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Abstract: Effective management within the human-dominated matrix, outside of formally protected areas, is of paramount importance to wide-ranging carnivores. For instance, the largest extant population of cheetahs *Acinonyx jubatus* currently persists on privately owned Namibian ranchlands, and provides an excellent case study to examine and design matrix conservation approaches. Although human caused mortality is likely the principal threat to this population, anecdotal evidence suggests that 'bush encroachment', the widespread conversion of mixed woodland and savannah habitats to dense, Acacia-dominated thickets, is another probable threat. A better understanding of cheetah habitat use, outside of protected areas, could be used to directly influence habitat management strategies and design local restoration and conflict mitigation efforts. To identify specific habitat characteristics associated with cheetah use, radio-telemetry locations were used to identify areas intensively visited by cheetahs on commercial Namibian farms. The habitat characteristics of these 'high-use' areas with adjacent 'low-use' areas were compared. A binary logistic regression model correctly categorized 92% of plot locations as high or low use, and suggested that cheetahs may be utilizing 'rewarding patches' with better sighting visibility and greater grass cover. The possible reasons for kudu Tragelaphus strepsiceros, Namibian cheetahs' preferred prey, exhibiting significantly lower abundance in high-use areas are discussed. Using habitat characteristics to identify areas intensively utilized by cheetahs has important implications for guiding future habitat restoration and developing effective predator conflict mitigation efforts.

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Managing the matrix for large carnivores: a novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling

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Abstract

Effective management within the human-dominated matrix, outside of formally protected areas, is of paramount importance to wide-ranging carnviores. For instance, the largest extant population of cheetahs *Acinonyx jubatus* currently persists on privately owned Namibian ranchlands, and provides an excellent case study to examine and design matrix conservation approaches. Although human-caused mortality is likely the principal threat to this population, ancedotal evidence suggests that 'bush encroachment', the widespread conversion of mixed woodland and savannah habitats to dense, *Acacia*-dominated thickets, is another probable threat. A better understanding of cheetah habitat use, outside of protected areas, could be used to directly influence habitat management strategies and design local restoration and conflict mitigation efforts. To identify specific habitat characteristics associated with cheetah use, we used radio-telemetry locations to identify areas used intensively by cheetahs on commercial Namibian farms. We then compared the habitat characteristics of these 'high-use' areas with adjacent 'low-use' areas. A binary logistic regression model correctly categorized 92% of plot locations as high or low use, and suggested that cheetahs may be utilizing 'rewarding patches' with better sighting visibility and greater grass cover. We discuss the possible reasons for kudu *Tragelaphus strepsiceros*, Namibian cheetahs' preferred prey, exhibiting significantly lower abundance in high-use areas. Using habitat characteristics to identify areas intensively utilized by cheetahs has important implications for guiding future habitat restoration and developing effective predator conflict mitigation efforts.

Introduction

While protected areas play an important role in large carnivore conservation, many carnivore species of concern are wide-ranging, and the existing reserve network is insufficient for their long-term conservation (Woodroffe & Ginsberg, 1998; Linnell, Swenson & Anderson, 2001; Woodroffe, 2001; Marker & Dickman, 2004). Designing effective conservation strategies in the human-dominated matrix, outside of formally protected areas, is critical for developing the most appropriate and effective conservation strategies.

Over the past century, the cheetah *Acinonyx jubatus* has experienced dramatic declines in population size and distribution. The largest surviving population is in Namibia, where an estimated 2500–3000 adult cheetahs persist (Morsbach, 1987). Nearly 90% of Namibia's cheetahs reside outside protected areas in *c.* 275 000 km^2 of privately owned commercial farmland in the north-central region (Marker-Kraus *et al.*, 1996). This unprotected rangeland matrix provides an excellent case study to examine interactions between cheetah habitat use, habitat degradation and other human impacts. Direct threats to cheetah populations, associated with human-caused mortality, have been well-documented (Marker-Kraus *et al.*, 1996; Marker & Schumann, 1998; Marker *et al.*, 2003*a*). Anecdotal evidence suggests that cheetahs may be influenced by habitat degradation associated with commercial cattle production. Ranchlands in north-central Namibia have undergone widespread 'bush encroachment', the conversion of grassland and woodland savannahs to dense, *Acacia*-dominated thornveld with minimal grass cover (Marker-Kraus *et al.*, 1996; de Klerk, 2004). Driven by factors including livestock overgrazing, altered fire regime and mega-herbivore removal (Barnard, 1998), this process has affected *c.* 12 million hectares (14%) of Namibian land within the last 50 years (Bester, 1996). Approximately half of bush-encroached lands fall within the north-central commercial farmlands (Bester,

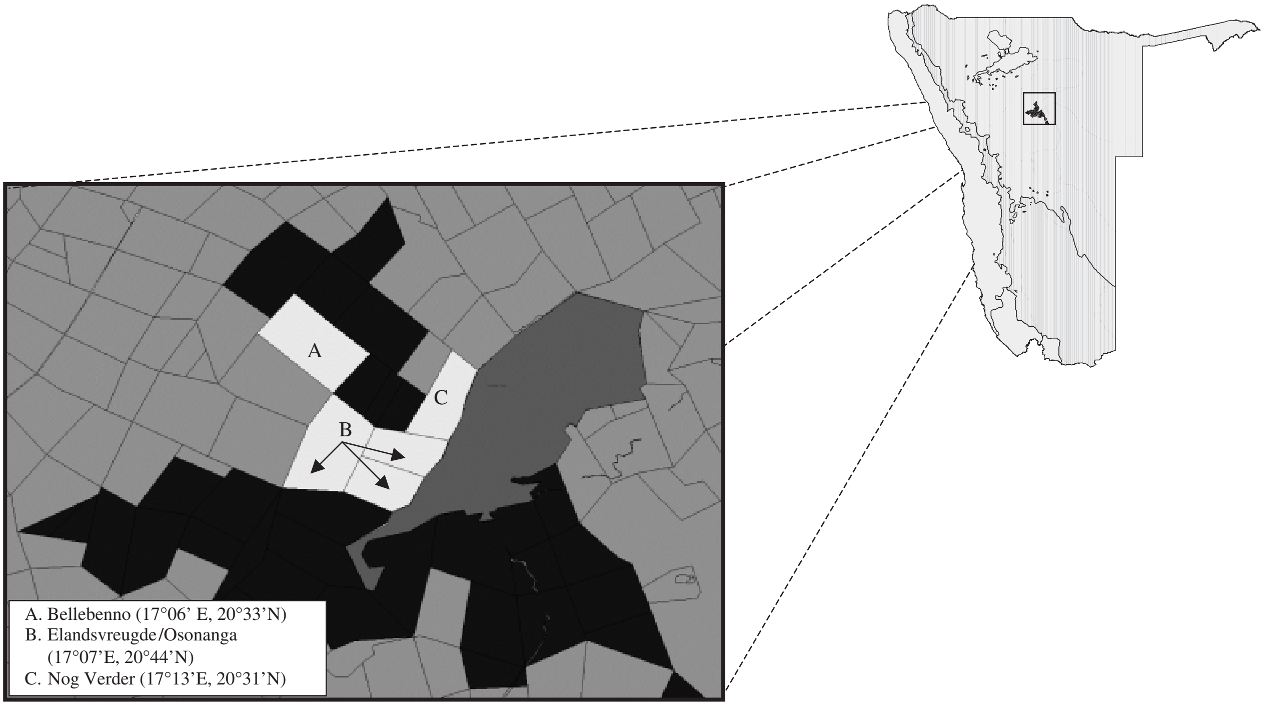

Figure 1 Location of the study site in north-central Namibia. Light grey areas indicate commercial farms, the dark grey area denotes the Waterberg Plateau Park (a protected area), the black area represents Waterberg Conservancy land, while the three study farms (Bellebenno, Elandsvreugde/Osonanga and Nog Verder) used to develop the habitat model are shown in white.

1996), reducing regional land productivity (Quan, Barton & Conroy, 1994; de Klerk, 2004). The impact of bush encroachment on cheetahs is poorly understood, but it is widely hypothesized to reduce hunting efficiency and prey abundance, alter prey distribution and decrease farmers' tolerance for predators by lowering stocking capacity of degraded land (Marker-Kraus *et al.*, 1996). However, despite the plausible detriments of bush encroachment to wildlife, there have been few attempts to document how Namibian wildlife species persist in the heavily altered thornveld landscape, particularly with respect to habitat use, density and distribution (N. D. Muroua, L. Marker, M. Nghikembua & R. M. Jeo, unpubl. data) and associated restoration implications. Moreover, this study provides a specific example of how spatial ecology can be used to design matrix conservation approaches. A better understanding of cheetah habitat can be used to design habitat management and restoration strategies and inform outreach efforts to local ranchers.

We used an 8-year radio-telemetry data set (Marker, 2002) that showed that cheetahs on Namibian ranchlands have exceptionally large home ranges, averaging 1651 km^2 and spanning several farms, with intensive utilization of small 'core' areas. We examined microplot-level habitat characteristics on three large, privately owned, ranches where we had radio-telemetry data and access permission. We sought to characterize cheetah high-use areas by using measured habitat metrics to develop a habitat selection model. This model provides information on cheetah habitat selection at a finer scale than described previously, supplying valuable data that can be incorporated into future land-use planning and restoration efforts for cheetah conservation. In addition, such basic habitat analyses could be used elsewhere to identify those areas most likely to be utilized by cheetahs as such areas represent places where conflict is most likely to occur, and pre-emptive conflict resolution strategies can be applied with the ultimate aim of reducing levels of both stock predation and cheetah removals (Angst, 2001; Stahl & Vandel, 2001; Stahl *et al.*, 2002; Treves *et al.*, 2004).

Materials and methods

Study area

Land-use management decisions in Namibia are often made by individual landowners at the scale of one or a few ranches. Thus, for effective habitat restoration, it is imperative to match the scale of analysis to the desired scale of restoration application (Morrison, Marcot & Mannan, 1998; Morrison, 2002). In addition, conflicts with farmers due to predation are normally localized events requiring individual farm consideration (Treves *et al.*, 2004; Wydeven *et al.*, 2004). Thus, the study area consisted of three ranches within the Waterberg Conservancy: Nog Verder (A), Elandsvreugde/Osonanga (B) and Bellebenno (C) (Fig. 1). We selected these ranches for several reasons: (1) because there was an overlap with the radio-telemetry data, (2) we had access permission and (3) they represented a range of

Table 1 Descriptive statistics of cheetah telemetry data used to calculate the 30% fixed probability kernels broken down by farm

		Number of locations			
Cheetah identity	Sex	BB	EO	NV	Years tracked
174	M	21	11	0	1995
559	M	2	3	0	1998
540	M	42	31	34	1997–1999
730	M	5	0	3	1996
152	F	0	13	0	2000
233	F	0	16	0	1996–2000
802	F	0	7	0	1998
Totals		70	81	37	1995–2000

BB, Bellebenno; EO, Elandsvreugde/Osonanga; NV, Nog Verder.

common management practices. Nog Verder (4465 ha) has been managed exclusively for cattle farming, Bellebenno (7300 ha) has been managed for both livestock and game farming and the Elandsvreugde/Osonanga complex (14 800 ha) is managed for game and small stock (goats).

The area falls within the 400–500 mm rainfall isopleth, with the majority of rain falling between November and April (Barnard, 1998), the topography is generally flat and elevation is *c*. 1500 m. Although no permanent rivers exist in the study area, each farm has several artificial waterholes, allowing livestock and game access to water year-round. The region falls within the thornveld biome (Barnard, 1998) dominated by *Acacia* and *Dichrostachys* bush species.

Geographic information system (GIS) micro-plot selection

The Cheetah Conservation Fund located radio-tracked cheetahs between 1995 and 2001, utilizing aerial tracking to minimize error (White & Garrott, 1986) and collecting data before 09:00 h to capture the highest activity period (Caro, 1994; Marker, 2002). An attempt was made to locate each individual on each weekly flight throughout collar lifetime (~2 years). Data were restricted to females and coalition males, because these groups are most likely to utilize optimal habitat and hold territories (Caro, 1994; Marker, 2002), thus providing the most relevant information for setting restoration goals (Morrison, 2002) and implicated in potential conflict with farmers (Knowlton, Gese & Jaeger, 1999; Landa *et al*., 1999; Sacks, Blejwas & Jaeger, 1999; Wydeven *et al*., 2004), respectively. Single males were not considered since they tend to occupy marginal habitat in the farmlands (Marker, 2002), and strong evidence for 'problem animals' being linked to juveniles or dispersing/transient individuals is, to date, inconclusive (Linnell *et al*., 1999; Stahl & Vandel, 2001). Furthermore, Marker *et al*. (2003*a*) found no evidence that cheetah age and/or sex structure were disproportionately represented in any confirmed conflict events on Namibian farmlands.

ArcView GIS (version 3.2, ESRI, Redlands, CA, USA) and the Animal Movement extension (Hooge, Eichenlaub & Soloman, 1999) were used to calculate a 30% fixed probability kernel within each study farm. Multiple coalition male and female cheetah telemetry data within farm boundaries were pooled and used to calculate each farm's high-use kernel. Elandsvreudge-Osonanga contained 81 pooled locations from four male coalitions (two represent 52%) and three female cheetahs (two represent 35%), Bellebenno contained 70 locations from four male cheetah coalitions (two represent 97%) and Nog Verder contained 37 locations from two male cheetah coalitions (one represents 92%) (Table 1). This study aims to investigate aggregated cheetah habitat use within a small subset of multiple cheetahs' home ranges. Therefore, conventional 'core area' calculation techniques were not necessarily applicable or practical, and a smoothing parameter was chosen somewhat arbitrarily, yet based upon noted studies suggesting narrow kernel bandwidths highlight finer-scale detail (Seaman & Powell, 1996; Powell, 2000). Use of a 30% fixed kernel was thus preferred. Between 20 and 25 circular plots with a 12 m diameter (113 m^2) were randomly selected within both high- and low-use areas on each farm, and the habitat characteristics of these plots were investigated.

Habitat characteristics

Information on habitat characteristics was collected during September–December 2002 and February–March 2003. We quantified six key habitat characteristics affected by bush encroachment that may additionally influence cheetah habitat preference within the thornveld, based upon the selection criteria identified by Whitmore (1981) and documented cheetah behavioural ecology (Caro, 1994; Marker, 2002). Habitat characteristics measured in each plot were: (1) shrub density (stems m^{-2}), (2) shrub species richness, (3) average shrub height, (4) percentage grass cover, (5) relative prey abundance estimated from prey scat frequency or number of individual scat piles and (6) sighting visibility. We estimated sighting visibility by positioning an observer at the centre of the plot with an eye level 65 cm above ground, simulating a cheetah's eye height (Marker & Dickman, 2003). A second person then walked away from the observer at a random compass bearing until the observer could no longer view them, and the sighting distance was measured using a rangefinder to the nearest metre. This was repeated three more times adding 90° to each previous bearing, and the mean visibility was calculated for each plot. Adequate sample sizes (at least 20) were estimated during the first phase of fieldwork by a running mean analysis (Rabinowitz, 1997) on each metric measured.

Statistics and model selection

Kolmogorov–Smirnov tests revealed that all data were non-normally distributed, warranting the use of non-parametric tests. For univariate analyses, high- and low-use habitat metrics were compared both within as well as pooled across all farms using the Mann–Whitney *U*-test (Fowler, Cohen & Jarvis, 1998). Correlations between habitat metrics were investigated using the Spearman rank correlation coefficient (r_s). Data were considered significant at $P<0.05$ and all tests are two-tailed unless otherwise stated. All data were entered and analysed using SPSS version 10.0 software (SPSS Inc., Chicago, IL, USA).

Collinearity was investigated to prevent including extraneous variables in the final model (Pearce & Ferrier, 2000). Binary logistic regression models (Brennan, Block & Gutierrez, 1986; Morrison *et al*., 1998; Soh *et al*., 2002; Hashimoto, Natuhara & Morimoto, 2005) were used to assess the factors associated with areas used intensively by cheetahs. Independent habitat variables for model minimization went through a forward selection process (Norušis, 2000). The first stage required building individual models with each individual variable (six models) and the constant. The model with the lowest −2 log likelihood statistic gives the highest predictive power (Kleinbaum & Klein, 2002), and was used as the root model. The process was then repeated, adding each variable not already in the model and comparing the differences in respective −2 log likelihood statistics. The most influential variable at each step was then considered for inclusion in the root model. If the addition of a variable significantly decreased the −2 log likelihood value (χ^2 test) of the root model, it was retained (Table 5). No more variables were added once there was no significant improvement in model fit.

The predictive accuracy of the final model was field calibrated by measuring habitat structure at 50 evenly spaced sites *c*. 1 km apart at Bellebenno Farm in October 2003. Model predictions of high- and low-use areas were compared with observed 30% probability kernels from radio-telemetry data. For increased rigour, a more stringent cut-off decision rule of greater than 0.75 was chosen, where a site would require a 75% or greater high use classification probability output from the model to be categorized as high use. Sensitivity analyses were then performed, and regression slopes for each significant variable were compared using a *t*-test. Minimum habitat threshold levels were explored under different management scenarios likely to be encountered on commercial farmlands, enabling recommendations to be made regarding possible habitat restoration protocols.

Results

Univariate habitat metric analysis

Sighting visibility was significantly greater in high-use areas on Bellebenno ($z=-3.315$, d.f. = 49, $P=0.002$) and Elandsvreudge/Osonanga ($z=-3.336$, d.f. = 73, $P=0.001$) while grass cover was significantly greater in high-use areas on Elandsvreudge/Osonanga ($z=-2.086$, d.f. = 73, $P=0.037$) and Nog Verder ($z=-2.599$, d.f. = 45, $P=0.009$). Shrub height was significantly shorter in high-use areas on Elandsvreudge/Osonanga ($z=-2.828$, d.f. = 73, $P=0.005$). When data were pooled, high-use areas were characterized by significantly greater visibility ($z=-4.333$, d.f. = 169, $P<0.001$), more grass cover ($z=-3.860$, d.f. = 169, $P<0.001$), more abundant prey ($z=-2.235$, d.f. = 169, $P=0.025$) and shorter shrub vegetation ($z=-2.196$, d.f. = 169, $P=0.028$) (Table 2).

Analysis of relative prey abundance revealed that kudu *Tragelaphus strepsiceros* were significantly less abundant in high-use areas on two of the farms, Elandsvreugde/Osonanga ($z=-3.228$, d.f. = 73, $P=0.001$) and Nog Verder ($z=-2.476$, d.f. = 45, $P=0.013$), and overall ($z=-4.002$, d.f. = 169, $P<0.001$) whereas oryx *Oryx gazella* and warthog *Phacochoerus aethiopicus* were significantly more abundant in high-use areas ($z=-3.455$, d.f. = 169, $P=0.001$; $z=-3.188$, d.f. = 169, $P=0.001$, respectively) (Table 3).

Shrub density and shrub height were both negatively correlated with sighting visibility ($r_s=-0.406$, d.f. = 169, $P<0.01$; $r_s=-0.267$, d.f. = 169, $P<0.01$, respectively), while relative prey abundance was positively correlated ($r_s=0.375$, d.f. = 169, $P<0.01$). Shrub height and relative prey abundance were both negatively correlated with grass cover ($r_s=-2.82$, d.f. = 169, $P<0.01$; $r_s=-0.278$, d.f. = 169, $P<0.01$, respectively). Shrub height was negatively correlated with shrub density ($r_s=-0.231$, d.f. = 169, $P<0.01$) (Table 4).

Multivariate model

Sighting visibility was best correlated with high-use areas, with grass cover also adding significantly to model fit (Table 5). The relative prey abundance was the next greatest contributor, but did not significantly improve the model fit ($P=0.16$) (Table 5), giving a final binary logistic regression model:

$$\text{Logit} = -2.835 + 0.034\,(\text{Sighting Visibility}) + 0.04\,(\text{Grass Cover})$$

Model calibration against radio-telemetry data at one site showed that overall, the model accurately classified 92% (46 of 50) of sites correctly: two of three high-use sites and 44 of 47 low-use sites (Fig. 2). However, when looking only at high-use predictive accuracy, the model classified five sites as high use, of which only two were correct (40%) (Fig. 2). Sensitivity analyses demonstrated that the likelihood of an area being classified as a high-use site was influenced slightly more by sighting visibility than by the percentage of grass cover ($t_1=6.306$, $P=0.10$).

Inputting various management scenarios into the model revealed that under low grass cover conditions, sighting visibility would have to be restored to greater than 95 m in order to achieve the threshold probability level (75%) of the

Table 2 Descriptive statistics of habitat characteristics measured in high- and low-use areas, for potential inclusion in the habitat model

	Farm			
	A	B	C	Overall
Shrub density				
High use	19.52 ± 10.79	34.92 ± 26.67	39.64 ± 20.03	31.89 ± 22.59
Low use	24.16 ± 12.44	33.14 ± 21.19	46.19 ± 27.1	33.74 ± 22.13
P	0.24	0.833	0.193	0.506
Species richness				
High use	4.72 ± 1.28	4.34 ± 2.29	4.08 ± 1.63	4.38 ± 1.87
Low use	4.84 ± 1.34	5.06 ± 1.22	4.1 ± 1.84	4.74 ± 1.47
P	0.69	0.089	0.669	0.191
Shrub height				
High use	1.45 ± 0.23	1.33 ± 0.37	1.28 ± 0.51	1.35 ± 0.39
Low use	1.61 ± 0.35	1.56 ± 0.27	1.2 ± 0.75	1.48 ± 0.49
P	0.112	0.005	0.494	0.028
Grass cover				
High use	37.8 ± 15.42	33.55 ± 21.02	51.6 ± 28.09	39.89 ± 23.01
Low use	29.4 ± 17.52	23.33 ± 16.82	30.71 ± 23.47	27.07 ± 18.99
P	0.078	0.037	0.009	0.000
Relative prey abundance				
High use	6.84 ± 2.69	10.11 ± 7.21	7.04 ± 2.85	8.31 ± 5.37
Low use	6.36 ± 3.39	7.06 ± 3.6	5.81 ± 2.8	6.52 ± 3.35
P	0.401	0.138	0.125	0.025
Sighting visibility				
High use	57.96 ± 13.46	75.01 ± 73.14	49.05 ± 39.91	62.79 ± 53.76
Low use	45.11 ± 15.39	34.21 ± 14.66	30.72 ± 14.02	36.64 ± 15.66
P	0.002	0.001	0.123	0.000

The mean values for each characteristic were compared between high- and low-use areas, both for each farm and across data pooled from all three farms, using the Mann–Whitney *U*-test for individual farms and the Kruskal–Wallis χ^2 approximation for pooled data. Farm A is Bellebenno (n=50), Farm B is Elandsvreugde/Osonanga (n=74) and Farm C is Nog Verder (n=46). ± represents the standard deviation.

site being classified as a high-use area; medium grass cover requires a visibility of >65 m and high grass cover requires 33 m (Fig. 3). Under a hypothetical scenario with low sighting visibility (set at 20 m), restoration of 88% grass cover would be required to reach the threshold level; medium sighting visibility (50 m) requires 51% cover, and high sighting visibility (80 m) only 15% (Fig. 4).

Discussion

Rewarding habitat patches

The unprotected commercial farmlands in north-central Namibia are one of the last remaining strongholds for free-ranging cheetahs (Marker-Kraus *et al*., 1996). As this crucial population is severely threatened by habitat degradation and conflict with farmers (Marker-Kraus *et al*., 1996), identifying factors important for habitat restoration and conflict resolution on a farm-level scale will be vital for guiding future conservation strategies. Of the habitat characteristics measured, sighting visibility and grass cover most accurately characterized cheetah high-use areas at the micro-habitat level within the bush-encroached farmlands. Interestingly, despite the probable ecological impacts of bush encroachment, bush density was not statistically significant on a plot-level scale and did not contribute significantly to the model. This supports the results of the macro-habitat study conducted in the area, which revealed that cheetahs did not preferentially select for sparsely bushed areas (Marker, 2002). Indeed, there is evidence that bush encroachment aids cheetah populations as it provides refugia and is positively associated with browsers such as greater kudu (de Klerk, 2004). Nevertheless, these results should not be taken to indicate that increasing bush density on the farmlands is having no effect on cheetah populations, but perhaps the effects are more indirect. Increased bush density and decreased grass cover could have important anthropogenic effects not measured here, such as reduced tolerance of farmers for predators on degraded farmland.

The fact that sighting visibility was the best predictor of high-use habitat suggests that cheetahs may be seeking out ‘rewarding patches’ within the farmland matrix to increase their hunting efficiency in two ways: (1) these areas are easier to move through and require less energy expenditure and (2) increased sighting distance increases the chance of sighting prey species per distance travelled. Observations of hunting behaviour in the Serengeti indicate that they frequently use the edges of more dense habitat patches to provide cover for stalking, and that they appear to configure their ranges to incorporate a mix of habitat types (Frame & Frame, 1980; Caro, 1994). Because cheetahs are diurnal predators that rely heavily on eyesight to locate prey, patches of better

Table 3 Frequency of prey scat piles found in sampled micro-plots, both within high- and low-use cheetah areas

	Farm			
	A	B	C	Overall
Kudu				
High use	1.1 ± 0.97	0.85 ± 0.8	0.8 ± 2.08	0.83 ± 1.35
Low use	1.65 ± 1.5	1.29 ± 1.2	1.62 ± 1.43	1.72 ± 1.48
P	0.31	0.001	0.003	0.000
Oryx				
High use	1.05 ± 0.94	1.69 ± 1.8	3.76 ± 2.45	2.8 ± 2.92
Low use	1.2 ± 1.2	1.71 ± 1.44	1.52 ± 1.36	1.36 ± 1.25
P	0.777	0.013	0.001	0.001
Warthog				
High use	0.8 ± 1.06	0.23 ± 0.6	0.56 ± 0.87	0.8 ± 1.23
Low use	0.65 ± 1.6	0.36 ± 0.84	0.29 ± 0.78	0.35 ± 0.99
P	0.28	0.004	0.129	0.001
Eland				
High use	1.15 ± 1.46	0.54 ± 1.2	0.32 ± 0.56	0.8 ± 1.43
Low use	0.75 ± 0.97	0 ± 0	1.05 ± 1.2	0.58 ± 0.96
P	0.485	0.041	0.012	0.702
Hartebeest				
High use	0.15 ± 0.49	0.85 ± 0.99	0.56 ± 0.87	1.31 ± 2.36
Low use	0.15 ± 0.67	0.43 ± 0.65	0.86 ± 0.91	0.64 ± 0.94
P	0.594	0.004	0.159	0.163
Steenbok				
High use	0.85 ± 0.99	0.15 ± 0.38	0.16 ± 0.47	0.55 ± 1.02
Low use	0.35 ± 0.67	0.36 ± 0.63	0.19 ± 0.51	0.56 ± 1.2
P	0.06	0.522	0.821	0.737
Duiker				
High use	0.1 ± 0.31	0 ± 0	0 ± 0	0.22 ± 0.63
Low use	0.1 ± 0.31	0.14 ± 0.53	0 ± 0	0.15 ± 0.56
P	–	0.286	–	0.411
Hare				
High use	1 ± 1.34	0.23 ± 0.6	0.4 ± 0.76	0.84 ± 1.81
Low use	0.7 ± 1.08	0.14 ± 0.36	0.29 ± 0.72	0.62 ± 1.12
P	0.492	0.317	0.486	0.908
Livestock				
High use	0.35 ± 0.59	0 ± 0	0.2 ± 0.82	0.14 ± 0.54
Low use	0.7 ± 1.13	0 ± 0	0.14 ± 0.48	0.38 ± 0.94
P	0.513	–	0.875	0.069

The mean frequencies were compared between high- and low-use areas on each farm, and the two areas were also compared across data pooled from all three farms, using the Mann–Whitney *U*-test for individual farms and the Kruskal–Wallis χ^2 approximation for pooled data. Farm A is Bellebenno ($n=40$), Farm B is Elandsvreugde/Osonanga ($n=75$) and Farm C is Nog Verder ($n=46$). ± represents standard deviation.

Table 4 Spearman rank correlation (r_s) matrix for habitat metrics ($n=170$)

	Species richness	Shrub height	Grass cover	Sighting visibility	Relative prey abundance
Shrub density	0.073	−0.231**	0.098	−0.406**	−0.129
Species richness	–	0.046	−0.176*	−0.104	0.092
Shrub height	–	–	−0.282**	−0.267**	−0.033
Grass cover	–	–	–	−0.014	−0.278**
Sighting visibility	–	–	–	–	0.375**

$P<0.05$ and $P<0.01$ levels (two-tailed) are denoted by * and **, respectively.

visibility would enable them to scan further for potential prey, which would be particularly valuable in the thornbush habitat, where visibility is often limiting. Therefore, hunting behaviour would be enhanced by having access to areas with longer lines of sight within the bush matrix.

Cheetahs also appeared to prefer areas of higher grass cover. Although grass cover and bush density were not correlated on a micro-habitat scale, it is probable that higher grass cover is more conducive to cheetah hunting techniques, providing them with better stalking grounds to get

Table 5 Forward model selection procedure summary for Namibian cheetah micro-habitat variables

Model	Sighting visibility (SV)	Grass cover (GC)	Relative prey abundance (RPA)	Shrub height (SH)	Shrub density (SD)	Shrub species richness (SSR)
Constant +	209.9[a]*	220.3*	228.4*	228.9	235.2	233.4
Constant + SV +		191.6[b]*	208.7	209.3	207.6	209.8
Constant + SV + GC +			186.4[c]	191.3	190.4	191.5

Cells display the −2 log likelihood statistic for the current model following their individual addition in the root model.

*Denotes statistical significance (change in −2 log likelihood deviance or χ^2). A significance level of $\alpha < 0.10$ was used in the criterion for variable inclusion.

[a]The lowest initial −2 log likelihood statistic developed in the root model.

[b]Grass cover was the second term added to the root model due to its significant deviance.

[c]Although the relative prey abundance produced the next greatest deviance, it was not significant ($P = 0.16$) and was not added to the current model. This also terminated the selection process as all other unselected terms were already less important than the relative prey abundance.

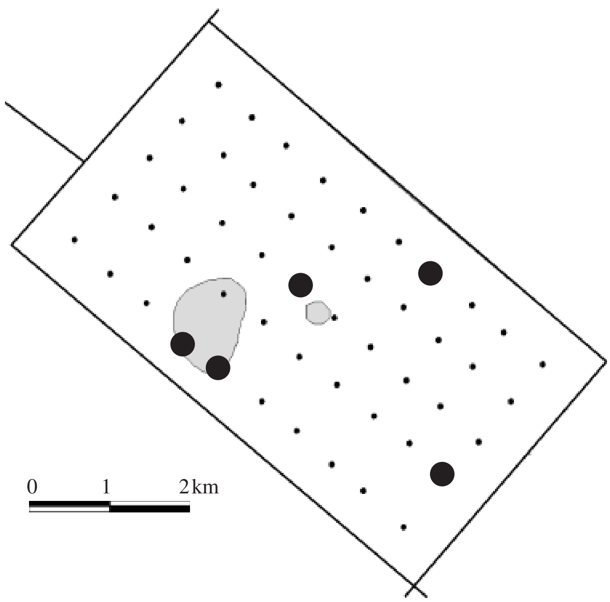

Figure 2 Model ground-truthing exercise, showing 50 sample grid sites on Bellebenno farm. Small circles represent sites predicted to be low-use areas, and large black circles represent high-use areas. The shaded region represents the 30% high use probability kernel calculated from the radio-telemetry data.

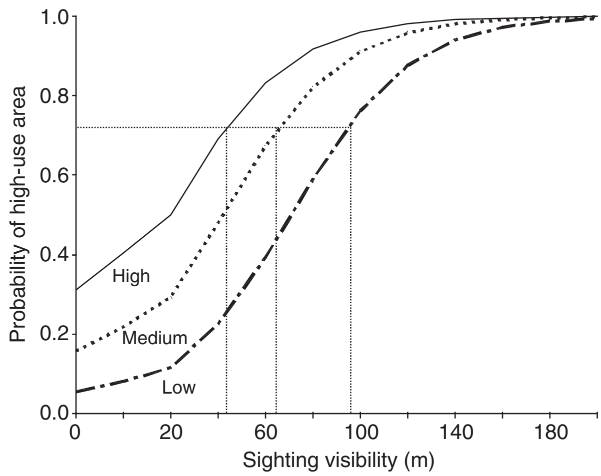

Figure 3 Effect of increasing sighting visibility distance on the probability of a site being a cheetah *Acinonyx jubatus* high-use area, at high (50%), medium (34%) and low (10%) grass cover levels. The horizontal line represents the threshold likelihood value of a site being classed as a high-use area (set at 0.75), while the drop-down lines indicate the sighting visibility distance that would have to be attained in order to reach the threshold level in each scenario.

closer to their prey, especially valuable in the thornveld where chase distances and velocity are likely to be limited by the surrounding bush. Areas supporting higher grass cover may also serve as refugia for hidden fawns or juvenile ungulate prey. While adult male coalitions can easily prey upon adult ungulates, Namibian cheetahs often prefer fawns and/or juvenile prey on commercial farmlands where springbok *Antidorcas marsupialis* have been eliminated (Marker-Kraus *et al.*, 1996).

Although cheetahs are opportunistic hunters, they appear to prefer kudu in the study area (Marker-Kraus *et al.*, 1996; Marker *et al.*, 2003*b*). Interestingly, separating out individual prey species with the relative prey abundance data set revealed that kudu were significantly more abundant in low-use areas. This suggests that habitat structure may be more important than absolute prey density. In the Serengeti, cheetahs seek out 'competition refugia' with lower prey densities to avoid interspecific competition with lions *Panthera leo* and hyenas *Crocuta crocuta* (Durant, 1998). Another wide-ranging carnivore, the African wild dog *Lycaon pictus*, also appears to avoid prey-rich areas because they are positively correlated with lions, a major cause of wild dog mortality in Kruger National Park, South Africa (Mills & Gorman, 1997). Such competitor avoidance behaviour is unlikely in central Namibia, where both lions and hyenas have been extirpated from the commercial farmlands (Marker-Kraus *et al.*, 1996). It is more plausible that the Namibian cheetahs prefer areas supporting lower densities of preferred prey due to a combination of better sighting visibility and greater grass cover increasing hunting efficiency. Furthermore, there may be an important anthropogenic component affecting cheetah spatial utilization on the farmlands, with high conflict with farmers in prey-rich areas

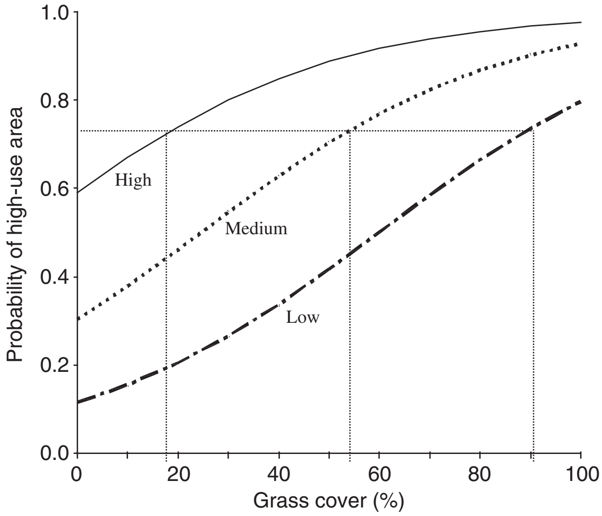

Figure 4 Effect of increasing the percentage of grass cover on the probability of a site being a cheetah *Acinonyx jubatus* high-use area, at high (80 m), medium (50 m) and low (20 m) sighting visibility levels. The horizontal line represents the 0.75 threshold likelihood value of a site being classed as a high-use area, while the drop-down lines indicate the percentage grass cover that would have to be attained in order to reach the threshold level in each scenario.

(Marker, 2002), but this was not quantified during the present study.

Although our findings could be used on a local scale to help guide predator management strategies, a relatively small telemetry data set ($n = 188$), number of individual/coalitions ($n = 7$) and farm replication ($n = 3$) warrant caution in interpreting or extrapolating on a regional scale at this point. In addition, due to small telemetry sample sizes, we could not separate out locations to test for seasonal or individual variation on a micro-habitat scale. However, Marker (2002) reported no significant seasonal variation in cheetah macro-habitat use. Pooling of telemetry data, to increase sample size, carries a few potentially spurious assumptions such as unequal representation of a few individuals or pseudo-replication (Hurlbert, 1984). Yet, the size of individual home ranges complicating logistics and farm access over such large areas, the small sample size of individual telemetry locations and the practicality of conducting the research on the most relevant management unit (farm) justify a farm-scale analysis. The temporal gap between the initial telemetry locations (1995) and the habitat measurements (2002–2003) is also cause for concern. However, our field observations over the duration of the telemetry study indicate that the macro-habitat structure within the study farms has remained relatively static. Despite these potential setbacks, we find merit in utilizing this data set principally because it is the largest available spatial data for cheetah in Namibia. Rather than waiting for large data sets on vulnerable, elusive species to transpire, we feel it is more important to draw conclusions with the available data that can provide some science-based foundations for guiding conflict resolution and management efforts. It is vital to start implementing effective management and habitat restoration as soon as possible in critical regions such as central Namibia. Revisiting this analysis with supplemental telemetry and even possibly fitness-related demographic data is certainly an area worthy of future investigation to enhance the overall habitat suitability assessment while promoting adaptive management.

Conservation implications

Incorporating statistically rigorous and systematic habitat-use analysis findings a priori to focal species restoration protocols is fundamentally important. These findings provide critical information regarding cheetah habitat selection on the scale most relevant to habitat restoration of north-central Namibian farmlands. Identifying these habitat metrics and the ability to project different management scenarios using a systematically constructed model is an indispensable conservation tool for restoring degraded habitat. The next step will be to investigate whether restored high-use habitat patches could be spatially configured to encompass a potentially viable cheetah population within those fragmented habitat patches available for conservation efforts. Because landowners volunteering for cheetah restoration will probably be few and far between, it will be crucial to understand minimal spatial requirements for setting restoration goals. Insights from this study could also provide a direction in developing a landscape or conservancy-scale GIS-based habitat suitability model to predict current cheetah high-use areas and prioritize areas for restoration. Given the fact that across much of the cheetah's range, its remaining populations are limited to small, fragmented patches of habitat, further developing and refining this model and its practical applications will be critical for cheetah conservation worldwide.

Our sampling design scale and the resulting predictive model also has the potential to be utilized efficiently to mitigate farmer–cheetah conflict. This model provides practical scope by proactively assisting farmers in avoiding potential conflict with cheetahs on their lands by identifying potentially high-risk areas through rapid field sampling within their borders. By identifying these areas, shepherds could be alerted to take additional caution and vigilance when grazing livestock in these areas, and placing exotic game camps or calving kraals within those areas should also be avoided, as they are particularly vulnerable to cheetah predation (Marker-Kraus *et al.*, 1996; Marker & Schumann, 1998). Due to the ambiguity of the relationship between cheetah age and sex structure and confirmed conflicts by farmers (Marker *et al.* 2003), it would also be worth revisiting this issue when more data become available.

For successful, long-term conservation, however, particularly for large carnivores, strategies must be developed that not only reduce conflict, but actually provide landowners with a financial incentive for maintaining wildlife on their land (Sillero-Zubiri & Laurenson, 2001; Nyhus *et al.*, 2005). Ecotourism is one such method and is becoming increasingly popular, both in southern Africa and elsewhere

(Lambretchs, 1995; Ohrling, 2000; Michler, 2002). This habitat model could also have valuable applications in this setting, as many species sought after by tourists, such as cheetahs, are elusive and rarely seen by chance (Sillero-Zubiri & Laurenson, 2001). Applying this model on farms catering to ecotourists would be a simple and valuable method for identifying areas where cheetah sightings could be most likely or directing some restoration to encourage cheetahs to visit specific areas accessible to tourists.

In today's human-dominated landscapes, relying on the preservation of large, contiguous tracts of pristine habitat within which to conserve large, wide-ranging carnivores is increasingly unrealistic (Woodroffe, 2000, 2001). Instead, widespread habitat degradation and fragmentation mean that conservation must increasingly be performed within relatively small, isolated habitat 'islands' (Wilcove, McLellan & Dobson, 1986; Newmark, 1996) amidst human-dominated matrix landscapes, which often do not represent the optimal ecological conditions for the species being managed. Further replicating these studies and developing their practical applications in terms of habitat restoration and conflict resolution could have critically important implications, not only for cheetah conservation but also through the application of this methodology to other species whose future survival relies upon conservation across broad tracts of human-dominated land.

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