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Original Article

An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (*Lycaon pictus*) inside and outside a protected area

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The energetic output of hunting African wild dogs *(Lycaon pictus)* is extremely high. Therefore, survival and reproductive success depend not only on the ability to secure prey but also on minimizing foraging costs. African wild dogs often coexist with lions *(Panthera leo)* and spotted hyenas *(Crocuta crocuta)*; these competitors can seriously increase foraging costs by kleptoparasitism. In this study, we empirically and experimentally assessed the risk and costs of kleptoparasitism for African wild dogs inside Hwange National Park, where hyena densities are high, and outside the park, where hyena densities are lower. Lion densities within the study area have been fluctuating. The risk and costs of kleptoparasitism were determined by comparing direct observations during hunt follows of radio collared African wild dog packs and by the use of experimental call-ups with African wild dog sounds inside and outside Hwange National Park. The risk of kleptoparasitism was found to be significantly higher inside the park. The time it took lions and hyenas to get to the kill site during African wild dog hunts was longer outside the park allowing the dogs a longer carcass access time. The found differences in risk and costs of kleptoparasitism could contribute to African wild dog habitat choice for the buffer zone outside Hwange National Park. As habitat choice in and around protected areas is often related to the possibility of exposure to an "edge effect," interspecific competition should be considered in the conservation strategy of African wild dogs. *Key words:* African wild dog, foraging efficiency, habitat choice, interspecific competition, kleptoparasitism, predator competition. *[Behav Ecol 22:985–992 (2011)]*

INTRODUCTION

In systems where species forage in the presence of others, they may use the opportunity to steal resources from other successful foragers rather than spending time to secure resources themselves (kleptoparasitism). In general, kleptoparasitism is predicted to increase with a high density of hosts relative to prey and increasing food item value and handling time (Ruxton and Moody 1997; Hamilton 2002; Broom and Ruxton 2003). Another factor that affects the likelihood of kleptoparasitism is search efficiency. When competitors differ in their ability to search for food, those with the lower search efficiency are more likely to use kleptoparasitism as a strategy to obtain food (Hamilton 2002). Kleptoparasitizing a competitor might not always be cost efficient as challenging a competitor takes time that could otherwise be spent searching for undiscovered food. But if there is a strong asymmetry in size or fighting ability, the likelihood of successfully stealing food from a weaker competitor is increased and the benefits of kleptoparasitism may become higher than of searching for food (Broom and Ruxton 1998; Creel 2001; Hamilton 2002). Diet composition is likely to affect the benefits of kleptoparasitism. For species feeding on static food items like plants, the main costs of foraging are related to locating food items (Shipman and Walker 1989). Therefore, kleptoparasites are likely to benefit by a reduction in search time. For species feeding on mobile food items like vertebrate prey, the main costs of foraging are related to capturing prey (Shipman and Walker 1989). Especially, large carnivores experience relatively high hunting costs with long high-speed chases and high costs of capturing and killing prey (Carbone et al. 2007). Therefore, kleptoparasites are likely to benefit not only by a reduction in search time but also by avoiding the costs of chasing and killing prey.

Kleptoparasitism has been documented for many different types of animals, such as birds (Brockmann and Barnard 1979; Skorka and Wojcik 2008), fish (Webster and Hart 2006), and mammals (Carbone et al. 1997; Gorman et al. 1998). One of the mammals regularly affected by kleptoparasites is the African wild dog *(Lycaon pictus)*, which often coexists with larger carnivores such as lion *(Panthera leo)* and spotted hyena *(Crocuta crocuta)*. African wild dog hunting success ranges from 44% up to as high as 91% (for an overview, see Creel S and Creel NM 1998), which contrasts with the lower hunting success of hyena (25–30%; Holekamp et al. 1997) and lion (27–30%; Funston et al. 2001). The high

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hunting efficiency of African wild dogs compared with lions and hyenas and their smaller body mass make them vulnerable for kleptoparasitism by these bigger carnivores. Although lions and hyenas largely rely on hunting and scavenging to secure food, both of these species are known to steal kills from African wild dogs (Estes and Goddard 1967; Reich 1981; Creel S and Creel NM 1995; Carbone et al. 1997; Gorman et al. 1998; Drouet-Hoguet 2007). Data from different ecosystems show that lions and/or hyenas affect African wild dogs indirectly by excluding them from habitat with high prey densities (Mills and Gorman 1997; Creel 2001) or directly by killing (Reich 1981; Ginsberg et al. 1995; Van Heerden et al. 1995; Woodroffe et al. 1997) and through kleptoparasitism (Estes and Goddard 1967; Reich 1981; Carbone et al. 1997; Gorman et al. 1998; Creel 2001).

African wild dogs are efficient hunters that rely on high hunting success rates at regular intervals. They use a widely foraging strategy, which comes with the benefit of increasing the likelihood of encounter and thus ensuring prey capture, but also comes with significant energetic costs (Huey and Pianka 1981). The energetic output of hunting African wild dogs is extremely high (Gorman et al. 1998; Rasmussen et al. 2008), with more than 1500 KJ burnt per 100 m run (Rasmussen 2009). Not only does the survival and reproductive success of African wild dogs largely depend on its ability to secure prey, foraging in itself is costly and therefore minimizing foraging costs also positively affects survival (Rasmussen et al. 2008). Lion and hyena interfere with this minimalization and can seriously increase foraging costs by kleptoparasitism (Gorman et al. 1998).

In this study, we empirically and experimentally assessed the risk and costs of kleptoparasitism for African wild dogs inside a protected area (Hwange National Park), where hyena densities are high (Elliot 2007; 0.113 animals/km^2), and in the buffer zone outside the protected area, where hyena densities are lower (Elliot 2007; 0.055 animals/km^2). Due to sport hunting, lion densities within the study area have been fluctuating (see Methods). We determined the risk and costs of kleptoparasitism by comparing direct observations of kleptoparasitism during African wild dog hunts and by the use of experimental call-ups with African wild dog sounds in areas inside and outside Hwange National Park.

METHODS

Study area

Hwange National Park is situated in the Northwest of Zimbabwe (19°00′S, 26°30′E). The Hwange region is classified as semiarid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the Northern boundary of Hwange National Park in an area of 6000 km^2 covering part of the National Park and its peripheral areas. The area inside Hwange National Park is a protected wildlife area managed by the Zimbabwe Parks and Wildlife Management Authority. The buffer zone outside the National Park is destined for photographic safaris and trophy hunting. Most of this land is either privately owned or state owned and managed by Forestry Commission. Over the years, hyena densities in the study area have been stable and the densities have been estimated to be around 0.113 animals/km^2 in the area inside the National Park and 0.055 animals/km^2 in the buffer zone outside the National Park (Salnicki 2004; Drouet-Hoguet 2007; Elliot 2007). In 2005, the lion density inside Hwange National Park was estimated to be 0.027 individuals/km^2, whereas, due to sport hunting, the lion density outside the park was estimated to be as low as 0.0007 individuals/km^2 (Davidson 2009). In 2007, the lion density inside Hwange National Park was estimated to be around 0.026 animals/km^2 and the lion density in the buffer zone had recovered to approximately 0.022 animals/km^2 due to a moratorium (Elliot 2007).

Species

African wild dogs are medium-sized social canids, forming packs of up to 20 adults and their dependent offspring (Creel S and Creel NM 1995; Woodroffe et al. 1997). They are crepuscular with hunts being most common at dusk and dawn or when sufficient moonlight is available (Fanshawe and Fitzgibbon 1993; Creel S and Creel NM 1995; Fuller et al. 1995; Rasmussen 2009). They hunt by sight sound and smell for small to large antelopes, with kudu (*Tragelaphus strepciseros*), impala (*Aepyceros melampus*), and duiker (*Sylvicapra grimmia*) being their main prey in and around Hwange National Park (Rasmussen 2009). Previous research has shown that there was no difference in territory size, foraging distance, and diet composition of African wild dogs inside and outside the National Park, indicating that prey availability is similar (van der Meer E, Rasmussen GSA, Muvengwi J, Fritz H, unpublished data).

African wild dogs have large home ranges, which on average range between 423 and 1318 km^2 (Woodroffe et al. 1997). With fewer than 8000 individuals left in the wild, African wild dogs are classified as endangered and consequently rank high for conservation (Hunter et al. 2010). Over the years, their numbers in the Hwange area have declined. In 1997, it was estimated that African wild dog densities in and around Hwange National Park ranged between 150 and 225 individuals (Rasmussen 1997; Woodroffe et al. 1997). More recent information suggests that there are approximately 50–70 individuals left in and around Hwange National Park (Zimbabwe Parks and Wildlife Management Authority 2009; Blinston et al. 2010).

Hunt follows

Data from 22 radio-collared African wild dog packs were collected by G.S.A.R. between 1991 and 2002, with a study duration of 29.5 ± 20.1 months (mean ± standard deviation) per pack. As soon as a pack had been located, it was monitored nonstop from a distance of $\geq$ 50 m for as long as practically feasible (maximum 28 days). The activity of the pack was monitored continuously either visually or from motion sensors incorporated in the radio collars and recorded at 5-min scan intervals. Whenever a change in activity mode or direction occurred, location fixes were taken by using triangulation or visual observations and a GPS unit. When kills were made, the number of dogs feeding on the carcass, feeding time, the time it took before kleptoparasites arrived at the kill (lapse time), and the outcome of the defense of the kill were observed and recorded. As feeding time can differ per individual, it was measured as the time the pack had access to the carcass in cases where the kill was kleptoparasitized, successfully defended, or when no kleptoparasites were present. We categorized the data into events inside the National Park and events in the buffer zone outside the National Park. Being kleptoparasitized was defined as having the carcass stolen by lion and hyena within 60 min after the actual kill. After this time, irrespective of pack size, all dogs within a pack would either be satiated or the carcass would be finished.

Call-ups

As the average pack size in our study area is approximately 4 individuals per pack and impala are a main part of the diet, a 2-min recording of 4 African wild dogs killing and eating an impala was used to call up lions and hyenas. In total, we selected 48 call sites along the Northern edge of Hwange

National Park, 24 inside the National Park and 24 in the buffer zone outside the National Park. Lion and hyena are known to respond to call-ups from a range varying between 2.5 and 3.2 km (Ogutu and Dublin 1998; Mills et al. 2001). Although it is possible that the sounds we used are less of a stimulus and therefore have a smaller range than the sounds of kills of larger prey species, hyena interactions, and hyena lion interactions that are generally used during call-up sessions to estimate population densities, we decided to be conservative and situate call sites at least 7 km apart in order to avoid attracting the same animal twice. We called lion and hyena up at 0530 h in the morning and 1800 h in the evening, the time frames at which African wild dogs normally hunt.

We parked the car at an open spot on the road and played the sound fragment at maximum volume in the north, east, south, and west direction. Sounds were played at high amplification with two 100 W speakers connected to a 250 W amplifier, powered by the vehicles 12 V battery. Each 8-min call-up session was followed by a 5-min pause. Under normal conditions, the average feeding time of African wild dogs in our study area is around 30 min (Table 1). Therefore, we repeated the 8-min session 3 times. After the third time, another 26 min were spent in silence at the call site to allow for late responses. In total, we spent 60 min at each call site. After a period of 60 min, responses by kleptoparasites are unlikely to result in a significant loss of the kill as in a natural situation by then all dogs in a pack will either be satiated or the carcass will be finished.

Species, time of response, and number of animals responding were noted. Call-ups carried out made with a minimum of 3 people to be able to monitor both the vocal and the visual responses in all directions. As in general there were just 1 or 2 animals responding, it was not difficult to keep track of the animals and avoid double counting. If an animal responded vocally and was thereafter seen at the kill site, only the time of the visual response was recorded. After each session, we checked the area within a range of 150 m around the call-up station for spoor.

As the time at which the responding animal was seen and the distance at which the sound travels could be influenced by vegetation density, each call-up was followed by a vegetation monitor to determine bush and tree densities following the method as described by Walker (1976). An imaginary cross was placed on top of the car; 4 vegetation plots were placed along those 4 lines at 50 m from the car. At each plot, we determined vegetation density (for details of the method used, see Supplementary Material) and measured visibility in the north, east, south, and west direction by having one observer sitting in the middle of the plot and a second person walk away with a Garmin GPS to measure the distance at which this person went out of sight for the observer.

As wind speed and light strength could potentially affect the response of hyenas and lions, we measured wind speed with the use of a Silva wind meter (Silva Sweden AB, Sollentuna, Sweden); light strength was determined using a digital lux meter (LX1010B) (Precisions Mastech Enterprises, Kwun Tong Kowloon, Hong Kong).

Statistical analysis

Hunt follows

As there was no or a very limited response of lion in the buffer zone outside Hwange National Park, we performed analyses for lion and hyena together or for hyena separately. We used a binary logistic regression model to calculate the probability of presence of lion and/or hyena. To identify the factors influencing the presence of lion and/or hyena, we used a backward stepwise selection procedure based on the likelihood ratio with successive removal of variables for which $P > 0.05$. For the analysis of successful and failed kleptoparasitism during African wild dog hunts, we only selected cases where lion and/or hyena responded within the first 60 min. The variables for the hunt follows were inside or outside Hwange National Park, time of hunt, and African wild dog pack size. The interaction between pack size and inside or outside Hwange National Park, and time of hunt and inside or outside Hwange National Park was also taken into account. We used a similar procedure to analyze the probability of success of defense of the kill when lion and/or hyena were present during African wild dog hunts, with the variables inside or outside Hwange National Park, African wild dog pack size, and the interaction between the 2.

We analyzed lapse time with the use of a backward generalized linear model with a gamma distribution. Two full models were built with an identity link or a log link. Based on the Akaike information criterion with a second order bias correction, we decided that the generalized linear model with an identity link and maximum likelihood estimates as the scale parameter method was the best-fitting model. Variables used in the analysis were inside or outside Hwange National Park, time of hunt, and African wild dog pack size. We also took the interaction between inside or outside Hwange National Park and time of hunt, and inside or outside Hwange National Park and pack size into account.

We used a linear regression model with a stepwise backward procedure to determine the relationship between number of hyena present and African wild dog pack size. Variables added to the model were African wild dog pack size and inside or outside Hwange National Park.

It has been estimated that African wild dogs have a stomach capacity of 9 kg (Creel S and Creel NM 1995; Pribyl and Crissey 1999). African wild dog consumption rate is likely to be affected by previous consumption, and therefore, African wild dogs might not always be able to consume 9 kg. As there was no information available about previous consumption, we nevertheless used 9 kg as a baseline to see whether African wild dogs would have potentially met their maximum stomach capacity or not; this measure was used to quantify the quality of the kill. In order to be able to calculate whether the stomach capacity of a pack was met or not met, for the denning season, we calculated the maximum capacity by multiplication of the amount of adults and yearlings in a pack $\times$ 9 kg and for the nomadic season we added the amount of pups $\times$ 9 kg divided by 2 to be conservative (following Creel S and Creel NM 1995; Rasmussen et al. 2008). We obtained prey masses, measured as the total body weight, from Rasmussen et al. (2008). The maximum stomach capacity of a pack was subtracted from the prey mass; if this resulted in a negative number, the pack was said not to have met its stomach capacity, and if this resulted in a positive number, the pack was said to have potentially met its stomach capacity. As there were a large number of cases where prey mass had not been estimated and therefore it could not be determined whether the stomach capacity had been met or not, we used a separate logistic regression model with only the cases where prey mass was known to calculate the probability of presence of lion and/or hyena in relation to whether the stomach capacity of the African wild dogs within a pack was met or not met. Backward variable selection was used with successive removal of nonsignificant variables.

We used a nonparametric point biserial correlation in order to establish whether differences in lion and/or hyena presence when the stomach capacity of the African wild dogs was potentially met or not met were related to African wild dog pack size and/or prey mass.

Call-up experiment

Similarly to the hunt follows, we performed analysis for lion and hyena together or for hyena separately. We used a binary

Table 1

Feeding times with and without kleptoparasites present, n = 492, 191 kill sites inside Hwange National Park and 301 kill sites outside Hwange National Park (HNP)

	Hyena		Lion and/or hyena	
Feeding time (min) mean ± SE	Inside HNP	Outside HNP	Inside HNP	Outside HNP
Kleptoparasitized	11.06 ± 3.61	18.71 ± 7.78	9.67 ± 4.48	18.71 ± 7.78
Defended	30.64 ± 5.64	41.25 ± 6.25	30.64 ± 5.64	41.25 ± 6.25
Not present	29.00 ± 1.92	31.08 ± 1.23	29.00 ± 1.92	31.08 ± 1.23

logistic regression model to calculate the probability of presence of lion and/or hyena. To identify the factors influencing the presence of lion and/or hyena, we used a backward stepwise selection procedure based on the likelihood ratio with successive removal of variables for which $P > 0.05$. For the call-ups, we made a selection of vegetation variables based on bivariate Pearson's correlations. As shrub measurements were strongly correlated with visibility, only visibility was used in the analysis. We chose canopy volume as the variable to represent trees as there was no correlation between canopy volume and visibility but canopy volume was significantly correlated with all other tree measurements. The variables used in the analysis of the experimental call-up response were therefore as follows: inside or outside Hwange National Park, time of call-up, wind speed, light strength, tree canopy volume, grass height, and visibility. Due to differences in land use, animals in the areas outside Hwange National Park are more likely to be exposed to human activity, which could possibly result in a shift in activity frame or a change in behavior and therefore could potentially affect the response to the call-ups. To test for possible differences in response related to differences in land use, we also took the interactions inside or outside Hwange National Park and time of call-up, visibility, or light strength into account. We analyzed the lapse time during the experimental call-ups for both hyena and lion together and hyena separate and used a backward linear regression model with the variables inside or outside Hwange National Park, time of call-up, wind speed, light strength, tree canopy volume, grass height, and visibility. All statistical analyses were performed with SPSS software for MS Windows release 16.0 (SPSS Inc., Chicago, IL).

RESULTS

Risk of kleptoparasitism

Both the hunt follows and the call-up experiment showed that the risk for African wild dogs to encounter lion and/or hyena was significantly higher inside Hwange National Park. The likelihood of presence of lion and/or hyena at an African wild dog kill site was higher inside the National Park ($B = 1.18$, standard error [SE] = 0.32, $P = 0.000$, Wald = 13.68) (Table 2). Pack size, time of hunt, or the interactions between these variables and inside or outside Hwange National Park did not have a significant effect ($P > 0.05$, Wald ≤ 4.78). We found a similar result for hyena only with the likelihood of presence of hyena being higher inside Hwange National Park ($B = 0.96$, SE = 0.33, $P = 0.004$, Wald = 8.48) (Table 2).

During the call-ups, there was a significantly higher response of lion and/or hyena inside Hwange National Park ($B = 2.26$, SE = 0.72, $P = 0.002$, Wald = 9.81) (Table 3). We found no significant effect for time of call-up, wind speed, light strength, tree canopy volume, grass height, visibility, or the interaction between inside or outside the National Park and time of call-up, visibility, or light strength ($P > 0.05$, Wald ≤ 2.49).

If only hyena responses were taken into account, we found no differences in the likelihood of response inside or outside Hwange National Park. Variables entered in the model were inside or outside the National Park, time of call-up, wind speed, light strength, tree canopy volume, grass height, visibility, and the interactions between inside or outside Hwange National Park and time of call-up, visibility, or light strength ($P > 0.05$, Wald ≤ 3.52).

Costs and circumstances

The presence of lion and/or hyena did not necessarily mean that African wild dogs lost their prey, as there was always a chance that they successfully managed to defend their kill. None of the variables added in the logistic regression model significantly affected the likelihood of the success of defense of a kill, whether it was tested for lion and/or hyena ($P >$ 0.05, Wald $\leq$ 1.85) or hyena separately ($P > 0.05$, Wald $\leq$ 0.84). If looked at the percentage of successful defenses and the percentage of cases where African wild dogs were kleptoparasitized, there was basically a 50–50 chance that they either lost or successfully defended their kill when hyena were present at the kill site (Table 2). When lion were present, African wild dogs always got kleptoparasitized (Table 2).

Table 2

Presence of kleptoparasites at African wild dog kill sites, n = 492, 191 kill sites inside Hwange National Park and 301 kill sites outside Hwange National Park (HNP)

	Hyena		Lion		Lion and/or hyena	
	Inside HNP	Outside HNP	Inside HNP	Outside HNP	Inside HNP	Outside HNP
Presence	13.09% ($n = 25$)	5.65% ($n = 17$)	3.14% ($n = 6$)	0 ($n = 0$)	16.23% ($n = 31$)	5.65% ($n = 17$)
Kleptoparasitized	6.28% ($n = 12$)	2.66% ($n = 8$)	3.14% ($n = 6$)	0 ($n = 0$)	9.42% ($n = 18$)	2.66% ($n = 8$)
Defended	6.80% ($n = 13$)	2.99% ($n = 9$)	0 ($n = 0$)	0 ($n = 0$)	6.80% ($n = 13$)	2.99% ($n = 9$)
Mean lapse time (min) ± SE	10.84 ± 2.83	18.80 ± 4.32	14.40 ± 6.38	0	11.33 ± 2.57	18.80 ± 4.32
Mean number ± SE	2.73 ± 0.55	2.75 ± 0.55	*	*	*	*

*No data available.

Table 3
Response call-up experiment, n = 48, 24 call sites inside Hwange National Park and 24 call sites outside Hwange National Park (HNP)

Species responding	Response inside HNP (no.)	Mean no. responding inside HNP ± SE	Mean lapse time inside HNP (min) ± SE	Response outside HNP (no.)	Mean no. responding outside HNP ± SE	Mean lapse time (min) outside HNP ± SE
Hyena	9	1.67 ± 0.29	30.11 ± 4.10	5	1.00 ± 0.00	32.40 ± 3.54
Lion	7	1.86 ± 0.40	13.57 ± 3.21	1	1.00	41.00
Jackal	9	1.78 ± 0.28	8.77 ± 3.71	9	1.67 ± 0.17	21.33 ± 5.11
Kite	9	1.30 ± 0.26	16.89 ± 3.80	9	1.10 ± 0.19	12.22 ± 3.10
African wild dog	1	2.00	54.00	2	2.50 ± 0.50	42.00 ± 5.00
Leopard	0	0.00	0.00	1	1.00	28.00

Lapse time of lion and hyena was significantly shorter inside Hwange National Park (B = −11.30, SE = 4.90, P = 0.021, Wald = 5.32) (Table 2). The time of day a hunt took place affected the amount of time it took before these kleptoparasites arrived with a longer lapse time during the morning hunts than during hunts that took place at night when there was sufficient moonlight (B = 14.35, SE = 4.57, P = 0.002, Wald = 9.86). African wild dog pack size and the interaction between inside or outside Hwange National Park and time of hunt, and inside or outside Hwange National Park and pack size did not affect lapse time ($P > 0.05$, Wald ≤ 3.49). If only hyena were taken into account, similar results were found, with a shorter lapse time inside the National Park (B = −14.47, SE = 4.22, P = 0.001, Wald = 11.75) (Table 2) and a longer lapse time during the morning hunts than during hunts that took place at night when there was sufficient moonlight available (B = 15.32, SE = 4.41, P = 0.001, Wald = 12.08). African wild dog pack size and the interaction between inside or outside Hwange National Park and time of hunt and inside or outside Hwange National Park and pack size did not affect hyena lapse time ($P > 0.05$, Wald ≤ 3.62). The lapse time for the experimental call-ups both for lion and hyena together and for hyena separate did not differ inside or outside Hwange National Park (lion and/or hyena: B = 11.40, SE = 5.61, $P > 0.05$, t = 2.03; hyena: B = 7.28, SE = 4.65, $P > 0.05$, t = 1.57) (Table 3). In both cases, lapse time was not affected by time of call-up, visibility, grass height, canopy volume, or wind speed (lion and/or hyena: $P > 0.05$, $t \leq 2.05$; hyena: $P > 0.05$, $t \leq 3.76$). Light strength did not affect lapse time when lion and hyena responses were combined (B = −0.00, SE = 0.00, P = 0.825, t = −0.23) but did seem to affect the hyena lapse times with a stronger light strength resulting in a longer lapse time (B = 0.002, SE = 0.001, P = 0.048, t = 2.21). Stronger light strengths occurred late in the morning or early in the evening, the longer lapse time associated to it might mean that these periods of time were on the margins of the temporal activity frames of the hyena, and it therefore took longer before there was a response.

The number of hyena interacting was significantly related to African wild dog pack size, with an increase in number of hyena interacting with an increase in African wild dog pack size (Figure 1) (mean ± SE = 2.74 ± 0.33, B = 0.46, SE = 0.05, P = 0.000, t = 8.46), inside or outside Hwange National Park, did not affect the number of hyena interacting. When tested without the extreme of a pack of 24 dogs versus 13 hyenas, a similar result was found (B = 0.31, SE = 0.07, P = 0.000, t = 4.28). There was a higher likelihood of lion and/or hyena being present at the kill when the stomach capacity of the African wild dogs would have been met (B = −0.73, SE = 0.35, P = 0.038, Wald = 4.32). When analyzed for hyena only, the same result was found (B = −0.73, SE = 0.36, P = 0.043, Wald = 4.10). This either indicates that the likelihood of lion and/or hyena presence is higher when relatively small packs kill an average-sized prey or when average-sized packs kill big prey. We found a significant correlation between lion and/or hyena presence and prey mass (lion and/or hyena: P = 0.016, r = 0.11; hyena: P = 0.012, r = 0.11), whereas there was no correlation between lion and/or hyena presence and pack size (lion and/or hyena: P = 0.231, r = 0.03; hyena: P = 0.172, r = 0.04).

DISCUSSION

In this study, we found that the risk of kleptoparasitism is significantly higher inside Hwange National Park. For hyenas, for both the hunt follows and the call-ups, this risk seemed to be directly related to densities (Table 4). During the hunt follows as well as the call-ups, virtually no responses of lions were noted outside Hwange National Park (Table 4). At the time of the hunt follows, the bias in response rate could have been the result of sport hunting in the buffer zone outside Hwange National Park, which resulted in low densities of lions and a female bias in adult sex ratio (Loveridge et al. 2007; Davidson 2009). Previous research has shown that adult male lions tend to obtain most of their food by scavenging from kills of lionesses and other predators (Scheel and Packer 1991), which is in accordance with our finding that only male lions responded to the call-up sessions (no data on sex of lions responding during the hunt follows were available). However, the call-ups took place after a moratorium was implemented and lion densities were recovering and close to equal inside and outside Hwange National Park (Elliot 2007). Although lion and hyena densities have been found to be positively related (Creel S and Creel NM 1996; Mills and Gorman 1997), lions and hyenas are known competitors (Funston et al. 1998). With hyena densities inside the National Park being double

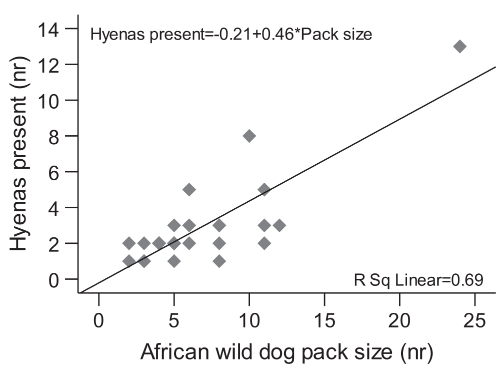

Figure 1
Number of hyenas present at African wild dog kill sites in and around Hwange National Park in relation to African wild dog pack size.

Table 4
Percentage of the population responding to call-ups (CU), densities based on Elliot (2007)

Species	Density inside HNP/km^2	Total present inside HNP CU area*	No. responding to CU	% Population responding to CU	Density outside HNP/km^2	Total present outside HNP CU area*	No. responding to CU	% Population responding to CU
Lion	0.026	22.347	13	58.17	0.022	18.583	1	5.38
Hyena	0.113	97.124	15	15.44	0.055	46.459	5	10.76

*Area covered inside Hwange National Park (HNP), 859.5 km^2, and area covered outside Hwange National Park, 844.7 km^2.

compared with outside the National Park (Elliot 2007), the competition rate between lions and hyenas will inevitably be higher inside Hwange National Park, which could possibly sensitize lions up to a point where they are overall more likely to respond to potential competitors. Prey density and distribution might also play a role as kleptoparasitism is generally considered to be lower with an increase in prey density (Broom and Ruxton 1998; Hamilton 2002).

Although hyenas have been found to kill African wild dogs (Creel S and Creel NM 1998), the main risk of encountering hyenas is related to kleptoparasitism. Lions on the other hand are known to be a common cause of death for African wild dogs (Mills and Gorman 1997; Creel S and Creel NM 1998). Due to a strong positive relationship between pack size, survival, and reproduction (Creel S and Creel NM 2002; McNutt and Silk 2008), in small packs, the loss of an individual can be detrimental for an entire pack of African wild dogs (Courchamp and Macdonald 2001; Rasmussen 2009). The fact that African wild dogs always lost their prey when encountering lions might be due to the fact that the risk of challenging a lion is not reduced to prey loss but might mean losing an individual and therefore the potential costs are too high to seriously attempt to fight.

Lions and hyenas were more often present at kills where the stomach capacity of African wild dogs of 9 kg (Creel S and Creel NM 1995; Pribyl and Crissey 1999) would have potentially been met, which seemed to be related to bigger prey rather than smaller pack sizes. This in itself is not surprising as with an increase in prey size, it is generally found that handling time and therefore the risk of kleptoparasitism increase as well (Ruxton and Moody 1997; Nilsson and Brönmark 1999; Hamilton 2002). There is a maximum to this increased risk as, according to the "apple model" of Broom and Ruxton (2003), the longer the prey has been handled the less value it will have, and therefore, individuals will only challenge when there is sufficient food remaining. The period of time where sufficient food remains for lions and hyenas to seriously challenge African wild dogs will inevitably be longer for bigger prey than for smaller prey, and it will therefore be more profitable to kleptoparasitize on bigger prey items.

We found that lapse time during morning hunts was shorter than during moonlight hunts. This most likely has to do with the fact that, with lions and hyenas being primarily nocturnal (Grinnell et al. 1995; Mills et al. 2001), there is a bigger overlap in activity time for lions, hyenas, and African wild dogs during the night compared with the morning. For hyenas, minimum lapse time during the hunt follows was 0 min, indicating that hyenas, as described in other studies (Estes and Goddard 1967; Reich 1981; Creel 2001; Rasmussen et al. 2008), start following hunting African wild dogs before they actually make the kill. This most likely also explains why the response to the call-ups is generally longer; the hyenas do not have the benefit of being able to follow the hunt from an early stage and therefore still need to travel a considerable distance to get to the call site. In 4 cases during hunt follows inside the National Park, hyenas were actually observed to interfere with the chase, whereas lions on the other hand were never observed to interfere with the chase. It is possible that, due to the small to medium prey sizes of African wild dogs, the benefits of kleptoparasitism for lions are relatively less compared with hyenas and that, unlike for hyenas, where kleptoparasitism appears to be an active strategy to obtain food, for lions, kleptoparasitism is more of an opportunistic event where, if they accidentally run into a pack of African wild dogs, they will steal the kill.

It took lions and/or hyenas longer to get to a kill site outside Hwange National Park. As, after killing the prey by disemboweling it, African wild dogs devour their prey as quickly as possible, this allows them more time to consume a substantial part of the prey themselves before being kleptoparasitized. Generally, hyenas seem to locate African wild dog kills more quickly in open habitat (Creel S and NM Creel 1996, 1998). Although vegetation density did not have an effect on the response time of lions and/or hyenas during the call-up sessions, it is possible that it does influence the response time during the hunt follows as vegetation density is likely to affect the ease with which hyenas are able to follow a hunting pack of African wild dogs. It is therefore possible that the found differences in lapse time reflect differences in vegetation density inside and outside Hwange National Park.

It has to be kept in mind that the small sample sizes, especially when testing for interactions, impose limitations. The small samples are largely due to the limitations in following hunts in thick bush and the large amounts of hunts and call-ups that need to be documented to be able to describe kleptoparasitism. Despite these limitations, we do feel some conclusions can be drawn.

Studies by Creel S and Creel NM (1996) and Mills and Gorman (1997) have shown that African wild dogs try to avoid competition with lions and hyenas by utilizing habitats in which lion and hyena densities are low, even when this might mean moving into an area with lower prey density. Like for other carnivore species, most of the mortality of African wild dogs occurs when they range beyond reserve boundaries into border areas where, because of a so called "edge effect," they get increasingly exposed to human activity resulting in mortality (Woodroffe and Ginsberg 1998; Woodroffe et al. 2004). Previous research has shown that, over the years, African wild dogs in Hwange National Park moved closer to or crossed the National Park's border increasingly exposing themselves to such an edge effect (van der Meer E, Fritz H, Blinston P, Rasmussen GSA). One of the factors contributing to this movement could be competition with lions and hyenas. In other African ecosystems, hyena presence at African wild dog kills varied between 18% (Selous, Tanzania) and 86% (Serengeti, Tanzania); when hyenas were present, the occurrence of kleptoparasitism varied between 0% (Kruger, South Africa) and 86% (Serengeti, Tanzania) (Creel S and Creel NM 1998). Although compared with these numbers, the pressure of kleptoparasitism inside and outside Hwange National Park might not be extraordinarily high, the differences in risk and costs of kleptoparasitism might nevertheless affect African wild dog habitat choice. Within Hwange National Park, African wild dogs lost their prey once out of every 11 hunts, whereas in the buffer zone outside the National Park, they lost their prey once out of every 38 hunts. Based on the model of Gorman et al. (1998), inside Hwange National Park, African wild dogs have to approximately spend an additional 5 h hunting to compensate for kleptoparasitism, whereas outside the National Park, this is an additional 3.5 h. On top of that, when the kill is being kleptoparasitized, African wild dogs have approximately an 8 min longer feeding time outside the National Park (Table 1). For African wild dogs, for which the "normal" 3.5 h hunting each day already brings them close to their physiological limits (Gorman et al. 1998), these differences in risk and costs of kleptoparasitism could influence habitat choice for the buffer zone outside Hwange National Park.

Like in and around Hwange National Park, habitat choice of African wild dogs in and around protected areas, due to differences in land use, is often related to the possibility of exposure to an edge effect (human activity resulting in mortality) (Woodroffe et al. 2004). Even when the pressure of kleptoparasitism seems to be relatively low interspecific competition is likely to play a role in habitat selection of African wild dogs and should therefore be taken into account in the conservation strategy of the species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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REFERENCES

Blinston P, Rasmussen GSA, van der Meer E. 2010. Painted Dog Conservation end of the year report 2010. [cited 2011 January 29]. www.painteddog.org.

Brockmann HJ, Barnard CJ. 1979. Kleptoparasitism in birds. Anim Behav. 27:487–514.

Broom M, Ruxton GD. 1998. Evolutionary stable stealing: game theory applied to kleptoparasitism. Behav Ecol. 9:397–403.

Broom M, Ruxton GD. 2003. Evolutionary stable kleptoparasitism: consequences of different prey types. Behav Ecol. 14:23–33.

Carbone C, Du Toit JT, Gordon IJ. 1997. Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? J Anim Ecol. 66:318–326.

Carbone C, Teacher A, Rowcliffe JM. 2007. The costs of carnivory. PLoS Biol. 5:0363–0368.

Courchamp F, Macdonald DW. 2001. Crucial importance of pack size in the African wild dog (*Lycaon pictus*). Anim Conserv. 4:169–174.

Creel S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conserv Biol. 15:271.

Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Anim Behav. 50:1325–1339.

Creel S, Creel NM. 1996. Limitation of African wild dogs by competition with larger carnivores. Conserv Biol. 10:526–538.

Creel S, Creel NM. 1998. Six ecological factors that might limit African wild dogs. Anim Conserv. 1:1–9.

Creel S, Creel NM. 2002. The African wild dog: behavior, ecology, and conservation. Princeton (NJ): Princeton University Press.

Davidson Z. 2009. Lion ecology and socio-spatial impact of trophy hunting in Zimbabwe [Doctorate thesis]. Oxford: Oxford University.

Drouet-Hoguet N. 2007. Influence des activités anthropogéniques sur le régime alimentaire et la réponse numérique de la hyène tachetée en savane arborée dystrophique dominée par l'éléphant [Doctorate thesis]. Lyon (France): l'Université Claude Bernhard.

Elliot N. 2007. A comparison of two methods for estimating population densities of lion (*Panthera leo*) and other large carnivores using spoor transects and call-up stations [Master thesis]. Oxford: Oxford University.

Estes RD, Goddard J. 1967. Prey selection and hunting behaviour of the African wild dog. J Wildl Manage. 31:52–70.

Fanshawe JH, Fitzgibbon CD. 1993. Factors influencing the hunting success of an African wild dog pack. Anim Behav. 45:479–490.

Fuller TK, Nicholls TH, Kat PW. 1995. Prey and estimated food consumption of African wild dogs in Kenya. S Afr J Wildl Res. 25:106–111.

Funston PJ, Mills MGL, Biggs HC. 2001. Factors affecting the hunting success of male and female lions in Kruger National Park. J Zool. 253:419–431.

Funston PJ, Mills MGL, Biggs HC, Richardson PRK. 1998. Hunting by male lions: ecological influences and socioecological implications. Anim Behav. 56:1333–1345.

Ginsberg JR, Alexander KA, Creel S, Kat PW, McNutt JW, Mills GL. 1995. Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. Conserv Biol. 9:665–674.

Gorman ML, Mills MGL, Raath JP, Speakman JR. 1998. High hunting costs make African wild dog vulnerable to kleptoparasitism by hyena's. Nature. 391:479–481.

Grinnell J, Packer C, Pusey AE. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? Anim Behav. 49:95–105.

Hamilton IM. 2002. Kleptoparasitism and the distribution of unequal competitors. Behav Ecol. 13:260–267.

Holekamp KE, Smale L, Berg R, Cooper SM. 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). J Zool. 242:1–15.

Huey RB, Pianka ER. 1981. Ecological consequences of foraging mode. Ecology. 62:991–999.

Hunter L, Woodroffe R, Flocken J, Sillero C. 2010. The fading call of the wild, a status update of 15 species of wild cats and canids. A report by the International Fund for Animal Welfare [Internet]. Yarmouth Port (MA): Panthera, the IUCN Canid Specialist Group, the IUCN Cat Specialist Group, and the Wildlife Conservation Society. [cited 2010 July 31]. Available from: www.ifaw.org/callofthewild.

Loveridge AJ, Davidson Z, Hunt JE, Valeix M, Elliot N, Stapelkamp B. 2007. Hwange Lion Project Annual Report 2007. Harare (Zimbabwe): Zimbabwe Parks and Wildlife Management Authority.

McNutt JW, Silk JB. 2008. Pup production, sex ratios and survivorship in African wild dogs, *Lycaon pictus*. Behav Ecol Sociobiol. 62:1061–1067.

Mills MGL, Gorman ML. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conserv Biol. 11:1397–1406.

Mills MGL, Juritz JM, Zucchini W. 2001. Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through play back recordings allowing for non-response. Anim Conserv. 4:335–343.

Nilsson PA, Brönmark C. 1999. Foraging among cannibals and kleptoparasites: effect of prey size on pike behaviour. Behav Ecol. 10:557–566.

Ogutu JO, Dublin HT. 1998. The response of lions and spotted hyenas to sound playbacks as a technique for estimating population size. Afr J Ecol. 36:83–95.

Pribyl L, Crissey S. 1999. Diets for African wild dogs (*Lycaon pictus*)—management guidelines. In: African Wild Dog SSP—Husbandry Manual. Brookfield (IL): American Association of Zoos and Aquariums [cited 2010 March 8]. www.nagonline.net/HUSBANDRY/husbandry_manual_chapters.htm.

Rasmussen GSA. 1997. Conservation status of the Painted Hunting Dog *Lycaon pictus* in Zimbabwe. Harare (Zimbabwe): Zimbabwe Parks and Wildlife Management Authority, Ministry of Environment and Tourism.

Rasmussen GSA. 2009. Anthropogenic factors influencing biological processes of the Painted Dog *Lycaon pictus* [Doctorate thesis]. Oxford: Oxford University.

Rasmussen GSA, Gusset M, Courchamp F, Macdonald DW. 2008. Achilles' heel of sociality revealed by energetic poverty trap in cursorial hunters. Am Nat. 172:508–518.

Reich A. 1981. The behaviour and ecology of the African wild dog *Lycaon pictus* in the Kruger National Park [Doctorate thesis]. New Haven (CT): Yale University.

Ruxton GD, Moody AL. 1997. The ideal free distribution with kleptoparasitism. J Theor Biol. 186:449–458.

Salnicki J. 2004. The home range area dynamics of spotted hyena (*Crocuta crocuta*) in the woodland habitat of Hwange National Park, Zimbabwe [Masters thesis]. Harare (Zimbabwe): University of Zimababwe.

Scheel D, Packer C. 1991. Group hunting behaviour of lions: a search for cooperation. Anim Behav. 41:697–710.

Shipman P, Walker A. 1989. The costs of becoming a predator. J Hum Evol. 18:373–392.

Skorka P, Wojcik JD. 2008. Habitat utilisation, feeding tactics and age related feeding efficiency in the Caspian Gull *Larus cachinnans*. J Ornithol. 149:31–39.

Van Heerden J, Mills MGL, van Vuuren MJ, Kelly P, Dreyer MJ. 1995. An investigation into the health status and diseases of wild dogs (*Lycaon pictus*) in the Kruger National Park. J S Afr Vet Assoc. 66:18–27.

Walker BH. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. S Afr J Wildl Res. 6:1–32.

Webster MM, Hart PJB. 2006. Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. Behav Ecol. 17:959–964.

Woodroffe R, Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. Science. 280:2126–2128.

Woodroffe R, Ginsberg JR, Macdonald D. 1997. Status Survey and Conservation Action Plan, The African Wild Dog [Internet]. Cambridge (UK): IUCN/SSC Canid Specialist Group. [cited 2010 June 28]. www.canids.org/species/lycaon_pictus.htm.

Woodroffe R, McNutt JW, Mills MGL. 2004. African wild dog (Lycaon pictus). Paragraph 6.5 in 2004 Status Survey and Conservation Action Plan, Canids: foxes, Wolves, Jackhals and Dogs [Internet]. Cambridge (UK): IUCN/SSC Canid Specialist Group. [cited 2010 June 28]. www.canids.org/species/lycaon_pictus.htm.

Zimbabwe Parks and Wildlife Management Authority. 2009. Harare (Zimbabwe): National Conservation Action Plan for Cheetahs and African Wild Dog in Zimbabwe.