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Original Investigation

Characteristics of African wild dog natal dens selected under different interspecific predation pressures

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ABSTRACT

To successfully reproduce, many carnivorous mammals need access to suitable den sites. Den site selection is often based on fitness related criteria like escape from predators, food availability and shelter from extreme weather conditions. African wild dogs are cooperative breeders that use a den to give birth to their offspring. They often co-exist with lions and spotted hyenas, both of which are known to kill African wild dog pups. Little is known about den site selection by African wild dogs. In this study, we compared vegetation characteristics and distribution of roads and waterholes around den sites and random sites, in areas with high and low lion and spotted hyena densities. In both areas, African wild dogs selected den sites in closed woodland with little visibility, which is likely to reduce detection by predators, increase the likelihood of escape when detected, and might provide shelter from extreme weather conditions. In the high predator density area, African wild dogs seemed to spatially avoid predators by selecting den sites in this type of habitat relatively further away from waterholes and roads. African wild dogs have high energetic costs of gestation. Therefore, even when predation risk is relatively low, they are likely to try to maximise their fitness by choosing a den site in habitat that will provide optimal protection for their offspring, leaving little additional options to respond to a higher predation pressure.

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Introduction

There are several carnivorous mammals that make use of a den to give birth to their offspring. For these animals, access to suitable den sites is often crucial for successful reproduction, and likely to affect population recruitment (Fernández and Palomares, 2000; Norris et al., 2002; Richardson et al., 2007). Studies on carnivorous mammals show that the main selection criteria for natal den sites are the provision of protection from predators (Pruss, 1999; Hwang et al., 2007; Lesmeister et al., 2008; Ross et al., 2010), close proximity of available food resources (Meriggi and Rosa, 1991; Eide et al., 2001; Ye et al., 2007; Szor et al., 2008) and provision of shelter from extreme weather conditions (Eide et al., 2001; Richardson et al., 2007; Ye et al., 2007; Szor et al., 2008). Other factors that have been found to affect natal den site selection are close proximity to water sources (Hwang et al., 2007; Ye et al., 2007; Szor et al., 2008), protection against flooding (Pruss, 1999; White et al., 2001; Benson et al., 2008) and low ectoparasite loads (Butler and Roper, 1996).

An increase in the human population worldwide has resulted in fragmentation of habitat available to wildlife, thus forcing animals to live in close proximity to humans (Woodroffe, 2000; Inskip and Zimmermann, 2009). Some animals have adapted their denning behaviour to humans and use manmade structures to den (Hwang et al., 2007; Herr et al., 2010; Gould and Andelt, 2011), or place their dens in close proximity to roads (Pruss, 1999; Hwang et al., 2007; Gould and Andelt, 2011) and/or human settlements (Meriggi and Rosa, 1991; Hwang et al., 2007; Gould and Andelt, 2011). Other animals deliberately try to avoid humans by selecting den sites away from human activity (Theuerkauf et al., 2003; Ye et al., 2007; Ross et al., 2010).

African wild dogs (*Lycaon pictus*) are one of the mammalian carnivores that make use of a den to give birth to its offspring (Reich, 1981; Malcolm and Marten, 1982). African wild dogs are cooperative breeders that live in packs (Reich, 1981; Malcolm and Marten, 1982). During the coldest months of the year (May–June), the alpha female gives birth to the pups in an underground den where they remain the first three months of their life (Woodroffe et al., 2004; Rasmussen, 2009). After weaning, a ‘baby-sitter’ may be left behind at the den to take care of the pups and protect them against predators when the pack goes hunting (Malcolm and Marten, 1982; Rasmussen, 2009). Like other carnivores (Ross et al., 2010; Arjo et al., 2003; Lesmeister et al., 2008; Schmidt et al., 2008), African

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wild dogs do not always dig their own den, but also make use of burrows excavated by other species, e.g. armadillo (*Orycteropus afer*) (Robbins and McCreery 2003; Woodroffe et al. 2004).

For African wild dogs the principal cause of natural mortality for both adults and pups is predation by lions (*Panthera leo*) (Reich, 1981; Woodroffe et al., 2004). Although spotted hyenas (*Crocuta crocuta*) are direct competitors of African wild dogs, and have been reported to disturb den sites and kill pups (Creel and Creel, 1998; Woodroffe et al., 2004), predation by this carnivore plays a lesser role (Creel and Creel, 1998; Woodroffe et al., 2004). Interspecific competition with lions and spotted hyenas has been found to affect both the distribution and abundance of African wild dogs (Reich, 1981; Creel and Creel, 1996; Mills and Gorman, 1997; Creel, 2001) and is therefore likely to play a role in den site selection. Previous studies have indeed shown that African wild dog dens were located in thickets to avoid encounters with these predators (Creel and Creel, 2002), or in steep terrain where lion densities are low (Van Dyk and Slotow, 2003).

Historically, persecution by humans has contributed to a high level of African wild dog mortality (Woodroffe et al., 1997, 2004; Van der Meer, 2011), and has been one of the most important causes of the decline in the African wild dog population in the last century (Woodroffe et al., 1997). Up to today a large proportion of African wild dog mortality can be contributed to road casualties, snares and animals being shot and poisoned (Woodroffe et al., 1997, 2004; Van der Meer, 2011).

As far as we are aware, there are no detailed studies of African wild dog den site characteristics. In this study, we compared vegetation characteristics and spatial distribution of den sites versus random sites, in areas with high and low densities of lions and spotted hyenas. We predicted that, in order to

provide optimal shelter and protection for their offspring, African wild dogs selected dens in closed vegetation with limited visibility. We expected this selection pattern to be more pronounced in the high predator density area. In order to reduce encounters with predators in the high predator density area, and encounters with humans in the low predator density area, we predicted that den sites in both areas would be situated far from roads. With a large proportion of kills made around waterholes (Van der Meer, 2011), we expected African wild dogs to reduce foraging distance by selecting den sites relatively close to waterholes.

Material and methods

Study area

Hwange National Park (HNP) is situated in the northwest of Zimbabwe (19°00' S, 26°30' E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. October is the hottest month with a mean daily temperature of 33.2 °C, July is the coldest month with a mean daily temperature of 4.1 °C. The mean annual temperature is 20.3 °C. During the cool dry season (May–August) frost occasionally occurs.

Data were collected along the northern boundary of HNP, in an area of 6000 km² covering part of the National Park and its peripheral area. HNP is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside HNP is designated for trophy hunting and, to a lesser extent, photographic safaris. Most of this land is privately owned or state owned, and there are several human settlements within the buffer zone (Fig. 1). In the buffer zone African wild dogs experience a

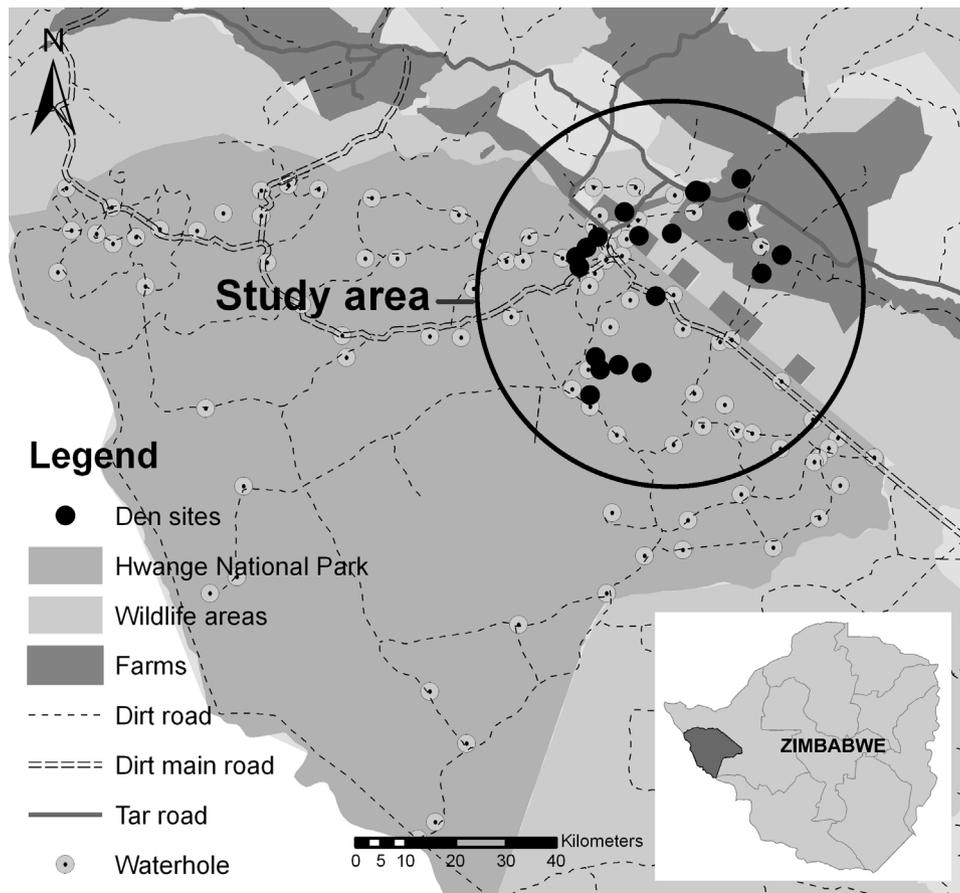


Fig. 1. Overview of the study area.

high level of mortality caused by human activity (Rasmussen, 1997; Van der Meer, 2011). In both areas the road network predominantly consists of dirt roads (low traffic density) that are used for game drives and hunts, and main dirt roads (medium traffic density) that serve as passage roads to areas with lodges. A tar road (medium to high traffic density) for regular traffic runs through part of the study area (Fig. 1). The vegetation is classified as typical southern African wooded savannah with patches of grassland, dominated by *Acacia*, *Baikiaea plurijuga*, *Burkea Africana*, *Combretum* and *Terminalia sericea* (Rogers, 1993). Prey species present in the study area include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*).

Predator densities

In 2005, lion densities inside HNP were 2.7 lions/100 km², whereas lion densities in the buffer zone outside HNP were as low as 0.06 lions/100 km² (Davidson, 2009). Over the years spotted hyena densities in the study area have been stable and densities have been estimated to be ca. 11.3 hyenas/100 km² inside HNP, and 5.5 hyenas/100 km² in the buffer zone outside HNP (Drouet-Hoguet, 2007). In 2009, there were approximately 50–70 African wild dogs in the study area (Zimbabwe Parks and Wildlife Management Authority, 2009; Blinston et al., 2010).

Protocol

African wild dog den sites were identified between 2001 and 2006 by radio tracking African wild dog packs and homing in on signals. In this study, we used 20 den sites, 10 den sites were situated in an area with relatively high predator densities and 10 den sites were situated in an area with relatively low predator densities. None of the den sites showed recent signs of fire or elephant damage. Random sites were selected by using a coordinate system where coordinates were generated randomly, coordinates that fell outside the home range of a given pack were discarded. We selected 20 random sites in the area with high predator densities and 20 random sites in the area with low predator densities.

Vegetation studies were carried out in 2007 between May and June, the months during which African wild dogs in the Hwange system give birth (Rasmussen, 2009). Vegetation characteristics at den and random sites were determined based on the method as described by Walker (1976). At each site, five vegetation plots were set at which vegetation and visibility measures were taken; one plot at the exact GPS point and four plots 50 m from this GPS point in each of the major compass directions (N, E, S, W). An average of the values for vegetation characteristics and visibility around these five plots was used in the final analysis.

At each site, we set a 10 m × 10 m plot to measure tree characteristics. Tree characteristics measured were tree height, canopy cover and stem density. Canopy cover was determined by measuring and multiplying the long and short diameter of the canopy. Stem density was determined by counting the number of stems including dead stems >2 m and regardless of whether one tree consisted of several stems.

Within the 10 m × 10 m plot we set a 5 m × 5 m plot to measure shrub characteristics. Shrub characteristics measured were shrub height, volume and density. Shrub density was determined by counting the number of shrubs within the plot. Shrub volume was determined by measuring the height, the short and the long diameter and using the formula: shrub volume = $\pi/4 \times$ long diameter × short diameter × height of shrub.

We randomly threw a 1 m × 1 m square within the 10 m × 10 m plot to measure grass height.

Visibility was estimated by positioning a seated observer at the centre of each plot at an eye level of 75 cm above ground, which

simulates an African wild dog's eye height. A second person walked away from the observer in each of the major compass directions (N, E, S, W) until the observer could no longer view him, and then whistled. After whistling, the second person started walking back towards the observer. As soon as the person was seen the observer whistled, the person walking stopped and recorded the distance between himself and the observer using a Garmin GPS.

At each site, the dominant vegetation species was recorded and the type of vegetation classified as bushland, woodland or grassland following Trochain (1957). Woodland was described as habitat dominated by trees with trees ≥ 3 m and less than 15 m distance between neighbouring trees. Bushland was described as habitat dominated by shrubs and a distance >30 m in between trees. Grassland was described as habitat dominated by grass and a distance of >30 m between shrubs and/or trees.

Distances to the nearest road and waterhole were calculated with the use of ArcGis[®] version 9.3. For an overview of the variables measured, see Table 1.

Statistical analysis

Previous research has shown that lions in the Hwange system select areas within 2 km from waterholes to hunt (Valeix et al., 2009a), and a large percentage of African wild dog kills is made within 2 km from waterholes (Van der Meer, 2011). We therefore divided distance to waterhole into two categories: <2 km from a waterhole, and >2 km from a waterhole.

African wild dog den site selection was analysed using a Jacobs index (Jacobs, 1974) according to the formula: $D = (r - p) / (r + p - 2rp)$, where r is the proportion of habitat used and p the proportion of habitat available (see Grignolio et al., 2003; Balestrieri et al., 2009). D ranges between -1 (strong avoidance) and $+1$ (strong preference), values close to zero indicate that habitat is used in proportion to its availability. We used a Jacobs index to test for preference or avoidance in relation to distance to waterhole, distance to road, visibility, vegetation type and dominant vegetation species. For the purpose of the den site selection analysis based on Jacobs' index, distance to road was divided into three categories: <500 m, 500–1500 m, and >1500 m from the road. Visibility was divided into the categories closed (≤ 25 m), medium (>25 m, ≤ 50 m) and open (>50 m) vegetation. Vegetation types were categorised as grassland, bushland or woodland.

Due to a relatively small sample size and a high occurrence of cell frequencies that equalled zero, the possibilities for additional testing of habitat selection were limited. Where possible, a binomial test was used to compare den site use versus availability, with the available proportion of habitat as the test proportion.

A binary logistic regression model was used to compare den sites selected versus random sites. In order to avoid multicollinearity and reduce the number of variables in the model we conducted a principal component analysis (PCA). PCA was conducted with orthogonal rotation (varimax). Sampling adequacy was verified with the Kaiser–Meyer–Olkin (KMO) measure, KMO = 0.73, all KMO values for individual items were ≥ 0.65 , which is above the acceptable limit of 0.5 (Field, 2009). Bartlett's test of sphericity ($\chi^2(15) = 146.54$, $p < 0.001$) indicated that correlations between items were sufficiently large for PCA. An initial analysis was run to obtain eigenvalues for each component in the data. Two components, vegetation cover and vegetation density, had eigenvalues over Kaiser's criterion of 1 and in combination explained 69.92% of the variance. Table 2 shows the factor loading after rotation. The variables distance to waterhole, distance to road, visibility and shrub density did not fulfil the criteria for PCA and were consequently excluded from the principal component analysis and treated as separate variables in the final analysis.

Table 1
Environmental characteristics of natal den sites and random sites in a high and low predator density area.^a

	High predator density area		Low predator density area	
	Natal den site (n = 10)	Random site (n = 20)	Natal den site (n = 10)	Random site (n = 20)
Distance to road (km)	1.07 ± 0.31	0.68 ± 0.14	0.35 ± 0.13	0.89 ± 0.21
Distance to waterhole	>2 km	<2 km	<2 km, >2 km	<2 km
Visibility (m)	30.38 ± 3.64	44.19 ± 6.02	22.98 ± 1.79	39.51 ± 4.23
Shrub height	55.11 ± 5.82	63.46 ± 5.87	67.77 ± 3.26	68.61 ± 5.82
Shrub volume	186.49 ± 54.97	194.20 ± 41.15	172.77 ± 23.06	314.71 ± 54.28
Shrub density per m ²	0.80 ± 0.16	0.52 ± 0.08	0.53 ± 0.06	0.67 ± 0.05
Tree height	385.19 ± 40.96	375.17 ± 32.98	435.20 ± 41.86	532.65 ± 30.86
Tree canopy cover	6.50 ± 1.73	8.73 ± 2.26	9.25 ± 2.20	15.88 ± 3.41
Tree stem density per m ²	0.12 ± 0.03	0.30 ± 0.08	0.21 ± 0.04	0.30 ± 0.07
Grass height	19.74 ± 2.46	26.14 ± 3.43	23.05 ± 2.73	18.19 ± 2.33
Vegetation type	Bushland/woodland	Bushland	Woodland	Woodland
Dominant species	Zambezi teak	Mixed	Mixed	Mixed

^a Values are mean ± SE or mode of nominal variable.

Variables entered in the binary logistic regression model were the categorical variables high or low predator density and <2 km or >2 km from a waterhole, and the continuous variables; distance to the road, visibility, shrub density, vegetation density and vegetation cover. In order to explore which vegetation characteristics determined den site selection in the high and low predator density area, all two-way interactions between high or low predator density and <2 km or >2 km from a waterhole, distance to the road, shrub density, visibility, vegetation density, vegetation cover were included in the model. With the lack of agreement on the best model approach to analyse behavioural data (Murtaugh, 2009), and the shortcoming of stepwise regression especially when dealing with small sample sizes (Whittingham et al., 2006), we decided to present the full model rather than perform an AIC-based or stepwise model selection (see Van der Meer et al., 2012). Before entering the variables into the model, we tested for collinearity by looking at tolerance statistics and variance inflation factors (VIF); tolerance for the variables added to the model was ≥0.75 and VIF's were ≤1.33.

All statistical analyses were performed with the use of SPSS software version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

Based on the Jacobs' preference index, both in the high and low predator density area African wild dogs selected den sites in closed woodland, >2 km away from waterholes (Figs. 2–4), and avoided medium to open bush and grassland, <2 km from a waterhole (Figs. 2–4). An additional binomial test showed that the proportion of den sites <2 km from a waterhole and the proportion of den sites >2 km from a waterhole differed significantly from the proportion of sites available (p = 0.01), with a lower proportion of den sites <2 km from a waterhole and a higher proportion of den sites >2 km from a waterhole relative to availability. In both the low and high predator density area Zambezi teak (*Baikiaea plurijuga*) dominated habitat seemed to be a preferred den site habitat (Jacobs index high predator density area; 0.75, Jacobs index low predator density area;

Table 2
Results of the principal component analysis, factor loading after rotation.^a

Item	Rotated factor loadings	
	Vegetation density	Vegetation cover
Mean tree height	0.46	0.52
Canopy cover (m ²)	0.74	0.55
Tree stem density (m ²)	0.72	0.37
Mean grass height	0.02	-0.89
Mean shrub height	0.88	-0.05
Shrub volume (m ²)	0.80	0.10

^a Factor loadings over 0.40 appear in bold.

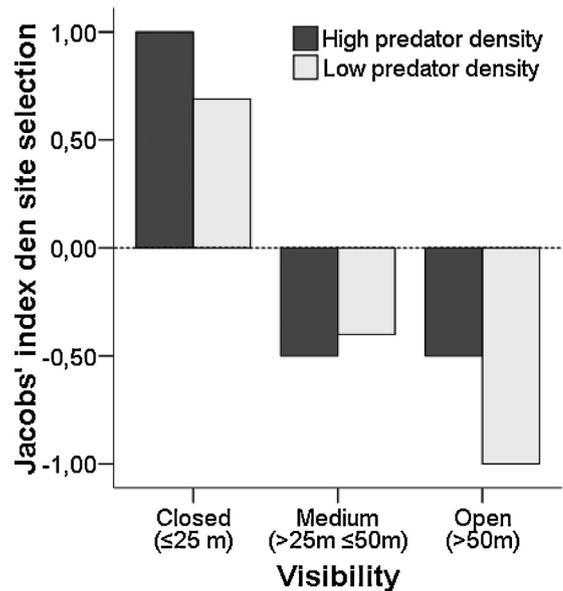


Fig. 2. Jacobs' index of African wild dog den site selection in relation to visibility.

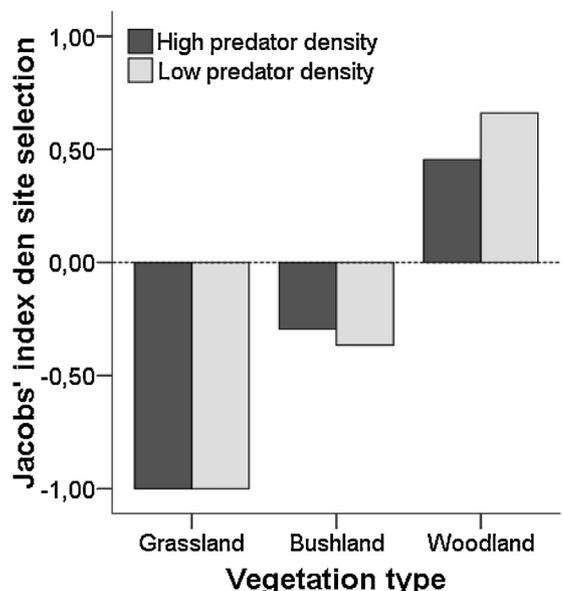


Fig. 3. Jacobs' index of African wild dog den site selection in relation to vegetation type.

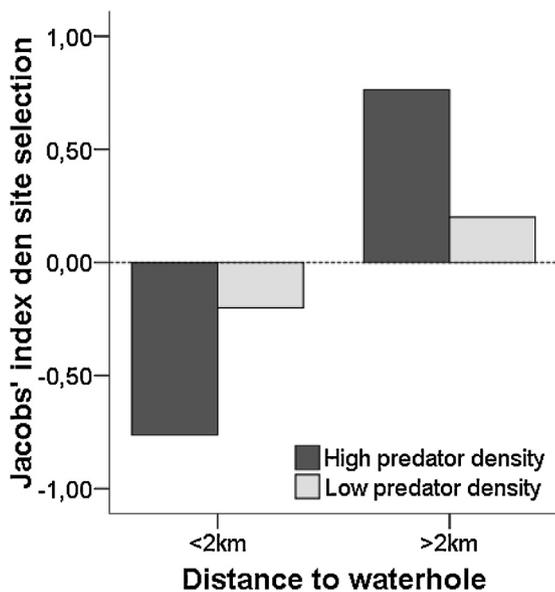


Fig. 4. Jacobs' index of African wild dog den site selection in relation to distance to waterhole.

0.78), none of the other dominant vegetation species were strongly preferred or avoided (all Jacobs indexes <0.5 and >-0.5).

In the high predator density area, African wild dogs selected den sites >1500 m away from the road and avoided den sites closer to the road (Fig. 5). In the low predator density area, they selected den sites <500 m from the road while avoiding den sites further from the road, especially den sites >1500 m from the road. In the high predator density area there seemed to be a stronger selection for den sites >2 km away from a waterhole, and avoidance of den sites <2 km from a waterhole, compared to the low predator density area (Fig. 4). An additional binomial test showed that, in the high predator density area, the proportion of den sites <2 km from a waterhole and the proportion of den sites >2 km from a waterhole differed significantly from the proportion of sites available ($p < 0.01$), with a lower proportion of den sites <2 km from a waterhole and a higher proportion of den sites >2 km from a waterhole relative to

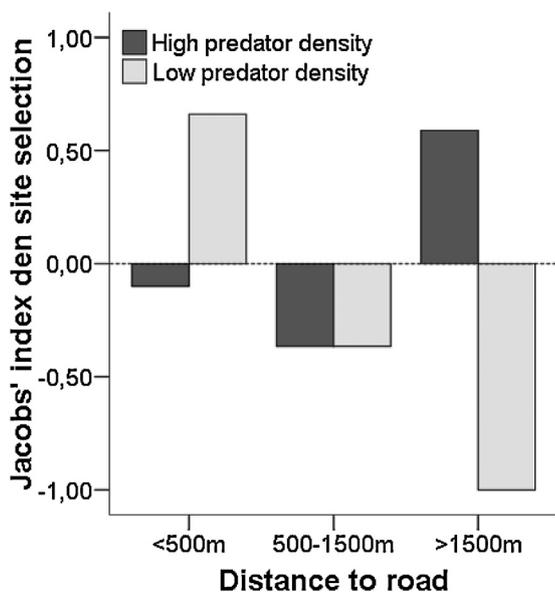


Fig. 5. Jacobs' index of African wild dog den site selection in relation to distance to the road.

Table 3

The binary logistic regression model for den site selection of African wild dogs.

	Coef	SE	Wald	df	P
Constant	20.06	9.21	4.74	1	0.03
Predator density (low predator density as reference)	-13.83	10.10	1.88	1	0.17
Distance to road	-2.46	1.74	2.00	1	0.16
Distance to waterhole (>2 km as reference)	-4.65	2.73	2.92	1	0.09
Visibility	-0.28	0.13	4.75	1	0.03
Shrub density	-11.05	5.42	4.15	1	0.04
Vegetation density	0.50	0.97	0.27	1	0.61
Vegetation cover	-0.70	0.83	0.71	1	0.40
Predator density \times Distance to road	4.32	2.24	3.73	1	0.05
Predator density \times Distance to waterhole	2.01	3.08	0.43	1	0.51
Predator density \times Visibility	0.08	0.18	0.19	1	0.66
Predator density \times Shrub density	8.29	5.87	2.00	1	0.16
Predator density \times Vegetation density	-1.93	1.46	1.75	1	0.19
Predator density \times Vegetation cover	1.93	1.08	3.18	1	0.08

availability. In the low predator density area there was no such difference between selected and available den sites ($p = 0.37$).

The binary logistic regression analysis showed that overall, African wild dogs selected den sites based on visibility and shrub density (Table 3). The likelihood of a site being selected as a den site increased with a decrease in visibility (coef \pm SE = -0.28 ± 0.13 , $p = 0.03$) and shrub density (coef \pm SE = -11.05 ± 5.42 , $p = 0.04$). Although the analysis based on Jacobs' index showed an effect of distance to waterhole, this effect was not significant in the regression analysis (coef \pm SE = -4.65 ± 2.73 , $p = 0.09$). Distance to road, vegetation density or vegetation cover did not affect overall den site selection (all $p > 0.16$) (Table 3).

The interaction between high and low predator density area and distance to road significantly affected den site selection (Table 3). In the high predator density area the likelihood of a site being selected as a den sites increased with an increase in distance to the road (coef \pm SE = 4.32 ± 2.24 , $p = 0.05$). None of the interactions between high and low predator density area and $<$ or >2 km from a waterhole, shrub density, visibility, vegetation density or vegetation cover significantly affected den site selection (all $p \geq 0.08$) (Table 3).

Discussion

We are aware of the limitations imposed by the small sample size on defining criteria used by African wild dogs to select natal den sites. However, with all known African wild dog dens being used in this study, we would like to stress the impossibility of having a large sample size of natal dens for a species that exists at low densities (see also Arjo et al., 2003 ($n = 8$), Fernández and Palomares, 2000 ($n = 7$)) and breeds cooperatively (see also Norris et al., 2002 ($n = 16$), Schmidt et al., 2008 ($n = 8$)), and would like to draw some prudent conclusions.

In this study, we found that for African wild dogs low visibility is a main den site selection criterion. Escape from predators has been shown to play an important role in natal den site selection (Pruss, 1999; Hwang et al., 2007; Lesmeister et al., 2008; Ross et al., 2010). While some studies have found that carnivores select dens with low surrounding vegetation in order to allow for an early detection of approaching predators (Zoellick et al., 1989), others have shown a preferential choice for den sites with dense and high surrounding vegetation that provides concealment from predators (Fernández and Palomares, 2000; Creel and Creel, 2002; Arjo et al., 2003). It is likely that for African wild dogs, in accordance with Creel and Creel (2002), the selection of den sites in habitat with limited visibility serves as a way to reduce the likelihood of detection by predators. In addition, once detected, thick bush might increase the chances for the pups to hide and escape predation.

Distance of the den site from waterholes might also contribute to the reduction of predation risk. In arid and semi-arid savannah systems large herbivores are more abundant in the vicinity of waterholes (Redfern et al., 2003; Valeix et al., 2009b). An aggregated distribution of prey inevitably affects the movement of predators. African wild dogs in the study area predominantly preyed on impala, kudu and duiker (Rasmussen, 2009), 73.0% of the impala, kudu and duiker kills were made within 2 km from a waterhole (Van der Meer, 2011). An African wild dog pack provides food for its pups by consuming large quantities of meat which are regurgitated upon return to the den (Malcolm and Marten, 1982). In order to reduce foraging distance, African wild dogs should select den sites relatively close to waterholes. However, the aggregation of prey around waterholes does not only affect African wild dogs, it also affects the movement of their competitors. Lions within the Hwange system have been found to reduce their search effort by selecting areas <2 km from a waterhole (Valeix et al., 2009a). With both lions and African wild dogs utilising the area <2 km from a waterhole to forage, it is likely that spotted hyenas, which scavenge on kills made by lions (Drouet-Hoguet, 2007) and steal kills from African wild dogs (Reich, 1981; Creel, 2001), can be regularly found within this 2 km radius as well. African wild dogs might therefore select den sites >2 km away from waterholes to reduce encounter rates with lions and spotted hyenas.

Prey has been found to show a diversity of behavioural adjustments in response to variations in predation risk (Valeix et al., 2009b; Périquet et al., 2010). Although short-term increased predation risk by African wild dogs had little effect on anti-predator behaviour of prey (Van der Meer et al., 2012), long term increased predation risk might affect prey behaviour. It is therefore possible that African wild dogs select den sites >2 km away from waterholes to avoid sensitising prey to their presence. An alternative explanation could be that woody cover has been found to be reduced in the vicinity of waterholes, especially within the first 2 km (Chamaillé-Jammes et al., 2009). This reduction was not consistently associated to elephant abundance or other herbivore related variables (Chamaillé-Jammes et al., 2009). With a preference for closed woodland, African wild dogs might therefore simply not be able to find suitable den site habitat close to waterholes. However, the fact that selection for den sites >2 km from a waterhole was more pronounced in the high predator density area seems to support the predator avoidance hypothesis.

When experiencing human disturbance, animals tend to stay further away from roads (Pépin et al., 1996; Kilgo et al., 2004). Although African wild dogs suffer a high level of persecution by humans (Woodroffe et al., 1997, 2004), they often use roads to travel and rest (Reich, 1981; IUCN/SSC, 2007). During this study tourism in Zimbabwe was low (Karambakuwa et al., 2011), therefore human disturbance in the high predator density area inside HNP was low. In the low predator density area in the buffer zone outside HNP, African wild dogs got exposed to a high level of mortality caused by human activity, e.g. road casualties and snares (Van der Meer, 2011). Despite this high level of human disturbance, African wild dogs selected den sites close to roads. In this study, human activity therefore does not seem to affect den site selection. In the high predator density area African wild dogs selected den sites further away from roads, with lions having the habit to travel along roads (Chardonnet, 2002), this might serve as a strategy to reduce the encounter rate with these larger carnivores.

Apart from protection from predators, den site selection has been found to be based on factors like food availability (Eide et al., 2001; Szor et al., 2008), thermal regulation and shelter from extreme weather conditions (Eide et al., 2001; Richardson et al., 2007; Ye et al., 2007; Lesmeister et al., 2008; Szor et al., 2008; Herr et al., 2010). African wild dogs selected den sites >2 km away from waterholes while most kills were made within 2 km from

waterholes. Both in the high and low predator density area, Zambezi teak (*Baikiaea plurijuga*) dominated habitat seemed to be a preferred den site habitat. As Zambezi teak is unpalatable (Holdo, 2003, 2007), herbivores do not occur in large numbers in Zambezi teak habitat (Ben-Shahar, 1996). Proximity of food resources therefore does not seem to play an important role in African wild dog den site selection.

Regardless of predator densities, African wild dogs seemed to preferentially select den sites in closed woodland with low shrub densities. This type of habitat is dominated by trees, which are likely to provide shade during the sunny days. Furthermore, closed vegetation with trees might provide relatively good protection against the cold nights as found during the reproductive months in the study area. Shelter from extreme weather conditions could therefore also play a role in den site selection by African wild dogs. The finding that African wild dogs selected den sites in habitat with low shrub density is likely to be a direct result of a preference for woodland. With none of the den sites being situated in grassland, den sites were situated in woodland and to a lesser extent bushland. Woodland is dominated by trees and will thus have a lower shrub density than bushland, which is dominated by shrubs. A preference for woodland therefore inevitably results in a preference for habitat with lower shrub densities.

When selecting a den site, carnivorous mammals often make use of burrows excavated by other species (Arjo et al., 2003; Lesmeister et al., 2008), e.g. Pallas's cats used Siberian marmot (*Marmota sibirica*) burrows (Ross et al., 2010), wolves used burrows dug out by Eurasian badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) (Schmidt et al., 2008). In some cases, den site selection by one species might therefore partly reflect den site selection pressures experienced by another species. African wild dogs have been reported to regularly make use of old aardvark burrows (Robbins and McCreery 2003; Woodroffe et al. 2004), which have sometimes been modified by warthogs (*Phacochoerus aethiopicus*) or spotted hyenas (Woodroffe et al. 2004; Knöthig 2005). The main enemies of aardvarks (lions, leopards (*Panthera pardus*) and spotted hyenas (Knöthig 2005)), largely overlap with those of African wild dogs. When selecting a den site, both species will therefore search for protection from similar predators. Within this study, we found no results that seemed to exclusively reflect aardvark selection criteria and could not be explained in terms of African wild dog ecology.

The time difference between the actual use of the natal den sites and measurement of the vegetation characteristics could have potentially created a bias in our results. Ever since 1992, the Hwange elephant population has been fluctuating around 30,000 animals (Chamaillé-Jammes et al., 2008). Although, in the Hwange system, at a landscape scale elephant induced changes to the vegetation were found to be limited (Valeix et al., 2007), at a micro-habitat scale elephants did alter vegetation (Valeix et al., 2011). Elephants and fire are the primary drivers of woodland change in African savannas (Holdo, 2007), their main effect being tree loss (Ben-Shahar, 1996). If fire and/or elephant impact has occurred, it is likely to have occurred at a similar level in the high and low predator density area, a comparison of den site characteristics is therefore likely to still produce meaningful results. Especially, as differences in den site selection in the high and low predator density area were based on spatial variables that are not subjected to rapid changes.

Regardless of predator densities, African wild dogs selected den sites in closed woodland with little visibility, which is likely to reduce detection by predators, increase the likelihood of escape when detected, and might provide shelter from extreme weather conditions. When predation risk was high, African wild dogs did seem to spatially try to avoid predators by selecting den sites in this type of habitat further away from waterholes and roads. African wild dogs have high energetic costs of gestation (Creel and Creel,

1991). Therefore, even when predation risk is relatively low, African wild dogs are likely to try to maximise their fitness by choosing a den site in habitat that will provide optimal protection for their offspring, leaving little additional options to respond to a higher predation pressure.

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