Brown hyaena and leopard diets on private land in the Soutpansberg Mountains, South Africa

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Introduction

Private land comprises a large proportion of the brown hyaena (*Hyaena brunnea*) and leopard (*Panthera pardus*) range, and is vital to their survival (Jacobson et al., 2016; Kent & Hill, 2013). Although prey availability is often highest in protected areas, private land used for game and livestock farming also hosts an abundance of wild and domestic prey (Balme, Slotow, & Hunter, 2010; Kinnaird & O'Brien, 2012).

Scavenging accounts for approximately 95% of the brown hyaena's dietary intake (Maude & Mills, 2005; Mills, 1984; Owens & Owens, 1978). Brown hyaenas depend on large carnivores such as the leopard to kill larger prey species (Mills, 2015; Slater & Muller, 2014; Stein, Fuller, & Marker, 2013). After feeding, leopards often become satiated before they can completely consume large prey animals, so they leave and return to the kill on subsequent occasions to feed further, providing ample scavenging opportunities (Karanth & Sunquist, 2000; Stein et al., 2013).

Studies that compare brown hyaena diets in areas where large predators are either present or absent show significant variation in patterns of consumption and food acquisition between these regions (van der Merwe et al., 2009; Yarnell et al., 2013). The degree of dietary overlap between brown hyaenas and leopards has, however, rarely been assessed, and this has never been studied in a montane area. We assessed the dietary composition of brown hyaenas and leopards and the degree of dietary overlap between these species in the Soutpansberg Mountains, South Africa. We also compared dietary composition with the relative abundance of prey species.

Methods

Study site

Data were collected from private properties in and around the Soutpansberg Mountains, Limpopo Province, South Africa (Fig. 1). The Soutpansberg Mountains range in altitude from 200 m to 1,748 m above sea level (Berger et al., 2003). Rainfall in the Soutpansberg Mountains ranges from 367 mm to over 2,000 mm per annum (Kabanda, 2003).

Variable climatic conditions and the mountains' undulating topography produce a myriad of biomes which host an extremely high level of biodiversity (Macdonald, Gaigher, Gaigher, & Berger, 2003). The most abundant prey species for large predators in the western Soutpansberg Mountains are bushbuck (*Tragelaphus scriptus*), Cape porcupine (*Hystrix africaeaustralis*), chacma baboon (*Papio ursinus*), greater kudu (*Tragelaphus strepsiceros*), and giraffe (*Giraffa camelopardalis*) (Chase Grey, Bell, & Hill, 2017). Much of the land in the mountains is unsuitable for farming and is used for leisure or ecotourism. Nearby lower lying areas are mainly used for livestock, game, and agricultural farming.

Within the mountains, leopards and brown hyaenas are the only resident large carnivores (Knott, Knott, Kruger, & Van der Waal, 2003). The leopard population in the western Soutpansberg Mountains is suffering a significant population decline (Williams, Williams, Lewis, & Hill, 2017), from 10.7 leopards per 100 km^2 in 2008 (Chase Grey, Kent, & Hill, 2013) to 3.7 per 100 km^2 in 2015 (Williams et al., 2017). Illegal human activity is driving high levels of leopard mortality (Williams et al., 2017). In 2015, brown hyaena density was estimated at 3.6 per 100 km^2 (Williams, 2017). Spotted hyaenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), and black-backed jackals (*Canis mesomelas*) pass through the area occasionally.

Dietary analysis

Scats were collected opportunistically in the western Soutpansberg Mountains from wild brown hyaenas (n = 137 scats) and leopards (n = 237 scats) between July 1, 2011 and December 31, 2015. Careful consideration of identifying features such as colouration, size, and weight was employed to ensure that scats were correctly assigned to species (Stuart & Stuart, 2003). Since there were no other large carnivores resident, confusion of scats from brown hyaenas and leopards with those from other species was unlikely.

Scats were placed in a wire sieve with 1 mm sized mesh and washed in water to remove all faecal matter (Kuhn, Wiesel, & Skinner, 2008). The contents of the scats were dried in the sun, then spread across a random sampling tray consisting of 36 or 100 numbered squares based on the size of the contents (Martins, Horsnell, Titus, Rautenbach, & Harris, 2011), and the macroscopic qualities of the contents were noted. For all brown hyaena scats and for 75 leopard scats, 40 hairs from every scat were selected at random: 20 hairs were used to create cuticular scale imprints (following Keogh, 1983) and 20 hairs were embedded in clear wax and cross-sectioned (following Douglas, 1989). For the remaining 162 leopard scats, cross-sectional analysis only was conducted. Cuticular imprints and cross-sections were carefully examined under a standard light microscope at 40-100x magnification. The species from which hairs originated were identified by comparing samples with a reference library of hairs collected from known mammal species and with published guides (Keogh, 1983; Seiler, 2010; Taru & Backwell, 2013), and we checked all species identifications at least twice to ensure accuracy.

Camera trapping

An array of 23 camera trap stations composed of two camera traps per station (Reconyx Hyperfire™ HC500 and HC600) was established in the western Soutpansberg Mountains (Fig. 1). The location and spacing of camera stations was optimised for estimation of leopard population density using a spatially explicit capture recapture framework (Williams et al., 2017). All camera stations collected photographs continuously from January 1, 2012 to December 31, 2015. The camera trap array covered an area of 73 km^2 at the onset of the study, but following one landowner's withdrawal from the survey and the subsequent relocation of five camera stations, the study area was reduced to 59 km^2 in late 2013 (Williams et al., 2017).

Statistical analysis

All occurrences of a prey item within a scat were calculated as a corrected frequency of occurrence (CFO) (Braczkowski, Watson, Coulson, & Randall, 2012; Henschel, Abernethy, & White, 2005). Employing the CFO accounted for occasions when more than one prey item was detected in a scat. For example, if two species were present in one scat, each species occurrence was weighted at 0.5 (Henschel et al., 2005; Karanth & Sunquist, 1995).

Dietary overlap between brown hyaena and leopard was calculated using Pianka's index (Pianka, 1973):

$$\alpha = \frac{\sum PiaPib}{\sqrt{\sum Pia^2 \sum Pib^2}}$$

where α equals the dietary overlap between species a and species b, Pia is corrected frequency of occurrence for species a, and Pib is corrected frequency of occurrence for species b. Results range from 0 (no overlap) to 1 (complete overlap) (Pianka, 1973) and values greater than 0.6 were deemed biologically significant (Navia, Mejía-Falla, & Giraldo, 2007). The relationship between the CFO of species in leopard scats and the CFO of species in brown hyaena scats was further tested using linear regression.

Camera trap data were used to estimate the relative abundance of potential prey species consumed by brown hyaena and leopard. Species abundance was calculated using a relative abundance index (RAI) (Negrões et al., 2010; O'Brien, Kinnaird, & Wibisono, 2003):

$$RAI_i = \left(\frac{\sum_j P_{ij}}{\sum_j tn_j}\right) * 100$$

where P_{ij} is the number of independent captures for *i*th species at *j*th camera trap location, and tn_j is the total trap-days at the *j*th camera trap location (Li, McShea, Wang, Shao, & Shi, 2010; O'Brien et al., 2003). Photographs of the same species taken at the same camera station occurring within a 60-minute interval were grouped as a single capture event (Negrões et al., 2010; Rovero & Marshall, 2009), and we excluded species < 1 kg since these are likely to be significantly underrepresented on camera images (Braczkowski et al., 2012; Henschel, Hunter, Coad, Abernethy, & Mühlenberg, 2011).

To determine the relationship between diet composition and prey abundance we used linear regression to test for associations between the RAI and the CFO of prey species in leopard and brown hyaena scats. We excluded Cape porcupine as it was an outlier due to its dense quills defending it from predators (Mori, Maggini, & Menchetti, 2014). Exclusion of this prey species revealed no further obvious influential cases, nor significant deviations from the assumptions of normality and homogeneity of residuals (Quinn & Keough, 2002). All statistical analyses were conducted in R v. 3.3.1 (R Development Core Team, 2017).

Results

Thirty-nine species of mammals were identified in brown hyaena scats and 24 species of mammals were detected in leopard scats (Table 1). Medium sized mammals was the category most frequently consumed by both species (38.80% of the brown hyaena diet and 50.49% in the leopard diet). The five most frequently consumed species by brown hyaena were bushbuck, chacma baboon, common duiker (*Sylvicapra grimmia*), common warthog (*Phacochoerus africanus*), and red duiker (*Cephalophus natalensis*). Three of these species (bushbuck, chacma baboon, and common duiker) also ranked highest in the leopard diet. Bushbuck was the most commonly consumed prey item for both brown hyaenas and leopards. Livestock (cows (*Bos taurus*), goats (*Capra aegagrus hircus*), and sheep (*Ovis aries*)) accounted for 7.23% of brown hyaena dietary occurrences. No livestock remains were detected in leopard scats. Dietary overlap between leopard and brown hyaena diet was biologically significant, with a Pianka's index of 0.817.

There was a significant positive association between the CFO of prey species in leopard scats and in brown hyaena scats (linear regression: $R^2 = 0.634$, $F_{(1,44)} = 76.17$, $p < 0.001$, gradient = 0.439, intercept = 1.22; Fig. 2a). The relationship remained significant when a potential outlier, bushbuck, was excluded (linear regression: $R^2 = 0.449$, $F_{(1,43)} = 35.02$, $p < 0.001$, gradient = 0.712, intercept = 0.11).

There was a significant positive relationship between the RAI of prey species and their CFO in the scats of brown hyaenas ($R^2 = 0.335$, $F_{(1,24)} = 12.07$, $p = 0.002$, gradient = 0.011, intercept = 2.69; Fig. 2b). No significant relationship was found between the RAI of prey species and their CFO in leopard scats ($R^2 = 0.128$, $F_{(1,15)} = 2.21$, $p = 0.158$).

Discussion

We found that there is high dietary overlap between leopards and brown hyaenas in the Soutpansberg Mountains. Although scat analysis does not definitively explain how prey remains are acquired (Mills & Mills, 1978; Nilsen et al., 2012), our findings support the hypothesis that hyaenas may be acquiring carcases from leopard kills.

Scavenging from an apex predator is primarily expected for medium- and large-bodied prey which are unlikely to be completely consumed by leopards immediately after making the kill (Stein et al., 2013; Yarnell et al., 2013), especially since successful brown hyaena hunts are mostly restricted to small- and very small-bodied species (Maude & Mills, 2005). The three most common species in the diets of brown hyaena and leopard are predominantly diurnal (bushbuck 67% diurnal; chacma baboon 99% diurnal; common duiker 78% diurnal: (Fitzgerald, 2015)) with warthogs and red duiker, the fourth and fifth most frequently consumed species by brown hyaena, both 94% diurnal in this area (Fitzgerald, 2015). These species would not be easily accessible to brown hyaenas when hunting, as brown hyaenas have a very low degree of activity during the day (Mills, 1984), so the most likely source of these species is scavenging. In contrast, 36% of leopard activity is during daylight in the Soutpansberg Mountains (Fitzgerald, 2015), and leopards have been observed to hunt diurnal prey at these times. Although it is possible that brown hyaenas have successful hunts during times when prey species are inactive, it is more likely that these species are scaveneged.

Scavenging the remains of animals that died from anthropogenic causes, as well as those that died naturally will also contribute to the brown hyaena's diet. The positive relationship between brown hyaena diet and prey abundance indicates a generalist diet that is common in scavengers (Maude & Mills, 2005). Leopards strongly prefer specific prey species weighing between 10 and 40 kg such as bushbuck (Hayward et al., 2006), which explains why we found no relationship between leopard diet and prey abundance, since very large and small species are not taken in relation to their abundance. Although brown hyaenas may acquire some of their food by scavenging from other predators such as caracals (*Caracal caracal*), these occur infrequently in the western Soutpansberg Mountains (unpublished data). Nevertheless, leopards appear to represent the greatest opportunity for scavenging in these mountains.

Of the species comprising the brown hyaena diet wild mammals predominated, but a low incidence of feeding on domestic livestock was also noted (7.23% of occurrences). Livestock depredation by brown hyaenas is rare; despite the presence of livestock in the diet of collared brown hyaenas in Botswana, they were never observed hunting livestock (Maude & Mills, 2005). No livestock remains were detected in leopard scats. Yet, leopards do occasionally attack livestock in the area (unpublished data). Therefore, it is likely that brown hyaenas may have secured some livestock remains from leopards residing at lower altitudes or by scavenging the remains of livestock that died from other causes such as disease, mismanagement, or roadkill.

Understanding diet, food acquisition, and interrelationships between predators that are exceedingly reliant on private land is crucial for their conservation. Our data show that brown hyaenas on private land in the Soutpansberg Mountains have a varied diet consisting of mostly wild mammals. High dietary overlap with leopards and evidence supporting scavenging behaviour suggests that leopards could potentially provide brown hyaenas with scavenging opportunities, and thus function as a keystone species for brown hyaenas on private land. Leopards are experiencing severe declines, both in the Soutpansberg Mountains (Williams et al., 2017) and globally (Jacobson et al., 2016). Conservation management plans that adopt a multi-species approach are required to preserve leopards and consequently provide food security for scavengers like brown hyaenas, which supply important ecosystem services through their feeding habits (Beasley, Olson, & DeVault, 2015).

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Table 1 Occurrence of mammalian prey species identified in brown hyaena and leopard scats collected in the western Soutpansberg Mountains, South Africa, between July 2011 and December 2015. Prey size groupings are based on classifications by Mills and Mills (1978).

	Brown hyaena (n=137)		Leopard (n=237)	
Prey species	Corrected Occurrences	Corrected frequency of occurrence %	Corrected Occurrences	Corrected frequency of occurrence %
Large mammals (> 50 kg)				
Blesbok, *Damaliscus pygargus*	1	0.73		
Blue wildebeest, *Connochaetes taurinus*			0.33	0.14
Bushpig, *Potamochoerus larvatus*	7.58	5.53	24	10.13
Common warthog, *Phacochoerus africanus*	9.17	6.69	6.33	2.67
Gemsbok, *Oryx gazella*	1	0.73		
Giraffe, *Giraffa camelopardalis*	1	0.73		
Greater kudu, *Tragelaphus strepsiceros*	8.08	5.9	6	2.53
Nyala, *Tragelaphus angasii*	5	3.65		
Sable, *Hippotragus niger*	0.33	0.24		
Waterbuck, *Kobus ellipsiprymnus*	1.83	1.34	4	1.69
Zebra, *Equus quagga*	1.75	1.28		
Domestic livestock				
Cow, *Bos taurus*	5.08	3.71		
Goat, *Capra aegagrus hircus*	4.33	3.16		
Sheep, *Ovis aries*	0.5	0.36		
Medium mammals (16 - 50 kg)				
Aardvark, *Orycteropus afer*	1.33	0.97		
Brown hyaena, *Hyaena brunnea*	1.17	0.85		
Bushbuck, *Tragelaphus scriptus*	20	14.6	80.83	34.11
Chacma baboon, *Papio ursinus*	11.83	8.64	16.83	7.1
Common duiker, *Sylvicapra grimmia*	10.25	7.48	15.67	6.61
Domestic dog, *Canis lupus familiaris*	0.5	0.36		
Grey rhebok, *Pelea capreolus*			1	0.42
Impala, *Aepyceros melampus*	8.08	5.9	3.83	1.62
Mountain reedbuck, *Redunca fulvorufula*			1.5	0.63
Small mammals (1 – 15 kg)				
African civet, *Civettictis civetta*	0.33	0.24		
Black-backed jackal, *Canis mesomelas*	1	0.73		
Cape porcupine, *Hystrix africaeaustralis*	0.67	0.49	5.17	2.18
Gambian giant rat, *Cricetomys gambianus*	1.25	0.91	1	0.42
Klipspringer, *Oreotragus oreotragus*			5.67	2.39
Large spotted genet, *Genetta maculata*	0.5	0.36		
Mongoose, Family: Herpestidae[†]	2.5	1.82		
Red duiker, *Cephalophus natalensis*	9.17	6.69	8.83	3.73
Rock dassie, *Procavia capensis*	1.33	0.97	12.17	5.13
Samango monkey, *Cercopithecus albogularis*	3.83	2.8	7	2.95

Sharpe's grysbok, *Raphicerus sharpei*	1	0.73		
Steenbok, *Raphicerus campestris*	0.5	0.36		
Thick-Tailed Bushbaby, *Otolemur crassicaudatus*			1	0.42
Vervet monkey, *Chlorocebus pygerythrus*	5.17	3.77	19.83	8.37
Yellow spotted dassie, *Heterohyrax brucei*	4.08	2.98	11.5	4.85
Very small mammals (< 1 kg)				
Four striped mouse, *Rhabdomys pumilio*	1.83	1.34	1	0.42
House rat, *Rattus rattus*	0.92	0.67		
Lesser bushbaby, *Galago moholi*	1	0.73		
Lesser red musk shrew, *Crocidura hirta*	0.75	0.55		
Namaqua rock mouse, *Aethomys namaquensis*			0.5	0.21
Rock elephant shrew, *Elephantulus myurus*	0.5	0.36	2	0.84
Swamp musk shrew, *Crocidura mariquensis*	0.83	0.61		
Woodland dormouse, *Graphiurus murinus*			0.5	0.21
Total		**100**		**100**

† It was possible to identify mongooses only to a Family level.

Fig. 1 Locations of brown hyaena and leopard scats collected, and minimum convex polygon (MCP) of the area covered by camera traps in the Soutpansberg Mountains.

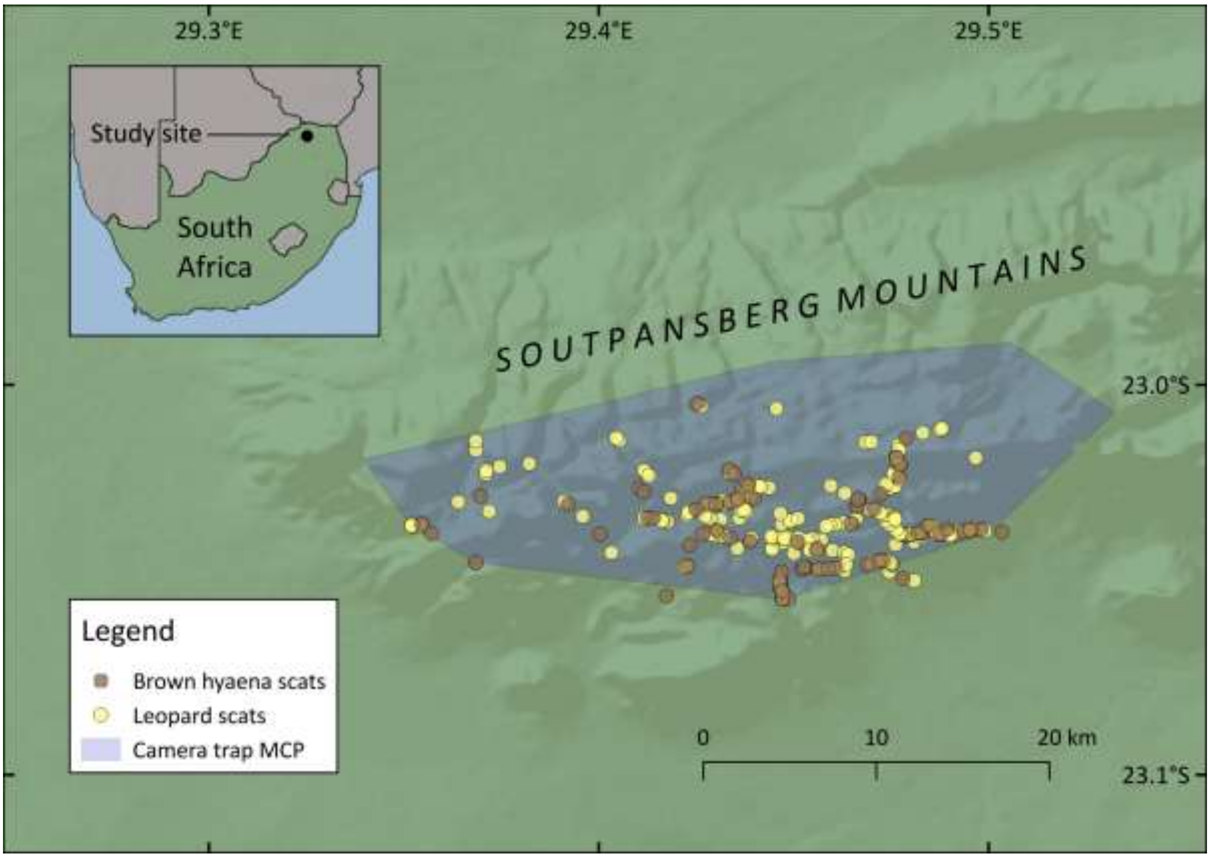
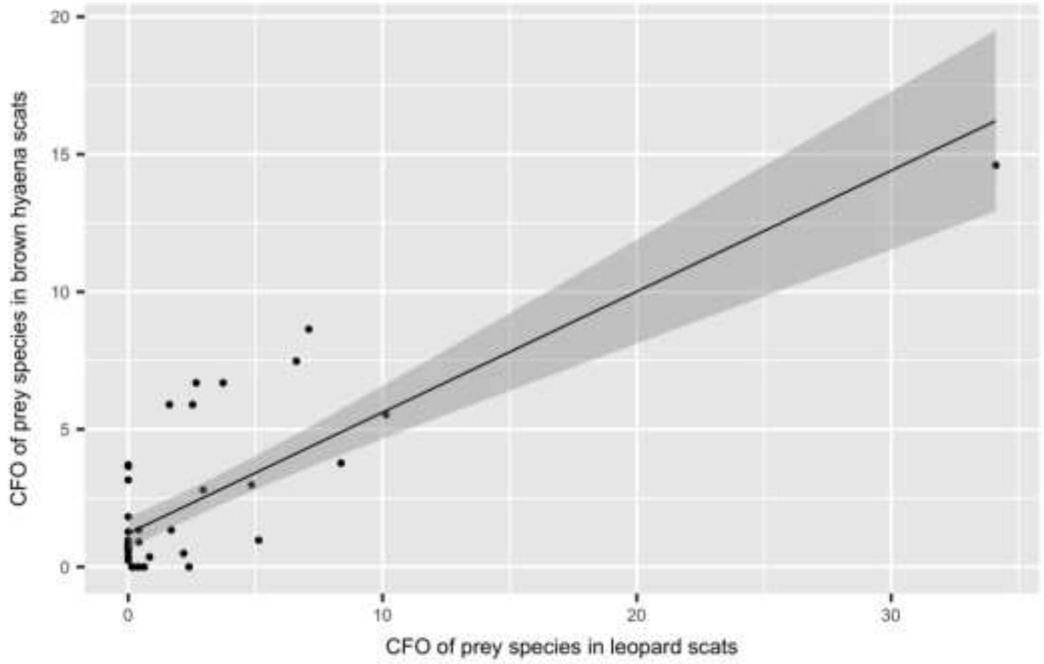


Fig. 2 (a) Corrected frequency of occurrence (CFO) of prey species in brown hyaena scats and corrected frequency of occurrence of prey species in leopard scats. (b) Corrected frequency of occurrence (CFO) of prey species in brown hyaena scats and relative abundance index (RAI) of prey species. Shaded area represents 95% confidence interval.

(a)



(b)