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Research report

Resource partitioning between black-backed jackal and brown hyaena in Waterberg Biosphere Reserve, South Africa

Rivona Ramnanan[1], Michelle Thorn[1], Craig J. Tambling[2] and Michael J. Somers [1, 3*]

[1] Centre for Wildlife Management, University of Pretoria, Pretoria, South Africa.

[2] Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, 6031, South Africa.

[3] Centre for Invasion Biology, University of Pretoria, Pretoria, South Africa. Email: mjs@up.ac.za

* Correspondence author

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Abstract

Understanding resource partitioning by predators is important for understanding coexistence patterns, with this becoming more relevant as historical food webs are altered through human impacts. Using scat analysis, we investigated the diet overlap of two sympatric meso-carnviores, the black-backed jackal *Canis mesomelas* and brown hyaena *Hyaena brunnea*, in Waterberg Biosphere Reserve, South Africa. Scats (n = 30 jackal, 42 brown hyaena) were collected in April 2012 from game and livestock farms. When comparing main prey categories (medium-large mammal, small mammal, fruit, invertebrate, reptile, and bird) we found little difference in diets, with both carnivores consuming predominantly medium-large mammals (10-100kg). Bushbuck *Tragelaphus scriptus* was the most commonly consumed large mammal species for both predators. Jackal and brown hyaena had, on average, 1.3 and 1.4 main prey categories per scat respectively which resulted in diet diversities of 3.9 for jackal and 2.5 for brown hyaena. Only jackal consumed livestock (which may have been scavenged), albeit in small amounts (< 5% frequency of occurrence). The high level of resource overlap was consistent with previous jackal–brown hyaena resource partitioning studies. Across a range of studies, resource overlap was higher when apex predator densities were lower. Thus, lower apex predator densities may restrict brown hyaena populations through the lack of carrion. At these lower brown hyaena densities, large mammal carrion, which brown hyaena rely on, may persist for longer. This persistence may enable jackals to increase their consumption of larger mammals, thereby reducing their reliance on rodents and small-medium sized mammals. Our results support the prediction that lower apex predator densities allow jackals to consume more medium to large mammals. However, diet overlap is only one of many niche axes that can assist in species co-occurrence, and further work is required to understand how jackal and brown hyaena interact at spatial, temporal and behavioural scales.

Introduction

Resource partitioning (temporal, spatial or trophic) between sympatric species is essential for their co-existence (Pianka 1973, Carvalho and Gomes 2004). For carnivores, resource partitioning varies in complex and dynamic ways (Azevedo et al. 2006), driven by variations in carnivore community composition, prey availability and landscape heterogeneity. This complexity is further exacerbated in human dominated landscapes where anthropogenic impacts can alter the carnivore community and available resources. Globally, carnivore communities are increasingly under threat from burgeoning human populations (Ripple et al. 2014), and in many cases large apex predators (e.g. lions *Panthera*

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leo) have been extirpated from many parts of their historical range, resulting in fundamentally altered carnivore communities.

In South Africa, apex predators such as lion and spotted hyaena *Crocuta crocuta* have been almost completely extirpated from non-protected areas (Hayward et al. 2007). Low density populations of cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, and African wild dog *Lycaon pictus* still exist outside of protected areas but are often heavily persecuted (Thorn et al. 2011). The removal of apex predators has created a void filled by competitively subordinate species such as black-backed jackal *Canis mesomelas* (hereafter referred to as jackal), caracal *Caracal caracal* and brown hyaena *Hyaena brunnea*. Consequently, as carnivore communities are altered under various land-use regimes, investigating how they partition resources will increase our understanding of their relative ecological roles which could be important for the conservation of these carnivores. Numerous studies have investigated the diet of jackal and brown hyaena in isolation, both inside and outside of protected areas, with brown hyaena considered obligate scavengers of large mammal carcasses (Mills 1990) and jackal alternating between active hunting of large mammals (Klare et al. 2011) and scavenging from large mammal carcasses (Fourie et al. 2015). However, little information exists on the competitive relationship between the two species from which inferences can be made about competition over scavenging resources and the extent of their niche overlap (but see van der Merwe et al. 2009, Yarnell et al. 2013). Even less attention has been given to interactions outside of protected areas, where human altered landscapes may further alter patterns of competition between jackal and brown hyaena. We used a short-term sampling period to investigate the diet of jackal and brown hyaena in Waterberg Biosphere Reserve, a landscape area characterised by high human modification and low apex predator densities.

Methods

Scats were collected in Waterberg Biosphere Reserve (24°04′30″S 28°08′30″E), Limpopo province, South Africa, which included a number of privately-owned commercial game and livestock farms. The vegetation in the region consists of Waterberg Mountain Bushveld (Mucina and Rutherford 2006) and rocky mountainous topography characterises the majority of the sampling area. Free ranging carnivores such as jackal, brown hyaena, caracal, African wild dog, cheetah and leopard occur in the area, with the latter three occurring at low densities (Thorn 2011, Ramnanan et al. 2013). Naturally occurring and artificially introduced and managed ungulates such as greater kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus*, steenbok *Raphicerus campestris*, duiker *Sylvicapra grimmia* and warthog *Phacochoerus africanus* are common.

Jackal and brown hyaena scats were collected opportunistically along roads between 16 and 25 April 2012 (Austral autumn season). Trained observers identified the scats to species level based on colour, shape and size. Seventy-two scats were collected (42 brown hyaena, 30 jackal) over an area of approximately 2,000km^2 with no clear spatial separation of jackal and brown hyaena scats across the region. The scats were washed in small cloth bags using a washing machine before being dried thoroughly (Johnson and Hansen 1979). Twenty hairs were randomly selected from each scat and cross sections were made from each following standard scat analysis protocols (Douglas 1989). Prey species were identified using reference keys (Keogh 1983, Buys and Keogh 1984). Contents of scats were separated into six categories, medium-large mammals (adults > 10kg [further subdivided by species for some analysis]), small mammals, invertebrates, birds, fruit and vegetation. These categories were used to facilitate the comparison of the diet of the two carnivores to similar studies conducted in the North-West province, South Africa, by van der Merwe et al. (2009) and Yarnell et al. (2013).

To assess if sufficient scats had been collected to adequately represent the diet based on: (a) the six main diet categories, and (b) all medium-large mammal species in addition to the remaining five main diet categories, we constructed species accumulation curves (replicated 1,000 times and assuming a random sample collection procedure) for jackal and brown hyaena using the R package Vegan (R Development Core Team 2011, Oksanen et al. 2012). Diet estimates were represented as frequency of occurrence (FO) and relative frequency of occurrence (RFO). FO refers to the proportion of each diet items from the total sample of scats and RFO refers to the proportion of each diet item from of the total number of diet items found (Loveridge and MacDonald 2003). Although it is recognized that biomass estimates are a more robust means to estimate resource use from scats (Klare et al. 2011), we restricted our analysis to FO and RFO to facilitate comparison to van der Merwe et al. (2009) and Yarnell et al. (2013) and because no correction factors are available for brown hyaena. To assess if (a) the consumption of the main diet categories and (b) the consumption of the medium-large mammal species in addition to the remaining five main diet categories differed between the two carnivores, a Log-Likelihood Ratio G test was conducted (Zar 1996). To further assess the similarity in the consumption of medium-large mammal species by the two carnivores we conducted a correlation analysis on the FO values. To generate variation around the estimated FO and RFO of each food category we bootstrapped both the FO and the RFO diet estimates by re-sampling the data 1,000 times to obtain 95% confidence limits. We only estimated FO for medium-large mammal species to reduce the importance of missing species in this category (see results – species accumulation curves).

Using Levins' index of niche breadth we estimated the diet diversity for each carnivore with respect to the six prey categories (Fedriani et al. 2000). In this study, the niche breath value can vary between one (one prey category present in the diet) and six (equal contribution of all six prey categories in the diet). We calculated Pianka's index (Pianka 1973) to assess the percent overlap in the six main diet categories between the two carnivores (van der Merwe et al. 2009, Yarnell et al. 2013). We similarly bootstrapped the niche breadth and Pianka index to estimate the 95% confidence limits for these measures. To assess how resource partitioning between the two carnivores compared to previous studies, we plotted our estimated Pianka index (+/- 95% confidence limits) along with Pianka estimates calculated using the same six categories from diet estimates collected on (1) ranchlands (apex predators absent, Yarnell et al. 2013), (2) a combination of ranchlands and protected areas (apex predators present and absent, van der Merwe et al. 2009) and (3) only protected areas (apex predators present, Yarnell et al. 2013). All statistical analyses were conducted using R (R Development Core Team 2011).

Results

Species accumulation curves for the six main food categories reached an asymptote between 20 and 25 scats for both predators (Figure 1). However, once medium to large mammal species were included as separate categories, accumulation curves suggested that some prey species may not have been detected with our sampling effort. Jackal and brown hyaena had, on average, 1.3 and 1.4 main prey categories per scat respectively which resulted in diet diversities of 3.9 for jackal and 2.5 for brown hyaena.

The diets of jackal and brown hyaena based on the six main prey categories were similar (G = 10.5, df = 5, p = 0.06) which resulted in a high niche overlap (0.95; CL = 0.89-0.99; Figure 2). Although medium-large mammals comprised the bulk of the diet for both carnivores (RFO: jackal = 42.2%, brown hyaena = 59.2%; Table 1) and bushbuck was the main species consumed by both carnivores (FO: jackal = 26.9%, brown hyaena 52.3%), when the medium-large mammal species were combined with the remaining five main prey categories, the composition of the diet differed significantly between jackal and brown hyaena (G = 37.6, df = 19, p < 0.01). This difference was driven primarily through the composition of the medium-large mammal species consumed, with 11 medium-large mammal species detected in the diet of jackal and brown hyaena respectively, but only seven of these were shared between the two carnivores (Table 2). However, those species that were shared were generally consumed often and equally between the carnivores resulting in the consumption of the medium-large mammal species being significantly correlated (t = 3.8, df = 13, p < 0.01, r = 0.72). After bushbuck, impala *Aepyceros melampus*; FO = 26.7% for jackal and blue wildebeest *Connochaetus taurinus*; FO = 22% for brown hyaena were the second most consumed prey species for each carnivore (Table

2). Livestock remnants were only found in jackal scats with cattle and goat each occurring in 3.3% of the jackal scats.

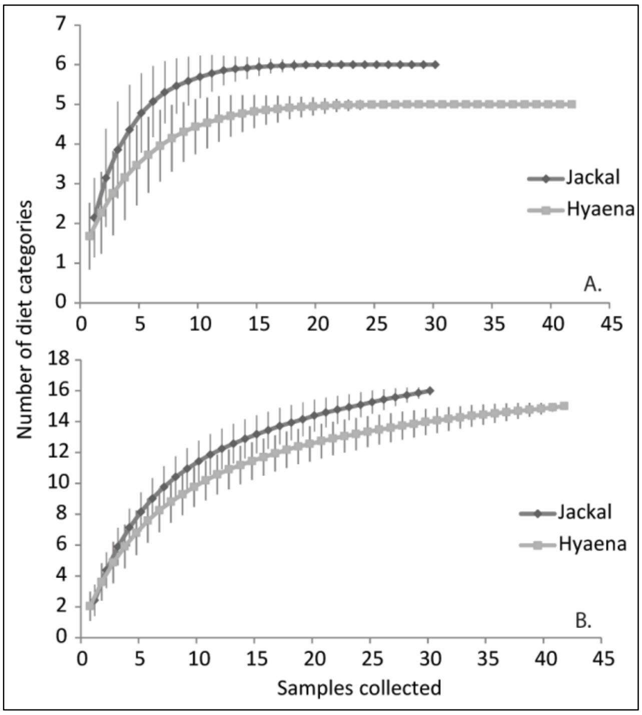

Figure 1. Species accumulation curves based on 1000 random re-sampling events for black-backed jackal and brown hyaena scat collection in Waterberg Biosphere Reserve, South Africa. (A) represents species accumulation curves based on the six main dietary groups identified, and (B) represents species accumulation curves based on the species specific delineation of medium-large mammals and the five remaining main diet categories.

Small mammals contributed considerably less than large mammals to the diet of both carnivores (RFO: jackal = 9.4%, brown hyaena = 8.4%, Table 2). Diet overlap using the six broad diet items was lowest in the presence of high densities of apex predators and highest in the absence (or low density) of apex predators (Figure 2).

Discussion

When considering broad diet categories, jackal and brown hyaena in Waterberg Biosphere Reserve had high resource use overlap, driven primarily by both species consuming predominantly medium- large mammals. In addition, not only did medium-large mammals dominate both carnivores' diet, but bushbuck was the most consumed prey item for both carnivores. Jackal and brown hyaena characteristically adapt to locally abundant resources (Klare et al. 2010, Slater and Muller 2014), which can vary seasonally (e.g. Kamler et al. 2012) or through periodic resource pulses (e.g. Fourie et al. 2015). This flexibility in diet from both species limits our ability to compare fine scale differences in our assessment of the diets of either jackal or brown hyaena with diet estimates obtained by van der Merwe et al. (2009 - scats collected year round but not separated by season) and Yarnell et al. (2013, scats collected in winter) because resource availability will undoubtedly change. In addition, we were unable to estimate resource (i.e. prey) availability in the current study because the sampling region was extensive and land use types varied considerably. Thus, for comparative purposes with previous studies we focused on the relative comparisons between jackal and hyaena diets for each site at each time period rather than on the absolute differences or prey composition or selection between studies.

The current assessment represents a low apex predator density environment, which we contrast against an apex predator free environment in Mankwe Wildlife Reserve, South Africa, a high apex predator density environment in Pilanesberg National Park, South Africa (Yarnell et al. 2013) and a mix of high apex predator and no apex predator environments (van der Merwe et al. 2009). For all assessments, diet overlap exceeded 0.53 with the lowest overlap recorded in the high apex predator density environment and the highest overlap (0.95 – current study) recorded in the low apex predator density environment. The apex predator free environment had a diet overlap of 0.87 which is similar to that of our current study where apex predators occur at a low density. Thus, these results suggest that diet overlap may be higher in areas with fewer or no apex predators and thus where carrion provisioning is lower.

Brown hyaena consumption of medium-large mammals is a function of the provision of carrion (Stein et al. 2013). In all assessments, brown hyaena consumed predominantly (> 68% FO) medium-large mammals, suggesting that both inside and outside of protected areas carrion is readily available for brown hyaena to scavenge from. In the absence of apex predators, jackal actively hunt and consume medium-large prey items (Klare et al. 2010). Thus, in the absence (or low density) of large predators as in our study region, jackal may be consuming medium-large mammals by actively hunting them. Three of the main prey species consumed by brown hyaena (and jackal), bushbuck, duiker and impala, can be killed by jackal (Kamler et al. 2010, Klare et al. 2010), but are also preferred prey of leopard (Hayward et al. 2006a, Swanepoel 2008) and African wild dog (Hayward et al. 2006b). Thus, although the exact source of carrion is unknown, jackal, in combination with the low density of large predators, are potentially providing carrion for brown hyaena in Waterberg Biosphere Reserve. This could also explain the significant correlation in medium-large mammal consumption between both carnivores. Therefore, at low apex predator densities, jackal and brown hyaena may feed on the same resource, with jackal consumption preceding brown hyaena presence at carcasses.

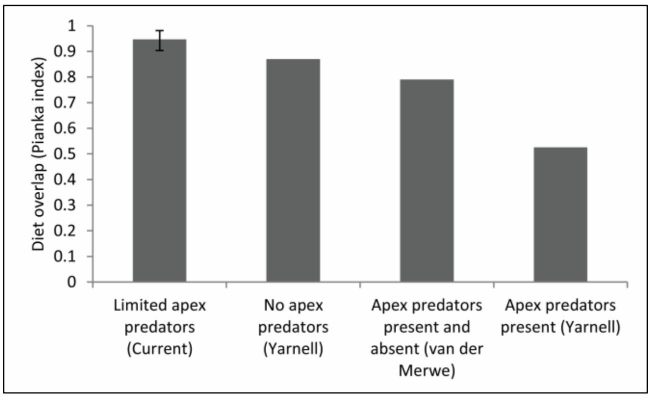

Figure 2. Comparison of Pianka indices reflecting niche overlap of the six main diet categories between jackal and brown hyaena diets in Waterberg Biosphere Reserve, South Africa. Apex predator presence and absence varies between studies, with the current study characterised by very low densities of apex predators. The ranchland component from Yarnell et al. (2013) is characterised by the absence of apex predators, van der Merwe et al. (2009) presents data from a combination of sites with and without apex predators and the reserve component of Yarnell et al. (2013) is characterised by high densities of apex predators. The error bar on the first bar is the 95% confidence limit resulting from the bootstrapping.

Table 1. Diet of jackal and brown hyaena in Waterberg Biosphere Reserve, South Africa, shown as the frequency of occurrence and relative frequency of occurrence, with 95% confidence limits in brackets. Values based on an analysis of scats (n = 30 jackal, 42 brown hyaena) collected in April 2012.

	Frequency of occurrence (%)		*Relative frequency of occurrence (%)*	
Food items	*Jackal*	*Brown hyaena*	*Jackal*	*Brown hyaena*
Medium-large mammals	90.0 (80.0-100.0)	100.0 (100.0-100.0)	42.2 (32.9-52.7)	59.2 (51.9-67.7)
Small mammals	20.3 (6.7-33.3)	14.3 (4.8-23.8)	9.4 (3.4-15.6)	8.4 (3.2-13.9)
Fruit	39.6 (23.3-56.7)	26.3 (14.3-40.5)	18.3 (11.3-24.6)	15.3 (8.8-22.1)
Invertebrate	32.9 (16.7-50.0)	17.0 (7.1-28.6)	15.1 (8.8-21.1)	9.9 (4.3-15.5)
Reptile	16.0 (3.3-30.0)	12.2 (4.8-23.8)	7.3 (1.8-12.7)	7.1 (2.5-12.8)
Bird	16.5 (6.6-30.0)	0.0 (0.0-0.0)	7.7 (2.6-14.3)	0.0 (0.0-0.0)

Table 2. Medium-large mammals consumed by jackal and brown hyaena in Waterberg Biosphere Reserve, South Africa, shown as the frequency of occurrence, with the 95% confidence limits in brackets. Values based on an analysis of scats (n = 30 jackal, 42 brown hyaena) collected in April 2012.

	Frequency of occurrence (%)	
Food items	*Jackal*	*Brown hyaena*
Bushbuck *Tragelaphus scriptus*	26.9 (10.0-43.3)	52.3 (38.1-69.0)
Mountain reedbuck *Redunca fulvorufula*	0.0 (0.0-0.0)	4.9 (0.0-11.9)
Common duiker *Sylvicapra grimmia*	10.0 (0.0-20.0)	14.0 (4.8-23.9)
Blue wildebeest *Connochaetes taurinus*	3.3 (0.0-10.0)	21.7 (9.5-35.7)
Impala *Aepyceros melampus*	26.9 (13.3-43.3)	19.0 (9.5-31.0)
Nyala *Tragelaphus angasii*	0.0 (0.0-0.0)	2.2 (0.0-7.1)
Common reedbuck *Redunca arundinum*	9.6 (0.0-20.0)	7.2 (0.0-16.7)
Kudu *Tragelaphus strepsiceros*	16.9 (3.3-30.0)	7.3 (0.0-14.3)
Blesbok *Damaliscus pygargus phillipsi*	0.0 (0.0-0.0)	4.7 (0.0-11.9)
Baboon *Papio ursinus*	0.0 (0.0-0.0)	2.4 (0.0-7.1)
Tssessebe *Damaliscus lunatus*	6.7 (0.0-16.7)	2.5 (0.0-7.1)
Warthog *Phacochoerus africanus*	3.2 (0.0-10.0)	0.0 (0.0-0.0)
Eland *Tragelaphus oryx*	6.7 (0.0-16.7)	0.0 (0.0-0.0)
Goat *Capra* sp.	3.3 (0.0-10.0)	0.0 (0.0-0.0)
Cattle *Bos* sp.	3.3 (0.0-10.0)	0.0 (0.0-0.0)

In the presence of apex predators, jackal will readily scavenge from carcasses (Fourie et al. 2015). Thus, it would be expected that jackal diets in the presence of apex predators should be dominated by medium-large mammals which are commonly predated by large predators (Clements et al. 2014). This, however, was not the case, with medium-large mammals found in only 40% and 57% of all scats in sites where apex predators were present (Yarnell et al. 2013) or partially present (van der Merwe et al. 2009). Brown hyaena densities are higher in areas with apex predators where carrion is provided (Yarnell et al. 2013). As a consequence, the consumption of carrion on landscapes where apex predators are present may be under intense scramble competition where brown hyaena may outcompete smaller jackal. Brown hyaena are also known to cache large prey items (Mills 1990), thus potentially removing this resource from the landscape, further preventing jackal from accessing it. Therefore, on protected landscapes in the presence of apex predators, jackal may be forced to actively hunt smaller prey items, whereas brown hyaena will scavenge larger prey items, thus reducing resource overlap.

Although we acknowledge that livestock remains found in scats may be from scavenged animals, jackal do predate on livestock, preying on sheep, goats, and cattle (Kamler et al. 2012). Our results indicated that livestock predation during our sampling period was low. We detected sheep, goat and cattle remains in less than 5% of jackal scats. The low levels of goat and cattle in the jackal diet (Table 2) suggest that livestock predation in Waterberg Biosphere reserve may not be as prevalent as in other regions in South Africa (Kamler et al. 2012). An abundance of wild prey species reduces the reliance of jackal on livestock (Kamler et al. 2012) and thus the game ranches in the region may be providing abundant resources that limit livestock predation, although without knowing the relative availbaility of wild and domestic prey this conclusion should be treated with caution. Our results also support the observation that brown hyaena do not often kill livestock (Maude 2005), as no livestock remains were found in the scats of brown hyaena in our region.

Scat analysis techniques have inherent biases that are often not accounted for. Our study was conducted over a short time span, and thus reflects a snapshot of the diets of these two species. As such, this assessment may not provide a true reflection of the long term diet in the region as resource pulses can have significant short term impacts on observed diet estimates (Fourie et al. 2015). Despite this, a comparison of the diet between the two species during the snapshot provides important information as both predators would be equally influenced by any environmental variability. In addition, scats collected over a short time period may suffer from a lack of independence (Davies-Mostert et al. 2010). Since brown hyaena also cache large food items (Mills 1990), the combination of this lack of independence between scats and the caching behaviour may have inflated the importance of medium-large mammals in the diet of brown hyaena (FO = 100%) in our study.

The current snapshot of jackal and brown hyaena diets in Waterberg Biosphere reserve, along with the previous studies conducted inside and outside of nearby protected areas indicates considerable overlap in resource consumption between the two species. This overlap will undoubtedly result in competition between the two species, which may be mediated by the relative density of brown hyaena and available resources (i.e. time of year and presence of apex predators). The use of carrion by jackal in the presence of apex predators may therefore be a function of the presence of brown hyaena, providing a mechanism that may explain the seemingly contradictory conclusions that apex predators have a significant influence on jackal diet composition in some studies (Fourie et al. 2015 – brown hyaena absent) but not in others (Brassine and Parker 2012, Yarnell et al. 2013 – brown hyaena present). Thus, further insights are needed to understand how the removal (or repatriation) of apex predators influences the relative relationship between jackal and brown hyaena from both numerical and behavioural perspectives. It must also be recognized that diet is only one of many niche axes that can be investigated to understand resource partitioning between sympatric species, and thus to fully understand the relationship between jackal and brown hyaena, space use, activity patterns and behavioural information will also be needed.

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Biographical sketches

Rivona Ramnanan is a veterinary science student at the University of Pretoria but previously studied wildlife management in the Centre for Wildlife Management, also at the University of Pretoria. Her interests are wide within the disciplines of wildlife biology and animal health.

Michelle Thorn is an independent researcher whose interests include patterns and determinants of mammal distribution, the development of practical field protocols for conservation monitoring and the management of human-animal conflicts.

Craig Tambling is a post-doctoral researcher with the Centre for African Conservation Ecology - Nelson Mandela Metropolitan University. His primary research interest lies in predator-prey ecology and in particular, understanding what drives predation patterns of carnivores and what the consequences of predation are for prey populations.

Michael Somers is the Director of the Centre for Wildlife Management and Core Team Member of the Centre for Invasion Biology at the University of Pretoria. His research interests are wide but he mostly works on the ecology, behaviour and conservation of carnivores in southern Africa.