Utilizing bycatch camera-trap data for broad-scale occupancy and conservation: a case study of the brown hyaena *Parahyaena brunnea*

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Abstract With human influences driving populations of apex predators into decline, more information is required on how factors affect species at national and global scales. However, camera-trap studies are seldom executed at a broad spatial scale. We demonstrate how uniting fine-scale studies and utilizing camera-trap data of non-target species is an effective approach for broadscale assessments through a case study of the brown hyaena *Parahyaena brunnea*. We collated camera-trap data from 25 protected and unprotected sites across South Africa into the largest detection/non-detection dataset collected on the brown hyaena, and investigated the influence of biological and anthropogenic factors on brown hyaena occupancy. Spatial autocorrelation had a significant effect on the data, and was corrected using a Bayesian Gibbs sampler. We show that brown hyaena occupancy is driven by specific co-occurring apex predator species and human disturbance. The relative abundance of spotted hyaenas *Crocuta crocuta* and people on foot had a negative effect on brown hyaena occupancy, whereas the relative abundance of leopards *Panthera pardus* and vehicles had a positive influence. We estimated that brown hyaenas occur across 66% of the surveyed camera-trap station sites. Occupancy varied geographically, with lower estimates in eastern and southern South Africa. Our findings suggest that brown hyaena conservation is dependent upon a multi-species approach focussed on implementing conservation policies that better facilitate coexistence between people and hyaenas. We also validate the conservation value of pooling fine-scale datasets and utilizing bycatch data to examine species trends at broad spatial scales.

Introduction

Carnivore species across the globe are in decline (Ripple et al., 2014). With an increasing human population, the biological traits of carnivores put them at high risk of extinction (Cardillo et al., 2004). Although some smaller species are plentiful and adaptable, many larger carnivores are vulnerable to extinction as a result of their narrow geographical ranges, small and isolated populations, low genetic diversity, specialized niche requirements, large home ranges, and propensity to compete with humans for the apex of shared food webs (Gittleman et al., 2001; Sillero-Zubiri & Laurenson, 2001). The key factors affecting carnivore survivorship are often interrelated; thus a connected and multifaceted approach is recommended in carnivore conservation (Winterbach et al., 2013).

Determining which factors influence species occupancy is vital for conservation, but this is often challenging for carnivores because of their secretive behaviour, nocturnal habits, low densities and broad spatial requirements that often extend beyond physical, administrative and political boundaries (Balme et al., 2010; Bischof et al., 2016; Chundawat et al., 2016). Camera traps are an increasingly popular tool in carnivore research and management because they overcome many of these obstacles (McCallum, 2013). They are affordable, can be deployed over large areas, and are able to collect continuous data non-invasively on even the most cryptic species. Accordingly, camera traps have

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the capacity to monitor species and inform conservation strategies at both national and global scales (Ahumada et al., 2016).

Despite this potential, few studies have examined carnivore occupancy, and the factors influencing occupancy, beyond the scale of single study sites (but see Karanth et al., 2011; Pitman et al., 2017a; Miller et al., 2018). This localized approach to monitoring generates a limited, and potentially biased, view of species ecology and behaviour. Recent collaborations have shown, however, that robust broad-scale species assessments are possible if researchers combine datasets from several single-site camera-trap surveys (e.g. Linkie et al., 2007; Miller & Grant, 2015; Tan et al., 2017). In addition, although many camera-trap surveys are established to monitor a single species, they also collect data on non-target species (Linkie et al., 2013). Such bycatch data can contribute towards assessments of non-target species if spatial violations are accounted for (Edwards et al., 2018). Occupancy modelling is forgiving of non-homogenous survey parameters and imperfect detection, and is therefore ideal for broad-scale collaborative analyses (MacKenzie et al., 2006). Occupancy modelling estimates the proportion of areas occupied by target species, and assesses which parameters affect utilization, through the examination of detection/non-detection data. Camera traps are ideal for collecting such data (O'Connell & Bailey, 2011). Compensating for potential false absences is an essential function of occupancy analysis, which distinguishes between a naïve occupancy estimate and the best estimate of true occupancy (MacKenzie et al., 2006).

A wide range of environmental, biological and anthropogenic factors can affect occupancy. In many cases, parameters associated with human disturbance and intraguild relationships have a greater influence on carnivore occupancy than environmental covariates (Schuette et al., 2013; Strampelli et al., 2018; Wang et al., 2018). For species that increasingly inhabit human-modified landscapes, a deeper exploration of how biological and anthropogenic factors affect occupancy is required.

We used camera trapping and single-season, single-species occupancy modelling to examine factors affecting brown hyaena *Parahyaena brunnea* occupancy across its South African range. Humans pose both direct and indirect threats to carnivores through habitat loss and degradation, prey depletion and poaching (Ripple et al., 2014). Private land used for farming comprises a large proportion of brown hyaena range, and is vital to their survival (Kent & Hill, 2013). Despite their ability to survive outside protected areas and in close proximity to people (e.g. Kuhn, 2014), brown hyaenas are subject to anthropogenic pressures, causing the species, which is categorized as Near Threatened, to come close to qualifying as threatened on the IUCN Red List (Wiesel, 2015). At present, research on brown hyaenas is predominately limited to geographically scattered,

small-scale studies. As a nocturnal and cryptic species, there is a paucity of data on the parameters affecting the species occupancy on a broader scale (Yarnell et al., 2016). By compiling data from 25 surveys into the largest detection/non-detection dataset collected on the species, our study makes a critical step towards filling this gap in ecological knowledge for protected areas and areas used for ecotourism. We also aim to demonstrate the potential for data initially collected to examine one target species, the leopard *Panthera pardus*, to provide a broadscale assessment of a bycatch species, the brown hyaena.

Study area

We collated data on brown hyaena detection and non-detection from 25 camera-trap surveys conducted across South Africa during 2013–2017 (Fig. 1, Table 1, Supplementary Material 1). The area surveyed totalled 7,705 km². Camera-trap survey sites within and outside formally protected areas were represented (21 formally protected sites and 4 privately protected sites). Although sites are either designated as protected areas by IUCN (UNEP-WCMC, 2018; Supplementary Table 1) or privately prioritize the conservation of native species, sections of KwaZulu Private Game Reserve and adjacent private properties, Lajuma and adjacent private properties, and Little Karoo are unprotected. All but three sites are fenced (Supplementary Material 1). However, even electrified perimeters are often permeable and brown hyaenas in protected areas may occupy home ranges that also include unprotected areas (Kesch et al., 2013, 2015; Miller et al., 2018).

An array of Panthera V-Series camera traps (models V4, V5 and V6; Panthera, New York, USA) monitored all sites except Mountain Zebra National Park, where Cuddeback Attack camera traps (Greenbay, Wisconsin, USA) were used. The location and spacing of camera stations was optimized for estimation of leopard population density using a spatially explicit capture–recapture framework at all sites other than Mountain Zebra National Park. The mean distance between camera-trap stations was $2.04 \pm$ SD 0.58 km and stations were dispersed evenly across survey sites. Camera stations consisted of pairs of camera traps mounted on poles or trees c. 40 cm above the ground, and 2–3 m from a road or trail. Camera stations were visited weekly or fortnightly to download images, change batteries and maintain the cameras. Although most surveys were initially established for leopard population monitoring, camera traps were placed in locations with a reasonable probability of detecting brown hyaenas but without guarantee of detection, thus reducing false absences and adhering to the requirements of occupancy analysis (Mackenzie & Royle, 2005; MacKenzie et al., 2006). Comparable detection probability for leopards and brown hyaenas was based on a similar
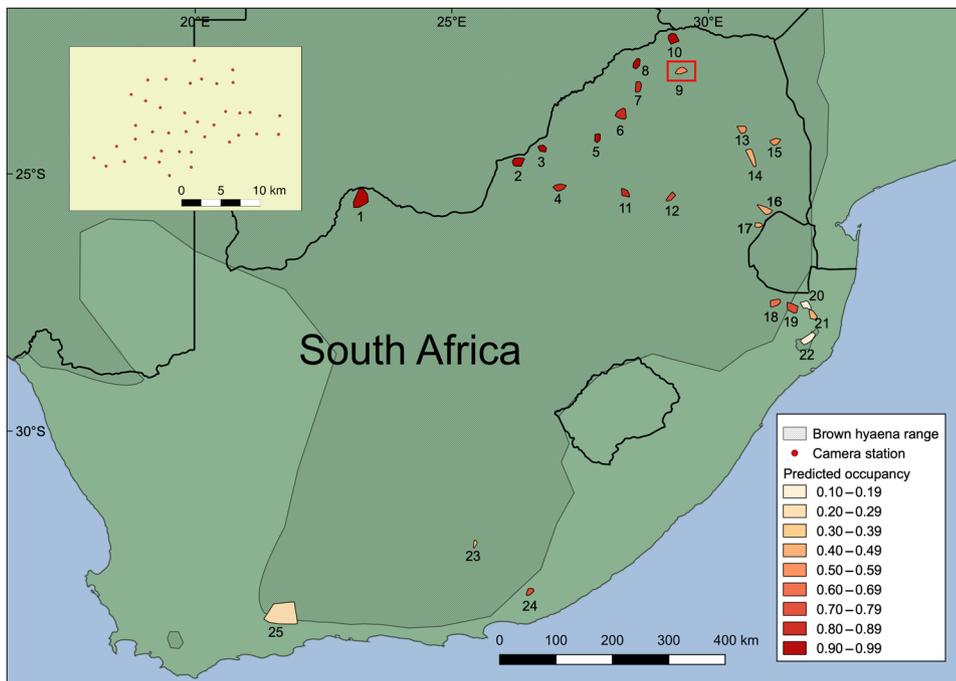
Fig. 1 Locations of the 25 camera-trap survey sites used to assess brown hyaena *Parahyaena brunnea* occupancy in South Africa. Names of numbered sites are in Table 1. Inset map shows camera station placement at one of the sites (no. 9, Lajuma and adjacent private properties) as an example. Brown hyaena range is from Wiesel (2015). Some of the survey sites lie outside this range (the global scale of the IUCN map lacks fine scale precision). Graduated shading of survey sites indicates predicted brown hyaena occupancy estimates averaged from camera-trap station estimates.

shoulder height (Estes, 1991), a preference by both species for travelling on roads and trails (Mann et al., 2015; Welch et al., 2016), and a high photographic capture rate. We tested photographic capture rate of hyaenas and leopards by placing a Reconyx Hyperfire HC600 no-glow infrared camera trap (Holmen, Wisconsin, USA), which has the fastest trigger speed and recovery time available (Trolliet et al., 2014), 2 m from the camera traps at one survey site (Lajuma and adjacent private properties). We detected a similar photographic rate using both models, thus confirming that all animals were detected despite brown hyaenas generally moving faster to cover larger daily distances than leopards (Mills, 1990; Swanepoel, 2008; Martins & Harris, 2013; Williams, 2017).

Methods

Four key categories of site covariates (habitat; relative sympatric predator abundance; human activity, e.g. people on foot and vehicles; relative abundance of medium- and large-sized prey species) were quantified from camera-trap and habitat data (Table 2). Habitat classifications from Department of Environmental Affairs Republic of South Africa (2015) were assigned to each camera-trap station using the Point Sampling Tool in *QGIS 3.0.1* (QGIS Development Team, 2018). Apex predator abundance was determined individually for cheetah *Acinonyx jubatus*, spotted hyaena *Crocuta crocuta*, leopard, lion *Panthera leo* and African wild dog *Lycaon pictus*. Prey with an average female weight of 15–50 kg were defined as medium-sized and those

> 50 kg were considered large-sized (following Mills & Mills, 1978). Small-bodied species have lower detection frequencies on camera traps (Henschel et al., 2011) and do not comprise a large proportion of brown hyaena diet (Williams et al., 2018), hence their exclusion. To ensure statistical independence between photographic events and to create a comparable baseline, consecutive photographs of the same species at the same station within 30 minutes were excluded (O'Brien et al., 2003). Species and human activity abundance were calculated using a relative abundance index: the number of single capture events per 100 camera-trap days (Treves et al., 2010; Carter et al., 2012). Site covariates with continuous relative abundance index values were standardized as z-scores because of the large range of values present (Harihar & Pandav, 2012).

To avoid multicollinearity disrupting clear outcomes in regards to detection probabilities (MacKenzie & Bailey, 2004), we tested relationships between each pair of covariates for multicollinearity, in *R 3.4.3* (R Development Core Team, 2017), using Spearman's rank correlation tests, and confirmed outcomes using the *R* package *VIF* (Lin et al., 2011). Any pairwise correlation coefficients with Rho > 0.6 in the same model were considered correlated and one covariate was excluded (Tan et al., 2017). Covariates with a variance inflation factor < 3 were retained (Wang et al., 2018).

Brown hyaena detection histories, with values of 0 (nondetection) and 1 (detection), were created to reflect the presence of brown hyaenas at each camera-trap station on each day of the survey. To meet the assumption of a closed population (Rota et al., 2009), data from only the first 40 days of each survey were used. The average number of days per

TABLE 1 Details of the first 40 days of camera-trap surveys for the brown hyaena *Parahyaena brunnea* at the 25 sites in the Eastern Cape, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, North West, and Western Cape provinces of South Africa (Fig. 1). No. refers to the numbered sites in Fig. 1.

No.	Survey site	Area[1] (km^2)	Year	No. of stations	Effort (trap-nights)	No. of brown hyaena captures
1	Khamab Kalahari Reserve	617	2016	40	1,592	339
2	Madikwe Game Reserve	327	2016	40	1,586	322
3	Atherstone Nature Reserve	156	2013	50	2,000	359
4	Pilanesberg National Park	247	2016	40	1,584	596
5	Welgevonden Private Game Reserve	146	2013	51	1,958	202
6	Lapalala Wilderness	385	2016	40	1,571	225
7	Wonderkop Nature Reserve	192	2013	52	2,032	116
8	Zingela Nature Reserve	186	2016	40	1,550	238
9	Lajuma and adjacent private properties	193	2014	39	1,560	104
10	Venetia Limpopo Nature Reserve	288	2016	40	1,583	135
11	Dinokeng Game Reserve	173	2016	36	1,440	44
12	Loskop Dam Nature Reserve	170	2016	34	1,359	63
13	Makalali Private Game Reserve	180	2015	40	1,513	54
14	Blyde River Canyon Nature Reserve	232	2016	31	1,200	1
15	Timbavati Game Reserve	167	2016	40	1,545	5
16	Barberton Nature Reserve	280	2016	33	906	6
17	Songimvelo Game Reserve	112	2016	27	1,027	45
18	Ithala Game Reserve	236	2013	36	1,378	193
19	KwaZulu Private Game Reserve and adjacent private properties	325	2015	62	2,417	342
20	Somkhanda Game Reserve and adjacent properties	229	2014	39	1,435	5
21	Manyoni Private Game Reserve	200	2015	40	1,593	35
22	Hluhluwe-iMfolozi Park	418	2017	46	1,632	8
23	Mountain Zebra National Park	73	2014	11	440	24
24	Kwandwe Private Game Reserve	135	2017	40	1,278	146
25	Little Karoo	2,038	2017	40	1,577	6

[1]Minimum convex polygon covered by camera-trap stations.

survey was 48 excluding Mountain Zebra National Park (367 days). The global model was tested for goodness-of-fit with detection histories collapsed into intervals of 4–7 days (MacKenzie & Bailey, 2004). Collapsing detection histories into eight 5-day intervals resulted in the lowest overdispersion statistic (ĉ) value, thus maximizing model fit (Supplementary Table 2). This length of time did not overcompress the statistical power of the data, accurately represented the rarity of the study species, and was in line with other large carnivore occupancy studies (Negrões et al., 2010; O'Connell & Bailey, 2011).

A two-step approach was used to examine factors influencing brown hyaena occupancy. In the first stage, single-season single-species occupancy analysis was conducted using the R package *unmarked 0.12-2* (Fiske & Chandler, 2011), to test the effect of covariates on occupancy (ψ) and probability of detection (p) without spatial autocorrelation. The effect of survey covariates were modelled on the probability of detection (Long et al., 2011). During this stage we identified site covariates to test during the second stage, a multivariate analysis with spatial autocorrelation.

Models were ranked using Akaike's information criterion (AIC), with higher-ranking models receiving the lowest AIC

values (Burnham & Anderson, 1998). The global model was assessed for goodness-of-fit using Pearson χ^2 tests (MacKenzie & Bailey, 2004) and normal dispersion using ĉ. Sites with an inflated ĉ value were removed to improve the goodness-of-fit before re-running the occupancy analysis (Meredith, 2008).

Summed model weights for biological and anthropogenic covariates > 0.10 were calculated to determine which covariates should be analysed for spatial autocorrelation in the next stage (Schuette et al., 2013; Tan et al., 2017). Summed model weights ≥ 0.5 showed a strong response and were retained (Barbieri & Berger, 2004).

The retained covariates were modelled for spatial autocorrelation in the second stage. By collating data from multiple sites in which the spacing of camera traps was optimized for another species, our dataset is likely to violate the assumption of independence between sampling sites in occupancy modelling and to suffer from spatial autocorrelation (Legendre, 1993; MacKenzie et al., 2002), especially given the tendency of brown hyaenas to travel up to 50 km per night (Mills, 1990). Spatial autocorrelation assumes that neighbouring camera stations have a greater likelihood of sharing a characteristic than more distant camera

TABLE 2 Site covariates for modelling brown hyaena occupancy across South Africa. Parameter and expected influence is provided for occupancy (ψ) where applicable.

Name	Description	Category[1]	Source	Parameter and expected influence
Habitat	Categorical, 35 land-cover classes	Habitat	2013–2014 South African National Land-Cover Dataset: DEA-CARDNO SCFP002[2]	ψ (*)
Cheetah *Acinonyx jubatus*	Numeric, detection frequency of cheetahs per 100 trap-days	Predator	Camera trap	ψ (+)
Spotted hyaena *Crocuta crocuta*	Numeric, detection frequency of spotted hyaenas per 100 trap-days	Predator	Camera trap	ψ (−)
Leopard *Panthera pardus*	Numeric, detection frequency of leopards per 100 trap-days	Predator	Camera trap	ψ (+)
Lion *Panthera leo*	Numeric, detection frequency of lions per 100 trap-days	Predator	Camera trap	ψ (−)
Wild dog *Lycaon pictus*	Numeric, detection frequency of African wild dogs per 100 trap-days	Predator	Camera trap	ψ (+)
Human	Numeric, detection frequency of human foot traffic per 100 trap-days	Human disturbance	Camera trap	ψ (−)
Vehicle	Numeric, detection frequency of vehicles per 100 trap-days	Human disturbance	Camera trap	ψ (−)
Prey	Numeric, detection frequency of medium and large prey species[3] per 100 trap-days	Prey abundance	Camera trap	ψ (+)

[1]Predator represents sympatric predator abundance.
[2]Department of Environmental Affairs Republic of South Africa (2015).
[3]Based upon average adult female weights and groups given by Mills & Mills (1978). Mean adult female weights from Skinner & Chimimba (2005).
*We expect this variable to be important, but as it is ordinal it is not meaningful to predict an overall direction.

stations, and can produce overestimated precision in occupancy estimates and underestimated standard errors (Latimer et al., 2006; Johnson et al., 2013).

Spatial autocorrelation was addressed by fitting Bayesian versions of the candidate set using the package *stocc 1.2.3* (Johnson, 2015) in *R*. A restricted spatial regression model was used to assess occupancy on all combinations of covariates with a summed model weight ≥ 0.5 (Broms et al., 2014).

The threshold for distinguishing spatial structure between camera-trap stations was set to 6.15 km, the mean radius of a brown hyaena home range, established from averaged brown hyaena home range estimates taken from 13 collared individuals in five of the survey sites (Supplementary Table 3). The Moran cut was 92.5 ($0.1 \times$ number of camera-trap stations, following Hughes & Haran, 2013). The detection and occupancy processes were assigned flat prior distributions with a Gamma distribution of 0.5 and 0.0005 (Johnson et al., 2013; Wang et al., 2018). The Gibbs sampler for each Bayesian model ran for 200,000 Markov-Chain Monte Carlo iterations with a burn-in period of 50,000 and a thinning rate of 10. Covariates with a 95% Bayesian credible interval that did not overlap zero were considered to have a significant association with brown hyaena occupancy (Wang et al., 2018). Model parameter convergence was assessed using Geweke diagnostic statistics and the $|Z| < 1.96$ scores (Wang et al.,

2018). The posterior predictive loss criterion (Gelfand & Ghosh, 1998) was compared between the Bayesian restricted spatial regression and non-spatial models for positive spatial autocorrelation.

Robustness for the restricted spatial regression model was assessed using the area under the curve (AUC) statistic (Broms et al., 2014; Wang et al., 2018). We inputted the median occurrences and spatially corrected ψ estimates at each camera-trap station with the package *ROCR* (Sing et al., 2005) in *R* to determine the AUC statistic.

Results

After removing 19 stations that captured brown hyaenas during every 5-day sampling interval (Supplementary Table 4), to reduce overdispersion, the final occupancy survey included 965 camera-trap stations and totalled 36,999 camera-trap days. Brown hyaenas were recorded at 630 camera-trap stations for a total of 2,862 independent capture events, resulting in an overall naïve occupancy of 0.65.

Effort and survey site affected probability of detection (Table 3). No covariates displayed multicollinearity so all were retained in the subsequent analyses ($r < 0.6$ and variance inflation factor < 3). Models with ΔAIC < 2 were included in the candidate set (Table 4). The global model

TABLE 3 Brown hyaena detection probability (p) models.

	AIC[1]	ΔAIC[2]	AICwt[3]	K[4]	−2ll[5]
p (effort + site)	6,962.54	0.00	0.68	27	6,908.54
p (effort + site + habitat)	6,964.01	1.47	0.32	28	6,908.01
p (site)	7,025.85	63.31	0.00	26	6,973.85
p (site + habitat)	7,027.16	64.62	0.00	27	6,973.16
p (effort + habitat)	7,664.26	701.72	0.00	4	7,656.26
p (effort)	7,672.35	709.81	0.00	3	7,666.35
p (habitat)	7,721.19	758.65	0.00	3	7,715.19
p (.)	7,730.18	767.64	0.00	2	7,726.18

[1]Akaike's information criterion.
[2]Difference in AIC between each model and top ranking model.
[3]AIC weight.
[4]Number of parameters.
[5]Twice the negative log-likelihood.

TABLE 4 Top ranked site occupancy models for brown hyaena occupancy (ψ) in South Africa.

Model	AIC[1]	ΔAIC[2]	AICwt[3]	K[4]	−2ll[5]
ψ (Cheetah + Spotted hyaena + Leopard + Lion + Wild dog + Human + Vehicle)	7,685.20	0.00	0.33	9	7,667.20
ψ (Cheetah + Spotted hyaena + Leopard + Lion + Wild dog + Human + Vehicle + Prey)	7,686.08	0.88	0.21	10	7,666.08
ψ (Cheetah + Spotted hyaena + Leopard + Lion + Wild dog + Human + Vehicle + Habitat)	7,687.03	1.83	0.13	10	7,667.03

[1]Akaike's information criterion.
[2]Difference in AIC between each model and top ranking model.
[3]AIC weight.
[4]Number of parameters.
[5]Twice the negative log-likelihood.

fitted the data well ($\hat{c} = 1.21$). Site covariates relating to the five sympatric predator, human and vehicle abundance had summed model weights > 0.5, and these were retained for the next stage of analysis (Table 5). Habitat and prey fell below this threshold and were therefore discarded from the second phase.

The restricted spatial regression model was more parsimonious than the non-spatial model (posterior predictive loss criterion: 2,606.07 vs 2,790.45), confirming that positive spatial autocorrelation influenced the data. Spotted hyaena and human abundance had a negative impact on brown hyaena occupancy, and leopard and vehicle abundance had a positive influence on brown hyaena occupancy (Table 6, Fig. 2).

Brown hyaenas are estimated to occur across 66% of the total sites surveyed ($\psi = 0.66 \pm$ SE 0.09) with site occupancy probability estimates of 0.12–0.98 (Supplementary Table 5). The majority of sites in eastern and southern South Africa had a lower mean occupancy estimate than those further north (Fig. 1). The AUC value was 0.74 for the restricted spatial regression model, suggesting reasonable levels of accuracy in our predictions of occupancy.

Discussion

Our study used a detection/non-detection dataset to identify, with a high level of confidence, a suite of four biological and anthropogenic factors that influence brown hyaena occupancy at a national scale. These findings suggest that camera-trap data focused on one species can provide useful data to determine broadscale occupancy trends of other, non-target species, provided the species share habitats and have similar-scale home range sizes. Our study enables us to make generalizations about variables influencing occupancy of brown hyaenas on a scale not previously possible for the species. The 25 survey sites incorporated a diverse array of environmental, biological, and anthropogenic conditions that are found throughout their international range. Our results therefore have conservation management implications applicable across the global range of the species, especially in protected areas and areas used for ecotourism.

The relative abundance of sympatric apex predators had the strongest influence on brown hyaena occupancy. Spotted hyaena relative abundance had a strong negative impact on brown hyaena occupancy, whereas the relative abundance of leopards showed a positive relationship with brown hyaena occupancy. Sympatric carnivore density estimations were not available as covariates in this study. We encourage future research to test brown hyaena occupancy against predator densities. Although relative abundance indices are not a substitute for density (Jennelle et al., 2002), relationships between brown hyaena occupancy and sympatric predator relative abundance mirror trends found when brown hyaenas cohabit with high densities of dominant

TABLE 5 Summed model weights of site covariates (Table 2) tested for brown hyaena occupancy (ψ) in South Africa.

Covariate	Summed model weights
Spotted hyaena	1.00
Leopard	1.00
Vehicle	0.99
Cheetah	0.97
Human	0.95
Lion	0.83
Wild dog	0.81
Prey	0.37
Habitat	0.26

TABLE 6 Parameter estimates and 95% credible intervals from a restricted spatial regression model assessing brown hyaena occupancy in South Africa. Beta coefficient estimates for each of the standardized covariates are reported as mean and standard deviation. Covariates with a 95% credible interval not overlapping zero are marked in bold to indicate there is a significant association between the covariate and brown hyaena occupancy. Model convergence was assessed using Geweke diagnostic statistics and the $|Z| < 1.96$ score.

Covariate	Mean ± SD	95% Credible intervals	Z score
(Intercept)	0.97 ± 0.13	(**0.72, 1.23**)	−1.54
Cheetah	0.26 ± 0.22	(−0.06, 0.67)	−0.84
Spotted hyaena	−0.42 ± 0.09	(**−0.60, −0.25**)	1.43
Leopard	0.15 ± 0.08	(**0.00, 0.30**)	−0.60
Lion	0.17 ± 0.10	(−0.03, 0.38)	−0.45
Wild dog	0.06 ± 0.10	(−0.14, 0.27)	−0.32
Human	−0.21 ± 0.06	(**−0.33, −0.09**)	0.30
Vehicle	0.24 ± 0.08	(**0.08, 0.41**)	−0.31

competitors. Spotted hyaenas present a competitive threat to the more submissive brown hyaena, through kleptoparasitism and occasionally as a source of mortality (Mills, 1990). Mills & Mills (1982) similarly showed that brown hyaenas avoided areas of high spotted hyaena density in the southern Kalahari, regardless of prey abundance. This negative relationship may explain why brown hyaena mean occupancy was lowest at survey sites in eastern South Africa. Many of the eastern sites support healthy populations of dominant competitors such as spotted hyaenas and lions. High densities of dominant predators can restrict the success of subordinate predators such as African wild dogs, brown hyaenas and cheetahs (Mills & Gorman, 1997; Marker et al., 2010).

The negative interspecific relationship and spatial separation between spotted and brown hyaenas can largely be attributed to environmental adaptability and diet. Brown hyaenas have a catholic and opportunistic diet, a secretive nature and low water requirements, which have enabled the species to survive in areas where less adaptable carnivores cannot persist (Maude, 2005). Spotted hyaenas, although also adaptable, have less plasticity in their habitat and prey requirements (Hayward, 2006; Schuette et al., 2013) and are highly vulnerable to persecution by humans on unprotected land, especially on livestock farms (Mills & Hofer, 1998). The brown hyaena's adaptability in diet and habitat requirements probably explains why we found that habitat characteristics and prey abundance had little effect on brown hyaena occupancy, as in other studies (Thorn et al., 2009; Williams, 2017).

Alternatively, some sympatric predators do not present a direct threat to brown hyaenas and may instead have a positive effect on brown hyaena success. The positive relationship we detected between relative leopard abundance and brown hyaena occupancy may be attributed to the environment leopards inhabit and their potential to provide a food source for scavengers. Leopards prefer areas away from urban development with few competitive apex predators and a high prey abundance (Gavashelishvili & Lukarevskiy, 2008; Steinmetz et al., 2013; Strampelli et al., 2018), and thus their presence may reflect more secure living

conditions for brown hyaenas. In addition, the brown hyaena is a poor hunter, and typically depends on scavenging to meet c. 95% of its dietary intake (Mills, 1984; Maude & Mills, 2005). It therefore relies on other large carnivores, such as the leopard, to kill larger prey species (Stein et al., 2013; Mills, 2015). In areas where leopards are present, brown hyaenas have a similar diet (Stein et al., 2013; Williams et al., 2018), which can be explained by a high frequency of observed scavenging incidents from leopard kills (76%; Stein et al., 2013).

Another factor that influences brown hyaena occupancy is anthropogenic activity. Brown hyaena occupancy was lower in areas with high human foot traffic. A similar trend was detected on private land in northern Limpopo Province, South Africa, where brown hyaena occupancy in unprotected farmland was negatively affected by high disturbance by people on foot (Williams, 2017). Striped hyaenas *Hyaena hyaena* also avoid human disturbance, with higher occupancy in rugged areas devoid of human activity and in areas with the greatest distance from human habitation (Singh et al., 2014). This finding fits well with the declines observed in carnivore populations globally as a result of human activity (Ripple et al., 2014).

Our finding that vehicle activity positively influenced brown hyaena occupancy was unanticipated, as we expected the abundance of vehicles to affect brown hyaena occupancy in the same manner as the relative abundance of people on foot. People on foot could represent threats to hyaenas such as poaching, legal hunting or control of damage causing animals, in addition to less threatening ecotourism or more general human activity. In contrast, vehicle-based ecotourism is conducted across many of our survey sites, and in these areas vehicles movements predominantly occur during the day, when brown hyaenas are resting, and thus pose a low risk.
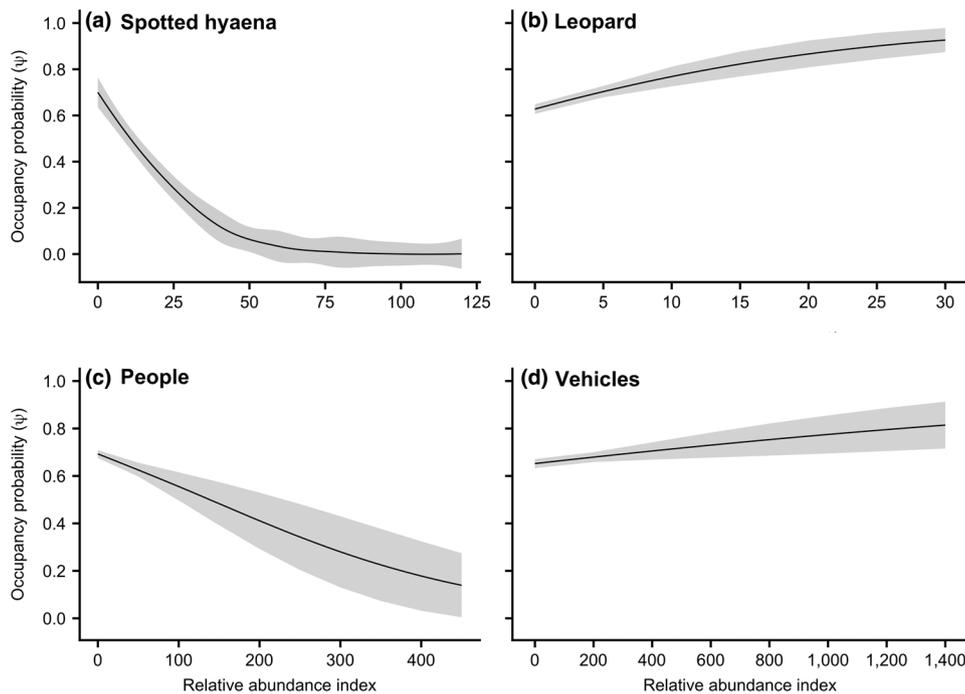
FIG. 2 Relationships between the probability of brown hyaena occupancy and relative abundance index (the number of single capture events per 100 camera-trap days) of (a) the spotted hyaena *Crocuta crocuta*, (b) the leopard *Panthera pardus*, (c) people and (d) vehicles. Shaded areas represent 95% confidence intervals.

People in vehicles are drawn to sightings of iconic animals, which could be more likely to occur in areas with preferable conditions for brown hyaenas (e.g. areas where human foot traffic is low and resources are abundant). Vehicle-based ecotourism may also contribute to anti-poaching efforts by providing additional surveillance (Baral, 2013).

Despite the large spatial scale of our study, private land used for farming was underrepresented in our dataset. Management of the analysed survey sites, especially in regards to fencing and supplementary feeding, may differ in unprotected land and we recommend further research to examine how these site-specific factors affect brown hyaena occupancy. Large predators such as spotted hyaenas, lions, cheetahs and African wild dogs have been largely extirpated from much unprotected land in southern Africa (Ray et al., 2005). The absence of these species leaves leopards and brown hyaenas as the only apex predator across much of their shared range. Our results suggest that such conditions promote high brown hyaena occupancy as long as human disturbance is minimized, emphasizing the potential importance of private land for brown hyaena conservation.

Carnivores occurring outside formally protected areas are particularly vulnerable to anthropogenic threats (Balme et al., 2010). With a severe decline in leopards already underway globally (Jacobson et al., 2016), conservation measures need to be established to preserve leopards on private land; our results suggest this will also aid brown hyaena conservation across their range. We thus recommend a holistic, multi-species approach that considers the entire large carnivore guild, rather than a single-species approach. Broader approaches to conservation that encompass multiple species or even entire landscapes are becoming increasingly popular, such as the focal species paradigm (Lindenmayer et al., 2014), which utilizes a suite of species, each of which is used to define various attributes in a landscape (Lambeck, 1997).

Areas with low human disturbance are also vital for brown hyaena conservation and should be prioritized for protection. This is easier to facilitate in protected areas, but outside protected areas private land used for wildlife farming tends to have lower levels of human disturbance than land used for livestock farming (Thorn et al., 2012). Wildlife farms provide a plentiful prey base for predators and abundant scavenging opportunities for brown hyaenas, both naturally and through meat discarded after commercial hunts. Scavengers such as brown hyaenas provide important ecosystem services to these areas through their feeding habits (Beasley et al., 2015). Despite the potential for wildlife farms to act as refuges for brown hyaenas, intolerance towards predators and subsequent persecution can be high on wildlife farms (Pitman et al., 2017b). Greater public education about the value of brown hyaenas and their dietary habits is therefore required.

Survey site and effort influenced brown hyaena detection probability. The effect of site variability on detection can be the product of a multitude of variables, including the density of brown hyaenas, animal behaviour, thickness of vegetation and seasonality (Tan et al., 2017). Although there are advantages of broad-scale studies, inconsistences in probability of detection highlight the importance of fine-scale or regional-scale surveys in conservation and incorporating a variety of knowledge sources, especially when constructing

locally specific management approaches (Raymond et al., 2010).

Finally, our case study is an example of how a collaborative approach that combines small-scale datasets and utilizes bycatch data can be a powerful tool to fit occupancy models at broader spatial scales. This approach can inform conservation management strategies at national or global scale when applied to species with a restricted international area of occupancy such as the brown hyaena. With limits of time, funding and resources challenging ecological research, this recycle and repurpose approach to data extends the potential of camera trapping to inform high-level wildlife management strategies. We suggest the development of better information sharing platforms to enable the collaborations necessary to share camera-trap data and conduct research at this scale. These platforms need to extend beyond the boundaries of protected areas, where research is frequently conducted. Collaborative data sharing from camera-trap owners outside protected areas will not only provide vital distribution and occupancy information but will also strengthen dialogues and relationships between conservation organizations, scientists and private landowners.

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