Mammalian Biology 81 (2016) 227–234

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original Investigation

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

S. Périquet[a,b,*], C. Mapendere[b], E. Revilla[c], J. Banda[d], D.W. Macdonald[e], A.J. Loveridge[e], H. Fritz[a,b]

[a] Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Université Claude Bernard Lyon 1, Bât Gregor Mendel, 43 Bd du 11 novembre 1918, 69622 Villeurbanne cedex, France
[b] CNRS HERD Program Hwange LTER, Main Camp Research, Hwange National Park, Zimbabwe
[c] Departamento Biología de la Conservación, Estación Biológica de Doñana (CSIC), Calle Américo Vespucio s/n, 41092 Sevilla, Spain
[d] Zimbabwe Parks and Wildlife Management Authority, PO Box CY140, Causeway, Harare, Zimbabwe
[e] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Oxfordshire OX13 5QL, UK

ARTICLE INFO

Article history:
Received 27 April 2015
Accepted 13 October 2015
Handled by Luca Corlatti
Available online 25 October 2015

Keywords:
Crocuta crocuta
Hwange National Park
Interference competition
Panthera leo
Predation risk

ABSTRACT

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

Introduction

Interactions among species regulate natural populations and shape community structure. Inter-specific killing is an extreme case of interference competition among carnivores (Donadio and Buskirk, 2006; Polis et al., 1989) and has been shown to occur amongst a wide range of species (Palomares and Caro, 1999). Predation by other carnivores is one of the main causes of juvenile mortality in some species (see Laurenson et al., 1995; Mills and Biggs, 1993 for wild dogs; Mills and Mills, 2013 for cheetahs) and might thus impact on population dynamics and recruitment. The protection of young animals may be the reason for many species to use dens (Carter et al., 2011; Tannerfeldt et al., 2002; Theuerkauf et al., 2003). In studies of predator avoidance, some suggested that individuals may use long term knowledge of their predators' space use (Fuller and Keith, 1981), but recent work suggests that their response can be reactive rather that predictive (Broekhuis et al., 2013).

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

* Corresponding author. Present address: Department of Zoology and Entomology, University of the Free State, Qwaqwa Campus, Private Bag X13, 9866 Phuthaditjhaba, Free State, South Africa. Tel.: +27 79 570 2683.
E-mail address: stephanie.periquet@gmail.com (S. Périquet).

http://dx.doi.org/10.1016/j.mambio.2015.10.005
1616-5047/

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

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

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

Material and methods

Study area

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

Movement data and predation risk by lions

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

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

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

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

We then quantified the presence of lions in the vicinity of a den at different spatio-temporal scales, representing the actual risk of encountering lions nearby the den. We defined ring buffers of 3 km,