Ecological and anthropogenic influences on space use by spotted hyaenas

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Abstract

Due to increasing human encroachment into the remaining habitat of many large carnivore species, there is an immediate need to understand the ecological and anthropogenic factors influencing carnivore space use decisions. In particular, knowledge of changes in space use in response to disturbance, and the costs associated with these changes, will be critical in guiding conservation efforts. To investigate the ecological factors influencing carnivore space use, we intensively radiotracked members of two large social groups (clans) of spotted hyaenas *Crocuta crocuta* in the Masai Mara National Reserve, Kenya. In addition, we studied the influence of livestock grazing by comparing space use between two study clans that differed dramatically in exposure to grazing. Logistic regression modeling indicated that space use in the absence of livestock was most influenced by the location of the clan's communal den. However, hyaenas were also found to select shrubland, areas of high prey density, and proximity to seasonal streams. Movements of hyaenas exposed to livestock grazing were most influenced by vegetation type, with a strong avoidance of open grass plains. Den location and prey density had less influence on space use decisions in the disturbed than the undisturbed clan. Livestock distribution did not directly influence hyaena movements either during daytime, when livestock were present, or at night. We suggest that direct livestock avoidance was unnecessary due to the observed increased use of vegetative cover by hyaenas exposed to grazing livestock. The greater distances from the den, and from areas of high prey density at which hyaenas were found in disturbed than undisturbed areas indicates potential energetic costs incurred by disturbed hyaenas. Our results therefore suggest that reduced vegetative cover, as is often found outside protected areas, may result in more dramatic modifications of hyaena movements in the presence of livestock.

Introduction

The presence of large carnivore populations is often critical for normal ecosystem functioning (Crooks & Soulé, 1999; Ripple *et al.*, 2001; Terborgh, 2001). But globally, large carnivores are in decline due to a combination of habitat degradation and direct human persecution (Weber & Rabinowitz, 1996; Woodroffe, 2001). Mortality associated with 'edge effects' even threatens the persistence of protected carnivore populations (Woodroffe & Ginsberg, 1998). Given the increasing fragmentation of carnivore habitat in an expanding matrix of agriculture and urbanization, there is an urgent need to understand the ecological factors, including various forms of human disturbance, that influence space use decisions by large carnivores. These data may be critical, for example, in guiding reserve design and management (Caro & Durant, 1995), and in assessing extinction risk and resilience of wildlife populations in response to disturbance (Arcese, Keller & Cary, 1997).

Animal responses to human disturbance represent trade-offs between optimal resource use and decreased risk of persecution (Gill & Sutherland, 2000). The overall importance to carnivores of resources within human-altered environments should therefore influence their responses to disturbance, as well as the costs associated with these responses. Quantification of these costs and trade-offs should increase our ability to forecast the consequences of disturbance, and the functional losses of carnivore habitat associated with human activity. Numerous studies have demonstrated carnivore avoidance of areas characterized by intense human activity (e.g. Van Dyke *et al.*, 1986; Gese, Rongstad & Mytton, 1989; Mattson, 1990; Reinhart & Mattson, 1990; Olson & Gilbert, 1994), yet few have attempted to quantify the trade-offs involved in disturbance response decisions (but see Gibeau *et al.*, 2002).

The majority of Africa's large carnivore species have experienced recent and often dramatic reductions in range, due largely to habitat conversion (Ginsberg & Macdonald,

1990; Nowell & Jackson, 1996; Mills & Hofer, 1998). Although the spotted hyaena *Crocuta crocuta* is no exception, it is currently listed as Lower Risk (IUCN, 2006), and this species occurs in relatively stable populations throughout much of its historic range, a fact attributed to its behavioral and ecological plasticity. As is the case with many African carnivores, hyaenas frequently share the landscape with livestock. In many systems worldwide, livestock often graze unguarded and are unlikely to serve as a disturbance to carnivores, but livestock in East Africa are usually closely guarded, and herders pose a direct threat to carnivores. Hyaenas are known to alter their patterns of activity in response to livestock grazing (Kolowski *et al.*, 2007), and to reduce use of intensely grazed areas over time (Boydston *et al.*, 2003*b*). Few other researchers have studied the effects of livestock on carnivore space use patterns (Chavez, 2006), and none have utilized a comparative study to identify the consequences and potential costs of this common disturbance. The primary objective of this study was to identify the factors influencing patterns of hyaena space use. By monitoring hyaenas in both disturbed and undisturbed environments within the same ecosystem, we attempted to isolate the influence of livestock grazing. In addition, by monitoring other important ecological variables, we attempted to identify the costs to hyaenas associated with this disturbance.

Within one large hyaena territory in the Masai Mara National Reserve, Kenya (hereafter the Reserve), Boydston *et al.* (2003*b*) showed that large areas that had been heavily used by hyaenas from 1988 to 1990, were avoided by hyaenas from 1996 to 1998. Ungulate and livestock sampling demonstrated that avoided areas were characterized by both the highest prey densities and the most intensive livestock grazing. These workers observed increased use by hyaenas of densely vegetated habitat corresponding in time with dramatic increases in local livestock grazing. However, before human activity can be causally linked with recent changes in the behavior of Reserve hyaenas, we need baseline knowledge of resource use by hyaenas in the absence of livestock grazing (Arcese & Sinclair, 1997; Caro, 1999). Here we used the Mara River (MR) clan, which defends a territory free from livestock grazing in the center of the Reserve, as a baseline control, and the Talek West (TKW) clan, which is exposed to daily livestock grazing, as our treatment group. Previous work demonstrated that, with the exception of the presence of livestock, these two clans are exposed to very similar ecological conditions, including prey density, lion *Panthera leo* density and the size and vegetation composition of their territories (Kolowski *et al.*, 2007). Therefore, differences in hyaena space use between these clans should represent behavioral changes in response to the presence of livestock. The results obtained by Boydston *et al.* (2003*b*) suggest that, over time, hyaenas have increased their use of vegetative cover, potentially as a refuge from grazing herds and pastoralists, and that these hyaenas may be unable to optimize utilization of prey resources within their territory. We therefore hypothesized that the presence of livestock grazing results in modified space use decisions by hyaenas willing to sacrifice optimal resource use for reduced threat of persecution. Specifically, we tested the following predictions: (1) densely vegetated habitats should be more heavily used by TKW than MR hyaenas; (2) prey distribution should be a less effective predictor of space use by TKW than MR hyaenas; (3) probability of use of a given area by TKW hyaenas should be negatively associated with intensity of use by livestock.

Materials and methods

Study area and study populations

This study was conducted in the Reserve from September 2002 to April 2004. The Reserve consists primarily of rolling grassland habitat and scattered shrubland with riparian forest along the major watercourses; this habitat supports a large diversity of resident ungulates including both grazing and browsing species. Sunset and sunrise times occurred around 18:45 and 06:30 h, respectively, with little seasonal variation.

We monitored individual hyaenas from two clans inhabiting group territories separated by c. 8 km. The MR clan defended a territory (31 km^2) near the center of the Reserve (Fig. 1) and included 28–38 individuals (eight adult females, five immigrant males). The TKW clan, which defended a territory (28.4 km^2) along the northern border of the Reserve (Fig. 1), served as our second study clan and contained 47–55 hyaenas (11 adult females, seven immigrant males). Approximately 80% of the landscape in both territories was open grassland, and stream density ranged from 0.9 km km^{-2} (MR) to 1.1 km km^2 (TKW). Due to its location along the Reserve border, and its proximity to a number of pastoral villages (Kolowski & Holekamp, 2006), the TKW territory was subjected to intense daily livestock grazing pressure. By contrast, no livestock were ever seen grazing within the MR territory during our study period.

Hyaena locations

We fitted 29 adult hyaenas from our two study clans with VHF radiocollars (Telonics Inc., Mesa, AZ, USA). The 12 MR hyaenas (seven females, five males) were each monitored for an average of 396 days (range = 98–578 days) during our study period, and the 17 TKW collared hyaenas (11 females, six males) for an average of 391 days (range = 66–608 days). Radiocollared hyaenas spanned a wide and similar range of social ranks in both study clans. We attempted to locate each collared individual daily. Most radiotracking was conducted from 05:30 to 09:00 h (42% of locations) and 17:30–20:00 h (34% of locations), but locations were collected throughout the day and night. To effectively assess the influence of daytime grazing on hyaena space use, monitoring of hyaenas outside of their primary active period (18:00–09:00 h; Kolowski *et al.*, 2007) was essential, so daytime locations comprised approximately one quarter of all tracking locations. The majority (66%) of all tracking locations were based on direct sighting of
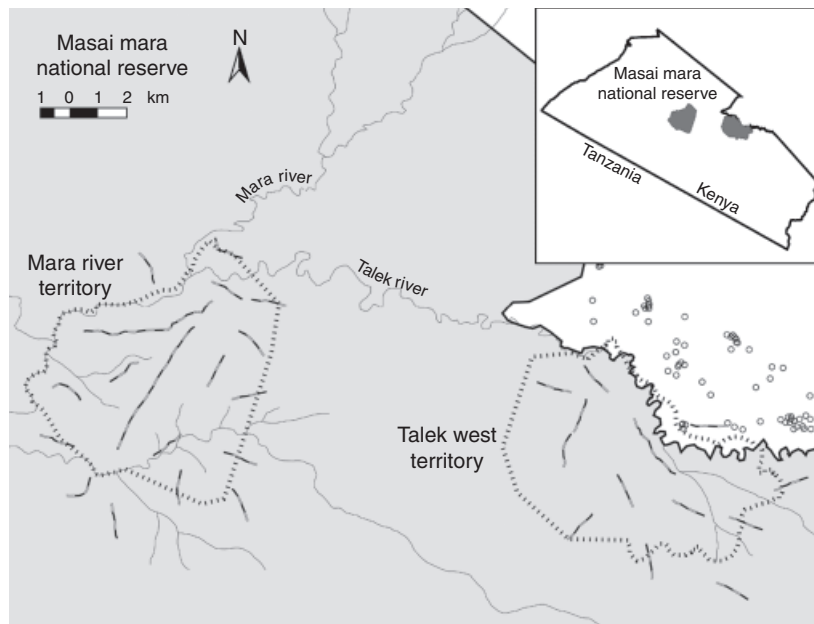
Figure 1 The location of the territory boundaries of the two hyaena study clans. Ungulate transects are shown with barred lines and Maasai villages within 2 km of the Reserve are shown with open circles. Selected rivers and streams are also shown.

hyaenas. When visual confirmation was not possible, we were able to localize the radio signal to an area typically < 200 m^2; therefore, spatial resolution of tracking locations was high in all cases. As individuals were rarely tracked more than twice a day, temporal autocorrelation was not a serious concern. However, we ensured that all locations for the same individual were separated by at least 1 h during their active period (a conservative minimum time estimate for an individual hyaena to cross its entire territory; (White & Garrott, 1990), and that only one location was collected per individual per day during resting hours.

Livestock distribution

To document the spatial distribution of livestock grazing, we conducted regular censuses in the Reserve portions of the TKW territory, which involved driving throughout the territory to obtain complete counts of sheep, goats and cattle. Herds were easily spotted in all habitat types thanks to the bells they wore, and the network of dirt roads and abundant hilltops from which we could scan surrounding terrain. To ascertain the extent of livestock movements into the Reserve, we conducted five censuses within each month, all sampling different 2-h intervals throughout the daytime hours. Based on observed grazing patterns inside the Reserve, we identified 09:00–18:00 h as 'grazing hours', 19:00–08:00 h as 'livestock-free hours', and considered the remaining hours as transition periods. Livestock are kept within fences at night in the villages near the Reserve.

We visually estimated the shape and size of each herd, and recorded a point location for the herd center using car-mounted GPS units by approaching the herds at close range. Herd shapes were then drawn in a GIS and filled with randomly located points according to the recorded herd size, with each animal represented as a single point. We then created a utilization distribution grid surface for the entire territory using fixed-kernel methods with values of each grid cell weighted according to the density of recorded livestock locations within and around each cell (Worton, 1989). Separate grids were created for each modeling period by pooling livestock locations from all censuses across the relevant months. The smoothing parameter for each grid surface kernel function was initially determined using the reference bandwidth value (Worton, 1995). If the resulting grid surface indicated areas of zero utilization between herds deep in the Reserve and herds entering the Reserve, the smoothing parameter was increased iteratively by 20 until at least low livestock utilization was indicated between these herds to more accurately reflect herd movement paths. Grid cell widths for created surfaces varied with the number and density of livestock points, but ranged from 40 to 100 m. Final grid cell values, referred to hereafter as livestock use values (LUVs) ranged from 0 to 100, with higher numbers indicating higher grazing intensity.

Ecological variables

In addition to livestock, we considered the influence of key ecological variables on hyaena space use, including dens, prey, watercourses and vegetation. Spotted hyaenas breed year-round in the Reserve (Holekamp et al., 1999). Cubs are typically born in an isolated natal den and, after 1–5 weeks (Kruuk, 1972; East, Hofer & Turk, 1989), moved to a communal den, where cubs of other clan females also reside until 8–9 months of age (Holekamp, Smale & Szykman, 1996). Typically a single communal den is used within a territory at any given time, but den locations in this region change, on average, every 1.5 months (Boydston, Kapheim & Holekamp, 2006). When females have den-dwelling cubs they are found closer to the communal den than they are

during other phases of their reproductive cycle (Boydston *et al.*, 2003*a*), and their core areas tend to be centered on communal den locations (Boydston, 2001). In addition to functioning as a refuge for vulnerable cubs (East *et al.*, 1989; Holekamp & Smale, 1998), the communal den also serves as a social center and site of sub-group assembly (Kruuk, 1972; Mills, 1990; Holekamp, Boydston & Smale, 2000). Thus, we expected that all clan members would exhibit space use patterns influenced by the communal den location. We recorded the coordinates and dates of usage of all MR and TKW communal dens occupied during the study period.

Water was not expected to be a limiting resource here, as permanent water occurs throughout the Reserve, and hyaenas living elsewhere within this ecosystem show little dependence on free water (Kruuk, 1972). However, the placement of water features may indirectly influence hyaena movements by providing cool daytime resting sites or by influencing preferred vegetative characteristics. Therefore, we obtained maps of permanent and seasonal streams digitized from aerial photographs (Boydston, 2001).

Spotted hyaena ranging patterns are influenced by the local distribution of prey resources (Mills, 1990; Hofer & East, 1993; Trinkel *et al.*, 2004). Within the Reserve, hyaenas in one studied clan generally used areas of higher prey density more frequently than areas of lower prey density (Boydston *et al.*, 2003*b*). Here, we characterized the availability of natural prey using multiple 1 km road transects distributed regularly throughout both territories (MR $n = 24$, TKW $n = 14$; Fig. 1). We counted all wild ungulates within 100 m of each third of each transect two to four times per month and assigned these counts to point locations (three per transect). Each point was assigned the mean number of prey counted ('prey value') on the corresponding transect section over the period of interest, with each transect section representing an area of 0.067 km^2 $(0.333 \text{ km} \times 0.2 \text{ km})$. For each modeling period, a prey distribution grid surface was then interpolated from these data points using inverse distance weighting. Final grid surfaces were composed of relatively large $500 \text{ m} \times 500 \text{ m}$ cells covering each territory to represent the coarse resolution of the field data. Each cell therefore represented the estimated prey value at that location based on transect points within and around each cell using the inverse distance weighting function.

Finally, we created vegetation maps for both clan territories based on a combination of three data sources: vegetation type reference points collected in the field, a 15 m resolution panchromatic Landsat 7 ETM + image and a 30 m resolution 6-band Landsat 7 ETM + image (both images from 4 February 2003). Vegetation reference points were recorded in both territories (MR $n = 899$; TKW $n = 1257$). A final vegetation map for each territory was digitized by hand in a GIS with three broad vegetation classes: riparian forest, shrubland and open grass plain. Shrubland was defined as a dense woody cover, the vast majority of which was *Croton* or *Euclea* bushes 1–2 m in height. Riparian forest often included this shrub layer but was distinguished by the presence of a tree canopy. Based on

the reference points, accuracy of each of the two final maps was > 92%. Satellite images were processed and georectified in Erdas Imagine 8.6 (Leica Geosystems LLC, Norcross, GA, USA).

Logistic regression models

Logistic regression modeling is a common statistical method used to calculate resource selection probability functions, whereby the probability that a location or area is used by an animal is a function of a set of habitat variables associated with that location (Manly *et al.*, 2002). Logistic regression models have the ability to incorporate multiple continuous and categorical variables, and model parameters can be straightforwardly interpreted in the form of odds ratios. The estimation of these models when using radio-telemetry data is commonly based on the comparison of a sample of locations used by an animal (i.e. tracking locations) with a sample of locations available for use (Manly *et al.*, 2002). We used logistic regression to model the probability that a location would be used by a hyaena as a function of the monitored variables described above. We compared ecological features associated with tracking ('used') locations of hyaenas to those associated with 5000 random ('available') locations identified within each clan territory. Variables identified in significant regression models are those that effectively differentiate between 'used' and 'available' locations, and therefore represent factors influencing hyaena space use decisions.

Each hyaena tracking and random location was associated in a GIS with specific values of the following predictor variables: distance to den, distance to nearest stream, distance to nearest permanent stream, distance to cover (i.e. shrubland or forest), prey value, LUV (for TKW models only) and vegetation class. Since den locations changed frequently, modeling of the influence of the den location was restricted to periods during which the den location either did not change at all, or moved < 1 km. In the latter case, the average UTM coordinates for all dens occupied within that modeling period represented the den location. Prey values and LUVs were based on separate livestock and prey distribution maps created for each modeling period.

Because reproductive state influences ranging patterns of adult female hyaenas (Boydston *et al.*, 2003*a*), we excluded locations at either natal or communal dens for females with den-dwelling cubs in order to reduce the influence of reproductive events on comparisons between the two clans. Additionally, since random locations had to be identified within an area 'available' to hyaenas (here the territory), we excluded hyaena locations collected outside territory boundaries (< 4% of locations per clan). In the TKW clan, since livestock data were only available for locations inside the Reserve, we also excluded TKW tracking locations outside the Reserve (an additional 3.6% of TKW hyaena locations). All spatial analyses were performed using either ArcView GIS 3.2 or ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), and the following program extensions: Spatial Analyst, Animal Movement Analyst

Table 1 Modeling periods during which den location was stable in the Mara River (MR) and Talek West (TKW) clans

Period	Dates	Days	Hyaenas (f,m)	Locs	Prey	Livestock
MR1	3 October 2002–21 December 2002	80	9 (6,3)	387	43.5	–
MR2	23 December 2002–30 April 2003	129	10 (6,4)	596	16.0	–
MR3	4 May 2003–1 February 2004	274	9 (5,4)	1249	54.3	–
Mean		161	–	744	37.9	–
TKW1	1 November 2002–6 April 2003	157	12 (6,6)	578	37.9	2266
TKW2	28 July 2003–2 November 2003	98	11 (6,5)	407	58.2	1046
TKW3	26 December 2003–6 February 2004	43	12 (8,4)	235	30.4	1078
TKW4	7 February 2004–30 April 2004	85	12 (7,5)	464	56.0	615
Mean		96	–	421	45.6	1251

Logistic regression modeling of space use was based on data collected only during these periods. Levels of prey and livestock for each period are represented by the mean # of ungulates per kilometer of transect and the mean # of livestock animals counted per census drive during each period, respectively. The total number of hyaena tracking locations for each period is also shown under 'Locs.'

(Hooge & Eichenlaub, 2000) and Grid Tools (Jenness, 2006).

Separate logistic regression models were created for each modeling period using the ecological variables as predictors and a binary ('used' vs. 'available') dependent variable. For each modeling period, all possible logistic regression models using all combinations of recorded variables were compared using information–theoretic methods and Akaike's information criterion values (AIC; Burnham & Anderson, 2002). All models within two AIC points of the optimal model were investigated and considered to have empirical support based on the data (Burnham & Anderson, 2002). We identified predictor variables that were included in all models in this initial subset, and ran a final logistic regression model that included only these variables. The significance of variables in the final model for each modeling period was based on the Wald statistic, and significance of each model was tested using likelihood-ratio tests.

We calculated odds ratios for each variable in each model to compare the relative influence of ecological variables among modeling periods and between clans. Here, we report modified odds ratios (MOR; Long, 1997) that represent the % change in probability of use associated with a biologically meaningful change in each predictor: an increase of 100 m for distance measures, 5 units for prey values and 10 units for LUVs. We used the average MOR for individual variables over all models within clans to qualitatively assess overall influence of independent variables on space use.

To investigate the influence of time of day on the relative importance of ecological variables, we used the above methods to create and compare separate logistic regression models within each modeling period based on hyaena locations collected either during grazing hours (09:00–18:00 h) or livestock-free hours (19:00–08:00 h), and assumed that prey distribution did not change significantly between these two time periods. While radiotracking, we noticed no obvious changes in prey distribution between day and night periods, but accurate nighttime assessments of prey distribution were impossible. Models referred to in the sections below are based on data from the entire 24-h period unless noted otherwise.

Results

We identified three modeling periods, each with a stable den location, for the MR clan, and four in TKW (Table 1). Natural prey abundance and livestock grazing intensity varied substantially among modeling periods (Table 1). Although the spatial distribution of prey also showed variability among modeling periods (data not shown), the spatial distribution of livestock in the TKW territory was consistent over time (Fig. 2); the monthly mean number of livestock counted per census was 1386 ± 181 (range: 106–3160; average herd size = 160, average # of herds = 8.1). The average proportion of hyaena tracking locations collected during livestock-free and grazing hours was 50.8 and 26.8%, respectively in MR, and 46.5 and 21.7%, respectively in TKW.

Variables influencing space use

All measured ecological variables, both continuous (Fig. 3, Table 2) and categorical (Fig. 4, Table 3), showed significant univariate differences between 'used' and 'available' locations. Hyaenas in both clans were found significantly closer to the den than expected in all modeling periods (Table 2). Except during one modeling period in TKW, hyaena locations in both clans were associated with higher prey values than were available locations (Table 2). On average, in both clans, hyaenas were found closer to vegetative cover and streams than was expected based on availability (Fig. 3), and hyaenas demonstrated a preference for shrubland habitat and avoidance of grass plains (Fig. 4). We found no evidence for avoidance of livestock use areas by TKW hyaenas (Table 2, Fig 3).

Final logistic regression models in each of three MR modeling periods generated similar results (Table 4). The most important predictor variable in all three final MR models was distance to the den. Distance to cover was excluded from the MR1 model, but all other final MR models included all possible predictor variables, indicating that all measured ecological variables influenced space use
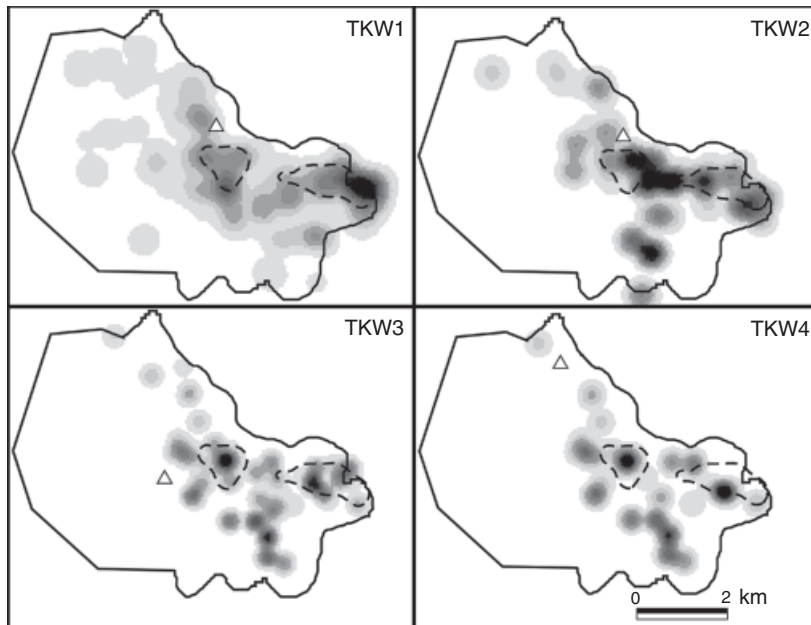
Figure 2 Livestock utilization distribution grid surfaces for each of the four modeling periods in the Talek West clan. Darker colors indicate higher intensity of use by livestock. The communal den location (triangles) used during each period, and the clan territory boundary is indicated on each map. The area that received the most intense livestock use over the whole study period (livestock core area) falls within the dashed lines.

decisions. All three MR models were highly significant based on the likelihood ratio test ($\chi^2 > 636.0$, $P < 0.0001$).

The relative importance of predictor variables varied among TKW modeling periods (Table 5). Distance to the den was an important predictor variable in all four TKW final models, but was not consistently the most important. Vegetation class was selected as the first or second most influential variable in all four TKW models. Surprisingly, LUV was selected as a predictor in only one final model (TKW1), with increasing livestock use associated with lower probability of hyaena use. Interestingly, in this model, increases in prey values reduced the probability of hyaena use. Furthermore, prey value was not selected for two of the four final TKW models. LUV value was also not an important variable in any models in TKW based on data collected during only livestock-free hours (data not shown). Although LUV was selected for in one of the four grazing-hours models, its coefficient was positive, indicating a positive relationship with probability of use by hyaenas (details provided in Supporting Information Table S1). Thus, as with the univariate tests, multivariate models indicated no direct avoidance of livestock by TKW hyaenas. All final models were highly significant based on the likelihood ratio test ($\chi^2 > 340.0$, $P < 0.0001$).

Spatial correlations

Ecological variables were not completely independent, and investigation of these intercorrelations is essential for a comprehensive understanding of model results. In particular, correlations between den location and ecological variables may lend insight into hyaena den site selection. Distance to the den was negatively correlated with prey values for six of the seven modeling periods (range:

$r = -0.05$ to -0.80), indicating that dens tended to be located in areas with higher than average prey values. In fact, a high correlation between den location and prey distribution in model TKW4 (the only r-value between any variables that was > 0.70) is likely the reason that prey value was not selected in this model. Finally, prey values and livestock use intensity were positively correlated in two TKW models but not the other (TKW1 $r = 0.17$, TKW2 $r = 0.34$).

Interclan comparison and the influence of grazing

The presence of livestock grazing was the only notable ecological difference between our two study clans, therefore a comparison of modeling results between the two clans should reflect the influence of livestock grazing on hyaena space use decisions. Distance to the den was consistently an important predictor of hyaena space use in both clans, and showed a similar degree of influence on model predictions in all models (Tables 4 and 5, Supporting Information Table S1). However, whereas distance to the den was consistently the most important predictor of MR hyaena locations, other variables, particularly vegetation class, were more important in some TKW models. The relatively weak influence of dens on space use by TKW hyaenas is clearly shown in plots of tracking locations relative to den locations: locations at which MR hyaenas were found cluster tightly around the den in each modeling period (Fig. 5) whereas this is far less apparent in TKW (Fig. 6). This result is remarkable considering that the average % of locations contributed by females with den-dwelling cubs to TKW models (24.3%; range: 9.7–56.3%) was higher than for MR models (19.3%; range: 10.3–27.1%). The influence of the den was
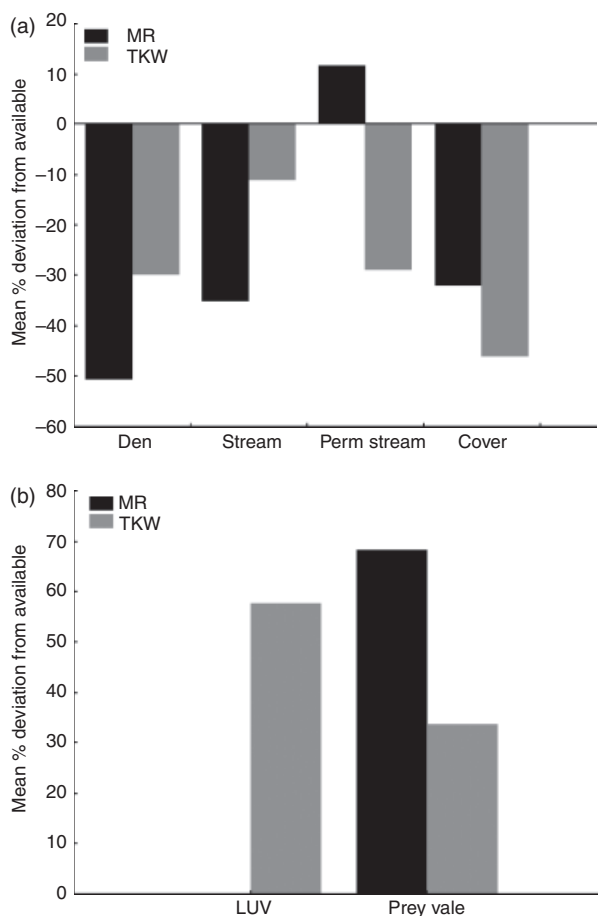
Figure 3 The mean % difference between values of continuous variables measured at hyaena locations ('used') and those measured at 5000 random locations ('available') within the respective clan territories. A % difference was calculated for each of three modeling periods in Mara River (MR), and four periods in Talek West (TKW); the mean of these values is indicated here. Variables in (a) represent distances; therefore negative deviation values indicate hyaena selection for proximity to these features. In contrast, positive values in (b) indicate hyaena selection for the corresponding variable. Variable descriptions, the data from each individual model and the associated statistical comparisons are shown in Table 2.

consistently important and positive in both grazing hours and livestock-free hours models in MR, yet in TKW, the influence of the den was highly variable in grazing hours models (Supporting Information Table S1).

Differences between clans in the relative influence of other important ecological variables were also evident. Although prey was selected as a significant positive predictor for all MR models, it was not consistently a positive or important predictor in TKW models (Tables 4 and 5) and in TKW1, areas used by hyaenas had lower prey values than did random locations. In the MR clan, prey values generally had a stronger influence on locations collected during livestock-free hours (mean MOR = +19) than during grazing hours (mean MOR = +4), which likely reflects increased hunting behavior during nighttime hours. However, this trend was not consistently evident for TKW
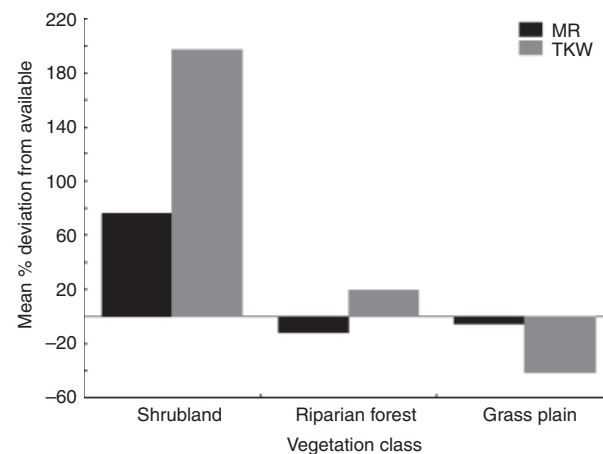

Figure 4 The mean % difference between the proportion of hyaena locations and the proportion of 5000 random locations ('available') within the respective clan territories that were located in each of three vegetation class. The mean % difference is indicated for all modeling periods in each clan. Here, negative deviation values indicate hyaena avoidance of particular habitat types. The data from each individual model and associated statistical comparisons are shown in Table 3.

Table 2 Comparison of 'used' and 'available' locations

	Den		Stream		Perm stream		Cover		LUV		Prey value	
	Used	Avail	Used	Avail	Used	Avail	Used	Avail	Used	Avail	Used	Avail
MR1	1275 ± 120	2972	253 ± 24	346	990 ± 49	851	332 ± 35	360	–	–	18.8 ± 0.7	15.5
MR2	1498 ± 112	3005	211 ± 16	346	946 ± 39	851	204 ± 19	360	–	–	17.1 ± 1.4	6.3
MR3	1457 ± 57	2631	211 ± 12	346	916 ± 27	851	199 ± 13	360	–	–	19.5 ± 0.4	17.4
TKW1	1855 ± 65	2546	**375 ± 24**	**359**	1248 ± 62	1507	163 ± 18	220	9.8 ± 0.9	7.6	**13.2 ± 0.5**	**13.5**
TKW2	1962 ± 74	2561	154 ± 20	359	1064 ± 57	1507	37 ± 10	220	22.9 ± 2.6	9.6	33.3 ± 1.1	21.0
TKW3	1372 ± 127	2131	451 ± 42	359	1115 ± 77	1507	90 ± 19	220	**7.8 ± 2.2**	**5.6**	15.1 ± 0.7	12.0
TKW4	2039 ± 135	3055	293 ± 22	359	862 ± 49	1507	184 ± 19	220	**6.7 ± 1.4**	**5.4**	32.6 ± 1.6	21.4

Mean values (±95% CI) of continuous variables recorded for hyaena tracking locations ('used'), and 5000 random locations ('avail') in the territories of the Mara River (MR) and Talek West (TKW) clans during each of the modeling periods delineated in Table 1. The first four variables represent the straight-line distances (m) to the communal den (Den), the nearest stream (Stream), the nearest permanent stream (Perm stream) and vegetative cover (Cover). Livestock use values (LUVs) and prey values represent intensity of use and were based on grid surfaces created from livestock censuses and prey sampling transects. Only values that did NOT differ between used and available based on 95% CI are in bold.

Table 3 The per cent of hyaena radiolocations ('used') and 5000 random locations ('avail') within the territories of the Mara River (MR) and Talek West (TW) clans that were associated with each vegetation class in each of the modeling periods delineated in Table 1

	Shrubland			Riparian forest			Grass plain		
	Used	Avail	χ_1^2	Used	Avail	χ_1^2	Used	Avail	χ_1^2
MR1	13.7	7.9	16.11*	7.0	13.2	12.63*	79.3	78.9	0.04
MR2	16.1	7.9	45.42*	13.9	13.2	0.22	70.0	78.9	24.73*
MR3	12.0	7.9	21.69*	13.9	13.2	0.41	74.1	78.9	13.62*
TKW1	38.9	16.8	163.39*	4.5	2.3	10.42*	56.6	80.9	180.51*
TKW2	72.2	16.8	695.93*	2.9	2.3	0.74	24.8	80.9	661.16*
TKW3	50.2	16.8	166.93*	1.7	2.3	0.34	48.1	80.9	147.63*
TKW4	38.8	16.8	134.57*	1.9	2.3	0.22	59.3	80.9	119.74*

*Significant χ^2 test statistic at $\alpha = 0.05$.

Table 4 Logistic regression results for Mara River (MR) modeling periods based on hyaena locations collected at all times of day and night

Model	Variable	Estimate	SE	Wald statistic	P
MR1	Distance to Den	−0.0009	0.00006	243.10	<0.0001
	Distance to Stream	−0.0032	0.00034	87.89	<0.0001
	Prey value	+0.0508	0.00926	30.06	<0.0001
	Distance to Perm	+0.0005	0.00015	10.66	0.0011
	Habitat			9.96	0.0069
	Shrubland	+0.3688	0.13065	7.97	0.0048
	Riparian Forest	−0.4533	0.15484	8.57	0.0034
MR2	Distance to Den	−0.0007	0.00005	190.56	<0.0001
	Distance to Cover	−0.0017	0.00027	38.03	<0.0001
	Prey value	+0.0245	0.00513	22.71	<0.0001
	Distance to Stream	−0.0015	0.00034	19.88	<0.0001
	Habitat			15.00	0.0006
	Shrubland	+0.2337	0.09964	5.50	0.0190
	Riparian Forest	+0.1179	0.10161	1.35	0.2459
	Distance to Perm	+0.0004	0.00014	9.72	0.0018
MR3	Distance to Den	−0.0009	0.00004	596.97	<0.0001
	Distance to Perm	+0.0010	0.00009	139.23	<0.0001
	Distance to Cover	−0.0016	0.00023	51.79	<0.0001
	Distance to Stream	+0.0017	0.00025	44.78	<0.0001
	Prey value	+0.0259	0.00519	24.91	<0.0001
	Habitat			19.97	0.0005
	Shrubland	−0.0480	0.08199	0.34	0.5582
	Riparian Forest	+0.3147	0.08145	14.93	0.0001

locations (Supporting Information Table S1). Although members of both clans showed selection for shrubland vegetation, comparison of odds ratios indicated a much stronger influence of this vegetation class on space use by TKW than MR hyaenas. The identification of a location as shrubland increased the estimated probability of identification as a 'used' location by an average of 22% in MR, but by 135% in TKW. The importance of shrubland was greatly increased during grazing hours relative to livestock-free hours in both MR (mean MOR = +81 vs. −3) and TKW (mean MOR = +257 vs. +111). However, these values indicate that selection for shrubland vegetation disappeared during livestock-free hours in MR, but remained strong during these hours in TKW (Supporting Information Table S1).

Discussion

Ecological variables influencing hyaena space use

Our first objective was to identify ecological factors influencing space use by spotted hyaenas. All the variables monitored here were important in predicting hyaena space use patterns, including vegetation type, water features and the distribution of prey. Given the social and reproductive importance of the communal den to *Crocuta*, we expected den location to have a strong influence on space use patterns, and in fact den location was an important predictor variable in all models. This indicates that the selection of den sites by female spotted hyaenas may have significant

Table 5 Logistic regression results for Talek West (TKW) modeling periods based on hyaena locations collected at all times of day and night

Model	Variable	Estimate	SE	Wald Statistic	P
TKW1	Distance to Den	−0.0014	0.00010	201.27	<0.0001
	Habitat			123.15	<0.0001
	Shrubland	+0.6059	0.10049	36.35	<0.0001
	Riparian Forest	−0.0439	0.17060	0.07	0.7968
	Distance to Perm	+0.0006	0.00012	22.94	<0.0001
	Prey value	−0.0430	0.00914	22.17	<0.0001
	LUV	−0.0162	0.00533	9.22	0.0024
TKW2	Prey value	+0.0733	0.00592	153.21	<0.0001
	Habitat			152.46	<0.0001
	Shrubland	+0.8041	0.12789	39.53	<0.0001
	Riparian Forest	+0.0489	0.22787	0.05	0.8300
	Distance to Den	−0.0009	0.00012	57.76	<0.0001
	Distance to Stream	−0.0023	0.00036	40.11	<0.0001
	Distance to Perm	+0.0005	0.00015	10.91	0.0010
TKW3	Distance to Den	−0.0007	0.00011	48.79	<0.0001
	Habitat			34.75	<0.0001
	Shrubland	+0.7455	0.19350	14.84	0.0001
	Riparian Forest	−0.4801	0.35379	1.84	0.1748
	Distance to Perm	−0.0005	0.00011	21.94	<0.0001
	Distance to Cover	−0.0025	0.00059	18.58	<0.0001
	Distance to Stream	+0.0011	0.00034	10.62	0.0011
TKW4	Habitat			116.15	<0.0001
	Shrubland	+1.1694	0.13708	72.78	<0.0001
	Riparian Forest	−0.9341	0.23941	15.22	<0.0001
	Distance to Den	−0.0004	0.00004	88.47	<0.0001
	Distance to Perm	−0.0008	0.00009	77.15	<0.0001
	Distance to Cover	+0.0018	0.00031	32.13	<0.0001

consequences for space use by all clan members. Den site selection in hyaenas is poorly understood. Hyaena dens were often associated with water features in both the Kalahari Gemsbok National Park (Mills, 1990) and the Mara Reserve (Boydston et al., 2006). Hyaenas in the Serengeti National Park typically selected dens located in the direction of large prey herds in the dry season (Kruuk, 1972). Spatial correlations in the current study also support the idea that changes in location of the den may be affected by local changes in the spatial distribution of prey.

Our models indicated that distribution of prey clearly influenced space use decisions made by hyaenas. Numerous studies have linked carnivore space use and the prey densities within their home ranges or territories (e.g. Schaller, 1972; Litvaitis, Sherburne & Bissonette, 1986; Avenant & Nel, 1998; Hopcraft, Sinclair & Packer, 2005), and the same association has been shown in *Crocuta*. For example, in southern Africa, hyaenas seasonally shifted movements within their territory to utilize areas with the most abundant prey resources (Mills, 1990; Trinkel et al., 2004), and extra-territorial movements increased as Serengeti hyaenas sought out distant migratory herds when local prey were scarce (Hofer & East, 1993). Similarly, our data, and those of Boydston et al. (2003b), provide direct, quantitative evidence that local movements of prey influence hyaenas' use of space within their territories, even on a relatively small scale.

We found water features and vegetation types to be important predictors of hyaena space use. Although water sources may influence movements of hyaenas in arid ecosystems (Tilson & Henschel, 1986; Cooper, 1989), it is unlikely that the hyaenas studied here were limited by the distribution of water. Woody vegetation tends to occur along all permanent and most seasonal streams in the Reserve, and so the importance of streams may reflect the hyaenas' preference for shrubland vegetation. MR hyaenas exhibited strong selection for streams relative to TKW hyaenas, with relatively weak selection vegetative cover. This is likely a result of selection by MR hyaenas for wet, muddy, concealed daytime resting sites in creek beds lacking continuous vegetative cover, which were more common in the MR than TKW territory. This conclusion is supported by the fact that selection for streams in MR was consistently stronger during daylight hours than during hours of darkness.

Influence of livestock grazing on hyaena space use

Our second objective was to compare space use patterns of hyaenas between MR and TKW territories, which differed in exposure to livestock grazing. Based on previous research (Boydston et al., 2003b), we predicted that vegetative cover would assume relatively low importance to hyaenas not exposed to livestock grazing. Although hyaenas in both
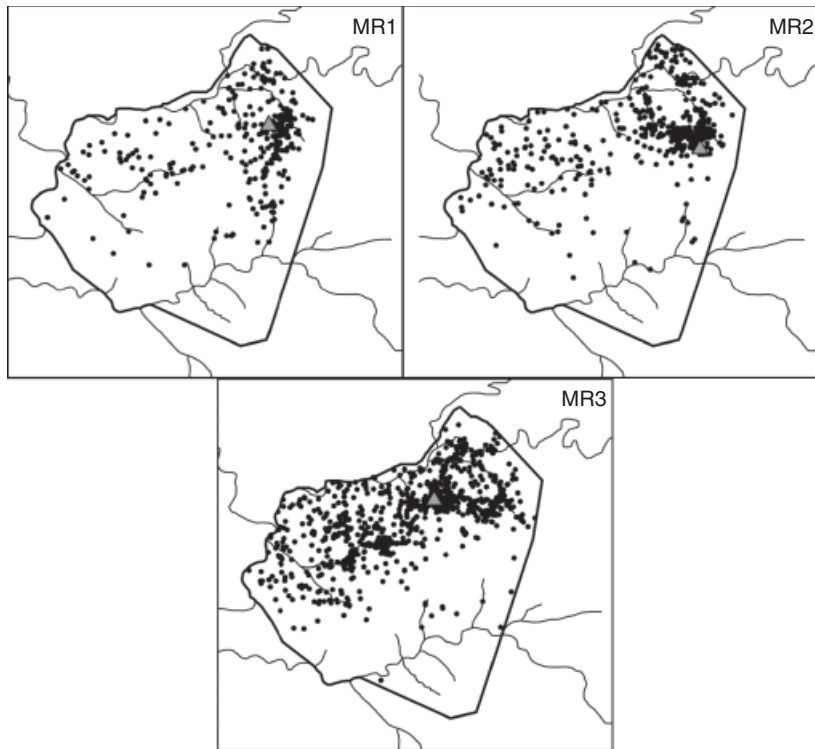
Figure 5 Locations at which adult Mara River hyaenas were radiotracked within their territory during three modeling periods (see Table 1). Locations at the communal den for females with den-dwelling cubs were excluded. Permanent and seasonal streams are indicated along with the communal den (gray triangle) used during each period.
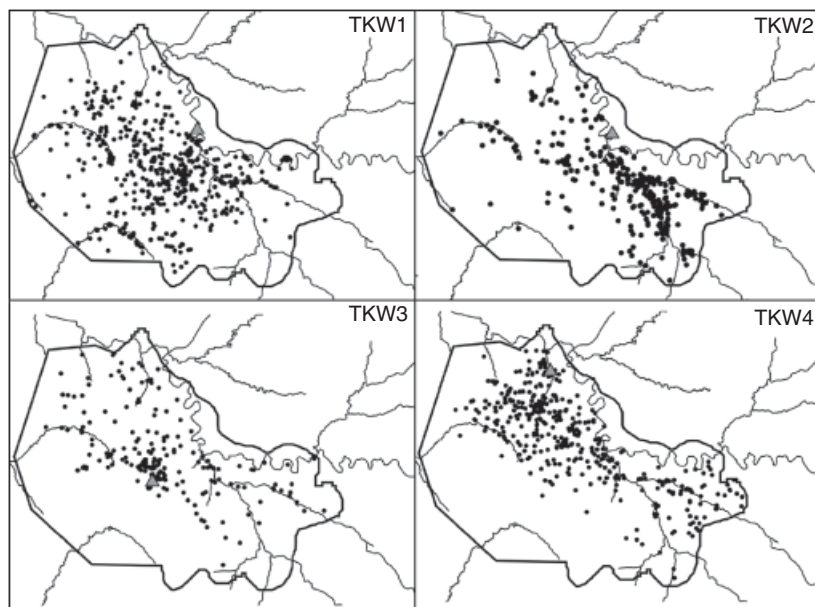

Figure 6 Locations at which adult Talek West hyaenas were radiotracked within their territory and within the Reserve during four modeling periods (see Table 1). Locations at the communal den for females with den-dwelling cubs were excluded. Permanent and seasonal streams are indicated along with the communal den (gray triangle) used during each period.

clans demonstrated selection for shrubland vegetation, logistic regression modeling confirmed that vegetation class was a more important predictor of space use patterns in TKW than in MR. Furthermore, models considering time of day indicated that selection by MR hyaenas for shrubland occurred almost exclusively during daylight hours, whereas selection for shrubland in TKW occurred both day and

night. Thus stronger selection for shrubland habitat in TKW appears to represent a behavioral modification reflecting reduced use of open areas resulting from grazing disturbance. Indeed, in three of the four TKW modeling periods, the den itself was located in areas providing vegetative cover while MR hyaenas consistently denned in open grassland. Yet, despite the use of relatively hidden

dens, movements of TKW hyaenas were still less influenced by the den relative to MR. This difference was clearly apparent even in simple plots of tracking locations (Figs 5 and 6), and existed despite a generally higher proportion of TKW locations being provided by females with den-dwelling cubs. The fact that vegetation class was a more important predictor variable than den location in two of the four TKW models suggests that TKW hyaenas may have been sacrificing proximity to the den for protective vegetative cover. Such a behavioral adjustment would therefore represent a potential energetic cost to hyaenas, particularly females with den-dwelling cubs, by preventing individuals from focusing their movements and resting sites around the communal den.

We also predicted that prey distribution would more effectively predict hyaena space use in livestock-free areas than in areas exposed to grazing. Hyaenas in livestock-free environments should make space use decisions based on the resources critical to their survival and fitness, whereas those exposed to disturbance may be forced to limit the cost of persecution at the expense of optimal resource use. Our results supported this prediction and suggest a second potential cost associated with increased dependence on vegetative cover: reduced ability to maximize proximity to prey resources. Interestingly, in the period during which hyaenas exhibited avoidance of areas with higher prey values (TKW1), livestock grazing levels were highest. However, we did not identify a consistent spatial relationship between prey values and LUVs.

Variables other than those monitored in this study, such as lion distribution and tourist activity, may potentially influence space use patterns of hyaenas in other systems, or of other carnivores. We did not take the distribution of either lions or tourist vehicles into account in our analyses because, although lions are a major source of mortality for Talek hyaenas (Watts, 2007), Boydston et al. (2003b) showed a positive spatial correlation between lions and Talek hyaenas, indicating that space use by these carnivores is influenced by similar ecological factors. In addition, clan comparisons here were not biased by differences in lion density, as lion numbers did not differ significantly between the MR and TKW clan territories (Kolowski et al., 2007). Similarly, although tourist use of the Talek area was estimated to be almost five times higher than that observed in the MR territory (Kolowski et al., 2007), hyaenas usually do not avoid tourist vehicles in the Reserve, even at close distances, due to frequent exposure and extensive habituation (K. E. Holekamp, unpubl. data). By contrast, hyaenas run away from pastoralists tending their herds on foot.

Given the temporal predictability of livestock grazing in the Reserve, and the direct threat that herders pose to hyaenas, we expected to find both direct avoidance of areas used intensely by livestock, and differential use of these areas between daytime and nighttime periods. However we documented little avoidance of livestock use areas in general, regardless of time of day. However, the reduced importance of the den and the remarkably strong influence of vegetation type during livestock grazing hours in TKW clearly suggest indirect effects of temporal patterns in grazing. Although lower daytime activity by TKW than MR hyaenas (Kolowski et al., 2007) may have reduced the need for direct avoidance by TKW hyaenas of areas used by livestock, our data suggest the availability of refugia (i.e. vegetative cover) during daytime rest periods is important in allowing shared use of space. Notably, during TKW1, the period of most intense livestock grazing, higher LUVs were associated with reduced probability of hyaena use and LUV was selected as an important model variable suggesting that direct avoidance of livestock, and their associated herdsmen, may be expected above some threshold grazing intensity.

Conclusions

The data presented here lead to three primary conclusions. First, patterns of space use by spotted hyaenas are determined by a complex interaction of multiple ecological factors, including prey distribution, vegetation types, landscape water features and most importantly, the location of the communal den. A complete understanding of space use in this species requires a more comprehensive understanding of the factors influencing den site selection than is currently available. Second, the effects of grazing on hyaena space use can clearly be more complicated than the simple direct avoidance documented by (Boydston et al., 2003b); presence of vegetative cover appears to be important in allowing the coexistence of livestock and hyaenas at a local scale. We demonstrated that daily, often intense livestock grazing pressure did not result in hyaena avoidance of grazed areas. However, although TKW hyaenas were largely able to maintain proximity to both the communal den, and to the areas within their territory that contained the highest prey densities, they clearly did so to a lesser extent than undisturbed hyaenas. We hypothesize that in the absence of vegetative cover this coexistence would not be possible, and that spatial avoidance of intensely grazed areas, either during grazing hours or at all times of day, would be dramatic. This is supported by the fact that the direct spatial avoidance of intensely grazed areas shown by Boydston et al. (2003b) occurred in large, open grass plains. Third, the more subtle responses to disturbance that we have demonstrated here are likely to result in temporal and energetic costs to hyaenas associated with more travel.

Documentation of behavioral responses to disturbance assumes its greatest utility to conservation when it is linked with demographic consequences (Caro, 1998; Gill & Sutherland, 2000). Clan size and birthrates in the Talek Clan from 1988 to 2003 were stable despite the fact that humans were a significant source of mortality for adults in this clan, and that annual human-caused mortality was more than four times greater between 1996 and 2003, than between 1988 and 1995 (H. E. Watts, unpubl. data). Given these data and the results presented above, it appears that these hyaenas have adjusted to coexist with the daily disturbance of livestock grazing without yet suffering measurable demographic consequences. However, increasing rangeland degradation outside the Reserve (Serneels, Said & Lambin,

2001), together with the increased threat of direct hyaena mortality associated with a growing human population, suggest that grazing pressure in the Reserve, and human-caused mortality among hyaenas, will continue to increase. Increased grazing pressure in and around the Reserve will most likely result in a reduction of critical vegetative cover, and lead to more acute behavioral responses to livestock grazing by hyaenas. Whether behavioral changes by hyaenas, such as increased use of vegetative cover (Boydston et al., 2003b; this study) and changes in activity patterns (Kolowski et al., 2007), or their apparent demographic resiliency, will continue to buffer these hyaenas from these increasing threats remains to be seen, and this population continues to be monitored. Further study is needed, however, to determine the extent to which the behavior of other large predators (e.g. cheetah Acinonyx jubatus, lion) in these ecosystems is influenced by livestock grazing.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Modified odds ratios for models created based on all hyaena tracking locations ('All'; Tables 4 and 5), and tracking locations from grazing hours (GH: 0900–1800 h), and livestock-free hours (LFH: 1900–0800 h). Numbers indicate the % change in probability of a location being identified as 'used' by a hyaena, that is associated with a 100 m increase in distance to the den, nearest stream, or vegetative cover, a 5-unit increase in prey value, and identification of a site as shrubland. Variables not selected for final models were assigned a value of 0. Only selected variables are shown.