12	–
VISIB + NB ENT	3	149.0	2.3	0.11	–
DWT + VISIB + NB ENT + DWT × VISIB	5	150.7	4.0	0.05	–
Null model	1	151.4	4.7	0.03	–
DWT	**2**	**151.7**	**5.0**	**0.03**	$X^2 = 7.99$ $p = 0.43$
VISIB	2	153.5	6.8	0.01	–
DWT + VISIB	3	153.7	7.0	0.01	–
DWT + VISIB + DWT × VISIB	4	155.3	8.6	0.004	–

NB ENT, number of entrances; VISIB, average visibility distance; DWT, distance to closest waterhole.

associated with a collared hyaena. For each day, we calculated the minimum distance from the hyaena to the den; then, we considered that the den was potentially visited on days when minimum distance <500 m (hyaenas travel an average of 1 km/h at night). A period of use was defined as at least five potential visits separated by less than a week, with at least two consecutive ones (see Appendix A for details). Based on this definition (i.e. an individual was consistently active in its vicinity), we reduced our sample size from 32 to 28 dens actually used. We also defined weekly den use by splitting the dataset into seven days periods. A den was considered as used if it was approached at least four days out of the seven.

For each den, we defined the duration of each period of use (in days) as well as the average duration of a period of use and the total duration of use being the sum of all periods of use. We used linear mixed models to detect any effect of proxies of predation risk on den use using distance to waterholes, number of entrances and visibility as explanatory variables. We defined individual hyaena ID and den ID nested within individual ID as random

variables for the analyses of average length of a period of use and the total length of use. We then built a set of generalized linear mixed models with a binomial error structure and the same random variables to model the effect of lion presence within a given distance of the den (3 km, 1.5 km, 1 km and 500 m) and during a given period (week of interest and the four weeks preceding the week of interest, each of them being a separate explanatory variable) on the probability of this den being used during a given week (i.e., the den was approached at least four days). We used the AICc to select the models best fitting the data used model averaging to calculate estimates (using standardized variables) following Richards et al. (2011) recommendations. Estimates are given with ± standard deviation (SD) unless stated otherwise. Statistical analyses were performed in R 3.0.2 (R Core Team, 2014) using packages 'lme4' and 'MuMIn'. There was no colinearity between the variables included in the models as suggested by the variance inflation factors that were all inferior to 2. In addition, we tested the goodness of fit of our models using Hosmer–Lemeshow test from the R package 'ResourceSelection'.

Table 2
Model selection for den use based on lion proximity to the den (distance) during the month preceding the week of interest. Best models used for model averaging are shown in bold with the corresponding results for the Hosmer-Lemershow goodness of fit test. ωAICc represent the AICc weight of each model within the complete set of 6 models.

Distance	Models	ΔAICc	ωAICc	Hosmer–Lemeshow test
3 km	**week-0 + week-1 + week-2 + week-3 + week-4**	**0.00**	**0.43**	$X^2 = 30.46$ $p = 0.0002$
	week-0 + week-1 + week-2	**0.74**	**0.30**	$X^2 = 25.4$ $p = 0.001$
	week-0 + week-1 + week-2 + week-3	**2.21**	**0.14**	$X^2 = 28.4$ $p = 0.004$
	week-0 + week-1	**2.45**	**0.13**	$X^2 = 15.12$ $p = 0.06$
	week-0	10.80	0.002	–
	null	20.66	0.00001	–
1.5 km	**week-0 + week-1**	**0.00**	**0.42**	$X^2 = 12.9$ $p = 0.12$
	week-0 + week-1 + week-2	1.18	0.23	–
	week-0 + week-1 + week-2 + week-3 + week-4	2.43	0.12	–
	week-0	**2.47**	**0.12**	$X^2 = 5.29$ $p = 0.73$
	week-0 + week-1 + week-2 + week-3	3.18	0.09	–
	null	5.86	0.02	–
1 km	**week-0 + week-1 + week-2**	**0.00**	**0.44**	$X^2 = 13.85$ $p = 0.09$
	week-0 + week-1 + week-2 + week-3	0.60	0.32	–
	week-0 + week-1 + week-2 + week-3 + week-4	1.90	0.17	–
	week-0 + week-1	**5.04**	**0.04**	$X^2 = 8.27$ $p = 0.41$
	null	5.86	0.02	–
	week-0	6.72	0.02	–
500 m	**week-0 + week-1**	**0.00**	**0.50**	$X^2 = 8.55$ $p = 0.38$
	week-0 + week-1 + week-2	1.78	0.21	–
	week-0	**2.86**	**0.12**	$X^2 = 6.19$ $p = 0.62$
	week-0 + week-1 + week-2 + week-3	3.76	0.08	–
	null	4.21	0.06	–
	week-0 + week-1 + week-2 + week-3 + week-4	5.74	0.03	–

Week-0: presence of lion during the week of interest, week-1 to week-4 presence of lions during the first to the fourth week preceding the week of interest.

Results

Den selection

Dens were not more likely to be located within hyaena core HRs than were controls ($z = 0.15$, $p = 0.88$, Fig. 2). Holes within both female pride and male lion core HRs were not less likely to be selected as dens than those outside lion core HRs (female: $z = 0.94$, $p = 0.35$; male: $z = 0.74$, $p = 0.46$, Fig. 2). The three models best explaining den selection by hyaenas included distance to water (estimate: 0.0002, 95% CI −0.00009 to 0.0007) and number of entrances (estimate: 0.77, 95% CI 0.08–1.5), both being positively correlated with den selection (Table 1, Fig. 3). The visibility (i.e. vegetation density) did not seem to affect den selection.

Patterns of den use

On average dens were used 1.8 ± 0.2 times (range 1–3) and for a total of 45.2 ± 5.8 days (range 12–108 days) over the four years of study. Around half of the dens were used more than once (15 of 32). We did not find any evidence that den use, in terms of duration of each period of use, average duration and total duration of use was influenced by distance to water, number of entrances or visibility. However, we found that the probability of a den being visited during a given week was negatively correlated with increasing lion presence in its vicinity (Tables 2 and 3, Fig. 4a). The negative effect of lion presence was stronger when they were closer to the den. For a given week, the negative effect correlation between lion presence within a given radius and the probability of the den

Table 3
Parameter estimates (with 95% CI) for den use based on lion proximity to the den. Estimates were calculated using model averaging on standardized variables.

Distance	Parameter estimation by model averaging on best models	
3 km	Intercept	−0.90 (−2.39 to 0.60)
	Week 0	−0.09 (−0.30 to 0.12)
	Week 1	−0.25 (−0.49 to −0.002)
	Week 2	−0.15 (−0.41 to 0.06)
	Week 3	−0.01 (−0.25 to 0.20)
	Week 4	−0.1 (−0.45 to −0.01)
1.5 km	Intercept	−0.77 (−2.29 to 0.76)
	Week 0	−0.15 (−0.38 to 0.07)
	Week 1	−0.18 (−0.47 to −0.01)
1 km	Intercept	−0.79 (−2.31 to 0.73)
	Week 0	−0.07 (−0.30 to 0.17)
	Week 1	−0.34 (−0.64 to −0.03)
	Week 2	−0.07 (−0.43 to 0.11)
500 m	Intercept	−0.76 (−2.29 to 0.77)
	Week 0	−0.18 (−0.43 to 0.06)
	Week 1	−0.22 (−0.56 to 0.01)

week-0: presence of lion during the week of interest, week-1 to week-4: presence of lions during the first to the fourth week preceding the week of interest.

being approached by hyaenas was still significant when considering the presence of lions during at least the two preceding weeks (at 1.5 km and 500 m) and even the four preceding weeks (at 3 km, Tables 2 and 3, Fig. 4b). Lion presence had the strongest effect during the first and the second weeks preceding the week of interest. Therefore, hyaenas appeared to be sensitive to the actual presence
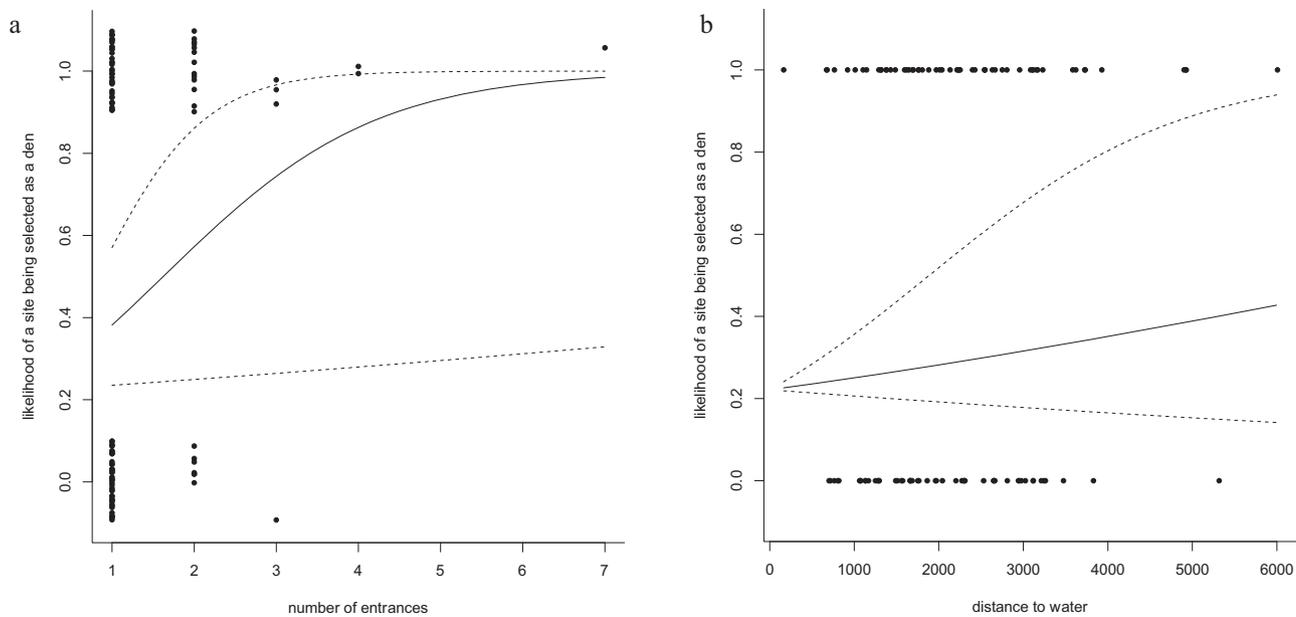
Fig. 3. Correlations between (a) the number of entrances and (b) the distance to water in meters and the likelihood of a site being selected as a den. Estimates were calculated by model averaging on the two best logistic regression models. Dotted lines represent lower and upper confidence intervals.
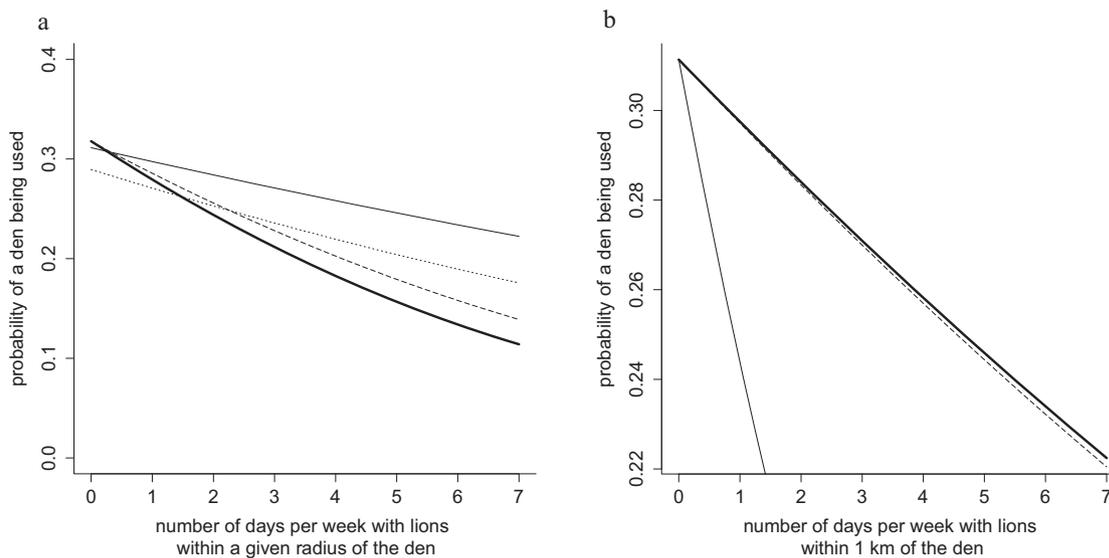

Fig. 4. Probability of a den being used when lions are present within a given distance with different time lags. (a) Correlation between the distance to lion during a given week and den use during the same week. Solid bold, solid thin, dashed and dotted lines show the effect of lion presence within 500 m, 1 km 1.5 km and 3 km radii respectively. Graphs for other time frames (presence of lions during the first, second third and fourth week preceding the week of interest) show the same pattern. (b) Correlation between the timing of lion presence within 1 km of the den and its use. Solid bold, solid thin and dashed lines show the impact of lion presence during the same week, the first and second preceding weeks respectively. Graphs for other distances (500 m, 1.5 km and 3 km) present the same patterns.

of lions at least up to 3 km of their potential dens and for at least a month after their passage. Nevertheless, the goodness of fit for models of lion presence within 3 km was weak (see Table 2) suggesting a weaker effect of lion presence at this distance when the time between lion presence and den use gest longer (Table 3).

Discussion

Hyaenas seem to select and use their dens depending on both habitat features and predation risk. Contrary to our expectations, dens do not tend to be located within hyaena core HRs. This could be explained by a different denning behavior of hyaenas in wooded savanna compared to open ecosystems. Despite the fact that dens are described as centers of social life in the Serengeti (Kruuk, 1972), we never observed large hyaenas gathering at dens in HNP. Nevertheless, the fact that they visited or approached the dens repeatedly might indicate that social relationships are occurring there. In addition, all dens were too small to provide shelter for adult hyaenas, despite that tracks showed intensive use by several adults suggesting that all clan members spent extended periods there with frequent visits regardless of their reproductive status. Thus, even though collared animals may not have had cubs of their own and were therefore enjoying a greater freedom of movement, their attendance to the den was likely to reflect the behaviour of lactating females.

Several species have been shown to avoid denning in areas intensively used by their predators, as is the case of both Cape foxes (*Vulpes chama*) and bat-eared foxes (*Otocyon megalotis*), who avoid black-backed jackals (*Canis mesomelas*; Kamler et al. 2012). We therefore expected that lion spatio-temporal space use would influence den selection and use by hyaenas. As the whole study area fell within at least one lion HR, hyaenas had no choice but to den within lion territories, as they did. However, hyaenas appeared to select dens based on environmental variables, such as distance to waterholes, which may lower their predation risk. Several species such as coyotes (Way et al., 2001) and raccoons (*Procyon lotor*, Henner et al. 2004) have been shown to select dens close to water sources. In semi-arid savannas, waterholes are key resources for water and prey but also attract predators (Valeix et al., 2009b). Despite the effect being weak in our study, we found that hyaenas avoid denning near waterholes, hence far from lions and prey concentrations, which matches results found for African wild dogs (*Lycaon pictus*) in the same study area (van der Meer et al., 2013). Flooding risk in HNP is limited to the immediate proximity of waterholes (in most of them water is artificially maintained during the dry season) and only one den was located within 500 m of a waterhole. Thus the avoidance of waterhole areas for denning is more likely due to lion presence than flooding risk. Yet, 74% of the dens were located within 3 km of a waterhole, a distance still allowing easy access to prey and water. Within this range of waterholes, the soil may also be more suitable for burrows (richer in clay and calcrete) than Kalahari sands. Soil type has indeed been shown to influence den selection in wolves and coyotes (Macdonald et al., 2004; Theuerkauf et al., 2003; Way et al., 2001). Hyaenas seem to prefer dens with several entrances, thus providing easier escape routes for cubs. East et al. (1989) also showed that communal dens usually have more than one entrance. Even though cubs are known to extend dens and are susceptible of opening new entrances, it is likely that hyaenas select for holes already with several entrances/exits. In addition, Moehrenschlager et al. (2007) showed that kit foxes were more likely to escape predators as the availability of refuge holes increased. Vegetation cover and density can also affect den selection (Arjo et al., 2003; Revilla et al., 2001). However, we did not find any significant correlation between vegetation density and den selection. It is possible that hyaenas rely more on olfactory and sound cues rather than visual ones to detect approaching predators. The senses of smell and hearing are indeed extremely well developed in hyaenas (Kruuk, 1972). Alternatively, the vegetation density may have been selected for by the species that initially created the burrow. For instance, only one of the control holes was located in grassland.

In Hwange, hyaenas use their dens for periods of about 45 days and re use approximately half of them. This pattern is similar to the one observed in the Masai Mara (Boydston et al., 2006), where hyaenas are known to vacate their dens and sometimes reuse them later (Kruuk, 1972). In HNP, hyaena den attendance seemed to be influenced by the actual predation risk of lions with the increased presence of lions close to a given den having a negative effect on the probability of the den being approached by hyaenas. The effect of lion presence seemed to be immediate and decreased in strength with the distance of lions from the den. In addition, hyaenas appeared to adjust their patterns of den attendance according to recent (up to at least two weeks and potentially even a month) lion presence in the vicinity of the den. It is likely that they respond to cues of lion presence such as scent-marks, urine or scats. It is also possible that hyaenas remember lion presence. Interestingly, this "ghost of lion presence" is strongest when lions were present during the first and second weeks preceding the week of interest and weaker when lions were present during the week of interest, suggesting that the decision to attend a den is based on an integrated knowledge of lion presence rather than their immediate

presence in the vicinity. This may reflect the fact that risk is greater when lions have settled in an area compared with when they are transient. Alternatively, the fact that den use during the same week increased for the females that we had marked (the ones that were not actually breeding) could also be interpreted in the following way: when lions are already present, it might be safer for the mother to wait for the lions to move away (to reduce the detection probability) while other females might increase the use to offer some protection. It appears that the strongest effect is observed the week after the presence of lions, once they have moved further away and therefore the immediate risk is reduced, but the overall risk is still high as lions are still close enough to still patrol the area. None of the other variables tested (distance to water, number of entrances and visibility) seemed to influence den use patterns in terms of total average duration and frequency of use. These parameters could be influenced by factors such as age of pups, prey and/or carcass availability in the vicinity or parasite load in the den.

Overall, den selection seemed to be influenced by proxies of predation risk (distance to waterholes and number of entrances) while knowledge of the current and past presence of lions appeared to be more important for den use. However, females with dependant offspring most probably cannot afford to stay away from the den for extended periods of time even if lions are in close proximity. It is thus likely that lactating females would be less sensitive to lion presence in the past that to their actual one when they have to visit the den to nurse their cubs. The presence of several dens in each clan HR may allow hyaenas to reduce risk of encountering lions by temporarily avoiding using dens when lions are in the vicinity or simply moving between dens. Thus, hyaenas appear to respond to lions in a reactive way rather than in a predictive way, like cheetahs do (Broekhuis et al., 2013) and make use of dens in risky areas only when their main competitor is absent. This shifting space use is similar to the pattern observed in prey responding to the presence of their predators (Fortin et al., 2005; Hernández and Laundré, 2005; Valeix et al., 2009a). Den use is therefore a dynamic process responding to the risk of predation by lions and can therefore be of significance for hyaena reproduction and dynamics. Given the recent increase in lion density in HNP following a moratorium on lion trophy hunting in the periphery of the park (lion density was just above 0.02 indiv./km^2 before 2005 and has reached 0.035 indiv./km^2 in 2010, Loveridge et al., 2010), the risk of encountering lions close to dens is likely to have increased as well. In the current framework of large carnivores and ecosystem conservation, it is therefore important to shed some light on how species affect each other, especially their reproduction success through cub/pup survival.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2015.10.005.

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