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Brown hyena habitat selection varies among sites in a semi-arid region of southern Africa

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Human/carnivore conflicts are common across the globe, and with a growing human population, this conflict is likely to increase as the space available to large carnivores is reduced. In South Africa, many small (< 400 km^2), fenced protected areas have reintroduced persecuted carnivores, such as brown hyenas (*Hyaena brunnea*). These reserves have great potential to conserve brown hyena populations; consequently, understanding the limitations that small, fenced reserves impose on space use patterns is needed. We investigated the home range (95% fixed kernel utilization distributions) and landscape determinants of habitat selection using resource selection functions for 10 brown hyenas in 3 separate fenced reserves. Home range sizes were consistently smaller in 2 of the reserves when compared to the third. Considerable variation in the selection of habitat features exists among individual brown hyenas and reserves. The most important landscape determinant driving brown hyena space use was distance to roads, with brown hyenas observed closer to roads when compared to random locations within their ranges. If this relationship with roads holds outside of protected areas, it could represent a considerable threat to the species. Thus, obtaining a better understanding of the influence of roads on brown hyenas represents an important focus for future research.

Key words: Eastern Cape, fenced reserves, home range, *Hyaena brunnea*, resource selection function, road ecology

In the last 50 years, the human impact on ecosystems has been greater than during any other time period in human history (Millennium Ecosystem Assessment 2003). Large carnivores face anthropogenic threats worldwide, specifically persecution, habitat degradation, and habitat fragmentation (Everatt et al. 2014; Groom et al. 2014; Ripple et al. 2014; Wolfe et al. 2015). Because large carnivores often occupy high trophic levels, their presence influences species at lower levels through trophic cascades (Ripple et al. 2014). Natural experiments, taking advantage of large carnivore management, have shown that large predators provide fundamental ecosystem and economic services that help maintain healthy and diverse ecosystems (Ripple et al. 2014). Additionally, carnivores play an important role in other ecosystem processes, for example, scavenging carnivores may provide regulatory services, such as waste removal, nutrient cycling, and disease regulation. Such services add stability to ecosystems and ensure energy flow through multiple trophic levels (DeVault et al. 2003; Wilson and Wolkovich 2011).

Large carnivore conservation in South Africa has benefitted from the establishment of fenced protected areas set aside to conserve biodiversity. Many small (< 400 km^2), private game reserves have been established in South Africa during the last 25 years to conserve biodiversity. In several of these areas, extirpated carnivores, such as brown hyenas (*Hyaena brunnea*), have been reintroduced (Hayward et al. 2007). Each reserve is typically separated from the surrounding areas by an electrified fence, effectively creating distinct ecological islands.

Despite the small size of these reserves, they can contribute to meta-population management strategies for endangered species (Davies-Mostert et al. 2009).

Fenced reserves, and the species within them, require careful monitoring and management as natural processes, such as immigration and emigration, are curtailed (Hayward et al. 2007). In addition, many of these small reserves in South Africa are smaller than the reported home range sizes of several carnivore species (e.g., Owens and Owens 1996; Houser et al. 2009; Funston 2011), making the assessment of carnivore space use and resource availability imperative if these small, fenced reserves are to provide conservation benefits for carnivores. Habitat selection is an important determinant of population persistence for many species, whereby factors such as resource availability and landscape attributes can strongly affect occupancy rates (Rostro-Garcia et al. 2015).

Brown hyenas are "near-threatened" (Wiesel et al. 2008), scavenging carnivores found throughout southern Africa, and they have been reintroduced into at least 5 small, fenced reserves in the Eastern Cape Province (Hayward et al. 2007). The main threats to this species outside of protected areas are conflicts with humans, particularly farmers who perceive them as a threat to livestock (Hofer and Mills 1998; Wiesel et al. 2008) and road mortality; inside protected areas, inbreeding depression can be a problem if outbreeding is prevented (M. Child, Red Data List, Endangered Wildlife Trust, Johannesburg, South Africa, pers. comm.). Brown hyenas have home ranges as large as 4,370 km^2 based on minimum convex polygon (MCP) methods and 2,570 km^2 based on kernel methods (Wiesel 2006). However, much of the research on the spatial ecology of brown hyenas has been conducted in large, open systems (e.g., Owens and Owens 1978; Mills 1990; Weise et al. 2015), where the focus has been primarily on home range sizes, thus limiting our understanding of the drivers of space use.

Due to the large number of small reserves in South Africa and their potential to provide conservation benefits to the brown hyena, it is important to understand the limitations imposed by the small size of the reserves on their spatial use and movement patterns. Accordingly, we investigated the space use patterns of brown hyenas in 3 small, fenced reserves in the Eastern Cape Province, South Africa, using Global Positioning System (GPS) data from multiple radiocollared individuals. We also investigated the potential drivers of brown hyena space use to better understand the factors that influence occupancy by brown hyenas at the landscape scale. Finally, because brown hyenas are elusive beyond small reserve boundaries (Mills and Hofer 1998), these reserve populations provide an ideal opportunity to investigate landscape variables that may promote or threaten the persistence of brown hyenas outside the boundaries of small reserves.

Materials and Methods

Study sites.—Brown hyena spatial data were collected from 3 sites in the Eastern Cape Province, South Africa: Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve (KPGR), and Shamwari Private Game Reserve (SPGR; Fig. 1). All are small, fenced reserves, ranging in size from 153 to 213 km^2. The perimeters have 2.4 m high, 5-strand electric game fences, which separate the reserves from private- or state-owned land. At MZNP, the only large carnivores present at the time of this study were cheetahs (*Acinonyx jubatus*) and brown hyenas. In KPGR and SPGR, many large indigenous carnivores (e.g., lion [*Panthera leo*] and cheetah) were reintroduced after having been extirpated from the Eastern Cape Province by the end of the 20th century; both reserves currently have relatively high predator densities (see Hayward et al. 2007). In 2002, 6 brown hyenas (4 adult females and 2 adult males) were reintroduced to SPGR, 3 from Thabo Thula and 3 free-roaming individuals, 1 captured in Benoni (Gauteng Province, South Africa) and 2 from areas close to the South African/Botswana border. In 2003, 6 brown hyenas (1 adult female, 2 sub-adult females, and 3 adult males) were reintroduced to KPGR from Thabo Thula in the North-West Province. In 2008, 3 brown hyenas (1 adult female, 1 adult male, and 1 sub-adult female) were reintroduced to MZNP from Mafunyane Game Reserve in the North-West Province, South Africa.

Telemetry data and home range estimates.—Brown hyenas (n = 3–4/site) were immobilized (Zoletil 20–50 mg, Virbac, Centurion, South Africa; Medetomidine 1–4 mg, Kyron Laboratories, Johannesburg, South Africa), collared, and monitored at each site to collect spatial data. The number of animals sampled at each site and the length of data collection varied among sites and was dependent on when brown hyenas were reintroduced and collar longevity (Table 1). The 3 individuals at MZNP were radiocollared for routine monitoring purposes by a South African National Parks (SANParks) veterinarian following standard SANParks operational protocol (Buss et al. 2005). Capture and handling protocols at KPGR were in accordance with the Rhodes University ethical standards protocol under the ethical clearance number ZOOL-11-2012; at SPGR, animal handling protocols were in accordance with The University of South Africa's ethical standards protocol under the ethical clearance number 2013/CAES/132. Protocols used in all study areas were also in accordance with American Society of Mammalogists' guidelines (Sikes et al. 2011). The radiocollars we used were either satellite GPS/GSM (MZNP) or satellite GPS/VHF (KPGR and SPGR) and all were manufactured by Africa Wildlife Tracking (Rietondale, Pretoria, South Africa). Wildlife managers at each site agreed to recapture animals and remove collars at the completion of monitoring.

Due to their nocturnal nature (Mills 1990) and inactivity during the day (Welch 2014), GPS fixes were recorded during the night and early morning for most individuals (Table 1). For home range analyses, GPS locations were reduced to 1 fix per night (between 2000 and 2200 h); at SPGR, the 1st available fix within this time period was selected, which was generally 2000. It is important to note that core areas will largely be determined by dens and resting areas and therefore by selecting only nightly fixes the data may be biased to periods of brown hyena activity, and therefore core areas may represent

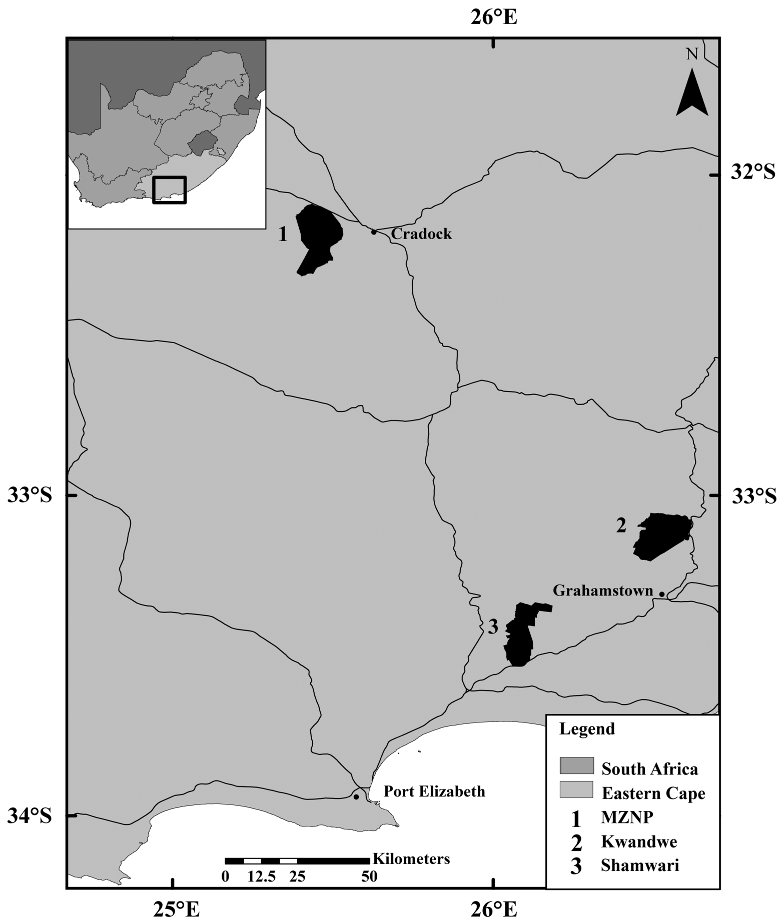

Fig. 1.—Locations of the 3 brown hyena study sites (MZNP [Mountain Zebra National Park], Kwandwe Private Game Reserve, and Shamwari Private Game Reserve) in the Eastern Cape Province of South Africa.

Table 1.—Data on 10 brown hyenas radiocollared in Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve (KPGR), and Shamwari Private Game Reserve (SPGR) in the Eastern Cape Province of South Africa (Ad = adult brown hyenas, S-Ad = sub-adults).

Reserve	BH I.D.	Sex (Age)	Start	End	GPS fix times (local time)
MZNP	BH1	♀ (Ad)	10 Oct 2008	05 Mar 2010	0200, 0500, 0800, 2000, 2300
	BH2	♂ (Ad)	10 Oct 2008	24 Apr 2009	0100, 0400, 0700, 2200
	BH3	♀ (S-Ad)	11 Oct 2008	30 Sep 2009	0100, 0400, 0700, 2200
KPGR	BH4	♂ (Ad)	18 Feb 2013	28 Feb 2014	1700, 2100, 0100, 0500
	BH5	♂ (Ad)	19 Feb 2013	28 Feb 2014	1700, 2100, 0100, 0500
	BH6	♀ (Ad)	13 Feb 2013	15 Nov 2013	1700, 2100, 0100, 0500
SPGR	BH7	♂ (Ad)	17 May 2014	14 Dec 2014	1200, 1800–0700 (every h)
	BH8	♂ (Ad)	01 Jul 2014	15 Dec 2014	1200, 1800–0700 (every h)
	BH9	♀ (Ad)	13 Sep 2014	14 Dec 2014	1200, 1800–0700 (every h)
	BH10	♀ (Ad)	24 Oct 2014	15 Dec 2014	1200, 1800–0700 (every h)

core areas of activity. One fix per day was chosen to eliminate autocorrelation and ensure statistical independence between successive locations (Newdick 1983; Tew 1989; Mizutani and Jewell 1998). This method provided a suitable number of fixes (≥ 50) for kernel home range analyses based on previous simulation data (Seaman et al. 1999). Individual home ranges were calculated using fixed kernel density estimators (Worton 1989; Seaman and Powell 1996). The 95% (home range) and 50% (core area) utilization distributions were calculated using home range tools (HRT) in ArcMap 9.3 (Rodgers and Kie 2011). We used the default smoothing factor (H_{ref}), which is generated automatically for each dataset (Worton 1995). For analysis, we multiplied the H_{ref} value by 0.70, because H_{ref} is known to over-smooth the data and exaggerate home range estimates (Bertrand et al. 1996).

Resource selection function covariates.—To identify environmental factors that influence home range use by brown hyenas, we selected 6 covariates a priori. Because we have little information on the factors that govern space use by brown hyenas, we selected broad covariates to reflect the potential influence of vegetation, anthropogenic activities, and terrain on space use. In each reserve, the vegetation was classified into either "dense vegetation" or "open areas" based on a visibility index, calculated using a modified point-centered quarter method and checker board (Bissett 2007). Visibility indices > 69 were considered open areas. At MZNP, open areas comprised 89% of the reserve, and the remaining 11% contained dense vegetation. In KPGR, open areas comprised 37% of the reserve and dense vegetation comprised 63%. In SPGR, open areas and dense vegetation were more equally divided, with 46% in open areas and 54% in dense vegetation. Because carnivores often use roads to traverse their ranges (Zimmermann et al. 2014), we calculated the Euclidean distance to roads (m) for each brown hyena location using ArcMap 9.3. Due to the small size of the reserves and the reportedly large home ranges of brown hyenas, we expected that fences would be encountered frequently. If fences provide barriers to movement, brown hyenas may spend a disproportionate amount of time near boundary fences. We therefore included the Euclidean distance to the boundary fence (m) for each brown hyena location using ArcMap 9.3. In semi-arid regions, drainage lines often provide areas of increased resources (Broten and Said 1995; Broomhall et al. 2003); consequently, brown hyenas may frequent such drainage lines when foraging. We calculated the Euclidean distance to drainage lines (m) for each brown hyena position using ArcMap 9.3. All 3 reserves lie in an area of undulating terrain, with elevations ranging from 170 to 1,960 m. A digital elevation model was created from a 20-m contour line shapefile, and from this model we created raster layers for both elevation and slope (degrees) to evaluate whether terrain-based factors may be influencing habitat selection by brown hyenas. Due to the strong differences in elevation for each reserve, we calculated the difference in elevation at each site by subtracting the minimum observed elevation from the elevation of each GPS location for each reserve. Therefore, results were standardized across all 3 reserves despite the large differences in elevation values (Table 2).

Resource selection functions.—Habitat selection was analyzed at the home range scale using resource selection functions (RSFs) to identify covariates that influence home range use (Johnson 1980). These analyses reveal patterns of selection by comparing observed locations (GPS data) to random available locations (pseudo-absences) within each individual home range (Keating and Cherry 2004) using logistic regression models (Manly et al. 2002). Observed locations were the same fixes used in home range analyses (1 fix per night) above. Additionally, it must be noted that these observed locations reflect nocturnal activity and these patterns might differ from resting or denning sites used by brown hyenas during the day. The number of random points generated was equal to the number of observed locations for each analysis (Klar et al. 2008). We found no evidence of colinearity among our predictor variables (Dellinger et al. 2013).

We generated RSFs for brown hyenas using mixed-effects general linear models with a logit link function. We constructed separate models for each reserve (i.e., we pooled all brown hyena data for each reserve) and included individual brown hyenas as random intercepts in each model. For each reserve, we constructed candidate models to examine the relationship between our response variable (presence or pseudo-absence) and various combinations of predictor variables. We did not include interactions, because we could not justify their biological relevance and wanted to keep the candidate model set as small as possible (Burnham and Anderson 2002). Model selection was performed by ranking each model based on its Akaike's Information Criterion (AIC_c) value (corrected for small sample size) and models were assessed based on their Akaike weights w_i (Burnham and Anderson 2002). Because there was no clear best model (see Supporting Information S1–S3), we averaged parameter coefficients across all models for each reserve with a cumulative Akaike weight > 0.9 (Symonds and Moussalli 2011). The relative importance of each variable in each reserve was estimated by summing the Akaike weights across models where each covariate was included (Burnham and Anderson 2002). To visually assess the influence of each continuous predictor variable on the probability of hyena presence, we plotted the average marginal probability of brown hyena presence as a function of the range of observed predictor variables. To do this, we fixed the value of our variable of interest at 100 values across its observed range and, for each value, predicted the observed probability of brown hyena presence while maintaining all other predictor variables (fixed and random) equal to their original input values (Elith et al. 2005). All analyses were conducted in R version 3.0.2 (see Supporting Information S4; R Development Core Team 2014).

Results

Home range sizes were variable among the 3 sites and ranged from 34 to 205 km^2, core area sizes ranged from 11 to 71 km^2 (Table 3; Fig. 2). Home range sizes were notably larger at MZNP, where all 3 individuals used most of the park, than at KPGR and SPGR, where our study animals only used certain portions of the reserves (Fig. 2).

We used model coefficient averaging because no model was selected as the best model; the top models for each reserve had Akaike weights ranging from 0.17 to 0.47 (MZNP: 0.18, KPGR: 0.47, SPGR: 0.17; Supporting Information S1–S3). After model averaging, the most important variables differed between the 3 reserves, and only the distance to roads

Table 2.—The wide range of environmental variables that exist within Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve (KPGR), and Shamwari Private Game Reserve (SPGR).

Environmental variable	MZNP	KPGR	SPGR
Change in elevation (m)	2–961	2–353	16–443
Slope (degrees)	0–56	0–36	0–40
Distance to drainage lines (m)	0–1,389	0–1,063	0–1,085
Distance to roads (m)	0–1,875	0–637	0–1,834

Table 3.—The 50% (core area) and 95% (home range) kernel utilization distribution estimates for individual brown hyenas (BH I.D.) in Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve (KPGR), and Shamwari Private Game Reserve (SPGR) in the Eastern Cape Province of South Africa. The corresponding *H* values (smoothing parameters) used and the number of GPS fixes used (*n*) are also indicated.

Reserve	BH I.D.	*n*	50% (km^2)	95% (km^2)	*H*
MZNP	BH1	388	46	192	1,428
	BH2	195	55	172	1,096
	BH3	337	71	205	1,193
KPGR	BH4	361	18	43	519
	BH5	366	30	80	653
	BH6	259	20	72	638
SPGR	BH7	212	13	51	522
	BH8	167	19	63	664
	BH9	94	11	34	533
	BH10	53	13	39	658

significantly influenced the probability of brown hyena presence in all 3 reserves (Table 4). Moreover, the distance to roads was the only variable to have the same significant relationship (positive or negative) with the probability of brown hyena presence across all reserves, whereby the probability of brown hyena presence increased with decreasing distance to roads (Table 4, Fig. 3a). This road effect was strongest for KPGR and weakest for MZNP (Fig. 3a).

The relative importance of the remaining variables differed among the reserves. The distance to drainage lines was the only other variable to have a consistent relationship among all 3 reserves, with the probability of brown hyena presence increasing closer to drainage lines, though not significantly so in all reserves (Table 4; Fig. 3d). In MZNP, along with the distance to roads and distance to drainage lines, the probability of brown hyena presence increased significantly in dense vegetation (Table 4). In KPGR, along with distance to roads and distance to drainage lines, the probability of brown hyena presence was significantly higher on steeper slopes (Fig. 3c) and at higher elevations within the reserve (Fig. 3b). In contrast, brown hyenas in SPGR were more likely to be found on flatter terrain (Fig. 3c) and at lower elevations (Fig. 3b).

Discussion

Our results showed that spatial use patterns by brown hyenas varied considerably among our 3 sites. Individual brown hyena home range sizes were 2–6 times larger in MZNP than in KPGR and SPGR, where all individuals occupied home ranges < 80 km^2 in size. Drivers of space use within home ranges also varied considerably among the 3 sites, with only the positive relationship between the distance to roads and brown hyena occupancy being a consistent influence on selection of home ranges. Observed variation in the importance of the covariates we examined suggests that brown hyenas can be flexible in their use of habitat at the landscape scale. However, we may also have omitted important explanatory variables that were not available to us, such as the occurrence or abundance of other large predators.

Home range estimates for brown hyenas in our study areas were comparable to kernel home ranges previously reported for brown hyenas (5.5–2,570 km^2; e.g., Skinner and van Aarde 1987; Skinner et al. 1995; Owens and Owens 1996; Maude 2005; Wiesel 2006). Most previous estimates were for brown hyenas that occupied areas not enclosed by fences, suggesting that either brown hyenas in small reserves need not range widely or that they are constrained by the fences. The home range estimates for brown hyenas in KPGR and SPGR were among the smallest estimates reported. It must be acknowledged, however, that many earlier studies used MCPs to estimate brown hyena home ranges, which may have resulted in over-estimates of their sizes (Harris et al. 1990).

All collared individuals remained inside their respective reserves during the study. This indicates that the populations are closed and that their use of space is restricted. Despite this, we found no indication that space use by brown hyenas was related to reserve boundaries, suggesting that the smaller home ranges we documented may not be an artifact of small reserve size. Despite the relative similarities in study sites, there was a considerable difference in home range sizes between KPGR and SPGR compared to MZNP (2–6 times larger). This observation might be explained by a combination of the following mechanisms. First, since brown hyenas are territorial (Owens and Owens 1979; Mills et al. 1980; Mills 1982), the considerably smaller home ranges in our reserves could have resulted from territory packing to reduce overlap between neighboring clans. Brown hyena densities are considerably higher in KPGR (14/100 km^2) and SPGR (8/100 km^2) than in MZNP (4/100 km^2—Welch 2014; C. Bissett, Rhodes University, Grahamstown, South Africa, pers. comm., February 2015; K. Müller, University of South Africa, Johannesburg, South Africa, pers. comm., February 2015), which could constrain individual space use. Second, the smaller home ranges observed at KPGR and SPGR could be related to strategies designed to avoid other large predators (Mills 1990). Lion density was high in both KPGR (5/100 km^2) and SPGR (13/100 km^2), whereas no lions were present in MZNP at the time of the study. Lastly, the large home ranges observed at MZNP could be associated with limited cultural inheritance of space, where knowledge of space is acquired from previous generations (Skinner et al. 1995). Initially, it was thought that these large ranges could be due to exploratory movements made prior to home range establishment (Weise et al. 2015), as brown hyenas had been reintroduced to MZNP only 2 weeks prior to the initiation of our study. However, upon further investigation, exploratory movements could not explain the larger home ranges, as home ranges for all 3 individuals were larger during the latter months of the study compared to the initial months following reintroduction. The populations of brown hyenas at KPGR and SPGR, however, were well established (about 10 and 12 years, respectively) by the time of our study and had originated from small founder populations. Consequently, territories were likely to have been established by closely related

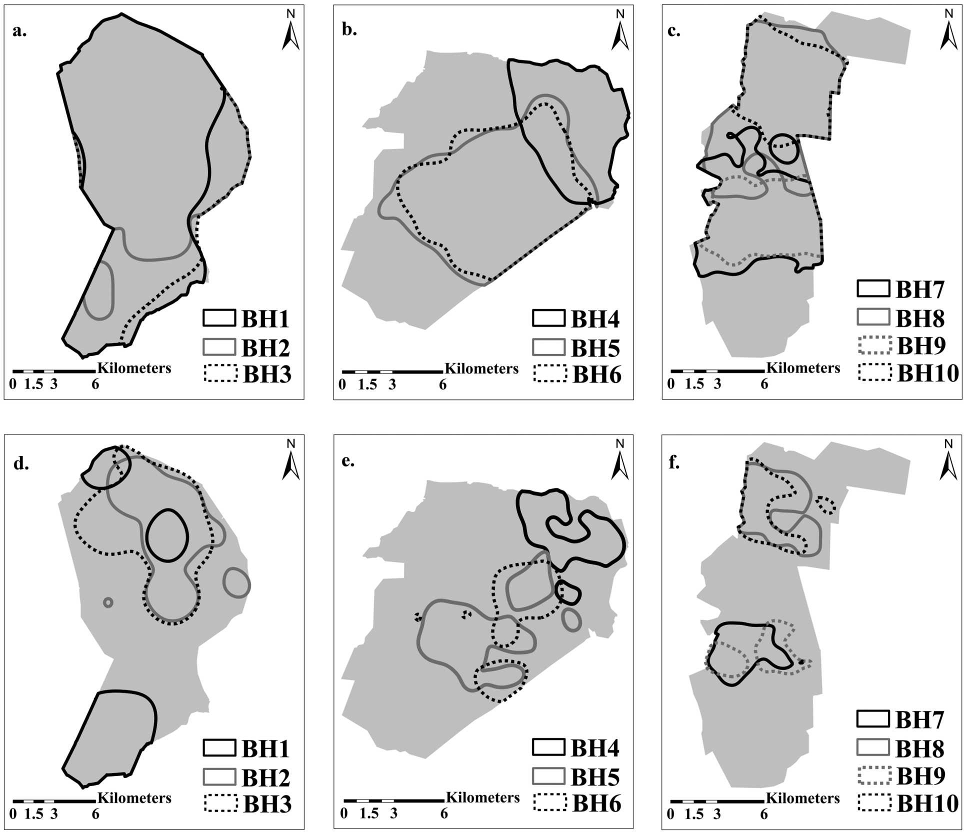

Fig. 2.—The 50% (core area) and 95% (home range) kernel utilization distribution estimates for individual brown hyenas at 3 sites in the Eastern Cape Province of South Africa. Mountain Zebra National Park (MZNP, a: home ranges, d: core areas), Kwandwe Private Game Reserve (KPGR, b: home ranges, e: core areas) and Shamwari Private Game Reserve (SPGR, c: home ranges, f: core areas).

Table 4.—Model averaged coefficients (β) and relative importance (R.I.) of the covariates investigated to explain the selection of home ranges by brown hyenas in Mountain Zebra National Park (MZNP), Kwandwe Private Game Reserve (KPGR), and Shamwari Private Game Reserve (SPGR) in the Eastern Cape Province of South Africa. * = statistically significant at $P \leq 0.05$.

	MZNP				KPGR				SPGR			
	B	SE	*P*	R.I.	β	SE	*P*	R.I.	β	SE	*P*	R.I.
Intercept	−0.06	0.05	0.27		0.00	0.06	0.95		0.03	0.10	0.80	
Drainage	−0.12	0.05	0.02*	0.91	−0.14	0.05	< 0.01*	1.00	−0.02	0.07	0.72	0.24
Roads	−0.13	0.06	0.02*	0.89	−0.27	0.05	< 0.01*	1.00	−0.19	0.07	0.01*	1.00
Slope	0.09	0.06	0.14	0.53	0.13	0.05	0.01*	1.00	−0.42	0.08	< 0.01*	1.00
Thicket	0.44	0.14	< 0.01*	1.00	0.02	0.10	0.86	0.27	−0.15	0.13	0.27	0.39
Boundary	−0.06	0.05	0.21	0.42	0.04	0.05	0.36	0.36	0.02	0.07	0.79	0.23
Elevation	−0.01	0.07	0.93	0.27	0.18	0.05	< 0.01*	1.00	−0.12	0.08	0.15	0.52

individuals, so knowledge of home range areas and space use may have already been acquired.

Among the 3 reserves, there was considerable variation in how individual brown hyenas used the landscape within their home ranges. This variation between reserves is highlighted in how elevation and slope influenced space use differently in KPGR and SPGR. In KPGR, individuals preferred more rugged and steep environments, whereas in SPGR individuals preferred flatter terrain. Despite considerable variation in habitat conditions among reserves, hyenas were positively associated with the proximity of both roads and drainage lines in all 3 study areas.

This preference for roads was highest in KPGR, where dense vegetation dominated the landscape (see "Materials and Methods"). This suggests that in KPGR, roads may provide foraging routes that reduce energy expenditures. A similar preference for roads has been observed in wolves (*Canis lupus*) in Scandinavia and is associated with reduced energy expenditure, territory maintenance, and as a means for increasing prey encounter rates (Zimmermann et al. 2014). However, roads were also important at MZNP, where the vegetation is predominantly open. Therefore, roads may also serve additional purposes such as territorial boundaries (Mills et al. 1980; Wiesel 2011), as suggested by the common occurrence of latrines and scent marks along road margins (R. Welch, pers. obs.). Furthermore, because brown hyenas often scavenge the kills of other large predators (Owens and Owens 1978;

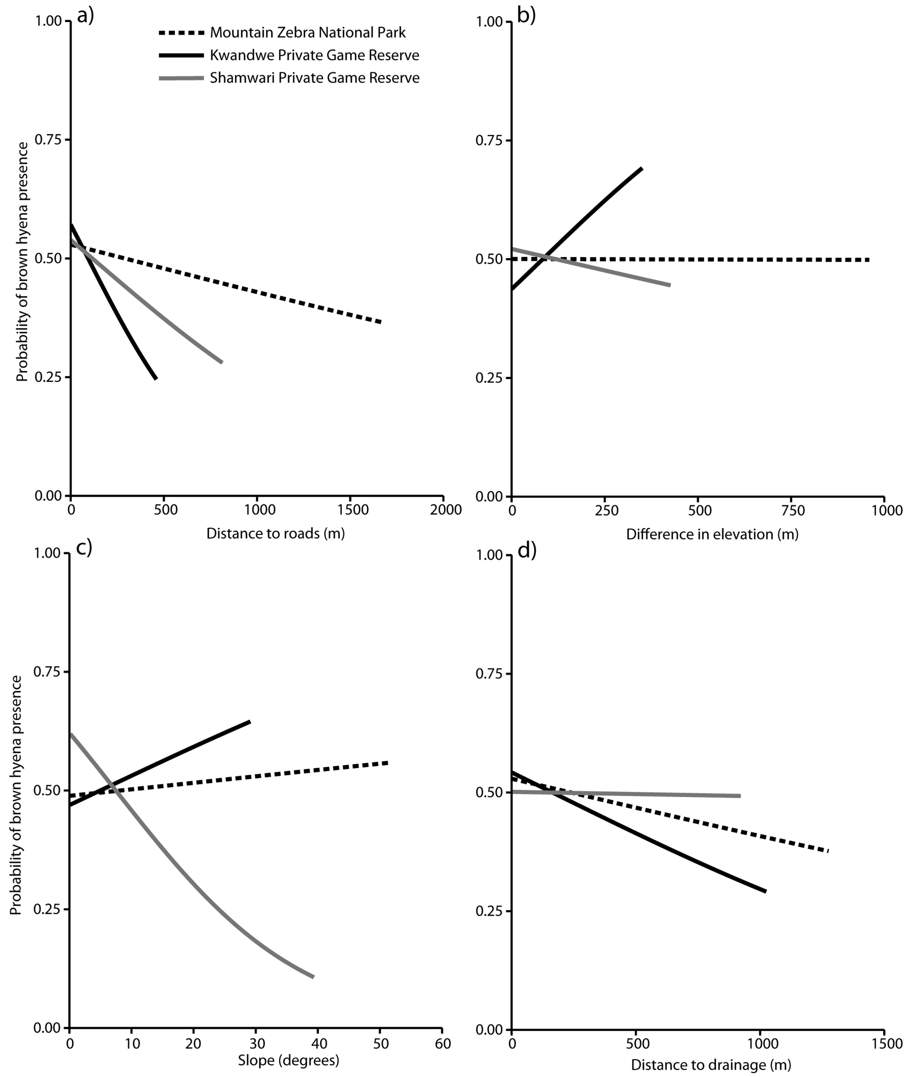

Fig. 3.—Average marginal probability of brown hyena presence in Mountain Zebra National Park, Kwandwe Private Game Reserve, and Shamwari Private Game Reserve in relation to a) distance to roads, b) relative difference in elevation among each reserve, c) slope, and d) distance to drainage lines.

Mills 1990), their use of roads could increase the probability of locating carrion as many large predators also preferentially use roads (Sunquist 1981; Zimmerman et al. 2014). However, using roads may also increase the chances of brown hyenas encountering other large predators, which could lead to agonistic interactions (Owens and Owens 1978). Camera-trap surveys at KPGR showed that other large predators also regularly used roads, providing support for this hypothesis (R. Welch, pers. obs.). If a similar pattern of road use exists outside of protected areas, brown hyenas may be in danger of road-related mortality when selecting tar roads as movement conduits. In Namibia, at least 2 brown hyena deaths per year are related to roads in areas where brown hyena densities are relatively low, and tar roads provide important territory boundaries (Wiesel 2010, 2011). Data for brown hyena road mortalities in South Africa are lacking (W. Collinson, Wildlife and Roads Project, Endangered Wildlife Trust, Johannesburg, South Africa, pers. comm., February 2015); however, because some brown hyena body parts are used for traditional medicines (Hofer and Mills 1998), many road-related deaths may go unreported.

Observed variation in the selection of habitat features among individuals and reserves suggests either that brown hyenas are adaptable in their response to landscape variability, or that our analysis omitted a key covariate. Space use by other large predators may, in turn, influence space use by brown hyenas (Mills 1990), and we suggest that this should be an important area of future research. The persistence of brown hyena populations in all 3 reintroduction sites demonstrates their resilience. We recognize that these reserves are small and enclosed, which may represent confounding factors, i.e., our results may have been strongly influenced by limitations on the space available within each reserve.

Nevertheless, information on habitat use is important for wildlife managers who are considering reintroducing brown hyenas into enclosed reserves. We suggest that the use of drainage lines by brown hyenas is associated with large carnivore kills and subsequent scavenging opportunities. In other areas, higher densities of brown hyenas have been observed in the presence of large predators (Yarnell et al. 2013). In contrast, brown hyena populations are suppressed in the presence of other large predators (e.g., spotted hyenas [*Crocuta crocuta*]; Mills 1990), and therefore differences in apex predator assemblages and densities may drive brown hyena selection patterns. Thus, in small reserves, brown hyenas may rely on the kills of large carnivores, suggesting that the presence of other large carnivores may be an important consideration when choosing future reintroduction sites. Roads are important in their use of space, possibly in providing foraging routes and as possible sites for intra- and inter-clan communications. Additionally, they may facilitate interactions with other large predators that provide scavenging opportunities for brown hyenas. If their relationship with roads is similar outside of protected areas, it could represent a considerable threat to the species from road-related mortality and warrants further investigation.

Acknowledgments

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Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Top candidate models predicting the probability of brown hyena presence in their home ranges (includes all models with a cumulative weight < 0.9) in Mountain Zebra National Park; numbers indicate covariates (1—boundary, 2—distance to drainage, 3—elevation, 4—distance to roads, 5—slope, and 6—vegetation).

Supporting Information S2.—Top candidate models predicting the probability of brown hyena presence in their home ranges (includes all models with a cumulative weight < 0.9) in Kwandwe Private Game Reserve; numbers indicate covariates (1—boundary, 2—distance to drainage, 3—elevation, 4—distance to roads, 5—slope, and 6—vegetation).

Supporting Information S3.—Top candidate models predicting the probability of brown hyena presence in their home ranges (includes all models with a cumulative weight < 0.9) in Shamwari Private Game Reserve; numbers indicate covariates (1—boundary, 2—distance to drainage, 3—elevation, 4—distance to roads, 5—slope, and 6—vegetation).

Supporting Information S4.—R code used to model the probability of brown hyena occurrence in the 3 study areas and plot the average marginal probability of brown hyena presence in relation to each covariate in each reserve.

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