Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana

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Keywords
competition; population density; brown hyena; spotted hyena; temporal activity; co-detection; camera trap; large carnivores.

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Editor: Matthew Hayward

Received 16 October 2020; revised 30 December 2020; accepted 15 January 2021

doi:10.1111/jzo.12873

Abstract

Large carnivore populations are declining worldwide due to anthropogenic causes such as habitat loss and human expansion into wild areas. Competition between large carnivores can exacerbate this decline. While brown hyena *Parahyaena brunnea* and spotted hyena *Crocuta crocuta* belong to the same family, they are rarely found in the same area or co-occur at low densities as spotted hyena are known to exclude brown hyena. In Central Tuli, Botswana, however, brown hyena and spotted hyena are both found at high densities. We undertook a camera trap survey in this area to estimate the densities of both species, and to examine temporal overlap and co-detection patterns of brown and spotted hyena. Estimated population densities based on spatial capture–recapture models were $10.5 \pm 1.9/100\ \text{km}^2$ for brown hyena and $14.9 \pm 2.2/100\ \text{km}^2$ for spotted hyena. These population densities are among the highest reported estimates in southern Africa. Strong temporal overlap was found between brown and spotted hyena, while there was no decrease in detection rate of brown hyena at camera sites where spotted hyena were also detected, which indicates that both hyena species did not tend to avoid encounters. Although both species compete for the same prey, we suggest as possible explanations that prey densities are high and that competition does not significantly negatively impact brown hyena, because brown hyena is a scavenger whereas spotted hyena scavenge and kill prey. With the found high densities of both carnivores, this study adds to the known variation in composition of existing large carnivore communities and suggests testable explanations for these densities.

Introduction

Most large carnivore populations worldwide are declining as a result of loss and fragmentation of habitat (Chapron *et al*., 2014), human expansion into wild areas (Yihune *et al*., 2009; Mponzi, Lepczyk & Kissui, 2014) and unsustainable trophy hunting (Treves & Karanth, 2003; Treves, 2009). Large carnivores are among those taxa most sensitive to these changes yet are economically important (in terms of benefits from tourism and depredation costs on domestic animals) as well as ecologically important (in terms of ecosystem functioning) (Naidoo *et al*., 2011; Ripple *et al*., 2014). Large carnivores may drive trophic cascades affecting large herbivore abundances and vegetation structure and composition, but also control other (small) carnivore populations (Ripple *et al*., 2014). Monitoring and understanding the distribution and population dynamics of these species are crucial for conservation (Williams, Nichols & Conroy, 2002; MacKenzie and Nichols, 2004).

While anthropogenic factors play a major role in the decline in large carnivore abundance, ecological factors can exacerbate this decline. The net effect of dominant carnivores on their subordinate competitors is usually negative and leads to a negative correlation in densities of subordinate and dominant competitors across ecosystems (Dröge *et al*., 2017). Subordinate competitors are subjected to two forms of competition: (1) exploitative competition, whereby one species outcompetes another for a limited resource through indirect interactions, and (2) interference competition, whereby one subordinate species is harassed, kleptoparasitized or killed by a dominant carnivore species (Linnell & Strand, 2000). Consequently, competition may potentially change and drive carnivore community patterns, determine niche partitioning and possibly limit coexistence of sympatric carnivores (Satgé, Teichmann & Christescu, 2017). In carnivore communities with species that experience strong interference competition, we can expect that the sympatric species differ in their spatial or temporal distribution or diet to facilitate coexistence (Di Bitetti *et al*., 2010; Comley *et al*., 2020).

The effects of dominant large carnivores on subordinate competitors are especially seen in Africa relative to most other parts of the world due to the rich, intact carnivore guild (Caro & Stoner, 2003). African large carnivore communities are typically characterized by the competitive dominance of spotted hyena *Crocuta crocuta* and lion *Panthera leo* (Mills, 2015). This competitive dominance affects the distribution and behavior of subordinate species when present, such as wild dog *Lycaon pictus* (Saleni *et al*., 2007; Dröge *et al*., 2017), cheetah *Acenonyx jubatus* (Hayward & Slotow, 2009; Droge *et al*., 2017), brown hyena *Parahyaena brunnea* (Mills, 1984; Hofer & Mills, 1998) and to a lesser extent leopard *Panthera pardus* (Balme *et al*., 2017; but see Ramesh *et al*, 2017; Comley *et al*., 2020).

Here, we estimate densities of spotted hyena and brown hyena, examine temporal overlap and co-detection patterns using camera traps Central Tuli, a protected area in southeastern Botswana. Spotted hyena are known to exclude brown hyena from areas where both species are present. For example, an increase in spotted hyena numbers in Kruger National Park resulted in a decrease in brown hyena density (Mills & Funston, 2003). Research by Williams *et al*. (2019) showed that spotted hyena relative abundance negatively impacted brown hyena occupancy. In central Tuli, a fairly complete large carnivore guild is present with leopard, spotted and brown hyena present in the area and lion and wild dog occasionally visiting the area. Despite Botswana's importance for brown hyena conservation, accurate density estimates are lacking, but see a summary of Botswana population estimates based on track counts in Winterbach *et al*., (2017). Our objective was to provide the first population estimates in central Tuli for brown and spotted hyena and a better understanding of brown and spotted hyena coexistence.

Materials and methods

Study area

The study area was located in Central Tuli, an approximate 600 km^2 protected area in South-East Botswana (Fig. 1). It is comprised of privately owned properties of which most host ecotourism lodges or private holiday houses and few properties have livestock with no fences between the individual properties. A 200-km^2 area was delineated in Central Tuli where a camera trap grid was used to sample both hyena species.

The dominant flora is riverine woodlands with large bands of large fever berry trees (*Croton megalobotrys*) and mopane (*Mopane-Combretum)* shrub savanna. Most precipitation falls during the wet summer months, spanning from November to April, with 350 mm average annual total rainfall. The carnivore guild consists of lion, leopard, spotted hyena, brown hyena, wild dog, aardwolf *Proteles cristata*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis*, African wildcat *Felis sylvestris lybica*, African civet *Civettictis civetta*, honey badger *Mellivora capensis* and small-spotted genet *Genetta genetta* all being present in the Tuli block.

Sampling design and field methods

Traditional population estimates of large carnivores, such as call-up stations and track counts, are notoriously unreliable (Norton, 1990; Belant *et al*., 2019), often have serious drawbacks (Belant *et al*., 2019) or are limited by logistical, financial, or time constraints. Camera trapping in combination with spatial capture–recapture (SECR) models has emerged as an effective alternative method to survey large carnivores that can be identified from their natural markings and calculate densities from mark–recapture data (Efford & Fewster, 2013).

A camera trapping survey was carried out from November 2019 to January 2020. The study area was divided into three parts. Every part was sampled for 24 days. Camera trap stations per part ranged from 11 to 14 (n = 14 in part 1, n = 11 in part 2 and n = 14 in part 3). Every camera trap station consisted out of two camera traps (27 Bushnell Trophy Cam HD Essential E3 cameras and 1 Crenova RD 1000 Trail Hunting Camera). Camera trap stations were placed at hyena latrines or at crossroads to maximize the capture probability of both hyena species. Camera trap stations were spaced 1.5–2.5 km apart and placed on trees 2–3 m from the latrines or from the middle of the road at a height of 40–60 cm. Cameras were

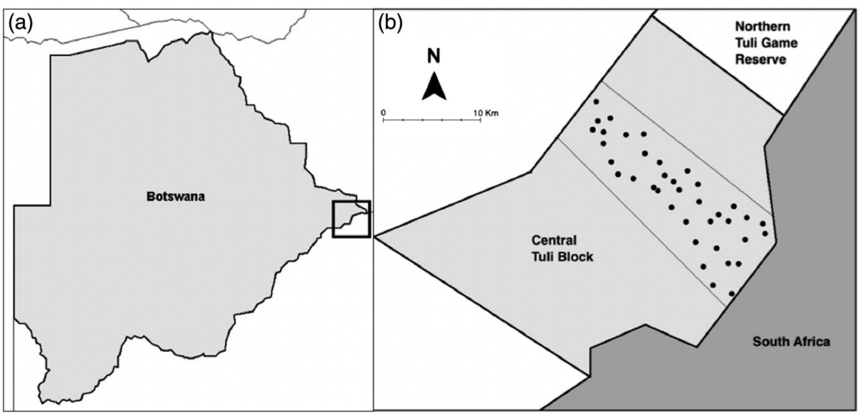

Figure 1 Map of (a) Botswana and (b) Central Tuli (pale gray) including the location of the survey area and the camera trap stations (black circles).

checked weekly to change batteries and download images. Cameras were set to run continuously and to take three photos per trigger with a 5-s delay between triggers with photograph quality of 16 M. Photographs that were recorded within 15 min of a previous photograph of the same species at the same camera trap station and could not be identified as a different individual were left out of the analysis as they cannot be considered an independent event (Kolowski & Forrester, 2017).

Because 2 camera traps were placed at a station, both left and right flank photographs could be obtained. Brown hyena were identified using their unique front leg stripe patterns and unique ear characteristics. Spotted hyena were identified using their unique spot pattern and other physical characteristics (e.g. body scars). A second observer separately identified brown and spotted hyena from the same photographs, and only individuals on which both observers agreed upon were used in the analysis. Cubs <1 year old were excluded from the analysis. Individual capture histories were constructed using 24-hour sampling occasions. Sex could not be determined for both hyena species on most photographs and was therefore left out of the analysis.

Density estimations

We used the 'secr' package in R (Efford, 2019) to estimate hyena densities. In 'secr' a maximum-likelihood spatially explicit capture–recapture framework is used and individual capture histories are combined with each individual's location where it was detected. Additionally, 'secr' produces two other parameters: the baseline encounter rate at the center of a home range g0, and σ describing how encounter rate decreases with increasing distance from the home range center. Two models were fitted for g0 including a learned response model (b, where hyena detection probability changes depending on previous captures) and a site learned response model (b_k, where hyena detection probability changes at a particular site once it is caught on camera) (Thornton & Pekins, 2015).

A habitat mask was created to represent habitat that is potentially the activity center for each hyena individual of the population being studied. We removed habitat outside the fence line from consideration due to no hyena movement outside central Tuli and increased human activity. A buffer of the maximum mean distance travelled (MMDM) was created using ArcGIS pro 2.4.2 (Esri Inc, 2019) around the camera trap grid based on recommendations by Tobler & Powell (2013) and Sharma *et al*. (2010).

Temporal partitioning

To examine temporal brown hyena–spotted hyena activity patterns, the coefficient of overlap (Δ) was calculated (Ridout & Linkie, 2009; Meredith & Ridout, 2014). To quantify the extent of overlap between both hyena activity patterns, a two-step procedure was performed. First, each activity pattern was estimated separately using kernel density estimation. Secondly, a measure of overlap between the two estimated distributions was calculated (Ridout & Linkie, 2009; Linkie & Ridout, 2011). Package *overlap* in R was used to do the analysis (Meredith & Ridout, 2016). Independent photographs were used as a random sample from the underlying distribution describing the probability of a captured event within any particular interval of the day. We used the estimator Δ_4 which is recommended for 'large' sample sizes by Ridout & Linkie (2009).

Spatial partitioning

In order to assess whether the presence of a species affected the detection probability of another species at a camera trap station, we used generalized linear modeling (GLM). Therefore, we used detection rate per camera trap station as response variable, calculated as the number of independent photograph events of a species divided by the number of 24-h trap days per camera trap station. A quasi-Poisson distribution was assumed, using a logarithmic link function, allowing for over/under dispersion from a standard Poisson distribution. Besides the detection rate per camera trap station for the other hyena species, the independent variables were as follows: (1) distance to koppies, since koppies can provide suitable den sites for rearing young, escaping from predators and harsh environmental conditions, factors all important in the survival of hyena species (Pokines & Peterhans, 2007; Holekamp & Dloniak, 2010) and (2) distance to water since sites close to water holes are characterized by high prey abundance and denser vegetation (Davidson *et al*., 2012). QGIS3 was used to calculate distance to koppies and water sources.

Results

We recorded 39 species of mammals based on 936 camera trap days. The number of independent photographs captured across camera trap stations for brown and spotted hyena was 448 and 335, respectively. Camera trap stations captured both hyena species at 33 camera trap stations (90%) and accounted for the majority of brown (97%) and spotted (98%) hyena captures.

For both hyena species, the b_k (site learned response) model was the best fitting model.

A total of 32 different brown hyena were captured on 213 sampling occasions. Individual brown hyena were captured on 1–23 sampling occasions (mean ± standard error / deviation = 7.1 ± 5.7) at 1–11 camera trap stations (mean = 4.9 ± 3.5) and were captured at all but two camera trap stations. Estimated brown hyena density was 10.6 ± 1.9/100 km^2 (Table 1).

A total of 46 different spotted hyena were captured on 261 sampling occasions. Individual spotted hyena were captured on 1-15 sampling occasions (mean = 5.7 ± 3.8) at 1-10 camera trap stations (mean = 4.3 ± 2.8), and spotted hyena were captured at all but two camera trap stations. Estimated spotted hyena density was 14.9 ± 2.2/100 km^2 (Table 1).

Detections of brown hyena were most common in the evening and early night (18:00 – 21:00 h) and in the early hours

Table 1 Model comparison table for SECR models for estimating brown and spotted hyena density and the two parameters baseline detection rate (g0) and sigma (σ)

Model	K[a]	Log Likelihood	AICc	ΔAICc	W_i	Density ± SE (Brown Hyena/100 km^2)
Brown Hyena						
$\lambda_0 \sim b_k$, $\sigma \sim 1$	5	−1307.034	2626.376	0.000	1	10.56 ± 1.92
$\lambda_0 \sim 1$, $\sigma \sim 1$ (null)	4	−1334.532	2678.546	52.170	0	10.47 ± 1.89
$\lambda_0 \sim b$, $\sigma \sim 1$	5	−1334.040	2678.080	54.012	0	10.72 ± 1.96
Spotted Hyena						
$\lambda_0 \sim b_k$, $\sigma \sim 1$	5	−1565.297	3140.594	0.000	1	14.90 ± 2.23
$\lambda_0 \sim 1$, $\sigma \sim 1$ (null)	4	−1580.630	3171.523	30.929	0	15.01 ± 2.25
$\lambda_0 \sim b$, $\sigma \sim 1$	5	−1582.187	3172.903	31.785	0	14.39 ± 2.16

Models were ranked according to their Akaike weights (Wi) based on the Akaike information Criterion for small samples (AICc), and only parameters included in models with AICc differences (ΔAICc) < 2 were averaged. In addition to the null model, two models were fitted for g0 including a learned response model (b) and a site learned response model (bk).

of the morning (01:00–04:00 h; Fig. 2). Spotted hyena were most frequently captured throughout the night, peaking in the early hours of the morning during 04:00–05:00 h. Temporal overlap between brown and spotted hyena was high based on kernel density estimates as indicated by the overlap coefficient estimate (Δ_4 = 0.80, 95% CI 0.73–0.85).

Brown hyena camera trap rate was not significantly related to spotted hyena camera trap rate, while distances to koppies and to water sources were also not significantly related to brown hyena camera trap rate (Table 2). Spotted hyena camera trap rate was not significantly related to distances to koppies and to water source (Table 2).

Discussion

In this paper, we assessed brown and spotted hyena densities, temporal overlap and co-detection patterns using camera trap data. As accurate population densities of these large carnivores are essential in successful conservation efforts and management implications (Williams *et al*., 2002; MacKenzie & Nichols, 2004), we present the first combined brown hyena and spotted hyena density estimates based on camera trapping. Using these data, we investigated whether densities of both hyena species were negatively correlated or whether there was a difference in activity during the day.

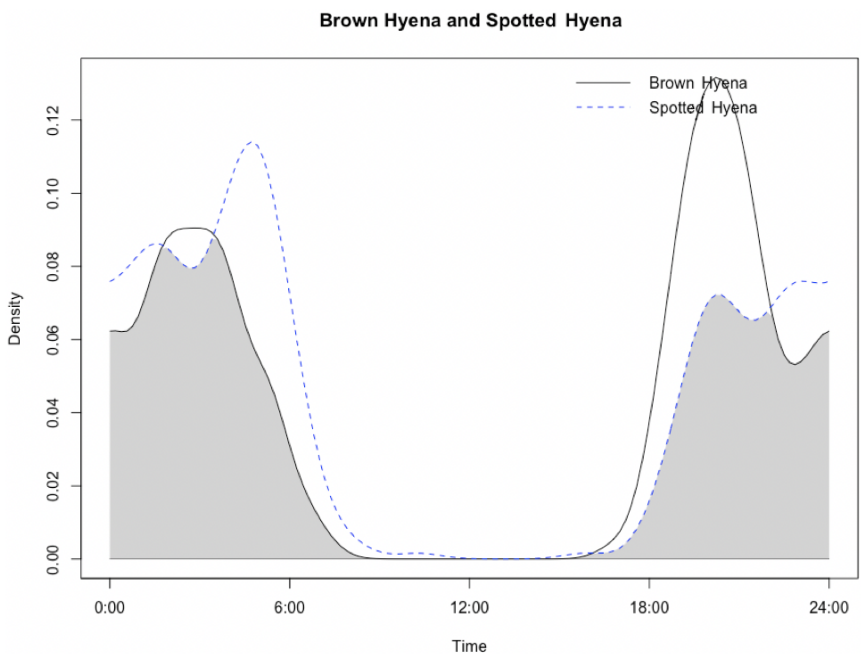

Figure 2 Density estimates of the daily activity patterns of brown and spotted hyena in central Tuli, Botswana. The solid lines are kernel density estimates for brown hyena, and the dashed lines are kernel density estimates for Spotted hyena. The overlap coefficient (Δ_4 = 0.80, 95% CI 0.73–0.85) is the area under the minimum of the two density estimates, as indicated by the shaded area in the plot.

Table 2 Variables from generalized linear models of brown and spotted hyena detections as is measured by camera trap rate in central Tuli, Botswana (*$P < 0.05$)

Variables	Brown hyena detections Estimate	SE	P-value	Spotted hyena detections Estimate	SE	P-value
SH-camera trap rate (total / camera trap days)	0.78	0.69	0.26			
BH-camera trap rate (total / camera trap days)				0.39	0.4682	0.41
	Brown hyena			*Spotted hyena*		
Distance to koppies (m)	−0.00013	0.00034	0.70	−0.00065	0.00052	0.21
Distance to water (m)	−0.000048	0.00076	0.95	0.00069	0.0089	0.44

For all variables, both the estimate and standard error (SE) are given with its corresponding *P*-value.

The density estimate for brown hyena is the highest reported estimate in Botswana and is among the highest reported estimates in southern Africa. Brown hyena density estimates vary across different areas: from 0.0/100 km^2–0.1/100 km^2 in Makgadikgadi Pans National Park, Botswana to 1.9/100 km^2–3.1/100 km^2 in the Ghanzi farms, Botswana (Winterbach *et al*., 2017) to 24.0/100 km^2 in Okonjima Nature Reserve in Namibia (Edwards, Heyns & Rodenwoldt, 2019) (Table 3). Similarly, the density estimate for spotted hyena is the highest reported estimate in Botswana and among the highest in Africa up to date. Cozzi *et al*. (2013) reported an overall density of 14.4/100 km^2 across the different habitat types in the Okavango Delta, Botswana while De Blocq (2014) reported a density of 10.6/100 km^2 in uMkhuze Game Reserve, South Africa, in a combination of camera trap and call-up studies (Table 3).

Carnivore density is positively related to prey abundance (Carbone & Gittleman, 2002; Karanth *et al*., 2004) as litter size and offspring survival increases (Fuller & Sievert, 2001). For example, Watts & Holekamp (2009) concluded that spotted hyena reproduction rates increase as a result of higher prey availability. For impala, which is the most abundant herbivore and main prey species in central Tuli, density was 32.9/km^2 (based on line transect data; Vissia et al. in prep.). As impala was the most important prey species in the diet of both spotted and brown hyena (through scavenging) in central Tuli (Vissia & van Langevelde. in prep.), the high impala density may explain the high densities for both brown and spotted hyena.

Our results did not demonstrate spatial and temporal partitioning between both hyena species. Temporal partitioning in activity patterns is thought to facilitate carnivore co-occurrence (Saleni *et al*., 2007; Hayward & Slotow, 2009; Dröge *et al*., 2017; Comley *et al*., 2020), but several studies quantifying temporal overlap between large carnivore species fail to show this temporal partitioning (Chaudhary *et al*., 2020). Temporal overlap between the two hyena species in central Tuli was high. As far as we know, no other study reported activity patterns for these two species in the same area. Furthermore, we found no evidence that the observed spotted hyena negatively affected the detection probability of brown hyena. In addition, distance to koppies and distance to water did not significantly influence brown or spotted hyena detection probabilities, suggesting that the distribution and movement of these species covered the whole area regardless topography of the landscape. Vegetation density could possibly influence detection probabilities since tree cover can act as refuges for safety from predators (Molina-Vacas *et al*. 2012).

Brown hyena are thought to compete with spotted hyena as both exploit shared resources (Mills, 1984; Mills & Funston, 2003; Yarnell *et al*., 2013). However, brown hyena rely on larger carnivores to kill larger prey species (Stein, Fuller & Marker, 2013; Yarnell *et al*., 2013; Mills, 2015) as scavenging could account for approximately 95% of the brown hyena dietary intake (Mills, 1984; Maude & Mills, 2005), and hence, both hyena species compete for the same resources. In central Tuli, the most numerous large carnivore species are spotted

Table 3 Brown and spotted hyena densities from previous studies in Southern Africa

Species	Location	Density/100 km^2	Method used	Reference
Brown hyena	Okonjima Nature Reserve, Namibia	24	Camera trap	Edwards, Heyns & Rodenwoldt, 2019
	Kwandwe Private Game Reserve, South Africa	14–19	Camera trap	Welch & Parker, 2016
	Ghanzi Farmlands, Botswana	2.3	Camera trap	Kent & Hill, 2013
	Makgadikgadi Pans NP, Botswana	0.05	Spoor count	Winterbach *et al*, 2017
Spotted hyena	Moremi Game Reserve, Botswana	14.4	Call-up	Cozzi *et al*., 2013
	uMkhuze Game Reserve, South Africa	10.6	Camera trap	De Blocq, 2014
	Ngamiland district, Botswana	10.1	Camera trap	Rich *et al*, 2019
	Etosha National Park, Namibia	2.1	Call-up	Trinkel., 2009
	Tsauchab River Valley, Namibia	0.85	Camera trap	Fouché *et al*., 2020

hyena and to a lesser extent leopard, which could provide scavenging opportunities for brown hyena (Mills, 1984; Stein, Fuller & Marker, 2013; Williams *et al*., 2018). For example, high brown hyena density on Kwandwe Private Game Reserve (Eastern Cape) was attributed to high carnivore densities and the resulting scavenging opportunities (Welch & Parker, 2016). Although an increase in scavenging opportunities as a result of high carnivore densities could facilitate hyena coexistence, other research has shown that spotted hyena densities negatively correlate with densities of the subordinate brown hyena (Mills, 1990; Mills & Funston, 2003). With the found high densities of spotted and brown hyena, this study adds to the known variation in composition of existing large carnivore communities and suggests testable explanations for these densities. Remarkably little research has been conducted on the potential of co-occurrence between brown and spotted hyena and more research related to diets, habitat use, densities and interference competition is needed to improve conservation efforts and facilitate brown and spotted hyena co-occurrence in other areas.

Acknowledgments

We thank the Botswana Ministry of Environment, Wildlife and Tourism and the Department of Wildlife and National Parks (DWNP) for granting permission to conduct this research in Botswana (research permit number: ENT 8/36/4XXXXIV (31)). We wish to thank M. Flyman and M. Somelokae from DWNP for their support and guests of Koro River Camp for their camera trap donations. This work was funded by Terra Conservancy Operations, Albert Hartog and the Timbo Afrika Foundation. In addition, we thank the different landowners for giving permission to include their properties in the study area. We thank staff members of Koro River Camp who assisted in the study.

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