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Foraging costs, hunting success and its implications for African wild dog (*Lycaon pictus*) conservation inside and outside a protected area

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Abstract

When selecting a habitat, animals utilize habitat in which they yield the highest rate of energy. Differences in foraging costs and hunting success are therefore likely to affect habitat choice. In a previous study, we showed that African wild dog *(Lycaon pictus)* packs with territories inside Hwange National Park (HNP), over the course of several years, moved their territories into the buffer zone outside HNP, where reproductive success was higher but anthropogenic mortality exceeded natality. In this study, based on long-term radio-telemetry data from 22 African wild dog packs, we analysed whether differences in foraging costs and hunting success could have contributed to this territorial drift. Taking seasonality and pack size into account, we determined foraging costs (foraging distance and chase distance) and hunting success (successful or failed chase) inside and outside HNP. Although we observed no difference in foraging costs, hunting success was higher outside HNP, which is likely to have contributed to the territorial drift into the buffer zone outside the protected area. This study shows the importance of taking factors affecting hunting success into account in the conservation strategy of African wild dogs.

Key words: African wild dog, anthropogenic mortality, conservation, hunting success, Lycaon pictus, prey density

Résumé

Pour choisir un habitat, les animaux sélectionnent celui où ils puisent le taux d'énergie le plus élevé. Ce sont les différences entre le coût de l'alimentation et la réussite de la chasse qui sont donc les plus susceptibles d'influencer le choix d'un habitat. Dans une précédente étude, nous avions montré que les meutes de lycaons (*Lycaon pictus*) qui ont des territoires à l'intérieur du Parc National de Hwange (HNP) avaient, au cours de quelques années, déplacé leurs territoires vers la zone tampon située à l'extérieur du HNP où le succès de la reproduction était plus élevé mais où la mortalité anthropogénique dépassait la natalité. Dans cette étude, basée sur des données radio-télémétriques de longue durée portant sur 22 meutes de lycaons, nous avons cherché à savoir si des différences de coûts de l'alimentation et de taux de réussite de la chasse avaient pu contribuer à ce glissement territorial. En prenant en compte la saisonnalité et la taille des meutes, nous avons déterminé le coût de l'alimentation (distance pour aller se nourrir et longueur des poursuites) et le taux de réussite de la chasse (poursuite réussie ou vaine) à l'intérieur et à l'extérieur du HNP. Nous n'avons observé aucune différence dans les coûts de l'alimentation, mais le taux de réussite de la chasse était plus élevé en dehors du HNP, ce qui pourrait avoir contribué au glissement territorial vers la zone tampon à l'extérieur de l'aire protégée. Cette étude montre qu'il est important de prendre en compte des facteurs qui influencent le taux de réussite de la chasse dans la stratégie de conservation des lycaons.

Introduction

Due to the difficulty of hunting large prey, foraging costs for large carnivores are usually high, making them

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vulnerable to historical and future extinction (Carbone, Teacher & Rowcliffe, 2007). For the widely foraging African wild dog (*Lycaon pictus*), foraging costs verge on the extreme (Huey & Pianka, 1981; Gorman *et al.*, 1998; Rasmussen *et al.*, 2008). To reduce these costs, wild dogs hunt cooperatively (Creel & Creel, 1995; Courchamp & Macdonald, 2001; Rasmussen *et al.*, 2008), select weak prey (Fitzgibbon & Fanshawe, 1989), and use barriers to increase hunting success (Rhodes & Rhodes, 2004).

Although at a continental scale, African wild dog density was related to prey density (Hayward, O'Brien & Kerley, 2007), at a local scale prey density seems a poor indicator of wild dog density (Mills & Gorman, 1997; Creel & Creel, 1998). African wild dogs often co-exist with lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*), both of which affect wild dogs by interspecific killing (Ginsberg *et al.*, 1995; Van Heerden *et al.*, 1995), and kleptoparasitism (Gorman *et al.*, 1998; Van der Meer *et al.*, 2011). Wild dog densities are generally low in areas where lions and spotted hyaenas are common (Creel & Creel, 1996; Mills & Gorman, 1997).

Animals should preferentially utilize habitats in which they yield the highest rate of energy (Rosenzweig, 1991). However, due to differences in land use, habitat choice around protected areas is often related to exposure to anthropogenic mortality (Woodroffe & Ginsberg, 1998; Woodroffe *et al.*, 2007). For example, mortality of lions moving outside Hwange National Park (HNP) was mainly due to trophy hunting and conflict with humans (Loveridge *et al.*, 2007). African wild dog packs with territories inside HNP, over the course of several years, moved their territories outside HNP, where reproductive success was higher but anthropogenic mortality exceeded natality (Van der Meer *et al.*, in press). Reproductive success of wild dogs depends on their ability to catch prey and on minimizing foraging costs (Rasmussen *et al.*, 2008). With a higher reproductive success outside HNP, we expected foraging costs to be lower, and hunting success to be higher outside HNP. In this study, we tried to determine whether differences in foraging costs and hunting success are likely to have contributed to the territorial drift into the buffer zone outside HNP.

Method

Study area

Hwange National Park covers c. 15,000 km in the north-west of Zimbabwe (19°00′S, 26°30′E). The region is classified as semi-arid with a mean annual rainfall of 606 mm (CV ≈ 30%) (Valeix *et al.*, 2009a). Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the northern boundary in an area of 5,500 km, covering part of HNP and its peripheral area. Hwange National Park is a protected wildlife area, without human settlements or main roads. The buffer zone outside HNP is designated for photographic safaris and trophy hunting, with human settlements, and a main tar road running through part of the buffer zone. African wild dogs experience a high level of anthropogenic mortality outside HNP (Rasmussen, 1997; Van der Meer *et al.*, in press).

Wild dog prey species present, include impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*). Spotted hyaena densities have been estimated at 11.3 hyaenas/100 km inside HNP, and 5.5 hyaenas/100 km outside HNP (Drouet-Hoguet, 2007). Due to trophy hunting, lion densities were likely to be lower outside HNP (2005 estimates; inside HNP 2.7 lions/100 km, outside HNP 0.06 lions/100 km (Davidson, 2009)).

Hunt follows

Data from 22 radio-collared African wild dog packs were collected by G.S.A Rasmussen between 1991 and 2002 (study duration 7–72 months/pack). Packs were observed from a vehicle. A directional antenna was used to locate, and keep track of a pack. As soon as a pack was located continuous observation was made from a distance of ≥ 50 m, for as long as practically feasible (1–28 days). Whether the pack was resting or moving was monitored visually, or from motion sensors in the collars, at 5-min scan intervals. Changes in activity mode or direction were recorded, and location fixes taken by triangulation or visual observations and a GPS unit. A hunt period was defined as the period from rest to rest within which a pack searched for prey. With the extensive road network in the study area, and wild dogs using roads to travel and rest (Reich, 1981), it was, in most cases, feasible to keep pace with the pack and follow their movements visually and/or by radio-telemetry.

Foraging costs were determined by measuring foraging distance and chase distance. Foraging distance is the distance travelled (walking/trotting) before a pack initiated a chase. A chase was defined as the high speed (running) pursuit of prey. Chase distance is the sum of all interfix distances during a chase and by default is an underestimate of the actual distance. Whether the pack was foraging or chasing was confirmed visually or by the speed at which the pack was followed via radio-telemetry.

Hunting success was determined by the percentage of successful chases. A chase was considered successful when resulting in a kill, only verified kills were included in the analysis. Where possible, the prey species chased was recorded visually. Although visual observations provide a reliable indicator for the consumption of medium to large prey, it can underestimate the consumption of small prey (Davies-Mostert *et al.*, 2010). Previous analyses of hairs extracted from wild dog faeces confirmed that, in this study, visual observations provided a reliable indicator of the consumption of small prey (Rasmussen *et al.*, 2008).

Hunt follows were classified as inside (n = 650) or outside HNP (n = 1071). Data were collected during the denning (when pups are too small to follow the pack on hunts and the pack needs to return to the den) and the nomadic season (when pups follow the pack on hunts). Hunts were categorized as morning (am), evening (pm) or moonlight (ml) hunts.

For an overview of the hunting parameters, see Tables 1 and 2.

Statistical analysis

Statistical analyses were performed for prey species for which $n \geq 10$ for all hunting parameters. Accordingly, prey species included in the analyses were impala (48.7% of the hunts), kudu (36.1% of the hunts) and duiker (15.2% of the hunts). For the analyses of the hunting parameters, with the exception of the quality of the kill, pack size was defined as the number of adults and yearlings active in prey procurement. Pups were not taken into account as they do not actively participate in the hunt. To ensure there were no underlying differences inside and outside HNP in variables that could affect the hunt, we tested for differences in: pack size of the hunts followed, the number of hunt periods per day, prey species selected and killed and the quality of the kill. All statistical analyses were performed with R software (R development Core Team).

Foraging costs and hunting success. Chase distance was logarithmically transformed to meet the normality assumption and analysed using a linear mixed effects model fit by restricted maximum likelihoods. We added inside or outside HNP, time of hunt, season (denning or nomadic), pack size and prey species, to the model as fixed effects. To test for possible effects of land use, we included the interactions inside or outside HNP × pack size, and inside or outside HNP × time of hunt. Pack identity was added as a random effect. As preliminary analysis showed

Table 1 Overview of African wild dog hunting parameters inside and outside Hwange National Park (HNP)

	Inside HNP	Outside HNP	Difference	*P*-value
Foraging costs				
Chase distance				
Mean ± SE	0.92 ± 0.15	0.63 ± 0.10	No	0.06
n	43	81		
Foraging distance				
Mean ± SE	5.05 ± 0.28	5.30 ± 0.24	No	0.28
n	116	182		
Hunting success				
Successful chases				
%	62.9	78.4	Yes	0.03
n	70	88		
Other				
Pack size				
Mean ± SE	5.72 ± 0.18	6.02 ± 0.17	No	0.26
n	197	279		
Hunt periods/day				
Mean ± SE	1.58 ± 0.06	1.68 ± 0.05	No	0.14
n	95	155		
Kg/ind/kill				
Mean ± SE	9.86 ± 0.66	10.26 ± 0.59	No	0.65
n	47	88		

Table 2 The average proportion of impala, kudu and duiker killed by African wild dog packs inside (n = 21) and outside Hwange National Park (HNP) (n = 18)

Prey species	Inside HNP Mean ± SE	Outside HNP Mean ± SE	Difference	*P*-value
Impala	0.34 ± 0.07	0.39 ± 0.07	No	0.65
Adult male	0.19 ± 0.06	0.41 ± 0.10	No	0.10
Adult female	0.25 ± 0.07	0.38 ± 0.09	No	0.33
Subadult male	0.04 ± 0.02	0.03 ± 0.02	No	0.91
Subadult female	0.06 ± 0.03	0.00 ± 0.00	Yes	0.02
Juvenile	0.13 ± 0.06	0.01 ± 0.01	Yes	0.05
Kudu	0.30 ± 0.06	0.41 ± 0.07	No	0.26
Adult male	0.12 ± 0.07	0.04 ± 0.03	No	0.46
Adult female	0.20 ± 0.07	0.23 ± 0.08	No	0.36
Subadult male	0.09 ± 0.05	0.13 ± 0.06	No	0.11
Subadult female	0.26 ± 0.09	0.26 ± 0.08	No	0.68
Juvenile	0.19 ± 0.07	0.18 ± 0.05	No	0.58
Duiker	0.21 ± 0.06	0.12 ± 0.03	No	0.31

no difference between an AIC-based and stepwise model selection, we used a backwards stepwise selection procedure with successive removal of variables for which $P > 0.05$ (see also Murtaugh, 2009).

Foraging distance was square root-transformed to meet the normality assumption. For the analysis of foraging distance, we used an identical model and selection procedure as for the analysis of chase distance.

Hunting success was analysed using a generalized linear mixed model fit by Laplace approximation, with binomial distribution and logit link. Fixed effects entered in the model were as follows: inside or outside HNP, time of hunt, season, pack size and prey species. The interactions inside or outside HNP × pack size and inside or outside HNP × time of hunt were included in the analysis. Pack identity was added as a random effect. Preliminary analysis showed no differences between an AIC-based and stepwise model selection, we therefore used a backwards stepwise selection procedure with successive removal of nonsignificant variables.

Hunting parameters and prey density. We used a Wilcoxon rank-sum test to test for differences in pack size during the hunts followed, the number of hunts per day and the quality of the kill inside and outside HNP.

Diet composition was analysed by, for each pack, calculating the proportion of impala, kudu, duiker and other species in the diet (inside HNP n = 204 kills, outside HNP n = 284 kills). A Wilcoxon rank-sum test was used to test for differences in diet composition inside and outside HNP. This analysis was performed for species, and the different age and sex classes (adult males, adult females, subadult males, subadult females, juveniles) for impala and kudu. For duiker, there were not enough cases where both age and sex were determined to perform a separate statistical analysis. Analyses were performed for both prey selected (=prey chased) and prey killed.

As an indicator of the quality of a kill, we used kilograms of prey available per individual wild dog at a kill. Prey masses were obtained from Rasmussen *et al.* (2008) (Table 3). In the denning season, prey mass was divided by the number of adults and yearlings in a pack, in the nomadic season, by the number of adults and yearlings, plus the number of pups divided by two (following Creel & Creel, 1995).

Prey densities for the study area were obtained from HNP waterhole census data provided by Wildlife Environment Zimbabwe. We analysed 1994 and 1995 data; the years where a sufficient number of waterholes were monitored outside HNP ($n \geq 10$). During the census, animals were identified as male, female, juvenile or unidentified. A Wilcoxon rank-sum test was used to test for differences in male, female, juvenile, unidentified and total densities of impala, kudu and duiker inside and outside HNP.

Table 3 Mean masses (kg) of main prey species eaten by African wild dogs in and around Hwange National Park

Prey	Adult male	Adult female	Adult sex ?	Subadult male	Subadult female	Subadult sex ?	Juvenile male	Juvenile female	Juvenile sex ?
Impala	45.7	38.5	42.1	35.6	31.4	33.5	22.7	17.7	20.2
Kudu	227.8	157.4	192.6	85.5	98.7	92.1	44.3	46.1	45.2
Duiker	18.7	20.7	19.7						

Results

Foraging costs and hunting success

Chase distance decreased with an increase in pack size (coef ± SE = −0.06 ± 0.02, $P < 0.01$). Chase distances for impala and kudu were longer than for duiker (both $P < 0.01$) (Table 4). Whether the chase took place inside or outside HNP did not affect chase distance ($P = 0.06$) (Table 1), nor did time of hunt or season (all $P \geq 0.12$).

Foraging distance increased with an increase in pack size (coef ± SE = 0.06 ± 0.02, $P < 0.01$). Whether the pack was foraging inside or outside HNP did not affect foraging distance ($P = 0.28$) (Table 1), nor did time of hunt, season or prey species (all $P \geq 0.18$).

The likelihood of a successful chase was higher outside HNP (coef ± SE = 0.76 ± 0.36, $P = 0.03$) (Table 1). Time of hunt, season, pack size and prey species did not affect hunting success (all $P \geq 0.20$).

Hunting parameters and prey density

Pack sizes of the hunts followed ($W = 25838.00$, $P = 0.26$) and the number of hunt periods per day ($W = 6647.50$, $P = 0.14$) were similar inside and outside HNP (Table 1).

Both inside and outside HNP, impala, kudu and duiker made up the largest proportions of the African wild dog diet (Table 2). There was no difference in the proportion of impala, kudu or duiker chased (all $P \geq 0.41$) or killed (all $P \geq 0.26$). A higher proportion of juvenile impala was chased ($W = 230.50$, $P = 0.05$) and killed ($W = 235.50$, $P = 0.05$) inside HNP. Although there was no difference in the proportion of subadult female impala chased ($W = 225.00$, $P = 0.19$), a higher proportion was killed inside HNP ($W = 243.00$, $P = 0.02$). The proportion of chased and killed adult male, adult female and subadult male impala did not differ inside versus outside HNP (all $P \geq 0.10$). Overall, African wild dogs primarily chased and killed adult impala (Table 2). The proportion of chased and killed adult male, adult female, subadult male, subadult female and juvenile kudu did not differ inside versus outside HNP (all $P \geq 0.11$). Overall, African wild dogs primarily chased and killed female and juvenile kudu (Table 2).

Whether a kill was made inside or outside HNP did not affect the kilograms of prey available per African wild dog ($W = 62112.50$, $P = 0.65$) (Table 1).

There was no difference inside versus outside HNP in male, female, juvenile, unidentified or total impala density ($W \leq 1359.00$, $P \geq 0.14$), nor was there a difference in male, female, juvenile, unidentified or total kudu density ($W \leq 1337.00$, $P \geq 0.10$) (Table 5). The density of male, female, juvenile and unidentified duiker was higher outside HNP ($W \leq 1311.50$, $P \leq 0.05$), so was the total density ($W = 1183.50$, $P < 0.01$) (Table 5).

Table 4 Chase distance (km) of the main prey species (impala, kudu, duiker), inside and outside Hwange National Park (HNP)

Species		Overall	Inside HNP	Outside HNP
Impala	Mean (km)	0.89	0.92	0.87
	SE	0.12	0.17	0.18
	n	43	20	23
Kudu	Mean (km)	1.15	1.46	0.99
	SE	0.21	0.38	0.26
	n	38	13	25
Duiker	Mean (km)	0.19	0.23	0.18
	SE	0.03	0.09	0.03
	n	43	10	33

Discussion

In this study, we observed no differences in foraging costs for African wild dogs inside versus outside HNP. However, hunting success was higher outside HNP.

Although some studies show no effect of pack size on hunting success and chase distance (Fanshawe &

Table 5 The density (nr/waterhole) of impala, kudu and duiker inside (n = 43) and outside Hwange National Park (HNP) (n = 21)

Prey species	Inside HNP Mean ± SE	Outside HNP Mean ± SE	Difference	*P*-value
Impala	31.09 ± 7.17	50.52 ± 14.42	No	0.11
Male	8.51 ± 1.85	17.43 ± 4.99	No	0.14
Female	19.42 ± 4.67	30.10 ± 9.61	No	0.21
Unknown	1.81 ± 0.86	1.33 ± 0.74	No	0.40
Juvenile	1.35 ± 0.65	1.67 ± 0.94	No	0.30
Kudu	28.33 ± 3.86	27.90 ± 3.97	No	0.57
Male	7.28 ± 1.05	4.29 ± 0.93	No	0.10
Female	18.77 ± 2.61	21.05 ± 3.36	No	0.36
Unknown	0.19 ± 0.10	0.19 ± 0.09	No	0.34
Juvenile	2.10 ± 0.65	2.38 ± 0.63	No	0.36
Duiker	1.26 ± 0.51	6.62 ± 1.97	Yes	<0.01
Male	0.16 ± 0.09	0.71 ± 0.36	Yes	0.05
Female	0.21 ± 0.13	1.33 ± 0.58	Yes	0.01
Unknown	0.28 ± 0.11	2.33 ± 0.92	Yes	0.03
Juvenile	0.61 ± 0.35	2.24 ± 1.35	Yes	0.05

Fitzgibbon, 1993), others show that an increase in pack size results in a higher hunting success and shorter chase distances (Creel & Creel, 1995). In this study, an increase in pack size resulted in a decrease in chase distance, but pack size did not affect hunting success once the chase was initiated (see also Rasmussen *et al.*, 2008). This might indicate that, as suggested by Rasmussen *et al.* (2008), with the excessive costs of chasing, packs use an 'all or nothing' strategy as soon as a chase has been initiated and energetic expenditure commences.

In accordance with other studies (Pole *et al.*, 2004; Rhodes & Rhodes, 2004; Hayward *et al.*, 2006; Mbizah, Marino & Groom, 2012), African wild dogs predominantly predated on impala and kudu. Differences in diet composition could not explain the observed differences in hunting success. With young animals being easy to capture (Husseman *et al.*, 2003; Pole *et al.*, 2004), a higher proportion of juvenile and subadult impala in the diet should result in a higher hunting success inside HNP, whereas in this study wild dogs experienced a lower hunting success inside HNP.

Some studies show that predators select habitat according to prey abundance (Murray, Boutin & O'Donoghue, 1994; Valeix *et al.*, 2009a). Others show that, regardless of prey abundance, predators favour habitat in which the probability of a kill is higher (Hopcraft, Sinclair & Packer, 2005; Balme, Hunter & Slotow, 2007). It is likely that both factors play a role and predators try to balance search efficiency and hunting success. There were no differences in impala and kudu densities, but duiker density was higher outside HNP. Duikers make up a relatively small proportion of the wild dog diet, especially if body mass is taken into account. Despite a higher duiker density outside HNP, the proportion of duiker in the diet was higher inside HNP. A higher duiker density is therefore unlikely to be a main reason for African wild dogs to move outside HNP.

Hunting success is affected by vegetation density (Creel & Creel, 2002; Husseman *et al.*, 2003). Inside HNP, there seems to be a higher availability of open vegetation (Van der Meer, 2011). With browsing and grazing herbivores utilizing open habitat to avoid short-term predation risk (Jarman, 1974; Fritz & Loison, 2006; Valeix *et al.*, 2009b), a higher availability of open habitat could result in a higher encounter rate of prey in this type of habitat. Pursuing prey in thick habitat increases the likelihood of a kill (Creel & Creel, 2002; Husseman *et al.*, 2003). The lower hunting success of wild dogs inside HNP might be the result of a higher encounter rate of prey in open vegetation.

Inside HNP, lions and spotted hyaenas were more often present at wild dog kills, it also took them a shorter time to locate the kill compared with outside HNP (Van der Meer *et al.*, 2011). With spotted hyaenas likely to locate wild dog kills more quickly in open habitat (Creel & Creel, 1998; Creel, 2001), this time difference could reflect the previously mentioned vegetation differences. With a higher level of competition inside HNP, it is difficult to disentangle the role predator competition and hunting success play in the habitat choice of African wild dogs. Both are likely to have contributed to the territorial drift into the buffer zone outside HNP. Hunting success and foraging costs affect reproductive success of wild dogs (Rasmussen *et al.*, 2008). With the excessive costs of chasing (Rasmussen *et al.*, 2008), a higher likelihood of a successful chase (higher hunting success), and a lower likelihood of the loss of a kill to larger predators, might have resulted in a higher reproductive success outside HNP.

Although African wild dog packs were observed undisturbed at close range (see also Estes & Goddard, 1967; Creel & Creel, 1995), following them by vehicle might have affected our results. Human activity, especially hunting, changes activity patterns of prey (Crosmary *et al.*, 2012) and increases flight initiation distance (Stankowich, 2008). An increase in flight initiation distance of prey, increases chase distance for wild dogs (Reich, 1981), which might affect the strength of the relationship between pack size and chase distance. Prey in photographic safari areas is regularly exposed to vehicles and mostly ignore them (see also Hunter & Skinner, 1998). Although packs were followed at the greatest distance possible, the potential impact on prey behaviour in the trophy hunting areas cannot be excluded. To test for a land use effect, we included the interactions inside or outside HNP × time of hunt, and inside or outside HNP × pack size, in our analyses. Neither of the interactions affected foraging costs or hunting success. In addition, we observed no difference in foraging costs, and a higher hunting success outside HNP. Therefore, the impact of our method on prey behaviour is likely to have been minimal.

Relying on visual observations could possibly create a bias towards more open areas. The additional use of radio-telemetry reduces this bias. With the large number of recorded hunt follows, the long study period and lengthy observation periods, we feel that the possibility for a bias was minimized, and hunts were followed in vegetation representative for the respective area. This is supported by the fact that we were able to successfully follow a large number of hunts outside HNP, where open vegetation is less available (Van der Meer, 2011). Even if biases might have occurred, they are likely to have occurred at a similar level inside and outside HNP, a comparison of hunting parameters will therefore still produce meaningful results.

This study shows that a higher hunting success outside HNP might have contributed to African wild dogs leaving the safety of HNP. Due to unaccounted effects of anthropogenic mortality, this movement did not result in an anticipated increase in fitness but instead resulted in a population decline (Van der Meer *et al.*, in press). Several other studies have shown that carnivores select habitat in which the probability of a kill is higher (Hopcraft, Sinclair & Packer, 2005; Balme, Hunter & Slotow, 2007). When determining a conservation strategy for carnivores, it is therefore important to not only consider factors like predator and prey densities, but also habitat features that affect hunting success. This will allow for a better prediction of carnivore movement and enable the use of conservation resources in areas where it is most needed.

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