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ANTHROPOGENIC INFLUENCES ON THE BEHAVIOR OF LARGE CARNIVORES IN THE NORTHERN SERENGETI ECOSYSTEM

By

Joseph Mark Kolowski

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ABSTRACT

ANTHROPOGENIC INFLUENCES ON THE BEHAVIOR OF LARGE CARNIVORES IN THE NORTHERN SERENGETI ECOSYSTEM

By

Joseph Mark Kolowski

Most large mammalian carnivores are in global decline, largely due to habitat loss and their involvement in livestock depredation. Increasingly, large carnivores are forced to adjust to living in landscapes characterized by human activity and disturbance. It is therefore critical to understand both the extent to which carnivores can adjust to human activities and the factors influencing human tolerance of their presence. Here I document the activity patterns and space use of three social groups, or clans, of spotted hyenas (*Crocuta crocuta*) in the Masai Mara National Reserve, Kenya that vary in exposure to humans, and investigate the degree to which these behaviors are influenced by human activity, primarily in the form of livestock grazing. I also investigate the issue of local tolerance of carnivores with an intensive study of livestock depredation.

Hyenas were active during 31.5 ± 2.7% of the 24-h period, and 96.2 ± 0.9% of all activity occurred from 1800–0900 h. Male spotted hyenas tended to be more active, and exhibit higher movement rates than females. Female hyenas in territories with daily livestock grazing showed lower activity and den use than hyenas in an undisturbed territory during the times of day when livestock grazing coincided with potential hyena activity.

Space use patterns of hyenas with no exposure to livestock grazing were influenced by the location of the communal den, and the distribution of prey,

vegetation types, and water features within their territory. Relative to this clan, hyenas exposed to livestock grazing showed a stronger avoidance of open grass plains and a weaker association with prey resources and den location. However, the distribution of livestock did not directly influence hyena space use patterns, indicating that increased use of vegetative cover by hyenas may be an important behavioral shift allowing temporary coexistence with livestock and their herdsmen.

Hyena home range size, core area size, and core area location were influenced by the presence of a refuse pit at the edge of one study clan's territory. The most common rank group utilizing the pit was low-ranking females, and regular pit users were more likely to be found near the pit during times of relative prey scarcity. These results indicate that human refuse at pastoral villages may increase hyena use of these environments, and that this use may vary on a seasonal and individual level.

Spotted hyenas, leopards (*Panthera pardus*) and lions (*Panthera leo*) were responsible for 53%, 32%, and 15% of attacks on livestock, respectively, that were documented along a Reserve border. Monthly depredation frequency was correlated positively with rainfall and negatively with natural prey abundance. The spatial location and size of local villages, and the fence type used at livestock enclosures influenced the vulnerability of these locations to livestock losses, with leopards and hyenas showing clear differences in selection of attack locations. Overall, improved fences, more watch dogs, and high levels of human activity were not associated with lower livestock losses to predators.

ACKNOWLEDGEMENTS

The research presented here was described in Animal Research Protocol No. 05/05-064-00, approved most recently on 3 May 2006 by the All University Committee on Animal Use and Care at Michigan State University (MSU). Throughout my tenure the Mara Hyena Project has been supported by NSF grants IBN0113170, IBN0343381, and IOB0618022 to Kay Holekamp. Throughout this program I personally received logistical and financial support from the College of Natural Sciences, the Department of Zoology, and the Ecology, Evolutionary Biology and Behavior program at MSU. In particular, the friendly and incredibly helpful staff of the Zoology Department office made navigating the waters of the MSU system manageable, and their assistance was always greatly appreciated.

I thank the Office of the President of Kenya for allowing us to conduct this research. I also thank the Kenya Wildlife Service, the Narok County Council and the Senior Warden of the Masai Mara National Reserve for their cooperation and assistance. I also thank the staff and management of Mara Intrepids Lodge for their support, logistical and otherwise, without which this study would not have been possible.

This dissertation was greatly improved by the insight and advice of my graduate committee, which included Joe Messina, Scott Winterstein, Laura Smale and my advisor Kay Holekamp. The logistical and financial support of Dr. Holekamp made it possible for me to live and work in Kenya for almost 3 years, allowing me to fulfill a nearly lifelong dream. I simply can't thank her enough for

making that possible. In addition, her support, guidance, and attention throughout this entire dissertation project was constant, it was critical to my success in completing this project, and it did not go unappreciated.

In spending close to 3 years in Kenya working on this project, I formed many friendships that made living away from home for so long not only bearable, but immensely enjoyable. Special thanks goes to the staff at Fisi Camp: John Keshe, James Kerembe, Moses Sairowa, and our askaris Stephen and Lesingo for keeping us safe, well-fed, and in good-spirits. In particular I thank John Keshe for his warmth and friendship throughout my time in Kenya. I would surely still be stuck on the Mara plains without the rescue efforts of Andrew Peart and his balloon crew, and the staff and guides of Base Camp who never hesitated to offer their help when needed. The work presented in Chapter 4 would not have been possible without the efforts of my livestock-conflict scouts: P. Mkurrana, D. Naurori, and D. Kasoe, the additional assistance of P. Naurori. Additionally, that research relied almost completely on the cooperation and participation of residents of our study area on the Koyake and Siana group ranches who provided their support, assistance and insight.

I would like to thank all the current and previous members of the Holekamp Lab, both graduate students, undergraduates, and field assistants that have been a part of the enormous effort required to keep the Mara Hyena Project going. Although many of these people, too numerous to name, have directly assisted me in one way or another on my way toward this degree, there are a few that deserve special mention. K. Kapheim and C. Beaudoin and J. Smith helped in the collection of field data that were used in this dissertation. Jaime Tanner and Heather Watts entered the program with me 6 years ago and have been my close friends ever since. They have supported me in innumerable ways since the very beginning and I can't thank them enough for what they've done. The importance of having a good office mate in one's intellectual, professional and personal development is often underestimated, but after spending my last years at MSU sharing an office with Kevin Theis, I will not be making that mistake. Despite his own, often intense workload, Kevin was always ready to answer a question, debate a relevant or irrelevant topic, or simply join in a voicing of frustration. His help, support and friendship throughout this process have been critically important. Kevin, Jaime and Heather also provided valuable comments and suggestions throughout all phases of my research and I am indebted to them for their help.

Much of the data presented in this dissertation were not easy to collect, and demanded long hours of radio-tracking at all hours of the day and night. Without the help of Sofia Wahaj and Matt Gibbons, one of which was present during almost all overnight hyena tracking sessions, these data would not have been collected. Somehow, Sofi and Matt persevered through all-night follows, dead car batteries in the middle of a dark grass plain, food deprivation, sleep deprivation, and the general uneasiness that comes with driving off-road in tall grass, in the dark. I am sure I have not thanked them enough for their part in maintaining my general sanity and contentment in the field, and in making this dissertation possible.

Many of my ideas regarding this dissertation were born from the earlier work of Erin Boydston, a previous member of the Holekamp Lab. Her excellent dissertation research paved the way for many of my ideas and objectives and I truly appreciate not only her previous efforts on the project, but also her assistance with my own research efforts here. I received critical assistance in the lab from undergraduates D. Katan, L. Kierepka and K. Lawracy as well as from S. Congdon who all provided helpful assistance with certain analyses. I thank Meredith Evans for helping with satellite image acquisition and analysis, Bilal Butt for freely sharing books, spatial data, and advice on a wide-array of topics, and Ashton Shortridge for taking the time to offer suggestions on spatial data analyses.

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INTRODUCTION

Worldwide, habitat suitable for wildlife is becoming increasingly rare due to human population growth and increasing rates of urbanization and habitat conversion. Because most mammalian carnivores exist at the top of their local food webs, they tend to range far more widely in search of food and mates than do other terrestrial mammals. As a result, carnivores may be more likely to come into contact with human populations than other species (Woodroffe 2001). Because large carnivores can rarely survive in human-altered habitats, they are particularly sensitive to habitat fragmentation (Woodroffe & Ginsberg 1998, 2000), and their low reproductive output and long-distance dispersal make them highly vulnerable to extinction (Sunquist & Sunquist 2001). However, their continued presence is often critical for proper ecosystem function (Berger 1999; Crooks & Soulé 1999; Ripple et al. 2001; Terborgh 2001).

Unfortunately, because local people often perceive predators as a direct threat to themselves or their livestock, sustained coexistence between humans and large carnivores is rarely possible outside of protected areas (Woodroffe & Ginsberg 2000). Therefore, as habitat is settled and developed, protected areas become the last remnants of suitable predator habitat. Today, however, even within these areas many carnivore populations continue to be affected by anthropogenic disturbance. Throughout the world, humans cause most adult mortality among large carnivores, including those inhabiting protected areas (Woodroffe & Ginsberg 2000). Not surprisingly, most adult mortality occurs when carnivores range beyond reserve borders. Thus, while habitat loss and persecution are restricting large carnivores to protected areas, 'edge effects' caused by human activity along reserve borders continue to reduce the viability of populations inside protected areas. As a result, research that investigates the effects of human activity on carnivores in and around protected areas, as well as the characteristics of human-carnivore interactions in these systems, becomes increasingly critical to the development and maintenance of carnivore conservation efforts around the world.

Despite the socio-political and economic complexities of carnivore conservation efforts, it is widely recognized that knowledge of the behavioral ecology of species of concern can be critical to successful management and conservation decisions (Caro 1999a). For example, detailed knowledge of behavior relating to a species' adaptability, flexibility, risk taking behavior, spacing, mating system, territoriality and habitat use are all directly related to their vulnerability to extinction and their resilience to disturbance or change (Arcese et al. 1997; Brashares 2003; Caro & Durant 1995; Weaver et al. 1996). Furthermore, behavioral data are critical to effective management of human-wildlife conflicts, as they inform the design of conflict prevention measures and identify the vulnerability of subsets of populations to conflict involvement (Arcese et al. 1997; Treves & Karanth 2003).

The Masai Mara National Reserve (hereafter the Reserve) in southwest Kenya offers an ideal setting in which to study human-carnivore interactions. The situation developing in the Reserve and surrounding areas typifies that facing numerous large carnivore species worldwide. Growth of local human populations in areas far north of the Reserve has sparked the clearing of savanna and woodlands to provide room for increased cultivation and settlement, constricting the habitat available to wildlife (Broten & Said 1995). Expanding cultivation, primarily in the form of large-scale wheat farming, has spread south toward the Reserve (Homewood et al. 2001) and has had the additional effect of limiting grazing land available to Maasai pastoralists (Serneels et al. 2001). Buffer zones surrounding the Reserve, which have traditionally been subjected to low intensity pastoralist or agropastoralist land use, are therefore becoming increasingly degraded (Serneels et al. 2001). Although livestock numbers have remained relatively stable in this region (Lamprey & Reid 2004; Serneels & Lambin 2001), livestock grazing inside the Reserve, though prohibited, has increased markedly in recent years and was described by the Kenya Wildlife Service as a 'rampant' problem in 1997 (Muriuki & Mulama 1997). Although herds are occasionally seen deep in the Reserve, the vast majority of trespassing occurs along the northeastern border (Muriuki et al. 2000). The human population itself is increasing along the Reserve border. All the lands bordering the Reserve to the north are communally owned, grazed and managed as "group ranches". On the Koyake group ranch, one of the largest group ranches bordering the northeastern portion of the Reserve, the human population is doubling every 15 years (Lamprey & Reid 2004), providing an increasing threat of direct persecution for carnivores ranging outside Reserve boundaries.

Although the spotted hyena (*Crocuta crocuta*), like most large African carnivores, has suffered a reduction in the extent of its historical range (Mills & Hofer 1998), it is recognized by the IUCN as a species of Lower Risk (IUCN 2006), and remains the most abundant and widespread large carnivore in Africa. The hyena's catholic diet has contributed to its ability to survive in diverse environments characterized by variable food resources, habitat characteristics, and competitors. Therefore, the responses of this species to human disturbances should represent conservative indicators of how other top predators, including those that are threatened and endangered, are likely to respond to similar perturbations. If human activity has negative effects on this highly adaptable and resourceful species, then the future of less resilient carnivore species in the same ecosystems is brought into serious question.

An intensive field study of the behavioral ecology of spotted hyenas in the Reserve began in 1988, under the direction of Dr. Laura Smale and Dr. Kay Holekamp, and continues to this day. The study has focused on members of a single hyena social group known as the Talek clan (which has since split into two clans; Talek West and Talek East) that defends a territory along the northeastern border of the Reserve. Due to its location, this clan has been exposed to increasing levels of human activity over the years of the study and currently interacts regularly with Maasai pastoralists and their livestock. The existence of this long-term study provided a unique opportunity to investigate the details of human-carnivore interactions in and around a protected reserve, and to incorporate detailed knowledge about the behavior and social structure of this species and about the individual identity of study animals.

The overarching objective of this dissertation research was to provide quantitative information on the effects of anthropogenic disturbances on spotted hyena movements and activity. However, whereas hyenas and other carnivores must adapt to the presence of humans in this and many other systems, so must humans adapt to the presence of carnivores. The Maasai people of Kenya that reside around the Reserve have a culture rich in pastoral tradition. Livestock play a central role in all aspects of their lives, and therefore conflict with large carnivores is an additional and inevitable component of their culture. Because the majority of carnivore mortality in protected areas is a result of human persecution, largely occurring outside reserve boundaries (Woodroffe & Ginsberg 2000), human-carnivore conflict must be mitigated, and tolerance of carnivores in human landscapes increased, to ensure the long-term persistence of many large carnivore populations. With this perspective, I focused one portion of my research on an investigation of carnivore-livestock conflict along the Reserve border. It is my hope that the results of this dissertation will be useful in guiding future management efforts in regard to spotted hyenas, as well as other large carnivores, and will elucidate the relationship between human activities and the carnivore populations struggling to exist in human-dominated landscapes. I also suggest that behavioral changes in animal populations subjected to varying degrees of human disturbance may be used as early indicators of potentially more severe consequences for population demography and viability.

I begin this dissertation, in Chapter 1, with an investigation into the activity patterns of spotted hyenas. Members of the Talek West clan have been monitored and closely observed since the start of this study in 1988. Because the clan territory is located along the heavily populated and intensely grazed northeastern border of the Reserve, this clan is subjected to frequent interactions with humans. Previous research suggested that hyenas in this clan have become more nocturnal over time, concurrent with an increase in the intensity of livestock grazing to which they were exposed (Boydston et al. 2003b). Similar modifications to activity patterns have been seen in numerous carnivore species resulting from either specific disturbances such as hunting or recreational activities (Kitchen et al. 2000; Olson et al. 1998), or from high overall levels of human activity and urbanization within territories (Ciucci et al. 1997; Lucherini et al. 1995; McClennen et al. 2001; Riley et al. 2003).

To address the question of whether Reserve hyenas exhibit similar activity pattern shifts in response to livestock grazing, I utilize a unique comparative approach, ideal for identifying the effects of human disturbance in natural settings (Arcese & Sinclair 1997; Caro 1999a). In 2001, I began studying hyenas in a clan located in the center of the Reserve, the Mara River clan. The territory defended by this clan is similar in all ecological aspects, including habitat and prey resources, to that of the Talek West clan, and it is located less than 6 km from the western edge of Talek West territory. However, due to its distance from the Reserve boundary, no livestock grazing occurs in the Mara River clan territory. Throughout this study this clan serves as a critical baseline control group and allows formal tests of predictions derived from hypotheses suggesting the effects of human activity on carnivore behavior. Specifically in this first chapter, I hypothesized that intense livestock grazing, which occurs during the day, has influenced the activity patterns of Talek West hyenas. I therefore predicted that differences in activity would be apparent between the Talek West and Mara River clans. In addition to providing detailed descriptive data on spotted hyena activity, including an investigation of the influence of sex and rank on activity, my results document clear differences in activity patterns between the two clans that correlate closely with the activity of grazing livestock. This chapter is currently in press at the *Journal of Mammalogy*, therefore references to it in Chapters 2–4 cite this manuscript.

Chapter 2 is a comprehensive investigation into the ecological determinants of space use in the spotted hyena and represents a logical continuation of the previous work of Boydston (2001) in the same Reserve. Here again I used a comparative approach to investigate the influence of livestock grazing on space use decisions by individual clan members. Although studies abound of space use by carnivores, few are able to associate space use with both landscape features and more variable ecological features such as prey distribution. Even fewer studies have investigated the influence of livestock grazing on the space use decisions of large carnivores and none of these have been conducted in East Africa. This chapter also focuses on the modifications in space use that may be available to spotted hyenas to minimize costs associated with livestock-related disturbance. Despite predictions to the contrary, data presented here indicate that Talek West hyenas did not actively avoid areas used by livestock, nor did they shift their temporal use of space to reduce use of heavily grazed areas during times of day when grazing herds were present. However, logistic regression modeling in both the Mara River and Talek West clan showed that the presence of vegetative cover, which has been shown to be highly variable over time in this ecosystem (Dublin 1995; Serneels et al. 2001), may be critically important to the successful coexistence of pastoralists and hyenas.

Although sheltered from most human activity, the hyenas in the Mara River clan were exposed for some time to the presence of an easily accessible, anthropogenic, non-livestock food source in form of a refuse pit near the border of their territory. In Chapter 3, I investigate the influence of this food source on the movement patterns of Mara River hyenas. I show not only that this small food source influenced movements of clan hyenas, but also that frequency of use of this food source was dependent on the local abundance of prey, and varied with an individual's social rank. These results are directly relevant to livestock depredation issues, as human refuse is often readily available near villages, and its presence has been suggested to influence rates of carnivore-human conflict (Beckmann & Berger 2003b) and livestock depredation rates (Mills & Hofer 1998). In addition, these findings indicate that behavioral variation among population subgroups may result in individual variation in susceptibility to edge effects. This chapter is currently under review at the *African Journal of Ecology*.

The dissertation concludes in Chapter 4 with a detailed investigation of the direct interactions between carnivores and Maasai pastoralists. There had been sporadic reports of livestock lost to hyenas, as well as leopards and lions, throughout the study since its inception (K. E. Holekamp, pers. comm.). However, the extent of these losses, the predators involved, and the factors influencing rates of livestock loss were all unknown. Here I document the extent of this depredation problem, and the relative involvement of each of the different predators present in the region. Most importantly, I show that livestock depredation has a clear and predictable association with rainfall, and that the rate of depredation at nighttime livestock corrals by leopards and hyenas is associated with fence type as well as by village location in the landscape. These findings and others result in clear recommendations for conflict mitigation that can be applied not only to this region but also across East Africa. Furthermore, the relationship of depredation rates to a combination of ecological and husbandry-related variables is supported by other recent work (Mech et al. 2000; Michalski et al. 2006; Ogada et al. 2003; Patterson et al. 2004); therefore, the implications of these results can potentially be applied to depredation management worldwide. This chapter was published in 2006 in *Biological Conservation*, therefore references to this chapter in earlier chapters cite this manuscript.

Because all Chapters presented here were prepared in manuscript form, and because the field work associated with these chapters, and the final preparation of the manuscripts was a truly collaborative effort, I have used the term “we” instead of “I” throughout the remainder of this dissertation, as I have done in the manuscripts themselves.

CHAPTER ONE

Kolowski, J.M., D. Katan, K. R. Theis, and K. E. Holekamp. 2007. Daily patterns of activity in the spotted hyena. Journal of Mammalogy (August issue).

CHAPTER ONE

DAILY PATTERNS OF ACTIVITY IN THE SPOTTED HYENA

INTRODUCTION

As in other mammals, the daily activity patterns of terrestrial carnivores result from both endogenous biological rhythms and behavioural adaptations to a changing environment (Daan 1981; Rusak 1981). Optimal patterns of activity reflect the influence of daily temperature variation (Avenant & Nel 1998; Garshelis & Pelton 1980), predation risk (Drew & Bissonette 1997; Geffen & Macdonald 1993; Lima & Dill 1990) and prey availability (Ferguson et al. 1988; Garshelis & Pelton 1980; Lariviere et al. 1994; Lode 1995). However, individual characteristics such as sex and reproductive condition may also influence patterns of daily activity (Daan & Aschoff 1982; Lariviere & Messier 1997; Paragi et al. 1994; Zalewski 2001). Furthermore, in gregarious carnivores whose societies are structured by linear dominance hierarchies, social status may also contribute to variation in activity patterns. Given increased human presence on landscapes worldwide, large carnivores have been shown to alter their natural patterns of activity to avoid human disturbances ranging from tourist or recreational activity (Machutchon et al. 1998; Olson et al. 1998) to direct exploitation by hunting (Andelt 1985; Kitchen et al. 2000). Therefore, where present, humans are likely to further influence observed activity patterns of free-living carnivores. Here we examine effects of these variables on activity patterns observed among spotted hyenas (*Crocuta crocuta*).

All four extant species in the family Hyaenidae are reported to be primarily nocturnal (Bothma & Nel 1980; Kruuk 1976; Mills 1984, 1990). However, the activity pattern of the spotted hyena, a gregarious carnivore found throughout sub-Saharan Africa, appears to be the most flexible, with activity often extending into periods of daylight (Kruuk 1972), or even occurring at mid-day (Rainy & Rainy 1989). The only systematic data describing *Crocuta*'s activity pattern come from the Serengeti ecosystem in Tanzania (Kruuk 1972) and from South Africa (Henschel 1986; Mills 1990). In both locations, hyenas exhibited a strongly nocturnal activity pattern with somewhat reduced activity during the middle of the night (Kruuk 1972; Mills 1990). However, within the Serengeti, the timing of evening activity peaks varied unpredictably over the course of months or weeks (Kruuk 1972). Furthermore, overall levels of hyena activity and movement rates were approximately twice as high in the Kalahari as in the Serengeti (Kruuk 1972; Mills 1990). Thus, patterns of activity are clearly variable in this species, yet sources of this variation remain unclear. Although Henschel (1986) documented sex differences in *Crocuta* activity and movement, the influence of social rank on these variables has yet to be investigated.

Our long-term study of spotted hyenas provides an opportunity to document in detail the activity patterns and movement rates of individual male and female *Crocuta* of various social ranks, and to investigate the influence of human presence on hyena activity. Livestock grazing has already been shown to influence patterns of space utilization by the *Crocuta* in our study population, and additional effects of grazing on hyena activity patterns were suggested by those data (Boydston et al. 2003b); however, the effect of daytime cattle grazing on carnivore activity patterns has not been investigated in any study system.

Our goals here were to (1) describe the general activity pattern and time budget of free-living *Crocuta* in Kenya, (2) investigate the influence of sex and social rank on activity patterns and time budgets and (3) investigate the effects of daytime human disturbance on hyena activity patterns and timing of den use. Because reproductive success among male hyenas is associated with their frequency of social interaction with the group's breeding females (East et al. 2003; Szykman et al. 2001), we expected that male movement and activity rates would exceed those of females, due to a need to regularly interact with as many females as possible. Because hyenas of low social rank have low priority of access to food resources, we expected they would exhibit higher activity and movement rates than hyenas of high rank. Finally, we were able to assess the influence of human disturbance on hyena activity patterns by comparing activity between members of neighboring social groups that differed in their exposure to both livestock grazing and tourist visitation during daylight hours. If hyena activity is affected by human presence on the landscape, then we expected activity rhythms to differ between these groups; specifically, hyena activity and den use in disturbed areas should be reduced when humans and cattle are present.

METHODS

Study area

Our study was conducted from 2001–2004 in and around the Masai Mara National Reserve (1500 km^2, hereafter the Reserve) in southwestern Kenya (1°40′S, 35°50′E). The Reserve consists primarily of rolling grassland and scattered bushland (predominantly *Croton* and *Euclea* species), with riparian forest along the major watercourses. Average annual rainfall in the study area from 2001–2004 was 1305 mm. Most rainfall occurs during two wet seasons: the "short rains" in November–December, and the "long rains" in March–May. Mean monthly daytime temperatures in 2003 averaged 28.3°C (range: 25.1–32.3°C), with the lowest temperatures occurring from May to July. Monthly nighttime temperatures averaged 13.8°C (range: 12.2–14.9°C). Because of the proximity of our study site to the equator, sunset and sunrise times varied little throughout the year with sunrise occurring from 0618–0648 h and sunset from 1828–1858 h.

Study populations

Spotted hyenas live in social groups called clans, and clan members cooperatively defend a stable group territory. Each clan contains one to several matrilines of adult females and their offspring, as well as one to several adult immigrant males. Clans are rigidly structured by hierarchical rank relationships (Frank 1986b; Kruuk 1972; Tilson & Hamilton 1984), with adult females socially dominant to immigrant adult males (Kruuk 1972; Smale et al. 1993). Subadult individuals of both sexes maintain their maternal ranks as long as they remain in the natal clan (Smale et al. 1993). Although females are generally philopatric (Frank 1986b), almost all natal males disperse between the ages of 2 and 5 years (East & Hofer 2001; Henschel & Skinner 1987; Van Horn et al. 2003). *Crocuta* clans are fission-fusion societies in which individuals travel, rest and forage in subgroups that typically change in composition many times each day (Holekamp et al. 1997a; Kruuk 1972). Female *Crocuta* bear 1–2 (rarely 3) young in isolated natal dens (Holekamp et al. 1996). Cubs are typically transferred to a communal den at 2–5 weeks of age where they reside for the next 7–8 months (Kruuk 1972). The communal den represents the social center of each clan's territory and most clan members visit it regularly. Den-independent cubs generally continue to nurse from their mothers until they are approximately 11–14 months old (Holekamp et al. 1996).

We monitored adult (>3 years old) members of three different clans. The adjacent territories of the Talek East (19.0 km^2, 29–35 members) and Talek West (28.4 km^2, 47–55 members) clans were both located mainly within Reserve boundaries but partially extended outside the northeastern border of the Reserve into lands occupied by Maasai pastoralists (Figure 1.1). The dominant land uses on Maasai-owned land were subsistence pastoralism and wildlife tourism. The Talek region supports the highest density of Maasai settlements along the entire northern border of the Reserve (Reid et al. 2003). Settlements within 2 km of this northeastern Reserve border supported roughly 12,000 cattle and 16,500 sheep and goats (Kolowski & Holekamp 2006), some of which were grazed illegally within the Reserve. Hyenas from both Talek clans have been killed at villages

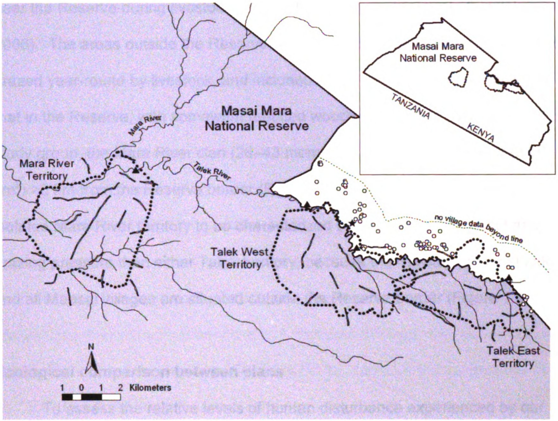


Figure 1.1. Territory boundaries (dotted lines) of the three monitored spotted hyena social groups (clans) in the Masai Mara National Reserve, Kenya. Triangles indicate the 4 main tourist lodges in the study area, open circles represent Maasai villages, and a star indicates the town of Talek. Prey sampling transects are indicated with checkered lines.

near the Reserve during livestock depredation attempts (Kolowski & Holekamp 2006). The areas outside the Reserve lying within the two Talek territories were grazed year-round by livestock, and included broad vegetation types similar to that in the Reserve, with somewhat reduced woody vegetative cover. Our 3rd study group, the Mara River clan (28–43 members), defended a territory (31.0 km^2) >6 km from the Reserve border (Figure 1.1). We expected the more isolated Mara River territory to be characterized by lower levels of tourist and grazing pressure than either Talek territory, because the majority of tourist lodges and all Maasai villages are situated outside the Reserve border (Figure 1.1).

Ecological comparison between clans

To assess the relative levels of human disturbance experienced by our study clans, we conducted monthly comprehensive livestock censuses in the Mara River territory (*n* = 18 months; Sept. 2002–Feb. 2004) and the Reserve portions of both the Talek West (*n* = 18 months; Sept. 2002–Feb. 2004) and East (*n* = 11 months; Sept. 2002–July 2003) territories. Censuses involved driving throughout each territory to obtain complete head counts for sheep, goat and cattle herds. Individual censuses were conducted at 2-h intervals throughout the day, with an initial census conducted as livestock herds entered the Reserve in the morning and a final census conducted as herds left the Reserve in late afternoon. However, censuses at these time intervals were not necessarily conducted on the same day; we completed one census during each 2-h interval once a month, with an average of five censuses per month (all at different times) in each territory.

As part of a larger ongoing study, behavioral observations of hyenas from each clan were conducted on average 22 days per month throughout the study period. Hyena observation "sessions" were conducted during all hours of the day and night but occurred primarily during the early evening (1730–2000 h) and late morning (0600–0830 h). To describe the timing and relative intensity of tourist use of our clan territories we recorded all instances of tour vehicles approaching hyenas during these sessions. These data were used to identify primary tourist use periods during the 24-h period and to calculate the frequency of vehicle approaches per hour of hyena observation during these periods in both the Talek and the Mara River territories.

In addition to human disturbance we assessed other ecological variables within each clan territory that might influence hyena activity patterns. We characterized the availability of natural prey to hyenas in each clan by counting all prey occurring along 1-km road transects in all three territories. Transects were located in open grassland to facilitate counting and were placed evenly throughout the territory, typically separated by less than 1 km (Mara River *n* = 24, Talek West *n* = 11, Talek East *n* = 13; Figure 1.1). We counted all wild ungulates within 100 m of each transect 2–4 times per month to estimate prey density values for both territories. Because lions are an important source of mortality for spotted hyenas (Kruuk 1972), we also recorded all observations of lions, either alone or interacting with hyenas, and calculated average lion group size and the relative frequency at which lions were observed within each territory.

Communal den use

The times of day at which females attend the communal den and nurse cubs may be influenced by human activity. We used two different methods to investigate whether the daily timing of den use in the two Talek clans (considered together here due to low sample sizes within each clan) differed from that observed in the Mara River clan. First, we utilized den observations lasting several hours to monitor fine-scale timing of den-use. Observers arrived at the communal den in the afternoon, before cubs emerged and before any other hyenas were present, and recorded both the time of arrival at the den of the first adult female or sub-adult, and the time at which den-dwelling cubs appeared above ground. We compared the Mara River and Talek clans with respect to the median time of first arrival and first cub appearance using a two-way test of independence to test for equality of medians (Sokal & Rohlf 1995).

Second, we utilized information collected during shorter-term behavioral observations at communal dens. Observers visited all active communal dens at least once every two days during regular morning and evening observation periods (see above). At each den visit, we conducted an initial scan to record which hyenas, if any, were present at the den at that time. We conducted subsequent scans of hyenas present every 10–15 minutes until a final scan was conducted before we left the den. We used logistic regression, with time as a single continuous predictor variable, to compare the Mara River and Talek clans with respect to the influence of time on the probability of observing any hyenas at the communal den. We performed separate regressions for each clan within each observation period (morning and evening) and individual model significance was assessed using a likelihood-ratio χ^2 test.

Hyena activity monitoring

We anesthetized 19 adult hyenas (11 females, 8 males) from two of the three study clans (Mara River *n* = 10, Talek West *n* = 9) with tiletamine/zolazepam (Telazol; W.A. Butler Company, Brighton, Michigan; 6.5 mg/kg) administered in a dart using a CO_2-powered rifle (Telinject Inc., Saugus, California), and fitted them with VHF radiocollars (Telonics Inc., Mesa, Arizona). Radiocollared hyenas were from a wide range of social ranks. To describe hyena activity patterns we utilized focal animal sampling with continuous recording of behavior. These sampling events (hereafter “follows”) lasted 2–15 h and were conducted at all times of day and night with the aid of night-vision binoculars and infrared spotlights. Although Talek East hyenas were included in analyses of timing of den use, they were not followed due to difficult terrain within their territory. Because we were interested in comparing movement rates of males and females without attachment to den sites, and because movements of female hyenas are influenced by the need to return to den-dwelling young (Boydston et al. 2003a), we only followed females without den-dwelling cubs.

Although we were unable to follow hyenas for complete 24-h periods due to logistical difficulties, we documented the 24-h activity pattern of each individual hyena by observing it during shorter follow segments that together generated a composite 24-h cycle. We attempted to complete this cycle as quickly as possible after its onset, with the average time necessary for completion being 31 days. Because 21% of the follow segments did not contribute to a composite 24-h cycle (e.g. due to hyena death or collar failure before cycle completion), analyses utilizing data from all recorded follow segments (i.e. from composite and incomplete 24-h cycles) are characterized by unequal sample sizes per hour-long time block. All analyses requiring equal sampling throughout the 24-h period utilize only data from composite 24-h cycles.

During each follow, we categorized the behavior of the focal hyena in every minute as traveling, nursing, resting, socializing, feeding, engaging in hunting, miscellaneous activity (standing, sniffing objects or the ground) or interacting with other carnivore species. We considered all behaviors other than resting and nursing as "active". When individuals were out of sight, we categorized animals that were clearly not resting (based on signal fluctuations, auditory clues, or obvious location changes) simply as "active", otherwise we recorded behavior and activity as unknown. We calculated the % time each hyena was active and engaged in each behavior during each hour block of each follow segment. Hour blocks with >20 min during which the animal was out of sight, or activity could not be assessed, were not included in hourly behavior and activity analyses, respectively. Follows were terminated when activity of the focal animal could not be conclusively determined for >20 consecutive minutes or when the focal animal was out of sight for >30 minutes within an hour block. Activity during composite 24-h follows is presented as the % of the entire 24-h period during which the animal was active. We also used composite 24-h follows to describe hyena time budgets, with the % time spent engaged in each behavior calculated out of the total minutes the animal was in sight during the 24-h period. To determine whether hyena activity was affected by human activity, we additionally compared individuals from the Mara River and Talek West clans with respect to % of total activity exhibited during daylight hours (0700–1800 h), as park regulations prevented public access to the Reserve between sunset and sunrise.

We calculated the length of all bouts of activity and inactivity; we defined the former as periods of at least 5 min of activity bounded on either end by 5 consecutive minutes of inactivity. We restricted analyzed bouts to those beginning and ending between 1800–0900 h to exclude long periods of daytime resting, and bout lengths were only calculated for follow segments lasting longer than 4 h. Bouts lengths were minimum estimates because some follows ended before bout completion. We identified cessation of daily activity as the time of morning after which no more than 10 consecutive active minutes were observed, and we identified onset of evening activity as the first afternoon time after which at least 10 consecutive active minutes occurred.

Because social interactions and group formation may be facilitated among distant hyenas through the use of long-distance vocalizations called whoops

(East & Hofer 1991b; Kruuk 1972), we also recorded all whooping behavior by focal hyenas to investigate its temporal distribution. As another measure of clan social activity we recorded the number of hyenas with the focal hyena every 10 min during follows, and further noted group size changes as possible within each 10 min interval. We then calculated the mean minimum hourly number of changes in group size using all composite 24-h follows.

To determine hourly movement rates, we recorded the locations of followed hyenas every 10 min and calculated straight-line distances between consecutive locations with Animal Movement Analyst (Hooge & Eichenlaub 2000) and ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California). Very few locations required the use of telemetry as followed hyenas were in sight, on average, for 98% of follow minutes. We then calculated average hourly movement rates for individuals based on composite 24-h follow cycles. Although we included only hour blocks with at least 4 locations per hour, we collected, on average, 140 of 144 possible locations per 24-h follow cycle.

In addition to the use of composite 24-h cycles to calculate mean % time active, and mean hourly movement rate for both daylight and the entire 24-h period, we used all individual follow segments to perform additional activity and movement comparisons, with data aggregated into 5 distinct diel periods. We excluded data collected from 1100–1400 h because negligible amounts of activity and movement were observed for any individual hyena during this time period. We divided the hours of darkness into 3 periods of equal length (night1: 1900–2300 h, night2: 2300–0300 h, night3: 0300–0700 h) and categorized the remaining hours as morning (0700–1100 h) and evening (1400–1900 h), based on average time of sunrise and sunset. We averaged hourly activity and movement rates within each of these 5 periods for each individual and made comparisons within time periods based on sex and clan. For comparisons of movement rates between males and females based on these 5 periods, we excluded all hour blocks during which the focal hyena engaged in a nursing bout to control for female movement limitations due to nursing demands. However, female movement rates based on 24-h follow cycles included follows during which nursing behavior was observed.

We categorized social rank for adult females as high or low relative to the median adult female rank. In analyses involving onset and cessation of activity, the sampling unit was the follow segment but in all other analyses, the sampling unit was the individual hyena. We averaged movement and activity data within sampling periods (e.g. hour, morning period) for individuals that were followed more than once during that period. Due to low sample sizes we compared mean proportions between groups using a nonparametric Mann-Whitney *U*-test, and compared frequency data using chi-squared tests.

Results in units of time are presented as medians because minutes are not on a strictly continuous scale; all other results are presented as means ± *SE*. Listed *p*-values are two-tailed unless research hypotheses generated clear directional predictions for group comparisons. For example, because we predicted males would show higher rates of activity and movement, and spend more time traveling than females, one-tailed tests were used for these comparisons. Statistical comparisons for all analyses were considered significant at $\alpha = 0.05$. All statistical analyses were conducted using the software package STATISTICA (StatSoft 2002).

RESULTS

We followed 19 different hyenas (11 females, 8 males) during 100 follow segments for a total of 628 h. The average length of follow segments was 6.3 h ± 3.3 h (*SD*). These segments resulted in 22 composite 24-h follow cycles for 16 different hyenas (11 females, 5 males). Four females and two males were followed for two 24-h cycles. Twenty-one follow segments did not contribute to a composite 24-h cycle.

General activity

The daily pattern of hyena activity was largely nocturnal with no clear peaks in activity throughout the night (Figure 1.2). In 16 follows of 11 different hyenas the time of cessation of daily activity could be determined, and yielded a median time of 0733 h (range: 0542–0918 h). The median time of onset of activity in 27 follows of 17 different hyenas was 1834 h (range: 1443–2037 h). The majority of activity observed during daylight hours occurred during the first two hours after sunrise (Figure 1.2). Based on composite 24-h follows, in which all hours were sampled equally, hyenas spent 31.5 ± 2.7% of their time active. During hours of darkness (1900–0600 h) hyenas spent 53.0 ± 4.1% of their time

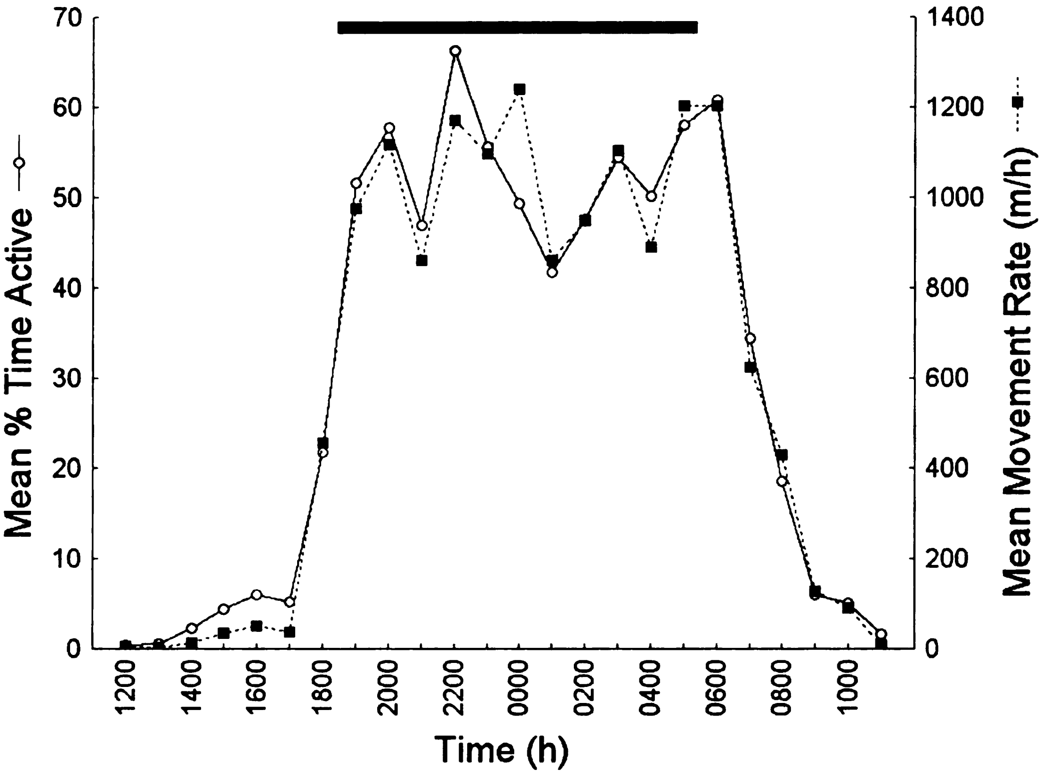


Figure 1.2. Activity pattern and movement rates of radiocollared adult spotted hyenas in the Masai Mara National Reserve, Kenya. Data are based on direct observations during long-term (2–15 h) follows of males and females. Number of individuals sampled varies per hour (*n* = 15–19). Plotted values for each hour (e.g. 1200 h) represent activity recorded in the following hour block (i.e. 1200–1259 h). The black bar extends over hour blocks characterized by darkness throughout the year.

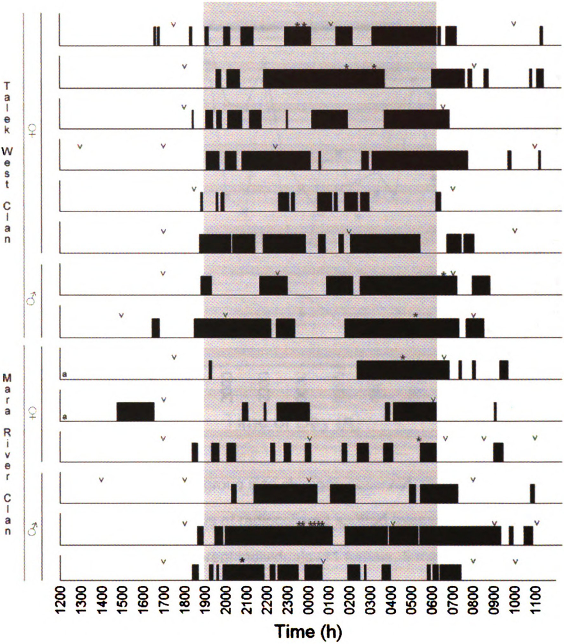
active, and 96.2 ± 0.9% of all activity occurred from 1800–0900 h. Only 9.7 ± 1.2% of their active minutes occurred during daylight hours (0700–1800 h).

Movement rates showed the same general pattern as activity (Figure 1.2); onset and cessation of movement were closely associated with sunrise and sunset and the majority of daytime movement occurred in the early morning. Using only composite 24-h follows, the mean movement rate for the entire 24-h period was 584 ± 64 m/h (range: 147–1185 m). Minimum nightly distance traveled based on follows $\geq$8.5 h in length ($\bar{x}$ = 11.4 h) averaged 12.4 ± 1.9 km (range: 3.5–21.7 km).

Duration of active bouts from 1800–0900 h averaged 62 ± 6.2 min, with 48% of active bouts being less than 30 min in duration (Figure 1.3). There was much individual variation in the timing and length of bouts of activity, and in the total amount of time spent active (Figure 1.3). Bouts of inactivity from 1800–0900 h averaged 53 ± 4.5 min in length. The longest recorded active bout during this period was for a male and lasted 383 min; the longest inactive bout was for a female and lasted 257 min.

Group size change showed a bimodal pattern (Figure 1.4). Not surprisingly, a similar pattern emerged from analysis of % time spent socializing, indicating that the majority of clan interactions occur either between 1900 and 2300 h or just after sunrise, between 0600 and 0700 h (Figure 1.4). Whoop vocalizations were recorded from 1829 to 0706 h and were equally likely to occur during all 2-h blocks from 1800–0800 h (χ^2_6 = 8.43, p = 0.209).

Figure 1.3. Bouts of activity (solid black bars) during 14 composite 24-h follow cycles for 13 individual radiocollared spotted hyenas. Active bouts were >5 consecutive active minutes bounded on both ends by 5 consecutive minutes of inactivity. Pictured 24-h cycles were those for which the night was described by no more than 2 follow segments. The letter “a” indicates a pair of follow cycles conducted on the same individual. Start and end points of each follow segment are indicated by a “v”. For example, the topmost follow cycle is composed of three nonconsecutive follow segments conducted from 1730-0100 h, 0100-1000 h, and 1000-1730 h. Asterisks indicate hunts and fresh kills on which the focal animal fed. Hours of darkness throughout the year fall within the shaded area.


Talek West Clan
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Time (h)

Figure 1.3.

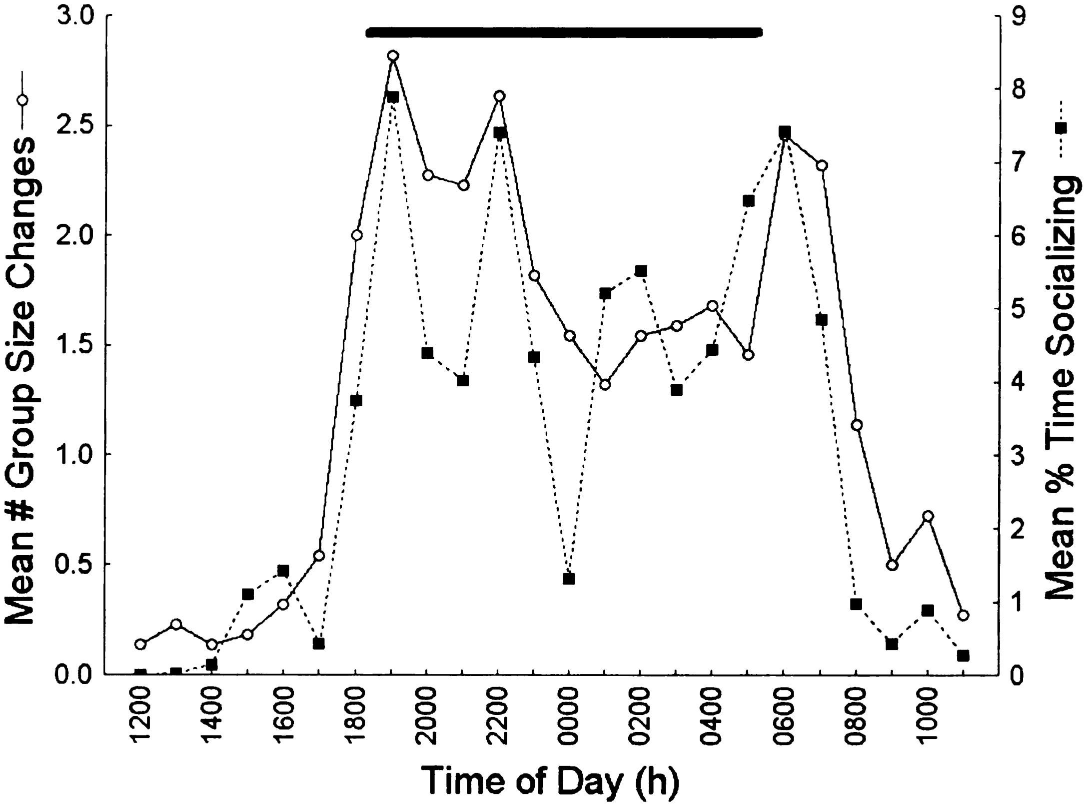

Figure 1.4. Mean number of group size changes observed and mean % time spent socializing during follows of radiocollared spotted hyenas. Data are from direct observations of 16 different individuals (11 female, 5 male) during 22 composite follows, each covering an entire 24-h period in nonconsecutive segments. Other notation is as in Figure 1.2.

Sex differences

Comparison of male and female time budgets, based on composite 24-h follows, revealed several differences. On average, males (n = 5) spent more time traveling (U = 11.0, one-tailed p = 0.031, Figure 1.5). Males also spent more time hunting than did females (U = 6.0, p = 0.015, Figure 1.5), but only 15 hunts were observed. Although focal females whooped during only 7 of 15 composite follows, focal males whooped during each of 7 composite follows. Mean whoop rates for the 11 females and 5 males were 0.04 and 0.34 times/h, respectively (U = 0.00, p = 0.002). Thus, males whooped 8.5 times more often than did females.

Although both sexes started activity at the same time of day, males tended to spend a larger portion of the 24-h period active (37.9 ± 5.7%) than did females (28.6 ± 2.7%, U = 16.00, one-tailed p = 0.097; Figure 1.6A, Table 1.1). The greatest sex differences in activity occurred in the morning time block (26.7 ± 10.1% and 11.0 ± 2.8%, U = 13.00, one-tailed p = 0.071; Table 1.1). Males showed clear peaks in activity from 2200–2300 h, and from 0600–0700 h, during which activity levels averaged close to 80% (Figure 1.6A), but comparable peaks in female activity were not apparent.

Males tended to exhibit higher movement rates than did females over the 24-h period (U = 14.00, one-tailed p = 0.063; Table 1.1) with the most obvious differences observed during the first half of the night (Figure 1.6B). Male movement rates peaked at 0000–0100 h, but female movements did not show a clear peak (Figure 1.6B). The maximum distance moved in a single hour was

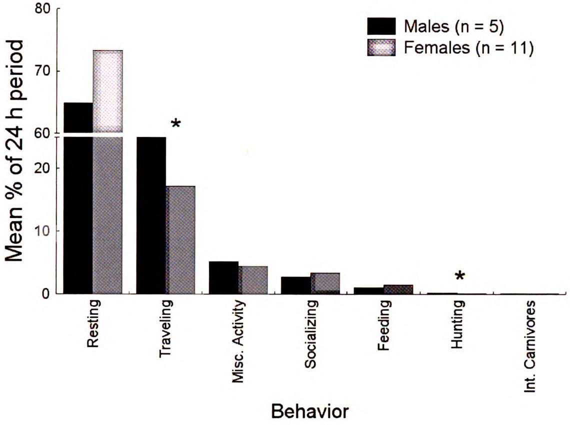

Figure 1.5. Mean % time spent engaged in various behaviors for 5 male and 11 female spotted hyenas during follows covering the entire 24-h period in nonconsecutive segments. Miscellaneous activity included standing, and sniffing objects or the ground. Traveling included both directed movement and wandering behavior. Significant differences (Mann–Whitney *U*-test, $p < 0.05$) are indicated by an asterisk.

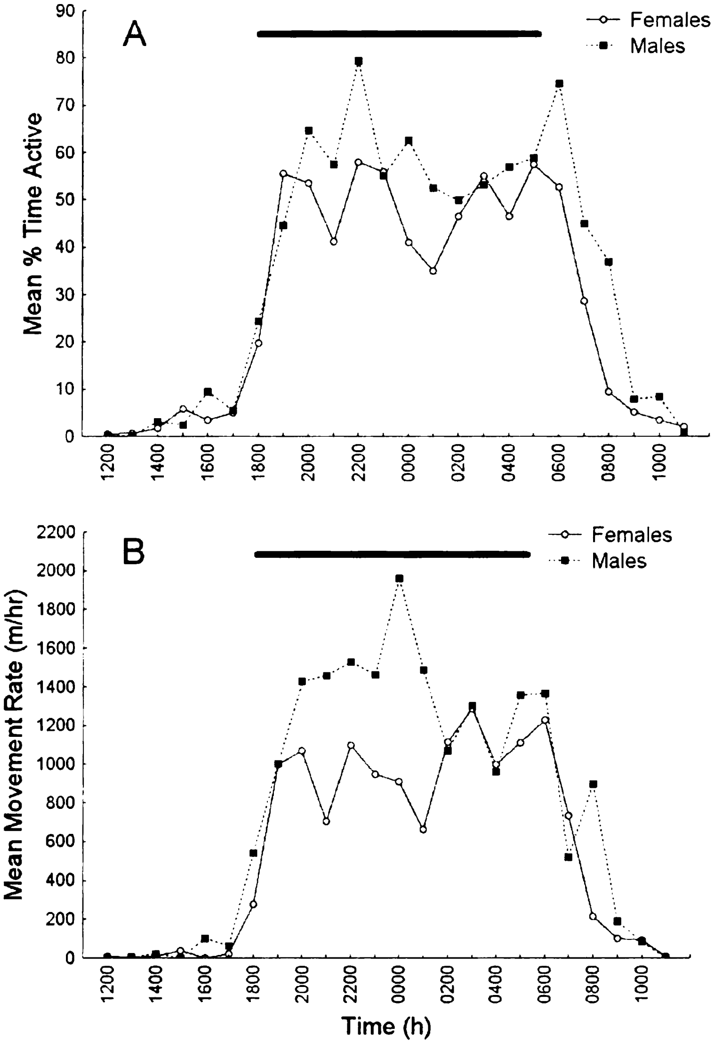

Figure 1.6. A) Sex differences in mean % time spent active by radiocollared adult spotted hyenas. Data are based on direct observation during long-term (2–15 h) follows of males and females. Number of individuals sampled varies per hour (females *n* = 9–11; males *n* = 5–8). Figure notation is as in Figure 1.2B. Mean hourly movement rates of radiocollared adult spotted hyenas excluding data collected during hour blocks when focal females nursed their cubs. Number of individuals sampled varies per hour (females *n* = 7–11; males *n* = 5–7).

Table 1.1. Mean (*SE*) activity and movement rates for male (M) and female (F) spotted hyenas in the Masai Mara National Reserve, Kenya. Time periods are as follows: Evening: 1400–1900 h; Night1: 1900–2300 h; Night2: 2300–0300 h; Night3: 0300–0700 h; Morning: 0700–1100 h.

	Mean % Time Active			Mean Movement Rate (m/h)		
	M	F	P^a	M	F	P^a
Evening	10.0(4.0)	8.0(2.2)	0.479	166(63)	82(25)	0.139
Night1	62.3(8.6)	52.1(7.0)	0.241	1474(255)	1014(265)	0.062
Night2	55.6(7.7)	44.6(7.3)	0.171	1540(374)	957(292)	0.238
Night3	59.4(14.6)	49.2(8.4)	0.211	1247(380)	1193(242)	0.500
Morning	26.7(10.1)	11.0(2.8)	0.071	445(124)	307(104)	0.190
24 h day[b]	37.9(5.7)	28.6(2.7)	0.097	737(137)	515(64)	0.063

[a] Based on results of one-tailed Mann–Whitney *U*-tests

[b] Based only on data from composite 24-h follow cycles

4680 m by a male hyena and 4513 m by a female. All movement rate averages are likely underestimates because extremely fast movement sometimes resulted in termination of follows.

Effects of social rank

Because we found clan differences in some measures of activity (see below), we restricted our analysis of social rank to those measures of activity that showed no differences between the clans. We pooled females from both clans resulting in use of 6 high-ranking (4 Talek, 2 Mara River) and 5 low-ranking (2 Talek, 3 Mara River) females. Based on composite 24-h follows, high-ranking females were no less active (26.7 ± 3.6%) than low-ranking females (30.9 ± 4.2%) over the 24-h period ($U = 11.00$, one-tailed $p = 0.233$). In addition, high- and low- ranking females showed no differences in the % time spent resting, hunting or traveling ($U > 7.0$, $p > 0.14$), and they showed similar movement rates during the 24-h period ($U = 13.00$, one-tailed $p = 0.358$). However, females of lower rank spent more time feeding (2.2 ± 0.4%) than did those of high rank (0.8 ± 0.3%; $U = 3.0$, $p = 0.028$).

Clan differences: Ecology

Monthly prey counts yielded estimates of prey density that did not differ significantly among the clans (Mara River = 196.6/km^2, Talek West = 210.8/km^2, Talek East = 181.9/km^2; Kruskal-Wallis test: $H_{2,48} = 2.17$, $p = 0.124$). The average size of lion groups seen within the territories of the two Talek clans ($\bar{x}$ =

3.9 ± 0.26) was no different than that of groups seen within the Mara River territory ($\bar{x}$ = 3.4 ± 0.30, U = 6284.5, p = 0.108). In addition, 1-2% of observation sessions included lions, either alone or with hyenas, in both Mara River and Talek territories.

Illegal grazing of cattle, sheep and goats inside the Reserve occurred nearly every day within the territories of both Talek East and West clans. Monthly livestock censuses recorded an average of 991 cattle and 1038 sheep and goats utilizing the area within the Talek West territory, and 515 cattle and 257 sheep and goats within the Talek East territory. Livestock grazing in the Talek area, whether inside or outside the Reserve, typically occurred from 0900–1800 h. In contrast, no livestock were ever seen in the Mara River clan's territory. Tour vehicles were present in all three territories primarily during only two periods each day: 0630–0900 h and 1630–1900 h. During these periods, researchers observed tour vehicles 4.8 times more frequently while observing hyena groups in Talek (East and West pooled) than in the Mara River territory.

Clan differences: activity and movement

Because males and females were not sampled equally between clans, and because we demonstrated differences in activity and movement rates between the sexes, comparisons of activity and movement between the Talek West and Mara River clans include only data from females. Female hyenas from the Talek West clan were followed 30 times for 206 total hours ($\bar{x}$ = 6.9 h/segment) and Mara River females were followed 29 times for 176 hours ($\bar{x}$ =

6.1 h/segment). Using composite 24-h follows, Mara River females (*n* = 5) were no more active (27.3 ± 4.0%) than were Talek West females (29.7 ± 3.9%, *n* = 6) over the 24-h period ($U = 0.715$, $p = 0.715$; Table 1.2). However, differences between clans were apparent in the timing of activity, with Mara River females showing more activity than Talek West females in the evening (one-tailed $p = 0.025$; Figure 1.7A) and during daylight hours (one-tailed $p = 0.034$; Figure 1.7A). In addition, the evening onset of socializing was delayed for Talek females relative to Mara River females (Figure 1.7B). Although females from both clans showed an early evening peak in % time spent socializing, that peak occurred 3 h earlier in Mara River than in Talek (Figure 1.7B). Comparisons of 24-h time budgets showed no differences between the two clans in % time spent engaged in any specific behaviors ($U > 7.0$, $p > 0.17$). Additionally, no differences were observed in overall movement rates or timing of movements during the 24-h period between females from the two clans (Table 1.2).

Clan differences: communal den use

We conducted 17 evening long-term observations at communal dens in Mara River and 28 in Talek. Den-dwelling cubs were first seen at communal dens earlier in the evening and at a wider range of times in Mara River (median = 1716 h; range = 1540–1854 h) than in Talek (median = 1844 h, range = 1738–1906 h; $p < 0.001$). In addition, time of arrival at the communal den of either an adult female or large subadult was earlier and more variable in Mara River

Table 1.2. Mean (*SE*) activity and movement rates for female spotted hyenas from either the Talek West (TW) or Mara River (MR) clans within the Masai Mara National Reserve, Kenya. Time periods as in Table 1 and daylight is 0700–1800 h.

	Mean % Time Active			Mean Movement Rate (m/h)		
	MR	TW	P^a	MR	TW	P^a
Evening	13.1(2.7)	3.9(1.7)	0.025^b	115(6)	70(33)	0.350^b
Night1	52.0(12.0)	52.2(9.2)	1.000	1026(569)	1009(339)	1.000
Night2	36.5(11.3)	51.3(9.5)	0.361	735(100)	1068(446)	0.643
Night3	37.1(7.4)	59.4(13.2)	0.144	993(301)	1361(377)	0.361
Morning	9.2(4.8)	12.2(3.8)	0.335^b	353(277)	292(122)	0.370^b
Daylight[c]	12.3(1.9)	6.9(1.9)	0.034^b	128(37)	108(45)	0.357^b
24 h day[c]	27.3(4.0)	29.7(3.9)	0.715	463(56)	558(109)	0.465

[a] Based on results of Mann–Whitney *U*-tests

[b] One-tailed *P*-values

[c] Based only on data from composite 24-h follow cycles

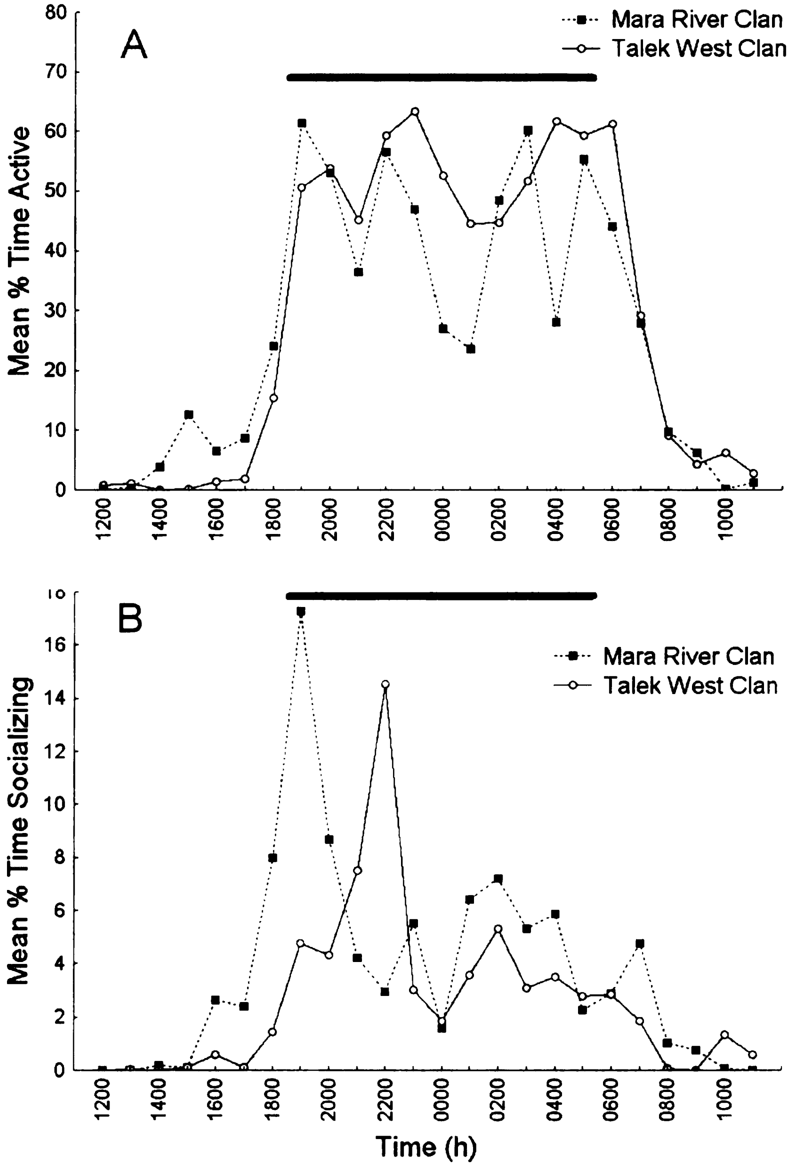

Figure 1.7. The mean % time spent A) active and B) socializing by radiocollared adult female spotted hyenas from two different social groups (clans). Data are based on direct observation during long-term (2–15 h) follows. Number of individuals sampled varies per hour (Talek West *n* = 5–6; Mara River *n* = 4–5 for activity and *n* = 3–5 for socializing). Figure notation is as in Figure 1.2.

(median = 1654 h, range = 1323–1853 h) than in Talek (median = 1834 h, range = 1730–1908 h; $p < 0.005$).

We recorded 3300 scans (morning: 1353, evening: 1947) at active communal dens in Talek East and West clans and 1562 scans (morning: 759, evening: 803) in the Mara River clan. Logistic regression indicated that time had a significant influence on the probability of Talek hyenas being present at the communal den in both the morning (Log-likelihood $\chi^2_1 = 11.778$, $p < 0.001$) and evening (Log-likelihood $\chi^2_1 = 53.022$, $p < 0.001$) periods; scans were more likely to reveal no hyenas late in the morning and early in the evening (Figure 1.8). In contrast, time did not influence hyena presence at communal dens during either the morning (Log-likelihood $\chi^2_1 = 1.130$, $p = 0.288$) or evening (Log-likelihood $\chi^2_1 = 0.704$, $p = 0.401$) observation periods in the Mara River clan (Figure 1.8). Therefore den use, as documented by both observation methods, appeared to begin later in the evening and end earlier in the morning in the Talek clans than in the Mara River clan, further reinforcing the apparent evening phase delay suggested by observed differences in the timing of activity and socializing.

DISCUSSION

General activity

Overall activity levels of Mara hyenas corresponded closely with those reported for *Crocuta* in South Africa (Kalahari Gemsbok NP: 31.5% of 24 h, 53.0% of nighttime—Mills 1990; Kruger NP: 27.5% of 24 h—

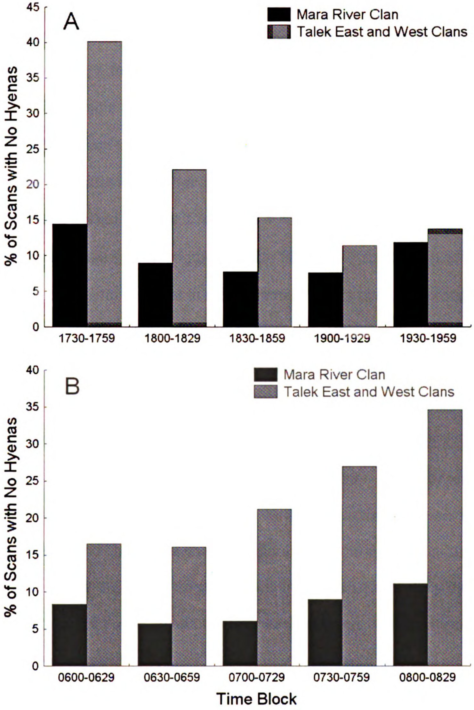

Figure 1.8. Percent of A) evening and B) morning scans at active communal dens in which no hyenas were present during each of 5 half-hour blocks for the Mara River Clan and the Talek East and West Clans.

Henschel 1986). Mara hyenas also spent amounts of time resting (70.7%) and traveling (19.9%) that were similar to those reported for Kalahari *Crocuta* (69% inactive, 23.6% foraging). However, Kalahari hyenas traveled more than twice as far each night ($\bar{x}$ = 27.1 km/night) than did Mara hyenas. This difference may reflect the much larger clan territories observed in the Kalahari ($\bar{x}$ = 1095 km^2), where prey densities are far lower than in Kenya (Mills 1990). The nightly distance traveled by Mara *Crocuta* ($\bar{x}$ = 12.4 km) matched more closely that of a followed female in Ngorongoro NP ($\bar{x}$ = 10.1 km—Kruuk 1972), where clan territories are more similar in size to those of Mara clans (Ngorongoro NP: $\bar{x}$ = 23.8 km^2—Honer et al. 2005).

As in previous studies, we observed activity onset to occur around sunset, with the majority of daytime activity occurring early in the morning (Kruuk 1972; Mills 1990). Like Henschel (1986), but in contrast to Kruuk (1972), we found little evidence of consistent peaks in activity through the night, likely resulting from a large degree of individual and nightly variation in activity. However, peaks in socializing and group size changes offer insight into the fission-fusion sociality of *Crocuta*. The majority of socializing within the clan, particularly by females, is conducted soon after onset of activity each evening. Groups formed during this period often remain relatively stable through the night until just after sunrise, when groups undergo additional reshuffling before the daytime rest period. We found the frequency of whooping activity to be constant throughout the night, as was also shown for males at dens in the Serengeti (East & Hofer 1991a).

Although activity graphs depicting an average activity pattern (as in Figure 1.2) are useful for describing general patterns, they fail to depict episodes of rest that may occur frequently and unpredictably throughout the night. Our study reports the first records of duration of active and inactive bouts for this species and indicates a highly punctuated pattern of nightly activity, with frequent bouts of inactivity interspersed among active bouts of highly variable duration. Individual differences in the timing and length of active bouts were remarkable, as has been observed in other large carnivores (Garshelis & Pelton 1980; Theuerkauf et al. 2003b). However, occasional and unpredictable group behaviors such as border patrols, lion-hyena interactions and inter-clan conflicts influenced timing and levels of nightly activity within individual follow segments, and replication within individuals would be necessary to adequately assess individual variation in activity. Previous studies of some felids have noted a detectable reduction in activity for multiple days after kill events (*Puma concolor*—Beier et al. 1995, *L. rufus*—Schmidt 1999). However, whereas felids may take several hours or days to consume a carcass, hyenas feed with remarkable speed (e.g. 18 kg food/h/hyena—Kruuk 1972) and commonly feed in groups, thus reducing the likelihood that single kill events would significantly influence patterns of activity.

Sex and rank differences

Because follows were logistically difficult, many of our analyses suffer from small sample sizes and few replicates within individuals, so factors such as weather and prey abundance may have influenced individual activity and movement estimates. We attempted to follow individuals exclusively during clear weather, and across a wide range of prey abundance conditions, but we were otherwise unable to control for these factors. Although previous studies have shown seasonal variation in hyena movements due to prey fluctuations (Hofer & East 1993a; Trinkel et al. 2004), these studies were conducted in areas where prey abundance in some regions decreased annually to near-zero values whereas the Reserve supports relatively stable resident ungulate populations throughout the year. Furthermore, when pooling females from both study clans, we found no correlation between local prey densities and hyena movement rates or activity, and two females that were followed in both periods of high and low prey density showed very similar activity rates (unpublished data). However, our sample sizes prevented us from specifically controlling for these factors and our results should therefore be interpreted with due caution.

We predicted, based on sexual selection theory, that the significant positive relationship between male reproductive success and time spent with receptive females (East et al. 2003; Szykman et al. 2001) would demand higher rates of movement and activity in males than in females. Indeed, like Henschel (1986), we found male spotted hyenas tended to be more active and to travel further than females during a 24-h period. Here, differences were most pronounced in the hours just after sunrise and sunset.

The African lion displays fission-fusion sociality similar to that of spotted hyenas, with group composition being both temporary and unpredictable (Schaller 1972). Although male lions of unknown or nomadic social status have been shown to range more widely than resident females during the night (Hemson 2003; Stander 1997), comparisons between males and females of the same resident pride have not been performed. The fission-fusion society of *Crocuta* is also remarkably similar in many respects to that of some primates, including spider monkeys (*Ateles* spp.—Chapman 1990; Symington 1990) and chimpanzees (*Pan troglodytes*—Lehmann & Boesch 2004). Although chimpanzees generally show no sex differences in their time budgets, males travel faster and cover greater daily distances than do females (Doran 1997). In spider monkeys, the fact that males range more widely, travel faster, and spend more time traveling than females within the shared group territory has been suggested to be the result of males monitoring females and patrolling territory boundaries (Shimooka 2005). Because participation in territory defense and border patrolling behavior is no more common in male than female *Crocuta* (Boydston et al. 2001), we believe the sex differences we observed reflect male monitoring of females rather than territory boundaries.

Although low-ranking female spotted hyenas range more widely than high-ranking females (Boydston et al. 2003a; Honer et al. 2005), we found no rank-related variation in movement rate or activity levels among the females followed here. We also found time budgets to be remarkably similar between high and low-ranking females with the exception of more time spent feeding by low-ranking females. Although high-ranking hyenas spend more time feeding than low-ranking clan members in competitive feeding situations (Frank 1986b), we suspect that low priority of access to kills forces low-ranking individuals to rely on lower quality food (e.g. bone) and may force them to engage in longer, more frequent feeding bouts over time. One would similarly predict low-ranking females to hunt more often than high-ranking females, and although our sample size for hunts was too small to detect rank effects, previous research has demonstrated this trend (Holekamp et al. 1997b).

Clan differences

Female hyenas in the Talek West Clan showed less daytime and early evening activity than did females in the Mara River Clan. In addition, the range of times utilized by Talek East and West females when attending the communal den was small relative to that of Mara River females, with Talek den use starting later in the evening and ending earlier in the morning. Various ecological differences might potentially have caused the observed differences in use of time between study clans, yet the Talek and Mara River territories differed very little except with respect to the intense daily exposure of Talek hyenas to the presence of tour vehicles and livestock.

Our data suggest that tour vehicle activity alone could not account for observed differences between clans with respect to hyena activity and den use. Despite an often heavy volume of tour vehicles from 0630–0830 h, when hyenas are generally active but before cattle enter the Reserve, we found no reduction in activity or movements of Talek females relative to Mara River females during this period. Additionally, despite constant tourist presence in Talek from 0630–0900 h, den use by Talek hyenas progressively decreased as the start of the grazing period approached. During the evening onset of hyena activity, when both tourist use and livestock activity was high in Talek, hyena activity was reduced, and both den use and peaks in socializing were delayed relative to those observed among Mara River females. Tour vehicles, while abundant in both Talek clan territories, do not pose a direct threat to hyenas and have been present in this ecosystem for more than three decades. Maasai herdsmen, however, represent a direct threat to hyenas, as humans are an important source of mortality for this population, second only to lions (Watts & Holekamp in review). Additionally, hyenas appear to perceive herdsmen as a threat because hyenas often flee from guarded cattle herds, whereas cattle left unattended by herders are not avoided (unpublished data). This response has also been noted among African wild dogs (Fuller & Kat 1990). Taken together, these observations suggest that cattle grazing, but not tourism, affected temporal distribution of activity among Talek hyenas.

Although the influence of human disturbance in the form of livestock grazing on the activity patterns of other carnivore species has not been investigated, similar activity shifts to those observed here have been described in response to a wide variety of anthropogenic disturbances with predictable temporal schedules. Carnivores that typically show some degree of diurnal activity have been found to increase or completely rely upon nocturnal activity when faced with the threat of hunting mortality (Andelt 1985; Kitchen et al. 2000) or harassment resulting from human recreational activities (Beckmann & Berger 2003a; Olson et al. 1998), except where spatio-temporal avoidance is possible

(Theuerkauf et al. 2003a). Similarly, daytime movements and activity have been reduced or eliminated among carnivores living in urban, or human-dominated landscapes (Ciucci et al. 1997; Lucherini et al. 1995; McClennen et al. 2001; Riley et al. 2003).

Although direct fitness costs might be expected to result from reduced diurnality in species adapted for daytime or crepuscular activity (e.g. cheetah, bears, coyotes), such direct costs are not expected in hyenas. Their night vision is believed to be as good as their day vision (Kruuk 1972), and variation in hunting success with time of day has not been reported. However there may be indirect fitness costs in this species when daytime activity is eliminated. For example, diurnal activity may reduce risk of predation on hyena cubs by lions, which are active almost exclusively at night (Schaller 1972; Stander 1992). Similarly, little daytime activity by predators was suggested to explain diurnal activity exhibited by female wolves with young cubs in an otherwise nocturnal group (Vilà et al. 1995). In addition, a reduction in the range of times available to females to nurse cubs at dens could potentially reduce overall numbers of nursing bouts, increase energetic stress on both cubs and mothers, and promote social conflict over den access. Although we did not observe enough nursing bouts or lion-hyena interactions in the three clans to address these hypotheses, long-term demographic data indicate no recent reductions in cub survival or clan size in the Talek area (Watts & Holekamp in review), suggesting that these indirect costs, while potentially important, have not reduced fitness in these hyenas.

We have shown that human disturbance in the form of livestock grazing, can alter patterns of activity and den use in this species. While it remains unclear what fitness costs might ultimately be incurred by spotted hyenas from disturbance-based alteration of normal activity patterns, documentation of behavioral changes such as these among large carnivores is critical to the development of our understanding of human-carnivore interactions and the extent to which carnivores can adapt to human presence. Changes in activity patterns or movements can potentially be used as early behavioral indicators of the extent and severity of human disturbance and may have other unforeseen consequences. For example, reduction of daytime activity by large carnivores might negatively influence monitoring efforts based on sighting data (Caro et al. 1998), or reduce the frequency with which tourists can observe these animals.

CHAPTER TWO

ECOLOGICAL AND ANTHROPOGENIC INFLUENCES ON SPACE USE IN THE SPOTTED HYENA (*CROCUTA CROCUTA*)

INTRODUCTION

It has become increasingly clear that continued presence of large carnivores is often critical to proper ecosystem function (Berger 1999; Crooks & Soulé 1999; Ripple et al. 2001; Terborgh 2001). However, large predators are in global decline due to a combination of habitat degradation and direct human persecution (Weber & Rabinowitz 1996; Woodroffe 2001), and mortality associated with "edge effects" threatens the persistence of even protected carnivore populations (Woodroffe & Ginsberg 1998). Given the increasing fragmentation of carnivore habitat in an expanding matrix of agriculture and urbanization, there is a critical 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 in response to disturbance or change (Arcese et al. 1997).

Because resources available to carnivores in areas influenced by human activity inevitably vary in quality, responses to human disturbance represent tradeoffs between optimal resource use and decreased risk of persecution (Gill & Sutherland 2000). With this perspective, the overall importance to carnivores of resources within disturbed environments should influence their response to disturbance, as well as the costs associated with this response. It is therefore essential to determine not only the factors influencing space use decisions, but also the costs and trade-offs associated with these decisions. For example, alterations in carnivore space use resulting from human disturbance may reduce exposure to humans and therefore the threat of human-caused mortality, yet access to critical prey or habitat resources may be compromised. Quantification of these costs and trade-offs will provide an increased ability to forecast the consequences of disturbance of varying degrees, and identify the costs to carnivores of functional habitat losses associated with human activity.

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; Mills & Hofer 1998; Nowell & Jackson 1996). Although the spotted hyena (*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. For example, spotted hyenas are found in habitats ranging from desert to rainforest, and occur in social groups (clans) ranging in size from 10 (Mills 1987) to 80 (Kruuk 1972). As is the case with many African carnivores, hyenas frequently share the landscape with human pastoralists; therefore livestock are a common landscape feature for many hyena populations. Whereas in many systems worldwide livestock left unguarded in pastures are unlikely to serve as a disturbance to carnivores, livestock throughout much of East Africa are closely guarded, and herders pose a direct threat to carnivores. Hyenas have been shown to alter their patterns of activity in response to livestock grazing (Kolowski & Holekamp 2007) and to reduce use of intensely grazed areas over time (Boydston et al. 2003b).

Multiple studies have demonstrated carnivore avoidance of areas characterized by intense human activity (wolves—Thurber et al. 1994; mountain lions—Van Dyke et al. 1986; coyotes—Gese et al. 1989; bears—Mattson 1990; Olson 1994; Reinhart 1990), yet few have attempted to quantify the trade-offs involved in disturbance response decisions (but see Gibeau et al. 2002). In addition, few researchers have investigated the influence of livestock on carnivore space use patterns (Chavez 2006), particularly where the presence of herds is associated with potential for direct persecution from herdsmen.

The primary objective of this study was to identify the factors influencing patterns of hyena space utilization. By describing these relationships concurrently for hyenas in both disturbed and undisturbed environments within the same ecosystem, we attempted to isolate the influence of livestock grazing on space utilization. In addition, by monitoring a number of potentially important ecological variables concurrently, we attempted to identify the potential costs to hyenas associated with this disturbance, in terms of their ability to optimize use of territory resources. Finally, we investigated the mechanisms by which hyenas exposed to livestock grazing may adapt to this disturbance.

Boydston et al. (2003b) showed that large portions of the territory of a clan of hyenas ("Talek" clan), in the Masai Mara National Reserve, Kenya (hereafter the Reserve) that were heavily used by hyenas from 1988–1990, were avoided from 1996–1998. Ungulate and livestock sampling demonstrated that avoided areas were characterized by both the highest prey densities and the most intensive livestock grazing in the territory. Consequently, the presence of livestock within the territory may have serious fitness implications for Talek hyenas in that effective habitat loss due to grazing might be associated with loss of access to critical prey resources. In addition Boydston et al. (2003b) demonstrated increased use of densely vegetated habitat corresponding in time with dramatic increases in livestock grazing within the territory.

Before human presence can be causally linked with recent observed changes in Talek hyena behavior, baseline knowledge of resource use patterns in the absence of livestock grazing must be described to allow separation of direct and indirect human influence from influences of the natural environment (Arcese & Sinclair 1997; Caro 1999a). The Mara River (MR) clan, which defends a territory free from livestock grazing in the center of the Reserve, served here as a baseline control. The results of Boydston et al. (2003b) suggest that Talek hyenas, over time have increased their use of vegetative cover, potentially as a refuge from grazing herds and pastoralists. Their results further suggest that Talek hyenas, due to the presence of livestock, were unable to utilize prey resources within their territory in an optimal fashion. We therefore hypothesized that the presence of livestock grazing as a frequent and intense disturbance results in adjusted space use decisions by hyenas that sacrifice optimal resource use, for reduced threat of persecution. Specifically, we tested the following predictions: 1) densely vegetated habitats should be less heavily used by MR hyenas than by Talek hyenas, 2) prey distribution should be a more effective predictor of space use by MR hyenas than Talek hyenas, and 3) probability of use of a given area by Talek hyenas should be negatively associated with intensity of use by livestock.

Herds grazing in the Reserve typically enter the park between 0800–1000 and leave by nightfall (Boydston et al. 2003b). Because livestock grazing is predictable in time and space, hyenas may restrict use of grazed areas to times of day when grazing is absent, and therefore minimize effective loss of habitat within the territory. This may be particularly true if avoided areas are resource-rich (Boydston et al. 2003b), because habitat available to hyenas is constrained by territorial boundaries and agonistic interactions with hyenas in neighboring clans. Such spatio-temporal shifts have been seen in a number of carnivores, with individuals increasing use of disturbed areas during daily periods when the disturbance was minimal or absent (Ciucci et al. 1997; Gibeau et al. 2002; Machutchon et al. 1998; McLellan & Shackleton 1988). We therefore tested the additional prediction that hyenas exposed to livestock should modify their temporal patterns of space use to minimize effective habitat loss. Specifically, we expected that: 1) Talek hyenas would be found in areas of high livestock disturbance more frequently during periods in each 24-h cycle when grazing is rare or absent than when grazing is frequent and, 2) hyenas would be found further from areas of the most intense livestock grazing during grazing periods, than during disturbance-free periods.

METHODS

Study area

This study was conducted from September 2002–April 2004 in the Masai Mara National Reserve in southwestern Kenya. The Reserve supports a large diversity of resident ungulates including gazelles (*Gazella thomsonii* and *G. granti*), impala (*Aepyceros melampus*), topi (*Damaliscus lunatus*), and giraffe (*Giraffa camelopardalis*). In addition, from August to October small resident populations of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) are joined by large migrant herds from Tanzania. The Reserve consists primarily of rolling grassland habitat and scattered shrubland with riparian forest along the major watercourses.

Study populations

We monitored individual hyenas from two clans in the Reserve. The Mara River (MR) clan defended a territory near the center of the Reserve (Figure 2.1) and included 28–38 individuals ($\bar{x}$ = 8 adult females, $\bar{x}$ = 5 immigrant males). The Talek West (TKW) clan defended a territory along the northwestern border of the Reserve (Figure 2.1) and contained 47–55 hyenas ($\bar{x}$ = 11 adult females, $\bar{x}$ = 7 immigrant males). Due to its location along the Reserve border, and its proximity to a number of pastoral villages (Kolowski & Holekamp 2006), the TKW clan territory is subjected to daily livestock grazing pressure. By contrast, no livestock were ever seen grazing within the territory of the MR clan during our study period.

Hyena locations

We anesthetized 29 adult hyenas (18 females, 11 males) from our two study clans with tiletamine/zolazepam (Telazol; W.A. Butler Company, Brighton, Michigan; 6.5 mg/kg) administered in a dart using a CO_2-powered rifle (Telinject Inc., Saugus, California), and fitted them with VHF radiocollars (Telonics Inc., Mesa, Arizona). The 12 hyenas (7 females, 5 males) collared in the MR clan had functional collars for an average of 396 d (range = 98–578 d) during our study period. The 17 collared hyenas (11 females, 6 males) in the TKW clan were monitored for an average of 391 d (range = 66–608 d). Radiocollared hyenas spanned a wide range of social ranks in both study clans. We made attempts to locate each collared individual on a daily basis. Most radiotracking was conducted during the morning (0530–0900 h) and evening (1730–2000 h), but additional locations were collected throughout the day and night. The majority (66%) of all tracking locations were based on direct sighting of hyenas (MR: 72%, TKW: 60%). When visual confirmation was not possible, we were able to localize the radio signal to an area typically $< 200m^2$; therefore spatial resolution of tracking locations was high in all cases. To avoid temporal autocorrelation in tracking locations, all locations for the same individual were separated by at least 1 hour, as that is a conservative minimum estimate for the time it takes an individual hyena to cross its entire territory (White & Garrott 1990). However, individuals were rarely tracked more than twice a day.

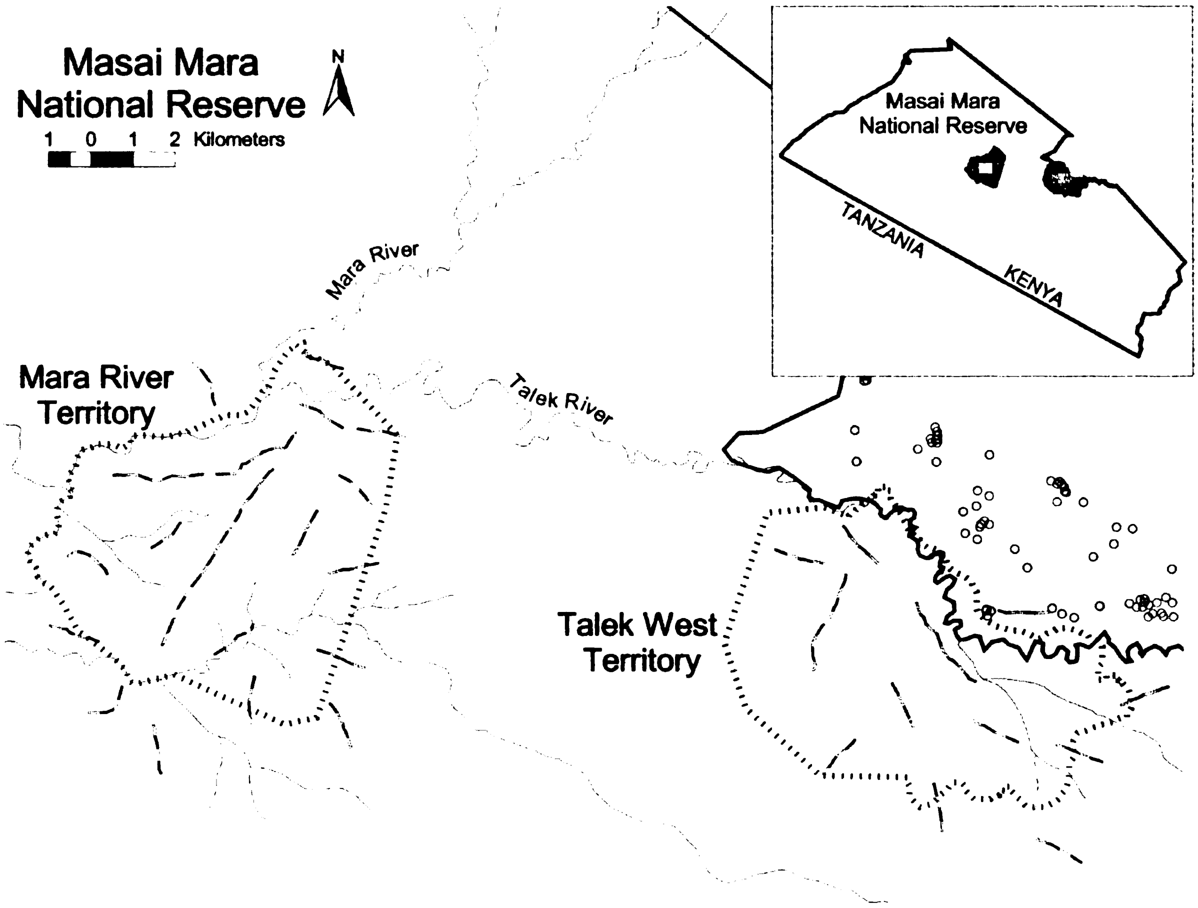

Figure 2.1. The location of the territory boundaries of the two study clans. Ungulate transects are shown with barred lines and Maasai villages within 2 km of the Reserve are shown with open circles. Note the extension of the Talek West territory outside the Reserve boundary.

Hyena clan territories

We identified territory boundaries of the MR clan based on a combination of territorial behavior and radiolocations of adult females. An initial Minimum Convex Polygon (MCP) was created using all recorded locations of communal dens (see "Dens" section below) and territorial behavior, which included boundary patrols, aggressive interactions with neighboring clans, and latrine sites (see descriptions of these behaviors in Henschel & Skinner 1991; Kruuk 1972; Mills & Gorman 1987). This polygon was then manually adjusted to align with natural boundaries known to limit hyena movement (i.e. the Mara River). Finally the polygon was expanded to match a 95% fixed-kernel home-range contour (Powell 2000; Worton 1989) created using all tracking locations of radiocollared adult females from June 2001–April 2004, where this contour extended beyond the MCP. This process was repeated for the TKW clan, but female locations here were limited to those collected after 1 April 2002, when a long-term fission event in this clan was conservatively estimated to have been complete. This fission resulted in creation of the Talek West and Talek East clans from a single "Talek" clan. The territory of the MR clan was 31.0km^2 and was based on 2407 tracking locations; the territory of the TKW clan was 28.4km^2 and was based on 1967 tracking locations.

Livestock distribution

To document the spatial distribution of livestock grazing, we regularly conducted comprehensive livestock censuses in the Reserve portions of the

TKW territory. Censuses involved driving throughout the territory to obtain complete counts of sheep, goat and cattle herds. Herds containing less than 500 head were estimated to the nearest 50 animals; herds containing >500 were estimated to the nearest 100 animals. Individual censuses within months were conducted at 2-h intervals throughout the day, with an initial census conducted as livestock herds entered the Reserve in the morning and a final census conducted as herds left the Reserve in late afternoon. However, censuses at these time intervals were not necessarily conducted on the same day; we completed one census during each 2-h interval each month, with an average of five censuses per month (all at different times). Livestock are corralled at night in the villages outside of the Reserve. Based on observed grazing patterns we identified the hours between 0900 to 1800 h as "grazing hours" (GH) and the hours from 1900 to 0800 h as livestock-free hours (LFH). We considered the hours from 1800 to 1900 h and 0800 to 0900 h as transition periods between grazing and livestock-free hours, because the timing of herd movement into and out of the park was somewhat variable.

We recorded a point location for the center of all herds using car-mounted GPS units by approaching the herds at close range, and estimated the shape and size of the area in which the herd was grazing. Herd shapes were then drawn in a GIS and filled with randomly located points according to the recorded herd size, with each cow represented by a single point location. Because livestock data were based on complete censuses rather than sampling transects, we did not use interpolation methods to create livestock distribution surfaces.

We instead created a utilization distribution grid surface for the entire territory using fixed-kernel methods with values of each grid cell weighted according to the actual density of livestock locations observed within and around each cell (Seaman & Powell 1990; Worton 1989). Grid surfaces were created for each month of the study as well as for larger time intervals, depending on the analyses, by pooling livestock locations (from censuses at all 2-hr intervals) across the period of interest. 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 late afternoon and early morning herd locations. This was done to ensure that grid surfaces reflected the fact that herds deep in the Reserve must have traversed the space between their grazing location and the Reserve border when not observed. Grid cell lengths for created surfaces varied with the number and density of livestock points, but ranged from 40–100m. Final grid cell values, referred to hereafter as livestock use values (LUVs) ranged from 0–100, with higher numbers indicating higher grazing intensity. Although all livestock in the area were counted, analyses utilized only herds recorded within the territory boundaries of our study clan.

Ecological Variables

Dens

Two types of dens, natal and communal, are utilized by spotted hyenas (East et al. 1989; Kruuk 1972; Mills 1990). Hyena cubs are typically born in a natal den at which no other litters reside. After a period of 1–5 weeks (East et al. 1989; Kruuk 1972), cubs are moved to the clan's communal den, which is often used concurrently by several litters of varying ages. Cubs in the Reserve reside at the communal den, on average, for the next 7–8 months (Holekamp et al. 1996), at which time they begin to follow their mothers throughout the territory and gradually gain independence. Typically a single communal den is used within a territory at any given time (Kruuk 1972; Mills 1990), but den locations may change frequently (e.g. every 1.5 months average for Talek Clan—Boydston et al. 2006).

When females have cubs at natal dens, they typically spend large portions of their time there. Once cubs are moved to the communal den, mothers spend less time at the den but often visit it at least twice a day to nurse their cubs (Kruuk 1972). When females have den-dwelling cubs they are found, on average, closer to the communal den than they are at other phases of their reproductive cycle (Boydston et al. 2003a), 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 center of social interaction and sub-group assembly for the clan (Holekamp et al. 2000; Kruuk 1972; Mills 1990). Thus, in addition to females with cubs, it was expected here that all other clan members would, to some extent, exhibit space use patterns influenced by the location of the communal den. We recorded the coordinates of all communal dens utilized by MR and TKW hyenas during the study period, as well as their dates of usage.

Water

Water was not expected to be a limiting resource here, as permanent water sources are found throughout the Reserve, and hyenas living elsewhere within this ecosystem show little dependence on free water (Kruuk 1972). However, the placement of water features may indirectly influence hyena movements, for example, by providing cool daytime resting sites or by influencing preferred vegetative characteristics. Therefore, we obtained maps in vector format of all permanent and seasonal streams digitized from aerial photographs (Boydston 2001) and, when necessary, streams were digitized directly in the field with a hand-held GPS unit.

Prey Distribution

Spotted hyena ranging patterns are influenced by the local distribution of prey resources (Hofer & East 1993a; Mills 1990; Trinkel et al. 2004), Within the Reserve, hyenas have been found to use areas of higher prey density more frequently than areas of lower prey density, except when disturbed by intensive grazing (Boydston et al. 2003b). Here, we characterized the availability of natural prey to hyenas in each study clan by counting all prey occurring along multiple 1-km road transects in both territories. Transects were located in open grassland to facilitate counting, were placed evenly throughout each territory, and were typically separated by less than 1 km (Mara River $n = 24$, Talek West $n = 14$; Figure 2.1). Because the primary prey species of Crocuta are ungulate grazers, we assumed that shrubland and riparian forest habitat, in which no prey transects were located, supported the lowest prey densities in each territory. We counted all wild ungulates within 100 m of each transect 2–4 times per month. Each kilometer of transect was divided into thirds, with the number of prey counted along each third associated with a midpoint for each section. Therefore, each km of transect was assigned three points, each with its own corresponding prey count for each sampling event. This allowed estimation of variability and spatial correlation in prey densities over short distances, as well as over the longer distances between transects. Each point was assigned the mean number of prey counted on the corresponding transect section (0.333 km * 0.2 km = 0.067km^2) over the period of interest ("prey value"). For each month, as well as for longer periods of analysis, a prey distribution grid surface was then interpolated from these data points using inverse distance weighting (power function = 2). Final grid surfaces were composed of relatively large 500 m x 500 m cells covering each territory to represent the course resolution of the field data. Each cell therefore represented the estimated prey value at that location based on transect points within and around each cells according the inverse distance weighting function.

Vegetation

Vegetation may influence hyena space use in a variety of ways. Vegetation classes may be effective indicators of other important ecological features such as diurnal resting spots or prey distribution. Additionally, dense vegetation may offer important refugia for hyenas in disturbed habitats, as indicated by Boydston et al. (2003b). Therefore, we created a vegetation map for each study clan territory based on a combination of three data sources: vegetation type reference points collected in the field, a 15m-resolution panchromatic Landsat 7 ETM+ image, and a 30m-resolution 6-band Landsat 7 ETM+ image. Both Landsat images were collected on 4 Feb 2003 and were geo-referenced using previously digitized road intersections and streams. Vegetation reference points were recorded in both territories (Mara River n = 899; Talek West n = 1257) during the last 11 months of the study period, during which all tracking locations were associated with a particular vegetation class at the time of collection. A vegetation map for each territory was digitized by hand in a GIS with three brad vegetation class: riparian forest, shrubland, and open grass plain (Figure 2.2). Shrubland was defined as dense woody cover, the vast majority of which was *Croton* or *Euclea* bushes approximately 2m in height. Riparian forest often included this shrub layer but was distinguished by the presence of a tree canopy. We assumed that these 3 classes were sufficient to describe the cover types available to hyenas, given the low diversity of vegetation types in this area and the overwhelming dominance of grass plains in both territories (~ 80% of territory area for each clan, see Figure 2.2).

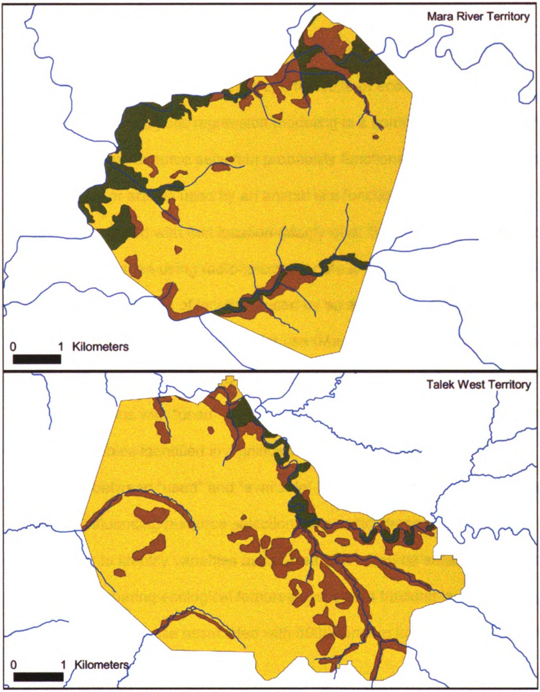

Figure 2.2. Vegetation class maps for the territories of the Mara River and Talek West hyena clans. Permanent and seasonal streams are shown in blue, and the three vegetation classes are grass plain (yellow), shrubland (brown) and riparian forest (green).

Logistic regression models

We used logistic regression models to identify relationships between observed hyena space use patterns and the suite of ecological variables described above. 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). The estimation of these functions when using radio-telemetry data is often 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). Characteristics associated with locations used by animals are then compared to those at available locations with "used" vs. "available" modeled as the binary dependent variable. Variables identified in significant models are those that effectively differentiate between "used" and "available" locations, and therefore represent the factors influencing resource selection by a particular species. We used this methodology to identify variables associated with resource selection in spotted hyenas by comparing ecological features associated tracking locations of spotted hyenas ("used") to those associated with 5000 random locations identified within each clan territory ("available").

Each hyena tracking location was associated in a GIS with specific values of the ecological variables described above. In order to model the influence of the den location, given that it was not constant throughout the study period, all modeling was restricted to periods during which den location did not change, or was moved less than 1 km. In the latter case, the average UTM coordinates for all dens occupied within that modeling period were used to represent one den location for the period. All locations, both “used” and “available”, were then assigned a distance to the average den location for each modeling period. In addition, each location was associated with a prey value and, for TKW only, a livestock use value, based on the grid cell value underlying the location. These cell values were based on separate livestock and prey distribution maps created for each modeling period. We then assigned each “used” and “available” location to a vegetation class based on the digitized vegetation maps (Figure 2.2). Finally, for each location, we calculated the distance to the nearest stream of any size, the nearest permanent stream and the nearest vegetative cover. Cover was defined here as all areas not classified as grass plain.

All spatial analyses were performed using either ArcView GIS 3.2 or ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California) with the help of a number of program extensions. Animal Movement Analyst (Hooge & Eichenlaub 2000) was used to create all MCPs and fixed kernel home ranges, and to calculate distances between point locations and specific habitat features. Association of point locations with the grid cell values of prey and livestock distribution grid surfaces was performed using the Grid Tools extension (Jenness 2006) and Spatial Analyst. Inverse-distance weighted surfaces for prey distributions were created using Spatial Analyst in ArcView and ArcGIS. Satellite images were processed and georectified in Erdas Imagine 8.6 (Leica Geosystems LLC, Norcross, Georgia).

Model creation procedure

Separate logistic regression models were created for each modeling period with the following predictor variables: vegetation class, distance to den, distance to nearest stream, distance to nearest permanent stream, prey value, and LUV (for Talek West models only). Because vegetation class was a categorical variable, it was modeled using grass plain as a reference category. Each model compared variables associated with random locations ("available") with the same variables measured for hyena tracking locations ("used"), using only hyena locations collected during that modeling period. Because reproductive state was found to influence ranging patterns of adult females hyenas (Boydston et al. 2003a), model comparisons between clans may be biased depending on the relative numbers of tracking locations for females with and without den-dependent cubs. Therefore all female locations were categorized according to whether or not each female currently had cubs residing at dens. We then excluded locations for females with den-cubs that were recorded at either natal or communal den locations. Additionally, since random locations had to be identified within an area deemed "available" to hyenas (here the territory), we similarly limited hyena locations for these analyses to those falling within territory boundaries. This resulted in a loss of less than 4% of tracking locations in each clan. In the TKW clan, since livestock data were only available for locations inside the Reserve, we also limited locations for analysis in this clan to those occurring inside the Reserve, resulting in a further loss of 3.6% of all tracking locations for TKW hyenas.

For each modeling period, all possible logistic regression models using all recorded variables were compared using information-theoretic methods (Burnham & Anderson 2002). These methods utilize Akaike's Information Criterion (AIC) values to incorporate both model parsimony and model fit to assist in selection of appropriate descriptive models. All models within 2 AIC points of the optimal model were investigated and considered to have empirical support based on the data (Burnham & Anderson 2002). We identified the predictor variables included in all models in this initial subset, and ran a final logistic regression model that including only these variables. The significance of variables in each final model was based on the Wald statistic, and overall 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 for the same clan, and between the clans themselves. In logistic regression, an odds ratio represents the change in the odds of the dependent variable being "true" (in this case being identified as a "used" rather than an "available" location), associated with a one-unit change in a predictor variable (e.g. 1m for distance variables). Here, we report modified odds ratios (Long 1997) that represent the % change in probability associated with a biological meaningful change in each predictor. For distance measures we used an increase of 100 m, for prey values an increase of 5 units (estimated density), and for livestock use values an increase of 10 units (% probability of livestock use). We used the average modified odds ratio for individual variables over all models within clans to qualitatively assess the overall influence of independent variables in the models on space use in each clan.

To investigate the potential influence of time of day on the relative importance of ecological variables, we used the above methods to run separate logistic regression models within each modeling period using hyena locations collected either during grazing hours (GH: 0900–1800 h) or livestock-free hours (LFH: 1900–0800 h). For this analysis and those described in the next section, we assumed that prey distribution did not change significantly between the GH and LFH hours. During radiotracking sessions we noticed no obvious changes in prey distribution between day and night periods and nighttime assessments of prey distribution were logistically impossible.

Analysis of spatio-temporal shifts in utilization

We used two different methods to investigate the possibility that hyenas in the TKW clan utilized spatio-temporal avoidance of livestock to prevent effective habitat loss. We first inquired whether livestock use values associated with hyena locations collected during GH were lower than those collected during LFH, as this would indicate increased use of disturbed areas when the disturbance is absent. We also asked whether the proximity of hyena locations to areas characterized by the most intensive livestock use differed between GH and LFH.

Tracking Locations and Livestock Use Intensity

Because livestock use intensity varied from month to month, we first investigated the relationship between the distributions of livestock and hyenas on a monthly basis. We created livestock utilization distributions, as described above, for each month of the study period and associated each hyena tracking location, based on date of collection, with the corresponding LUV for the location. We included only tracking locations falling within both Reserve and clan territory boundaries, and excluded seven months when <20 tracking locations were collected during either GH or LFH. First, we compared monthly LUVs of hyena locations to the average LUV of all cells within the Reserve portion of the TKW territory. We considered hyenas to have avoided livestock when the 95% confidence interval for the mean hyena location LUV did not overlap with the overall territory LUV. Within each month, we then calculated the average LUV of hyena locations collected during GH and LFH. If spatio-temporal avoidance was occurring, we expected LUV values to be higher for locations collected during LFH. We compared mean values in a paired *t*-test using months as sampling units. The latter analysis was then repeated using individual hyenas as sampling units instead of months. For these comparisons, we assigned LUVs to hyena locations based on a livestock utility distribution created using livestock data from all months during which the individual was monitored (using all herds plotted during this period). We included only individual hyenas that were tracked >20 times during both GH and LFH. Included hyenas were all monitored continuously for at least 18 months. We used independent sample *t*-tests to compare average LUVs for locations collected during GH and LFH for each hyena, and a paired *t*-test, using hyenas as sampling units, to assess the overall difference between LUVs of GH and LFH locations.

Tracking Locations Relative to Livestock Core Area

The second method used to determine whether TKW hyenas avoided livestock examined locations of tracked hyenas relative to the area(s) in which the most intense livestock use occurred throughout the study period (livestock core area: “LCA”). The LCA was identified as the area within the 50% contour of a fixed-kernel livestock utility distribution based on all herds recorded in the TKW territory throughout the entire period during which each hyena was radiotracked. Each hyena location was assigned a distance to the LCA, and was also categorized as being within or outside this area. We recorded the proportion of GH and LFH hyena tracking locations that fell inside the LCA, as well as the average distance to the LCA for both sets of locations. Proportions and mean distances were calculated on a monthly basis, excluding seven months where <20 locations were collected during GH or LFH. Mean distances were compared using *t*-tests and proportions were compared using χ^2 tests. Overall differences between GH and LFH locations in the distance to the LCA were compared using a single paired *t*-test and months as sampling units.

RESULTS

Logistic regression models

Modeling Periods

We identified three modeling periods for the MR clan, which averaged 161 d in length (range: 80–274 d), during which the location of the den did not change more than 1km (Table 2.1). We identified 4 such periods for the TKW clan that

Table 2.1. Periods identified in the study period during which den location was stable in the Mara River (MR) and Talek West (TKW) clans. Logistic regression modeling of resource 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/km of transect and the mean # of livestock animals counted per census drive during each period, respectively.

Period	Dates	Days	Hyenas (f,m)	Tracks	Prey	Livestock
MR1	10/03/02 – 12/21/02	80	9 (6,3)	387	43.5	–
MR2	12/23/02 – 4/30/03	129	10 (6,4)	596	16.0	–
MR3	5/04/03 – 2/01/04	274	9 (5,4)	1249	54.3	–
TKW1	11/01/02 – 4/06/03	157	12 (6,6)	578	37.9	2266
TKW2	7/28/03 – 11/02/03	98	11 (6,5)	407	58.2	1046
TKW3	12/26/03 – 2/06/04	43	12 (8,4)	235	30.4	1078
TKW4	2/07/04 – 4/30/04	85	12 (7,5)	464	56.0	615

averaged 96 d (43–157 d; Table 2.1). After excluding a small subset of locations, as described above, the mean number of tracking locations per period was 744 in the MR clan (range: 387–1249) and 421 locations in the TKW clan (range: 235–578; Table 2.1). The average proportion of MR locations collected during LFH and GH for these modeling periods was 50.8% and 26.8%, respectively. The average proportion of TKW locations collected during LFH and GH was 46.5% and 21.7%, respectively.

Univariate Comparisons ("Used" vs. "Available" Locations)

Prey distribution grid surfaces indicated variability in both the distribution and abundance of prey among modeling periods for both clans (Table 2.1, Figure 2.3 and 2.4). Livestock utility distribution grids showed similarly high variability in intensity of grazing among modeling periods in TKW (Table 2.1, Figure 2.5), but the spatial distribution of livestock, in contrast to that of prey, appeared stable over time (Figure 2.5). The monthly mean number of livestock counted per census in the TKW territory was 1386 ± 181 (range: 106–3160).

We identified clear differences between used and available locations in both clans based on simple univariate comparisons. In fact, all measured ecological variables, both continuous (Figure 2.6, Table 2.2) and categorical (Figure 2.7, Table 2.3), showed significant differences between used and available locations. Hyenas in both clans were located significantly closer to the den than expected in all modeling periods (Figure 2.8 and 2.9), and, with the exception of one modeling period (TKW1), hyena locations were associated with higher prey values than were available locations. Univariate comparisons showed no

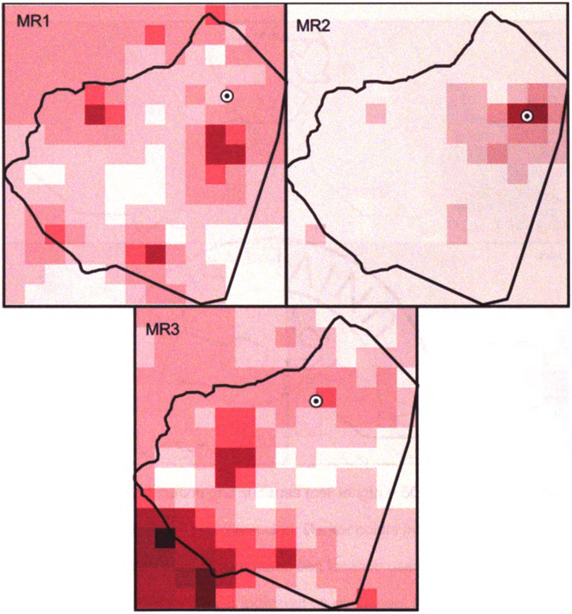

Figure 2.3. Prey distribution grid surfaces (cell length = 500 m) for each of the 3 modeling periods for the Mara River clan. Darker colors indicate higher estimated prey densities. The communal den location used during each period, and the clan territory boundary, is indicated on each map. Note that prey distributions indicated outside territory boundaries are not accurate.

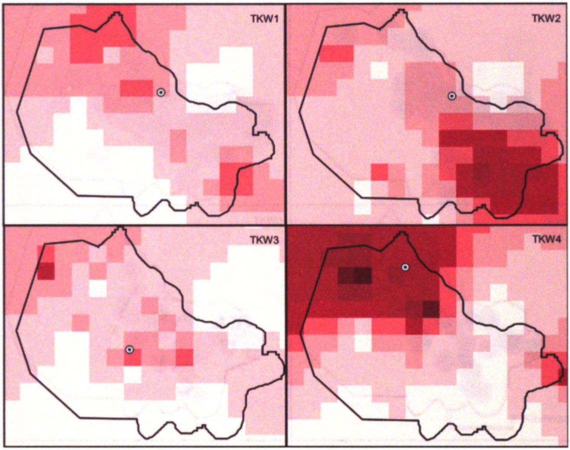

Figure 2.4. Prey distribution grid surfaces (cell length = 500 m) for each of the 4 modeling periods for the Talek West clan. Darker colors indicate higher estimated prey densities. The communal den location used during each period, and the clan territory boundary is indicated on each map. Note that prey distributions indicated outside territory boundaries are not accurate.

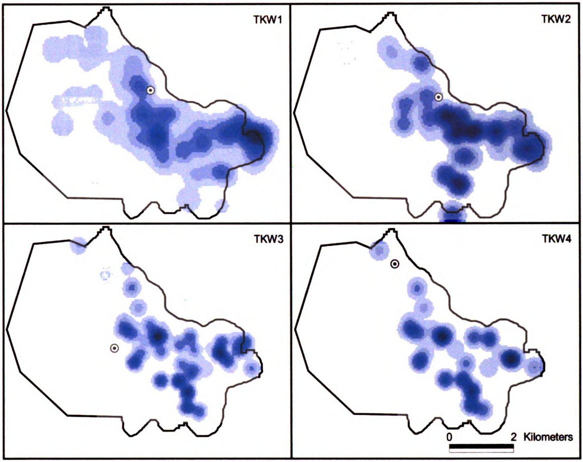

Figure 2.5. Livestock utility distribution grid surfaces for each of the 4 modeling periods in the Talek West clan. Darker colors indicate higher intensity of use by livestock. The communal den location used during each period, and the clan territory boundary is indicated on each map.

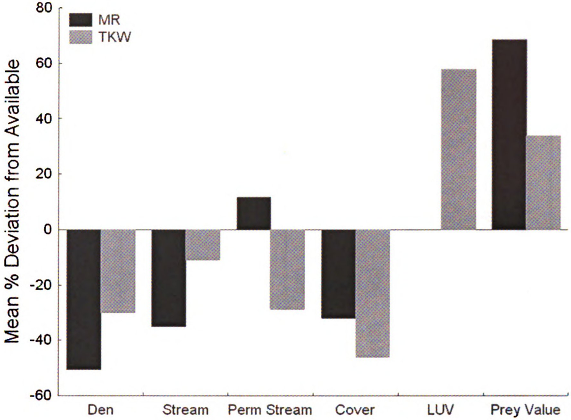

Figure 2.6. The mean % difference between values of continuous variables measured at hyena locations ("used") and those measured at 5000 random locations ("available") within the respective clan territories. A % difference was calculated for each of 3 modeling periods in Mara River (MR), and 4 periods in Talek West (TKW); the mean of these values is indicated above. The first 4 variables represent distances; therefore negative % deviations indicate hyena selection for proximity to these features. Variable descriptions, the data from each individual model, and the associated statistical comparisons are shown in Table 2.2.

Table 2.2. Mean (95% CI) values of continuous variables recorded for hyena tracking locations ("used"), and 5000 random locations ("available") within the territories of the Mara River (MR) and Talek West (TKW) clans. The first three variables represent the straight-line distances (in meters) to the communal den (Den), the nearest stream (Stream), nearest permanent stream (Perm stream) and nearest vegetative cover (Cover). Livestock use values (LUV) and prey values were based on grid surfaces created from livestock censuses and prey sampling as described above. Only values that did NOT differ based on 95% CI are in bold.

	Den		Stream		Perm Stream		Cover		LUV		Prey Value	
	Use	Avail	Use	Avail	Use	Avail	Use	Avail	Use	Avail	Use	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

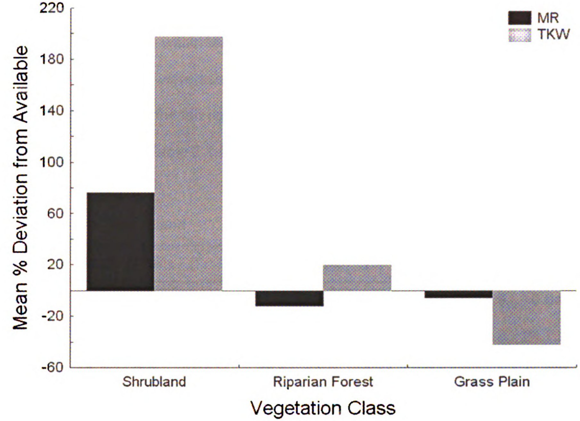

Figure 2.7. The mean % difference between the proportion of hyena locations and the proportion of 5000 random locations ("available") within the respective clan territories that were located in each of 3 vegetation class. The % difference was calculated for each of 3 modeling periods in Mara River (MR), and 4 periods in Talek West (TKW); the mean of these values is indicated above. The data from each individual model and associated statistical comparisons are shown in Table 2.3.

Table 2.3. The percent of hyena radiolocations ("used") and 5000 random locations ("available") within the territories of the Mara River (MR) and Talek West (TW) clans that were associated with each of three vegetation classes. Periods indicated on the left represent time periods during which hyena locations were collected (see Table 2.1 for period descriptions and location sample sizes).

	Shrubland			Riparian Forest			Grass Plain		
	Used	Avail	χ^2_1	Used	Avail	χ^2_1	Used	Avail	χ^2_1
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 $\alpha = 0.05$.

Figure 2.8. Locations at which adult male and female Mara River hyenas were radiotracked within their territory during 3 modeling periods (see Table 2.1). Locations at the communal den for females with den-dwelling cubs were excluded. Permanent and seasonal streams are indicated along with the communal den (orange triangle) used during each period.

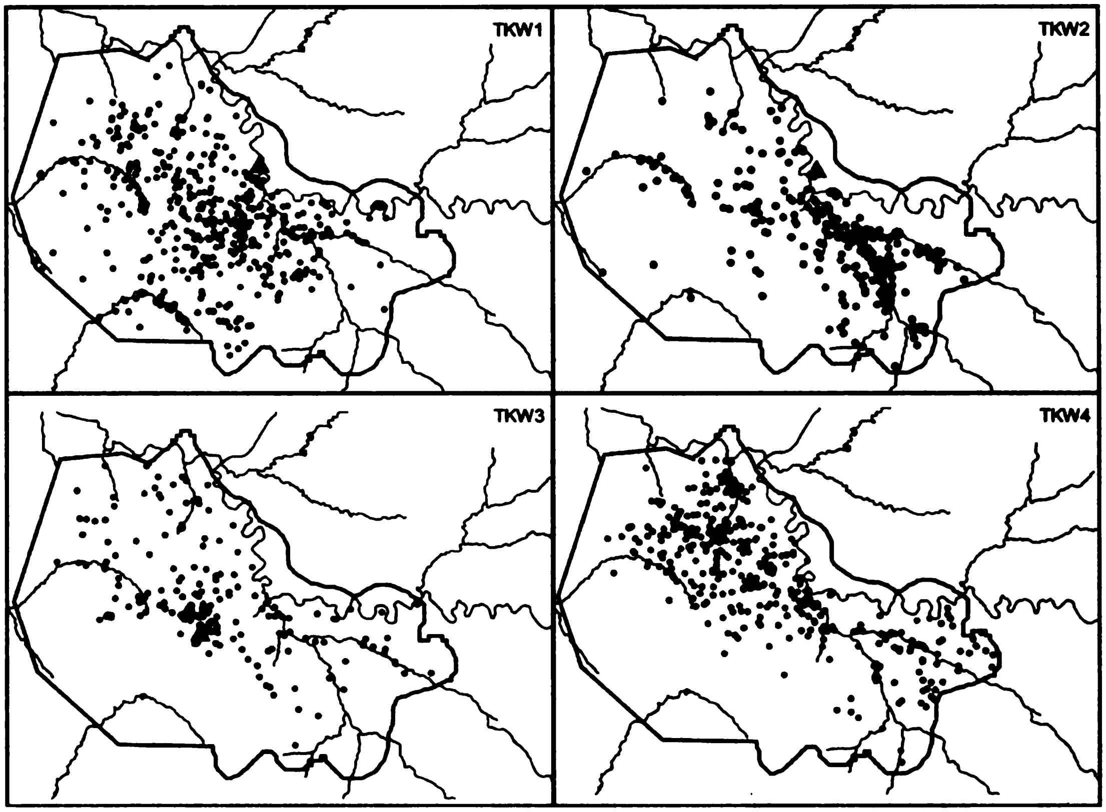

Figure 2.9. Locations at which adult male and female Talek West hyenas were radiotracked within their territory and within the Reserve during 4 modeling periods (see Table 2.1). Locations at the communal den for females with den-dwelling cubs were excluded. Permanent and seasonal streams are indicated along with the communal den (orange triangle) used during each period.

avoidance of livestock use areas relative to available locations, with data from all modeling periods indicating either hyena selection for areas of higher livestock use, or no difference in livestock use values between TKW used and available locations. MR hyena locations were consistently closer to streams in general, and further from permanent streams than were available locations. However, locations for TKW hyenas did not show a consistent relationship with water features except for an apparent selection for areas close to permanent streams. With respect to vegetation class, hyenas in both clans showed selection for shrubland and corresponding avoidance of grass plains, relative to their availability, though this appeared to be a much stronger tendency in TKW.

Multivariate Analysis - Mara River Clan

Final logistic regression models in each of 3 modeling periods for the MR clan generated similar results (Table 2.4, A.1). The most important predictor variable in all 3 final models was distance to the den. Except for exclusion of distance to vegetative cover from the MR1 model, final models included all predictor variables. All 3 models were highly significant based on the likelihood ratio test ($\chi^2 > 636.0$, $p < 0.0001$).

Multivariate Analysis - Talek West Clan

The relative importance of predictor variables varied, sometimes dramatically, among modeling periods for the TKW clan (Table 2.5, A.2, A.3, A.4, A.5). Distance to the den was an important predictor variable in all 4 final models, but was not consistently the most important. Vegetation class was selected as the first or second most influential variable in all 4 models. Livestock use value

Table 2.4. Logistic regression results for Mara River modeling periods based on hyena locations collected during all times of day and night.

Model	Variable	Estimate	SE	Wald Stat.	*P*
MR1	Dist to Den	- 0.0009	0.00006	243.10	<0.0001
	Dist to Stream	- 0.0032	0.00034	87.89	<0.0001
	Prey Value	+0.0508	0.00926	30.06	<0.0001
	Dist 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 F.	- 0.4533	0.15484	8.57	0.0034
MR2	Dist to Den	- 0.0007	0.00005	190.56	<0.0001
	Dist to Cover	- 0.0017	0.00027	38.03	<0.0001
	Prey Value	+0.0245	0.00513	22.71	<0.0001
	Dist 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 F.	+0.1179	0.10161	1.35	0.2459
	Dist to Perm	+0.0004	0.00014	9.72	0.0018
MR3	Dist to Den	- 0.0009	0.00004	596.97	<0.0001
	Dist to Perm	+0.0010	0.00009	139.23	<0.0001
	Dist to Cover	- 0.0016	0.00023	51.79	<0.0001
	Dist 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 F.	+0.3147	0.08145	14.93	0.0001

Table 2.5. Logistic regression results for Talek West modeling periods based on hyena locations collected during all times of day and night.

Model	Variable	Estimate	SE	Wald Stat.	*P*
TKW1	Dist 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 F.	- 0.0439	0.17060	0.07	0.7968
	Dist 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 F.	+0.0489	0.22787	0.05	0.8300
	Dist to Den	- 0.0009	0.00012	57.76	<0.0001
	Dist to Stream	- 0.0023	0.00036	40.11	<0.0001
	Dist to Perm	+0.0005	0.00015	10.91	0.0010
TKW3	Dist 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 F.	- 0.4801	0.35379	1.84	0.1748
	Dist to Perm	- 0.0005	0.00011	21.94	<0.0001
	Dist to Cover	- 0.0025	0.00059	18.58	<0.0001
	Dist 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 F.	- 0.9341	0.23941	15.22	<0.0001
	Dist to Den	- 0.0004	0.00004	88.47	<0.0001
	Dist to Perm	- 0.0008	0.00009	77.15	<0.0001
	Dist to Cover	+0.0018	0.00031	32.13	<0.0001

was selected as a predictor in only one final model (TKW1), with increasing livestock use associated with lower probability of hyena use. Interestingly in this model, increases in prey values reduced the probability of hyena use of territory locations, and prey value was not even selected for 2 of the 4 final models. All 4 final models were highly significant based on the likelihood ratio test ($\chi^2 > 340.0$, $p < 0.0001$).

Interclan Comparisons

A comparison of model results between the MR clan (where no livestock grazing occurred) and the TKW clan, where livestock grazing was common, revealed some important similarities and differences. Distance to the den was consistently an important predictor variable of hyena use in both clans, and showed a similar degree of influence on model prediction over all models (Table 2.6). However, although distance to the den was consistently the most important predictor of MR hyena locations, other variables, particularly habitat type, were more important in some TKW models. Because we could not exclude all locations from females with den-dwelling cubs, there was the potential for these females to contribute unequal amounts of locations to each model data set, and lead to spurious conclusions regarding the influence of the den. However, the average % of locations contributed by females with den cubs to TKW models was 24.3 (range: 9.7–56.3%), and 19.3 (range: 10.3–27.1%) for MR models, indicating that differences between clans in the influence of the den were not due to clan differences in the reproductive states of monitored females. In addition, in the TKW modeling period during which more than half the locations came from

Table 2.6. Modified odds ratios for models created based on all hyena tracking locations ("All"; Table 2.4 and 2.5), 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 hyena, that is associated with a 100 m increase in distance to the den, nearest stream, or vegetative cover, and a 5-unit increase in prey value. Variables not selected for final models were assigned a value of 0. Not all selected variables are shown.

	Den			Prey			Shrub			Stream			Cover		
Model	All	LFH	GH	All	LFH	GH	All	LFH	GH	All	LFH	GH	All	LFH	GH
MR1	-8	-11	-10	+29	+30	0	+45	0	+97	-27	-14	-46	0	0	0
MR2	-6	-6	-10	+13	+13	+13	+26	0	+115	-14	-13	-17	-15	-10	-14
MR3	-9	-8	-13	+14	+18	0	-5	-8	+31	-15	-8	-45	-15	-16	0
Mean	-8	-8	-11	+19	+20	+4	+22	-3	+81	-19	-12	-36	-10	-15	-5
TKW1	-13	-10	-10	-19	-20	-23	+83	+32	+111	0	+12	-9	0	0	0
TKW2	-9	-9	0	+44	+56	+31	+124	+67	+321	-20	-15	-22	0	0	0
TKW3	-7	-5	-9	0	0	0	+111	0	+190	+11	+17	0	-22	-16	-35
TKW4	-4	-6	+5	0	-10	+32	+222	+303	+406	0	-11	0	+19	+29	+31
Mean	-8	-8	-4	+6	+7	+10	+135	+111	+257	-9	+1	-8	-3	+3	-4

females with den cubs, the model indicated den location was less important than prey distribution and vegetation class.

Differences between clans in the relative influence of additional ecological variables were also evident. Although MR hyenas consistently avoided permanent streams (of which there were few) but selected sites closer to streams in general, the relationship between these watercourses and TKW hyena locations was unclear. Similarly, although prey was selected as a significant positive predictor for MR models, the TKW models indicated an inconsistent relationship between hyena space use and prey distribution (Table 2.5 and 2.6). Although members of both clans showed selection for shrubland vegetation, comparison of odds ratios indicates a much stronger influence of this vegetation class on hyena space use decisions in the TKW clan (Table 2.6). 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.

Temporal Differences in Model Results

Separate models based on locations collected during GH and LFH (Tables A.6 – A.19) indicated some obvious temporal variation in space use patterns by hyenas in both clans. For example, variables related to vegetative cover generally had a stronger influence on locations collected during GH than during LFH (Table 2.6). Because much of the vegetation in the Reserve is associated with water features, distance to streams is almost certainly related to selection for cover as well as moist/muddy resting areas. In the MR clan, distance to stream was a stronger predictor variable for locations collected during GH (Table 2.6), when hyenas spend most of their time resting in shaded muddy areas, but the relationship between space use and water features was not as clear in the TKW models. In both clans, the importance of shrubland was greatly increased during GH, which undoubtedly represents, at least in part, selection for shade cover. However, selection for shrubland vegetation remained during LFH in TKW, but disappeared during LFH in MR. Although distance to cover was consistently lower at hyena locations than at random locations in both clans (Table 2.2), distance to cover was not a consistently important predictor of hyena space use based on multivariate modeling in either clan and did not show clear temporal trends in model influence (Table 2.6). This may be because selection for vegetative cover was described more effectively by the vegetation class variable, leaving little variation in space use to be described by the distance to cover variable. In the MR clan, prey values generally had a stronger influence on locations collected during LFH than during GH (Table 2.6), which likely reflects increased hunting behaviour during nighttime hours. However, this trend was not consistently evident for TKW locations. Although variable in its importance among models within clans, the influence of the den appeared consistent overall between GH and LFH (Table 2.6).

Spatial Correlations

Ecological variables were not completely independent, and investigation of these intercorrelations is essential for a comprehensive understanding of modeling results. In particular, correlations between den location and the relevant ecological variables may lend insight into hyena selection of den locations within the territory. Distance to the den location was negatively correlated with prey values for 6 of the 7 modeling periods (Table 2.7), indicating that dens tended to be located in areas with higher than average prey values. This trend can be seen clearly when den locations are overlaid with prey distributions (Figures 2.3 and 2.4). In fact, the 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 as a predictor in this model. In the TKW clan, the relationship between den location and livestock grazing intensity was less clear, but it is remarkable that in 2 of the 4 models for this clan, correlations indicated the location of den sites in areas subjected to higher than average usage levels by livestock (Table 2.7, Figure 2.5). Finally, because the ultimate goal of the modeling was to investigate costs associated with livestock as a disturbance, we were interested in the relationship between prey values and livestock use intensity. Here also correlations did not show a clear relationship between the variables, with 2 of the 4 models indicating that areas of high livestock use were associated with high prey values (Table 2.7). For all correlations p-values are not presented because they would be heavily influenced by the extremely large sample sizes (> 5000 points).

Table 2.7. Pearson correlation coefficients between 3 ecological variables used in logistic regression modeling of space use by members of the Mara River (MR) and Talek West (TKW) clans. Variables listed are the distance to the communal den location (Dist to Den), the livestock use intensity value (LUV) and the prey value. Correlations are based on all locations used for modeling during each period (i.e. 5000 random locations plus all tracking locations for the period).

Period	Dist to Den * Prey Value	Dist to Den * LUV	LUV * Prey Value
MR1	- 0.24	–	–
MR2	- 0.58	–	–
MR3	+0.22	–	–
TKW1	- 0.34	- 0.35	+0.17
TKW2	- 0.14	- 0.40	+0.34
TKW3	- 0.05	+0.02	- 0.04
TKW4	- 0.80	+0.13	- 0.18

Spatio-temporal avoidance

We did not identify a clear relationship, within months, between livestock use values (LUVs) associated with hyena tracking locations and the average LUV of the TKW territory (Table 2.8). Data from only 3 of 13 months indicated that hyenas used areas characterized by lower intensity of livestock use than that available overall in their territory. Interestingly, during 4 of the 13 months, hyena locations had higher LUVs than the average territory value, indicating selection for areas used by livestock. This overall lack of avoidance of livestock use areas is supported by the lack of significance of LUV as a predictor variable in 3 of the 4 logistic regression models discussed above.

Despite an overall lack of avoidance, there is still an opportunity for hyenas to modify their use of disturbed areas on a temporal level. However, we found little evidence of this in TKW hyenas. Livestock use values did not differ between hyena locations collected during GH and locations collected during LFH on a monthly level (n = 13 months; t = 1.11, p = 0.289 Table 2.8), or at the level of the hyena (n = 11 hyenas; paired t = -1.22, p = 0.25; Table 2.9). At a courser scale, hyenas tended to be found in the area of the most intense livestock grazing (LCA) less often during GH than during LFH, but these differences were not significant (Table 2.10). In addition there was no difference between LFH and GH in the average distance to the LCA at which hyenas were tracked, using individual months as samples (n = 13 months, t = -0.699, p = 0.498; Table 2.9).

Table 2.8. Monthly livestock use intensity values (LUVs) for radiolocations of adult hyenas in the Talek West clan (95% CI) collected during the entire month (Overall Hyena), during only grazing hours (GH: 0900–1800 h) and livestock-free hours (LFH: 1900–0800 h). For comparison, the average LUV for all cells in the clan territory for each month (Territory) is also presented. Months with < 20 radiolocations in any time block were excluded. When the average LUV of hyena locations is significantly greater than the territory LUV, “S” indicates selection for livestock use areas relative to availability, and “A” indicates avoidance.

		Livestock Use Values				
Mo-Yr	n (LFH, GH)	Overall Hyena		Territory	LFH	GH
Sep-02	125 (56,22)	10.2 (3.6)		9.4	11.9 (5.7)	10.3 (10.4)
Oct-02	126 (66,20)	6.9 (1.6)	A	9.1	9.1 (2.6)	3.4 (1.7)
Dec-02	114 (53,25)	4.9 (1.7)		5.1	6.3 (1.5)	2.2 (1.6)
Feb-03	154 (67, 43)	1.4 (0.5)	A	3.6	1.1 (0.2)	1.3 (0.6)
Mar-03	163 (97,24)	14.4 (3.5)	S	7.9	17.0 (5.0)	13.7 (8.1)
Apr-03	110 (41,24)	5.2 (1.4)		4.0	5.0 (3.0)	7.7 (2.8)
Sep-03	116 (39,44)	17.0 (4.2)	S	4.8	20.7 (6.7)	12.4 (5.1)
Oct-03	186 (94,23)	8.4 (2.2)		6.5	10.1 (3.1)	13.5 (8.6)
Nov-03	169 (87, 33)	2.7 (1.2)	A	4.3	3.7 (2.2)	1.5 (0.3)
Dec-03	203 (90,47)	10.6 (1.5)	S	5.2	9.2 (3.5)	9.3 (5.1)
Jan-04	160 (55,49)	2.7 (1.3)		2.4	3.1 (2.1)	2.3 (1.3)
Feb-04	201 (107,32)	6.0 (1.1)		6.4	6.6 (3.1)	6.8 (7.7)
Mar-04	216 (107,40)	6.0 (1.8)	S	3.0	5.9 (1.8)	10.6 (7.7)

Table 2.9. Average livestock use intensity values (LUVs) for radiolocations of adult hyenas in the Talek West clan (95% CI) collected during grazing hours (GH: 0900–1800 h) and during livestock-free hours (LFH: 1900–0800 h). LUVs were derived from fixed-kernel grid surfaces based on all herds observed during the monitoring period of each hyena. Hyenas monitored for < 18 months were excluded. For comparison, the average LUV for all cells in the Reserve portion of the clan territory, based on entire study period, was 12.6 (18.6). There was no overall difference in average LUV of locations from GH and LFH using individual hyena means as samples (paired $t = -1.22$; $p = 0.25$).

Hyena	*n*	Mean LUV - LFH	*n*	Mean LUV - GH
ALI	110	30.9 (4.5)	56	29.5 (6.9)
ATH	75	24.3 (5.1)	23	25.5 (11.0)
CSN	78	11.9 (3.3)	22	18.6 (6.5)
FOZ	66	24.6 (5.1)	25	26.2 (8.8)
LDV	81	21.3 (4.5)	30	29.1 (8.8)
MALI	146	24.9 (3.9)	67	24.5 (6.1)
MIG	60	16.9 (3.5)	30	20.1 (5.9)
MLN	112	20.3 (3.9)	46	20.3 (5.9)
MRPH	129	24.3 (3.3)	60	21.3 (4.9)
NICK	110	24.0 (3.7)	47	21.6 (6.3)
VGS	113	18.5 (3.7)	42	19.2 (6.9)
Overall $\bar{X}$	11 hyenas	22.0 (2.9)	11 hyenas	23.3 (2.4)

Table 2.10. Monthly average distances to, and % inside, the livestock core area (LCA) for hyena radiolocations collected during grazing hours (GH: 0900–1800 h) and livestock-free hours (LFH: 1900–0800 h). The LCA was the area of most intense livestock use during the study period. Months with < 20 radiolocations in any time block were excluded, except for the last row.

	# of Locs.	% in LCA			Distance to LCA		
Mo-Yr	LFH, GH	LFH	GH	χ^2_1	LFH	GH	*t*
Sep-02	(56, 22)	10.7	9.1	0.05	1520	1305	0.98
Oct-02	(66, 20)	9.1	0.0	1.95	1497	1610	-0.51
Dec-02	(53, 25)	7.5	0.0	1.99	1402	1777	-2.14*
Feb-03	(67, 43)	6.0	2.3	0.80	825	881	-0.38
Mar-03	(97, 24)	16.5	4.2	2.42	691	920	-1.00
Apr-03	(41, 24)	4.9	12.5	1.24	912	484	2.04*
Sep-03	(39, 44)	0.0	0.0	–	747	818	-0.56
Oct-03	(94, 23)	6.4	17.4	2.86	788	844	-0.32
Nov-03	(87, 33)	4.6	0.0	1.57	729	874	-1.29
Dec-03	(90, 47)	6.7	2.1	1.31	938	1004	-0.66
Jan-04	(55, 49)	10.9	6.1	0.75	970	1342	-2.09*
Feb-04	(107,32)	7.5	6.3	0.06	1475	1950	-2.70*
Mar-04	(107, 40)	11.2	7.5	0.44	1390	837	3.05*
All Mo.	(1277, 518)	10.1	9.5	0.17	1016	1030	0.32

* Significant test statistic (either χ^2 or *t*-statistic) at $\alpha = 0.05$

DISCUSSION

Ecological variables influencing hyena space use

The first objective of this study was to identify the ecological factors influencing space use in spotted hyenas. All the independent variables monitored here were identified as important in predicting hyena space use patterns to some extent, including vegetation types, water features, and the distribution of prey resources. Given the social and biological importance of the communal den to *Crocuta*, as discussed above, we expected den location to have a strong influence on space use patterns. Model results reinforced this prediction with den location selected as an important predictor variable in all models. This indicates that the selection of den sites by females in this species may have serious consequences for space use patterns of all clan members. Den sites selected by wolves have been associated with avoidance of the territory edge (Ciucci & Mech 1992), villages, forest edges and intensively used roads (Theuerkauf et al. 2003c). It has also been suggested that wolf dens may be located in areas providing a stable food supply (Ciucci & Mech 1992). In contrast, den selection by Iberian lynx (*Lynx pardinus*) appeared unrelated to prey densities or vegetation structure, but was closely associated with features of the microhabitat at the den itself (Fernandez & Palomares 2000).

Den site selection in hyenas is poorly understood. Hyena den location was often associated with water resources in both the Kalahari Gemsbok National Park (Mills 1990) and the Mara Reserve (Boydston et al. 2006), and hyenas in the Serengeti National Park typically selected dens located in the direction of large prey herds in the dry season (Kruuk 1972). The data shown here lend support to the idea that changes in location of the den site may be associated with local changes in the spatial distribution of prey, as prey values were negatively correlated with distance to the den during all but 1 of the 7 modeling periods. This trend was particularly strong in models MR2 and TKW4, where dens were clearly located in areas of high prey density (Figure 2.2 and 2.3).

Regardless of its influence on den site selection, the distribution of prey clearly influenced space use decisions made by Reserve hyenas. Univariate comparisons and multivariate models for 6 of the 7 modeling periods indicated that prey numbers were significantly higher at "used" locations than at "available" locations, demonstrating selection for prey-rich areas by hyenas in both clans. Numerous studies have demonstrated a link between carnivore space use and the prey densities within their home-ranges or territories (e.g., bobcat—Litvaitis et al. 1986, caracal—Avenant & Nel 1998, lion—Hopcraft et al. 2005; Schaller 1972), and the same association has been shown in *Crocuta*. For example, in southern Africa hyenas 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 hyenas sought out distant migratory herds when local prey were scarce (Hofer & East 1993a). Similarly, our data, and those of Boydston et al. (2003b), provide direct, quantitative evidence that local movements of prey influence hyenas' use of space within their territories.

Water features were found to be important predictors of space use in both clans. Although the location of water sources is suggested to influence movements of hyenas in arid ecosystems (Cooper 1989; Tilson & Henschel 1986), it is unlikely that the hyenas studied here are limited by the presence of water on the landscape. Because vegetation is clearly influenced by streams and rivers in the Reserve (Figure 2.2), the importance of streams may simply reflect the documented selection for shrubland vegetation. MR hyenas exhibited stronger selection for streams than did TKW hyenas. This is likely a result of selection for wet, muddy, concealed daytime resting sites in non-vegetated creek beds, which were more common in the MR than TKW territory. This conclusion is supported by the fact that selection for streams in MR was strongest during the daylight hours.

The influence of livestock grazing on patterns of space use

The second objective of this study was to compare space use patterns of hyenas between territories that differed in exposure to livestock grazing. With this comparison, we investigated the broad hypothesis that livestock grazing was influencing hyena space use decisions. Because Boydston et al. (2003b) found increased use of vegetative cover over time by Talek hyenas associated with a concurrent increase in livestock grazing within their territory, we predicted that vegetative cover would assume relatively low importance to hyenas not exposed to livestock grazing. Although hyenas in both clans demonstrated selection for shrubland and avoidance of grassland relative to its availability, logistic regression modeling confirmed our prediction, and indicated that vegetation class was a more effective predictor of space use patterns in TKW than in MR. Furthermore, models separated by time of day indicated that the selection by MR hyenas for shrubland occurred almost exclusively during the day, yet selection for shrubland in TKW was apparent regardless of time of day. Therefore, reduced use of grass plains and increased use of shrubland habitat in the TKW relative to MR clan appears to represent a behavioral modification resulting from the long-term disturbance of grazing, as opposed to a daily response to the immediate presence of livestock. These data support the suggestion by Boydston et al. (2003b) that observed changes in use of vegetative cover over time in the Talek clan resulted from increased exposure to livestock grazing.

Although den location was an important predictor of space use by members of both clans, it was not consistently the most important predictor in TKW models, and the reduced influence of the den on hyena locations in TKW relative to MR is striking even on simple plots of tracking locations (Figure 2.8 and 2.9). This difference between clans was clear despite a generally higher proportion of locations coming from females with den cubs in TKW.

The fact that vegetation class was a more important predictor variable than den location in 2 of the 4 TKW models may indicate that TKW hyenas were sacrificing proximity to the den for selection of vegetative cover. It is important to note that in all but the TKW3 period, TKW hyenas chose to den along or near the Talek River, which serves as the border of the Reserve in this area. Numerous Maasai villages are located <1 km from this Reserve border (Kolowski &

Holekamp 2006). In addition, all livestock herds entering the Reserve must cross this river, and often did so within 200 m of these den locations (J. M. Kolowski, pers obs.). Although human disturbance has been associated with den abandonment in coyotes (Bekoff & Wells 1982) and wolves (Ballard et al. 1987), these hyenas seem to have selected particularly disturbed areas for their den locations, and the reasons for this remain unknown. However, despite the fact that TKW hyenas denned along this river for 17 of the 20 months of our study period, the den exerted a strong influence on TKW space use in all modeling periods, even during hours when livestock were present. Notably, in all cases, these river dens were associated with dense shrubby vegetation and, in some cases, with riparian forest habitat.

Because previous research indicated that areas heavily grazed by livestock tended to have high prey densities (Boydston et al. 2003b), and because any avoidance of livestock within a territory should result in sub-optimal resource use, we also predicted that prey distribution would therefore be a more effective predictor of hyena space use in livestock-free territories. In other words, hyenas 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. Although prey distribution was important in predicting MR hyena space use in all modeling periods, the influence of prey distribution on TKW hyena space use was inconsistent, and varied in direction and importance among modeling periods and between models based on locations collected during grazing hours and livestock-free hours. Interestingly, the period during which hyenas exhibited avoidance of areas with higher prey values (TKW1) was that during which livestock grazing was observed to be most intense.

Based on data from our 4 modeling periods, we did not identify a consistent spatial relationship between prey values and livestock use values. The lack of a positive correlation between these variables indicated that the cost to hyenas of avoiding livestock, in terms of loss of prey resources, was not particularly high. Notably, although a strong positive correlation did exist between these prey value and livestock use value in TKW2, prey distribution was the most effective predictor of hyena space use for that period, indicating selection for prey rich areas despite heavy use by livestock in these same areas. Nevertheless, we found no consistent relationship between grazing intensity and prey distribution among modeling periods.

Variables other than those monitored in this study (e.g. lion distribution and tourist activity) may potentially influence space use patterns of hyenas in other systems or of other carnivores. We did not take the distribution of either lions or tourist vehicles into account in modeling the space use of Reserve hyenas for the following reasons. Although lions are a major source of mortality for Talek hyenas (Watts & Holekamp in review), Boydston et al. (2003b) showed a positive spatial correlation between lions and hyenas in the Talek clan territory, indicating space use by these carnivores is influenced by similar ecological factors. In addition, we have shown previously that lion density did not differ between the MR and TKW clan territories (Kolowski & Holekamp 2007). Therefore, we were confident that lions were not likely to directly influence hyena space use at the scale of interest here, or bias comparisons between the two study clans.

We also did not incorporate tourist vehicle distribution into modeling efforts. Tourist use of the Talek area was estimated to be almost five times higher than that observed in the MR territory (Kolowski & Holekamp 2007). However, tourist distribution is almost completely dependent on the distribution of charismatic wildlife (e.g. cheetah, elephant, lion); a category in which hyenas are generally not included. Therefore the local spatial distribution of tourist vehicles is not predictable over time, making vehicle distribution mapping highly dubious. Furthermore, hyenas have not been shown to avoid tourist vehicles in the Reserve, even at close distances, due to frequent exposure and habituation (K. E. Holekamp, unpublished data).

Numerous studies have shown carnivores to utilize spatio-temporal avoidance to accommodate human activity or disturbance in their territories. For example, grizzly bears have been shown to increase their use of areas near roads at night, when vehicular traffic was relatively light (Gibeau et al. 2002; McLellan & Shackleton 1988). Wolves in Italy used paved roads, villages and rubbish dumps almost exclusively at night (Ciucci et al. 1997). And in British Columbia, portions of rivers heavily used by anglers received relatively more night use from grizzly bears than portions with fewer anglers (Machutchon et al.

1998). Even in this hyena population, we found that use of areas around Maasai villages occurred almost exclusively at night (Kolowski & Holekamp 2006).

Given the temporal predictability of livestock grazing in the Reserve, and the direct threat that herders pose to hyenas, we expected areas used heavily by livestock to be used to a greater extent by hyenas during the night, when this disturbance was absent. However we found no evidence of this. We documented little avoidance of livestock use areas in general, and no consistent differences in the use of these areas based on time of day. TKW hyenas appear to have adjusted to the presence of livestock within their territory, and their increased use of vegetative cover apparently allows hyenas to continue to make space use decisions based on den location and prey distribution, regardless of time of day, or livestock distribution. Although reduced daytime activity by TKW relative to MR hyenas (Kolowski et al. 2007) may have reduced the need for direct avoidance by TKW hyenas of areas used by livestock, our data suggest the availability of refuges during daytime rest periods is important in allowing shared use of space.

However, we found some evidence suggesting that there may be a threshold level of grazing intensity, beyond which new patterns of space use may be required. Livestock use values were unimportant in predicting hyena space use patterns in all logistic regression models except TKW1, when livestock grazing was most intense, and when higher livestock use values were associated with a lower probability of hyena use. During December, February and March of this period, the % of locations in the livestock core area (LCA) was always higher during livestock-free hours (LFH) than during grazing hours (GH), and locations during LFH were on average closer to the LCA than those collected during GH (though neither trend was significant). Thus it may be that, at the levels generally observed during this study (except during TKW1), direct avoidance of livestock was not necessary, and increased use of vegetative cover was adequate to accommodate the disturbance.

Conclusions

The data presented in this chapter lead to two primary conclusions. First, and most broadly, patterns of space use in this species are the result of a combination of multiple ecological factors, including prey distribution, vegetation types, water features on the landscape, and is most strongly influenced by 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.

Second, given the relationship between the distribution of livestock, vegetation and hyena space use, we can also conclude that the presence of vegetative cover appears to be critical in allowing the coexistence of livestock and hyenas at a small spatial scale. We demonstrated that daily, often intense livestock grazing pressure did not result in measurable spatial avoidance of grazed areas and that despite this disturbance, TKW hyenas were largely able to modify patterns of space use to maximize proximity to the communal den and to the areas within their territory that contained the highest prey densities. 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 spatial avoidance of intensely grazed areas shown by Boydston et al. (2003b) occurred in areas of open plain containing virtually no dense vegetative cover.

Documentation of behavioral responses to disturbance assumes its greatest utility to conservation when it is linked with demographic consequences (Caro 1998; Gill & Sutherland 2000). A detailed investigation into the demography of the Talek Clan from 1988 to 2003 indicated that the population was stable, and birthrates did not decline over this time period. This was despite the fact that humans were a significant source of mortality for adult hyenas in this clan, and that the annual mortality rate due to humans was more than 4 times greater from 1996–2003, than from 1988–1995 (Watts & Holekamp in review). Given these data and the results presented above, it appears that hyenas living along this Reserve border have adjusted to coexist with the daily disturbance of livestock grazing, and importantly, have not yet suffered measurable demographic consequences due to either this disturbance, or the increased source of mortality associated with their proximity to the Reserve border. It is unlikely that growth of the local human population will result in a dramatically increased livestock population, given that livestock numbers have remained relatively stable over the last 20–30 years, and that current per capita stock numbers are thought to be unsustainable (Lamprey & Reid 2004; Serneels &

Lambin 2001). However, a combination of degradation of rangeland outside the Reserve (Serneels et al. 2001) and the increased threat of direct hyena mortality associated with a growing human population, suggests that grazing pressure in the Reserve and human-caused mortality will continue to increase over time. Whether behavioral changes, such as increased used of vegetation (Boydston et al. 2003b), and this study) and changes in activity patterns (Kolowski & Holekamp 2007), or demographic resiliency (Watts & Holekamp in review) will continue to buffer these hyenas from these increasing threats remains to be seen.

CHAPTER THREE

Kolowski, J.M., and K. E. Holekamp. In review. Effects of an open refuse pit on space use patterns of spotted hyenas. African Journal of Ecology.

CHAPTER THREE

EFFECTS OF AN OPEN REFUSE PIT ON SPACE USE PATTERNS OF SPOTTED HYENAS

INTRODUCTION

Patterns of space use by large carnivores are determined by a multitude of factors including availability of water, den sites, cover from predation or climate (Ewer 1973) and competition (Durant 1998), but are often most closely associated with the distribution and abundance of prey (Hofer & East 1993b; Mills & Knowlton 1991; Spong 2002). Numerous species utilize human-provided food sources as components of their diet (e.g., *Canis lupus*—Fuller & Keith 1980; *Vulpes vulpes*—Doncaster et al. 1990; *Ursus americanus*—Herrero 1983; *U. arctos*—Knight & Eberhardt 1985; *Crocuta crocuta*—Mills & Hofer 1998). It has been shown these anthropogenic resources influence carnivore movements (Ciucci et al. 1997; Craighead & Craighead 1971), home range size (Blanchard & Knight 1991; Hidalgo-Mihart et al. 2004), and population density (Fedriani et al. 2001; Fuller & Keith 1980). Additionally, the presence of these resources may influence the frequency of human-carnivore conflict by increasing carnivore densities (Yom-Tov et al. 1995), or by shifting populations (Beckmann & Berger 2003b) or individuals (Knight et al. 1988; Lunn & Stirling 1985) toward human-dominated areas. Resulting conflicts may cause property damage (e.g. livestock), human injury, and even increased carnivore mortality, with these areas acting as population sinks (Knight et al. 1988). As human population growth and habitat conversion proceed at increasing rates, human-carnivore conflict, particularly livestock depredation, threatens to impede large carnivore conservation efforts where carnivores share the landscape with humans. However, few studies have investigated the influence of human-provided food sources other than livestock on the movements and space use of potential livestock predators.

Seasonal variation in the use of refuse sites has been documented in a number of carnivores and is often associated with variation in prey availability and seasonal variation in nutritional requirements (Craighead & Craighead 1971; Lucherini & Crema 1994; Salvador & Abad 1987). It is also likely that variable nutritional demands of different age/sex classes, and reduced competitive ability in social carnivores of low social rank, may result in variation in the use of these resources at the level of the individual. Identification of the animals most likely to utilize human-provided food sources may help to identify the existence of potential "problem individuals" (see review in Linnell et al. 1999), and the factors that may lead to their destructive behavior. However, few studies have investigated individual variation in the use of refuse sites by large carnivores (but see Lunn & Stirling (1985) and Rogers et al. (1976)).

Spotted hyenas (*Crocuta crocuta* Erxleben) are important predators of livestock throughout East Africa (Kolowski & Holekamp 2006; Kruuk 1981; Ogada et al. 2003). Although *Crocuta* feed primarily on freshly killed ungulates that they hunt themselves (Gasaway et al. 1991; Kruuk 1972), hyenas are opportunistic foragers and efficient scavengers that have been observed to feed on a huge variety of food items including insects, birds, rodents and even garbage (Cooper et al. 1999; Henschel & Skinner 1990; Mills & Hofer 1998). It has been suggested that refuse and livestock carcasses at pastoral villages may influence the frequency of hyena visits to these areas and ultimately, livestock depredation rates (Kolowski & Holekamp 2006; Mills & Hofer 1998).

Our goal here was to document the influence of a single human refuse source on the space use patterns of adult hyenas, and to investigate the influence of hyena social rank and local prey abundance on variation in the use of this food source. We capitalized on a natural experiment in which a refuse site was closed midway through intensive monitoring of individual hyenas whose defended group territory contained the refuse site.

METHODS

Study population and habitat characteristics

Our study was conducted from June 2001 through April 2004 in the Masai Mara National Reserve (hereafter the Reserve) in southwestern Kenya. The 1500 km^2 Reserve consists primarily of rolling grassland and scattered bushland (predominantly *Croton* and *Euclea* species), with riparian forest along the major watercourses, and supports a large diversity of resident ungulates. From August to October, the Reserve also supports large migratory herds of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*). Due primarily to its diversity and abundance of predators, as well as the seasonal influx of migratory ungulates, the Reserve is Kenya's premier wildlife tourist attraction (Norton-Griffiths 1995), and supports 24 permanent tourist camps and lodges (Walpole et al. 2003). Although many are located just outside the Reserve boundary, a small subset of lodges (~20%) is located within the Reserve itself, and this study focuses on one of the latter.

Spotted hyenas live in social groups called clans, and clan members cooperatively defend a stable group territory. Each clan contains one to several matrilines of adult females and their offspring, as well as a variable number of adult immigrant males. Clans are rigidly structured by hierarchical rank relationships (Frank 1986b; Kruuk 1972; Tilson & Hamilton 1984) that determine priority of access to food, and all adult females are socially dominant to immigrant males (Kruuk 1972; Smale et al. 1993). Subadult individuals of both sexes maintain their maternal ranks as long as they remain in the natal clan (Smale et al. 1993). Although females are generally philopatric (Frank 1986b), virtually all natal males disperse between the ages of 2 and 5 years (East & Hofer 2001; Henschel & Skinner 1987; Smale et al. 1997). *Crocuta* clans are fission-fusion societies in which individuals travel, rest and forage in subgroups that typically change in composition many times each day (Holekamp et al. 1997a; Kruuk 1972). Female *Crocuta* bear 1–2 (rarely 3) young in isolated natal dens (Holekamp et al. 1996). Cubs are typically transferred to a communal den at 2–5 weeks of age where they reside for the next 7–8 months (Kruuk 1972). The communal den represents the social center of each clan's territory and most clan members visit it regularly.

We monitored individuals from a single clan (the Mara River clan) that defended a territory (31 km^2) near the center of the Reserve (Figure 3.1). The clan included 32–43 individuals ($\bar{x}$ = 8 adult females, $\bar{x}$ = 5 adult immigrant males), and each hyena was individually recognized by unique spot patterns. A single tourist lodge, which maintained an unfenced refuse pit approximately 300 m from the periphery of its grounds, was located near the northern boundary of the Mara River clan territory (Figure 3.1). Garbage, mainly composed of food refuse from tourist and staff dining halls, was deposited daily into an earthen pit, usually between 0900–1000 h. The pit was closed on 12 October 2002 and all garbage was removed from the site. In the following weeks the pit was filled with soil, and native shrubs and trees were planted.

Data collection

We anesthetized and radiocollared 6 adult female hyenas from the Mara River clan of variable social rank, and made attempts to locate each individual on a daily basis. On average, we collected 15 telemetry locations per month for each collared hyena. The majority of radiotracking was conducted during the morning (0530–0900 h) and evening (1730–2000 h), but additional locations were collected during mid-day and throughout the night. In addition to tracking efforts, we made regular visits to the refuse pit at all times of day; however, hyenas were only observed at the site when fresh refuse was present. During these observation sessions we recorded the number and identity of hyenas present, as well as the presence of other species at the site.

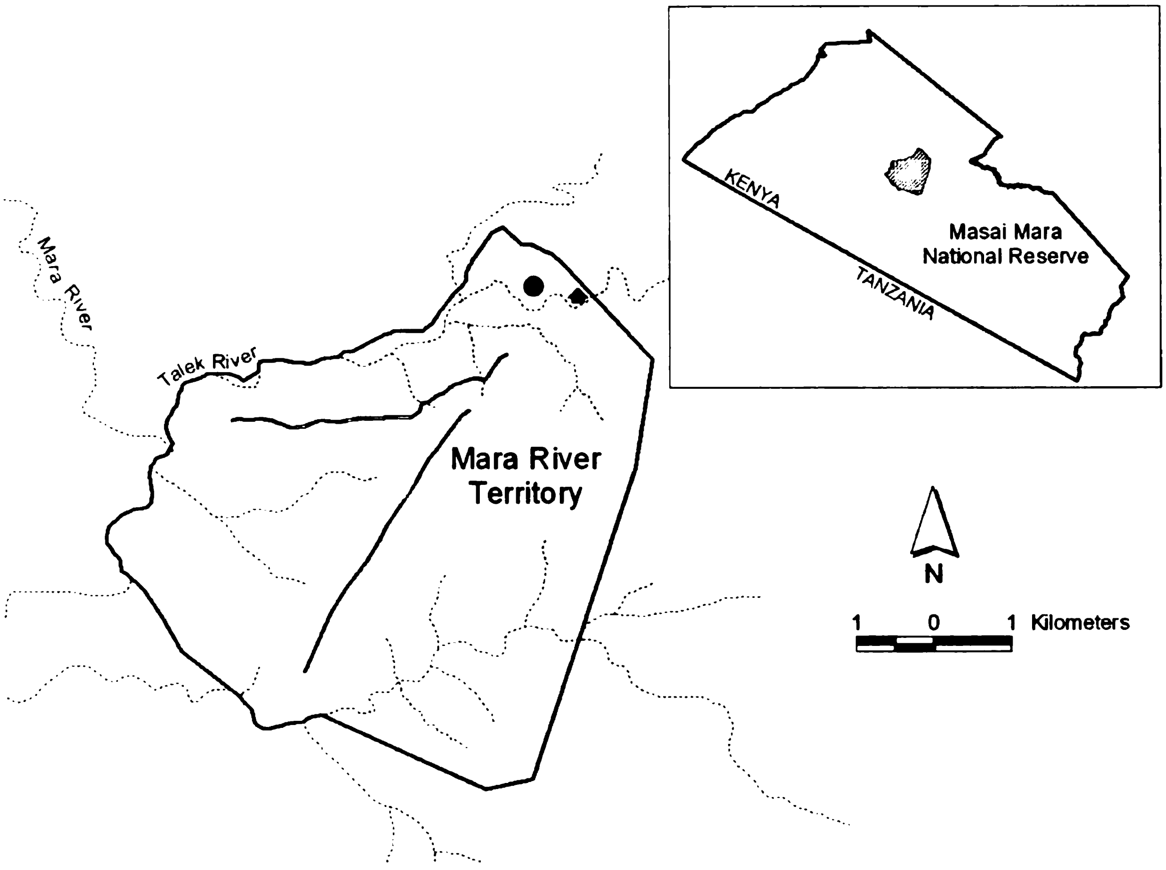

Figure 3.1. Territory of the Mara River hyena clan and its location within the Masai Mara National Reserve. Hatched lines represent ungulate prey sampling transects. The refuse pit (filled circle) and tourist lodge are also indicated.

Using tracking locations from 5 of the 6 monitored adult female hyenas (one female was not monitored after pit closure), we compared space use patterns before and after pit closure using the following variables: 95% fixed kernel home range size, 50% fixed kernel home range (core area) size, presence/absence of the refuse pit within the core area, and average hyena distance to the refuse pit. Home range size during the full 16-month pre-closure period was strongly influenced by the consecutive use of communal dens separated from each other by as much as 6 km. We therefore limited the pre-closure locations to those collected in the 10 months prior to pit closure, when consecutive den locations were consistently only short distances apart (this held for the remainder of the study period). Because space use of female hyenas is dependent on whether they have cubs residing at the communal den (Boydston et al. 2003a), we categorized all pre-closure locations for each female with respect to whether or not she had den-dwelling cubs. We then randomly subsampled locations collected in the 19-month post-closure period for each female to equalize the number of locations collected before and after closure with and without den-dwelling cubs (minimum of 20 locations per female pre- and post-closure). Because female space use is even further restricted during use of natal dens, we excluded locations collected at these dens from all analyses. Using this restricted dataset, we calculated a single 95% and 50% home range (with smoothing factors determined by least squares cross-validation—Seaman & Powell (1996)), and an average distance at which each female was tracked from the refuse pit, for the pre- and post-closure periods.

The pooling of locations to calculate home range and core area size, while necessary due to sample size requirements, prevented statistical comparisons of these variables before and after pit closure. We compared average distances to the refuse pit before and after closure using a Wilcoxon matched-pairs test. All distances and fixed kernel home ranges were calculated using Animal Movement Analyst (Hooge & Eichenlaub 2000) and ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California).

Because variability in prey abundance over time may influence space use patterns, we monitored prey abundance within the clan territory throughout the study period. As a monthly index of local prey abundance, we counted the total number of wild ungulates within 100 m of 2 4-km transects twice each month (Figure 3.1), and calculated the average number of prey animals counted per sampling event. Prey abundance was estimated based on 10 months of sampling data during the pre-closure period and compared, using a *t*-test, to an estimate based on the same 10 months during the post-closure period to control for the seasonal ungulate migration.

To investigate the influence of social rank on individual variation in space use relative to the refuse pit, we conducted two separate analyses with females assigned to low or high rank categories relative to the median adult female rank. Individual ranks were assigned based on the outcomes of dyadic agonistic interactions as in (Holekamp & Smale 1990). Immigrant males were treated separately as the lowest ranking group. First, to qualitatively compare use of the pit between individuals of different ranks, we calculated the proportion of tracking locations collected within 500m of the refuse pit for those adult females tracked for ≥12 months while the pit was in use. Second, independent of radiotracking, we documented the composition of hyena groups observed feeding at the refuse pit based on 18 observation sessions. We compared the proportion of these sessions recording the presence of low-ranking females, high-ranking females and immigrant males. We then compared the number of hyenas present from each rank group at these visits using a Friedman ANOVA, with the number of hyenas from each rank group representing three repeated samples for each observation session. Each rank group contained a total of five individuals in this pre-closure period.

To investigate the influence of natural prey abundance on use of the refuse pit, we compared pit utilization during months of high prey abundance, when migratory herds were present in the clan territory, to months when only resident herds were present. Migration months were defined as those months when wildebeest were seen within the territory as no resident herds of wildebeest utilize this portion of the Reserve. We focused only on hyenas that were closely monitored in the pre-closure period (≥12 months of tracking), and that were known to use the site with some frequency (>5% of locations within 500 m of the refuse pit). We compared the relative frequency of locations of these hyenas (pooled) within 500 m of the refuse pit during migration months and non-migration months using a chi-square test.

All tests were considered statistically significant at $\alpha = 0.05$ (two-sided), and all analyses were conducted using the STATISTICA software package (StatSoft 2002). Descriptive statistics are presented as means ± *SE* throughout.

RESULTS

Observations of refuse pit use

At least one clan member was present at 18 visits by researchers to the refuse pit. During these sessions an average of 5 hyenas were seen at the site (range: 2–14). The hyenas were often joined at the refuse pit by savanna baboons (*Papio cynocephalus*), warthogs (*Phacochoerus africanus*) and various species of vultures. Most edible items were typically consumed within 1–2 hrs of refuse deposition. Typically only a subset of the hyenas present, if any, was observed to feed, due to direct and sometimes aggressive competition with warthogs and baboons. At least one subadult hyena was present at 44% of these sessions, the youngest of which was approximately 13 months. None of the subadults were accompanied by their mothers and no hyenas <1 year old were observed at the refuse pit.

Effect of refuse pit on clan space use

We collected a total of 1830 locations from 6 radiocollared females, with each female monitored for an average of 20 months. Based on locations from the 5 females monitored before and after pit closure, home range in the 10 months prior to closure was 10.9 km^2 ($n = 385$ locations), and 13.9 km^2 ($n = 385$

locations) in the 19 months after closure (Figure 3.2). The pre-closure core area was 1.6 km^2 and included the refuse pit as well as 2 of the 6 communal dens utilized during this period (Figure 3.2A). After pit closure the core area no longer included the pit, was almost half its previous size (0.9 km^2), and contained 7 of the 11 communal dens utilized during the post-closure period (Figure 3.2B). Distance to the pit was significantly smaller during the pre-closure period ($\bar{x}$ = 1.87 ± 0.09 km) compared to that in the post-closure period ($\bar{x}$ = 2.23 ± 0.07 km; $Z = 2.00$, $p < 0.043$; Table 3.1). Differences in space use between the pre- and post-closure periods could not be explained by differences in prey abundance. Average monthly prey counts were similar in the pre- and post-closure periods (pre: $\bar{x} = 294$, post: $\bar{x} = 394$; $t = -0.522$, $p = 0.607$).

Individual variation in refuse pit utilization

Of 6 radiocollared females, four (2 high-ranking and 2 low-ranking) were monitored for $\geq$12 months during operation of the refuse pit. The two high-ranking females were tracked within 500m of the pit on only 2 of 179 (1.1%) and 4 of 202 (2.0%) occasions, respectively. In contrast 29.8% of 178 locations, and 26.2% of 183 locations for the two low-ranking females were within 500m of the pit. Seventy-five percent of 18 refuse pit observation sessions recorded low-ranking adult females present, whereas only 43% and 32% recorded the presence of immigrant males and high-ranking females, respectively. At the same 18 sessions these three rank groups were not represented equally

Table 3.1. Average distances (*SE*) of adult female hyena tracking locations to the refuse pit for the 10 months prior to the closing of the pit (pre-closure) and the 19-months following the closure (post-closure). The rank group of each hyena is indicated after each name (H=High, L=Low).

		Mean Distance (km) to Refuse Pit	
Hyena	# of Tracks per Period	Pre-Closure	Post-Closure
NANA(H)	130	2.19 (0.14)	2.51 (0.13)
ATAR(L)	119	1.89 (0.18)	1.98 (0.15)
BACK(L)	96	1.58 (0.18)	2.07 (0.13)
WND(L)	21	1.57 (0.38)	2.62 (0.22)
CHAC(L)	20	1.39 (0.19)	2.25 (0.32)
Pooled Locations	385	1.87 (0.09)	2.23 (0.07)

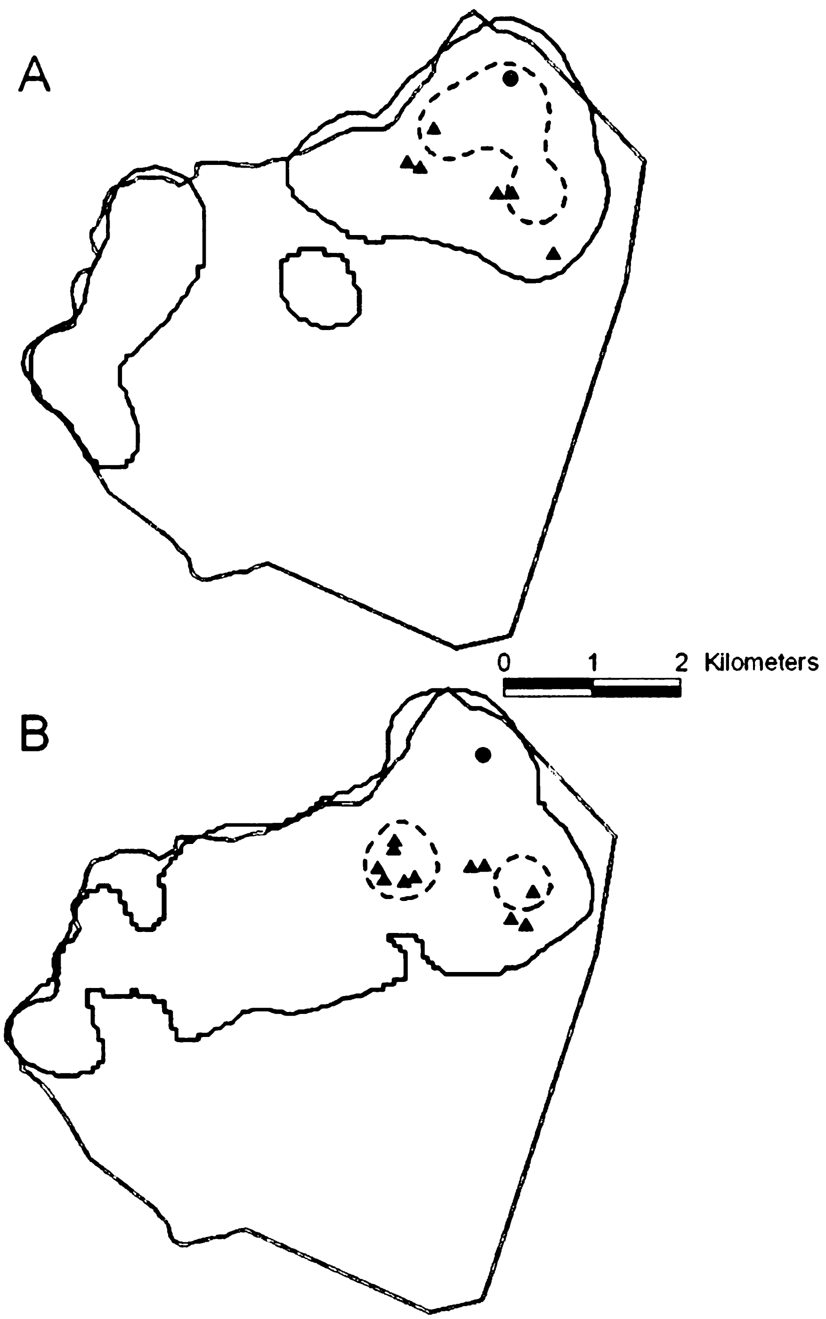

Figure 3.2. The 95% home ranges (solid dark lines) and 50% core areas (dotted lines) based on locations from 5 radiocollared adult female hyenas collected during the 10 months before (A) and 19 months after (B) closure of the refuse pit. Pit location is indicated as in Figure 3.1, and the locations of all communal dens utilized during the respective periods are indicated by solid triangles.

(Friedman ANOVA $\chi^2 = 15.5$, $p < 0.0005$), with low-ranking females being the most numerous individuals at the refuse pit (Figure 3.3).

Influence of natural prey abundance on refuse pit utilization

Migratory herds were present in the study area for 3 of the 9 months for which both prey and tracking data were available during operation of the refuse site. Unfortunately, only two females in the clan met our criteria for this analysis, yet clear trends were shown by these individuals. These two females were tracked to within 500 m of the pit significantly less often during migration months (12.0% of all tracks) than during non-migration months (38.0% of tracks; $\chi^2 = 19.24$, $p < 0.0001$).

DISCUSSION

In carnivore studies, utilization of human-provided food resources such as those available at garbage dumps often results in reduced individual or group home ranges (e.g. *C. latrans*—Hidalgo-Mihart et al. 2004, *U. arctos*—Blanchard & Knight 1991) or core areas (e.g. *Mungos mungo*—Gilchrist & Otali 2002). These observed reductions are presumed to result from a reduction in foraging space requirements due to the addition of a predictable, concentrated food supply . Here, the female group home range was smaller during operation of the refuse pit, yet core area size was smaller following closure of the pit. This discrepancy is probably related to the importance of the communal den in hyena society. Although its influence on space use varies with rank and reproductive

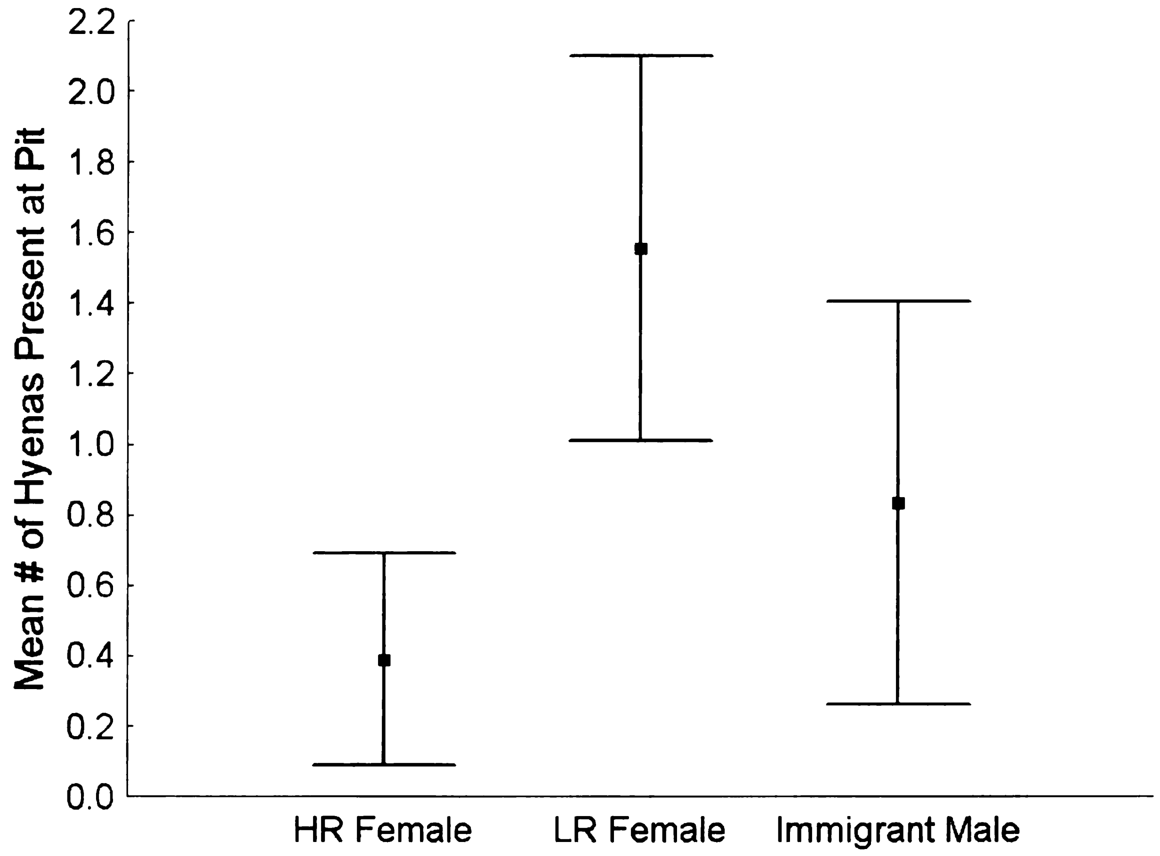

Figure 3.3. Mean number of high-ranking (HR) females, low-ranking (LR) females, and immigrant male hyenas (5 individuals per group) that were seen at 18 refuse pit observation sessions. Sessions included were those at which at least one hyena was observed. Whiskers indicate 95% confidence intervals.

condition, space use by all female clan members is highly influenced by the location of the communal den (Boydston et al. 2003a). It appears that during its operation, the refuse pit became a focal point of activity for at least some clan members, resulting in an expanded group core area that contained communal den locations and the refuse site. Unlike in garbage-feeding banded mongoose and baboon groups, where core areas were centered on refuse site locations (Altmann & Muruthi 1988; Gilchrist & Otali 2002), the location of the communal den likely dictates the location of hyena clan core areas. And, further, the location of the den appeared to be independent of the pit location, because den location was similar between the pre- and post-closure periods (Figure 3.1).

Use of the refuse pit was most common among low-ranking females, particularly during times of prey scarcity, though there was notable variation in pit utilization within rank groups. For example, at least one low-ranking uncollared female was seen only once at the refuse pit, and an uncollared high-ranking female was observed at the pit with some regularity. Based solely on rank and its associated priority of access to food, we expected immigrant males to be most dependent on alternate food resources, yet immigrant males were less common at the refuse site than low-ranking females. This likely resulted from exclusion of immigrant males at the pit by the higher-ranking female hyenas. Notably, frequent refuse pit users in our study were not infirm or consistently old, and all were known to be capable of making kills and consuming ungulate carcasses.

The observed shifts in space use, and the propensity of certain clan members to frequent the refuse pit are particularly interesting as they relate to human-carnivore conflict. We suggest that the relatively frequent use of the refuse pit by low-ranking individuals is related to their low priority of access to kills in the clan territory. This skewed utilization of human food sources has been similarly shown in polar bears (Lunn & Stirling 1985) and black bears (Rogers et al. 1976; Young & Ruff 1982), where subadults (particularly males in black bears) were the most common age group at garbage dumps. This has been suggested to result from the increased nutritional stress (Lunn & Stirling 1985), ranging behavior (Rogers et al. 1976) or necessity of avoiding intraspecific competition (Young & Ruff 1982).

If human refuse attracts hyenas to pastoral villages then, given our results here, we would expect low-ranking hyenas to be more likely to visit these villages and perhaps also to opportunistically attack corralled livestock there. From 2001–2005, 11 known hyenas from two clans defending territories along the Reserve border were found with neck snares, often set at livestock enclosures. Seventy-three percent of these were either immigrant males or low-ranking natal hyenas. During the same period, six of the seven hyenas from these clans that were either killed during livestock depredation attempts or found dead near villages were also low-ranking. While the possibility exists that low-ranking hyenas are more likely to seek out and attack livestock directly, our space use data suggest that garbage alone can influence movements of hyenas, particularly those of low rank, and that these individuals may therefore be more likely to participate in depredation events.

The potential of the presence of human-provided food sources to influence carnivore space use patterns is well documented. A wolf pack in Italy focused their nightly movements around garbage dumps (Ciucci et al. 1997), and there is a long history in North America of both black bears (Herrero 1983; Rogers et al. 1976) and grizzly bears (Craighead & Craighead 1971) visiting garbage dumps with remarkable frequency and predictability. Beckmann and Berger (2003) have related use of these dumps by black bears to an increase in direct conflict with humans, but this problem may be exacerbated when sources of garbage occur in the vicinity of livestock. In an earlier study we showed that larger pastoral villages along the Reserve border were more likely to suffer livestock losses to hyenas, and suggested that large villages may be more attractive to foraging hyenas due to the larger amounts of refuse produced by them (Kolowski & Holekamp 2006). We have shown here that even small sources of human refuse have the ability to alter hyena space use patterns and result in disproportionately frequent use of these areas. As refuse and livestock carcasses are common around many pastoral villages surrounding the Reserve, it seems likely that regular nightly movements into village areas by Reserve hyenas (Kolowski & Holekamp 2006) are associated with utilization of this resource. Because increased hyena use of these village areas is associated with more frequent hyena attacks on livestock (Kolowski & Holekamp 2006), the ability of human refuse to influence hyena movements makes the presence of these food sources in and around pastoral villages a potentially serious obstacle to efforts to reduce the frequency of livestock depredation events.

CHAPTER FOUR

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CHAPTER FOUR

SPATIAL, TEMPORAL, AND PHYSICAL CHARACTERISTICS OF LIVESTOCK DEPREDATIONS BY LARGE CARNIVORES ALONG A KENYAN RESERVE BORDER

INTRODUCTION

Human activity has caused a global decline in many large carnivore species (Fuller 1995; Nowell & Jackson 1996). As a result, large carnivores have disappeared from areas of high human density, and the current risk of extinction to a given predator species is closely linked with its level of exposure to human populations (Woodroffe 2001). Although habitat conversion, declining natural prey populations, and commercial exploitation have contributed to carnivore losses, active persecution by humans, based on real or perceived threats to themselves and their livestock, appears to be the most important factor in observed declines (Woodroffe 2001). Large carnivores, humans and their livestock have coexisted for millennia, but recent decades have seen dramatic increases in the frequency of human-carnivore conflict, resulting mainly from an exponential increase in the human population (Conover 2002; Woodroffe 2000).

In the face of such persecution, protected areas are fast becoming the last refugia for many large African predators (Mills 1991), all of which have experienced significant declines in recent decades (Ginsberg & Macdonald 1990; Mills & Hofer 1998; Nowell & Jackson 1996; Ogutu et al. 2005). However, even within protected areas, humans often remain the main source of mortality to large carnivores (Woodroffe & Ginsberg 1998), with smaller reserves surrounded by dense human populations being particularly susceptible to species loss

(Brashares et al. 2001; Harcourt et al. 2001). Given current rates of habitat conversion and human population growth, expansion of African reserves is unlikely, yet few of Africa's existing reserves are large enough to maintain viable populations of wide-ranging predators (Brashares et al. 2001). Therefore, conservation of large African carnivores is likely to depend on networks of smaller reserves, buffer zones, and private and communal lands, where successful conservation will be closely linked with an ability to resolve human-carnivore conflicts and minimize numbers of carnivores killed by people (Woodroffe 2001). To succeed in these efforts, park managers, biologists, and indigenous people must coordinate efforts to understand the circumstances surrounding conflicts involving large carnivores, and combine systematic data with local experience to identify factors that may mitigate conflict (Treves & Karanth 2003).

The Masai Mara National Reserve, Kenya (hereafter the Reserve) is one of East Africa's most popular game viewing locations, largely because it supports a high density of large carnivores (Ogutu & Dublin 1998; Ogutu & Dublin 2002). With the passage of the Land Group Representatives and Land Adjudication Act of 1968, much of the communal land immediately north of the Reserve was opened to demarcation into group ranches to formalize security of land tenure for the predominantly pastoral resident Maasai people (Kimani & Pickard 1998). By the late 1970s all rangelands surrounding the Reserve had been assigned to group ranches, 4 of which currently surround the Reserve: Lemek, Ol Kinyie, Koyake and Siana. The rangeland within these group ranches was intended to act as a buffer zone, protecting known wildlife dispersal areas from habitat conversion, and separating the protected area within the Reserve from expanding commercial agriculture to the north (Serneels et al. 2001). However, as available rangeland north of the ranches is lost to agriculture and the human population continues to grow (by an estimated 4.4% per annum on the Koyake group ranch (Lamprey & Reid 2004)), carnivore-livestock conflict is inevitable and likely to increase. To avoid the establishment of population "sinks" surrounding the Reserve, in which human-caused mortality limits survival of predators dispersing from the Reserve (Woodroffe & Ginsberg 1998), livestock depredation and the resulting persecution of carnivores must be minimized.

Rates of livestock depredation by large carnivores can be influenced by local environmental conditions such as abundance of natural prey (Meriggi & Lovari 1996; Mizutani 1999; Polisar et al. 2003; Stoddart et al. 2001) and rainfall (Patterson et al. 2004; Woodroffe & Frank 2005), as well as socio-ecological factors including livestock husbandry practices (Ciucci & Boitani 1998; Madhusudan 2003; Meriggi & Lovari 1996; Ogada et al. 2003; Stahl et al. 2001) and characteristics of attacked farms, villages, and livestock enclosures (Mech et al. 2000; Ogada et al. 2003). However, few studies have concurrently investigated the influence of both environmental and socio-ecological factors on livestock depredation, and even fewer have combined this knowledge with consideration of the behavior and movements of monitored predators. Our goal was to elucidate relationships between various ecological factors and temporal variation in conflict frequency in the vicinity of the Reserve, and to assess the influence of village and enclosure characteristics on relative vulnerability to carnivore attack. Finally, the concurrent long-term study of spotted hyenas (*Crocuta crocuta*) in our study region provided a unique opportunity to associate detailed data on hyena movements with hyena depredation behavior.

METHODS

Study area

Geography and Climate

Our study was conducted along the northeastern border of the Masai Mara National Reserve (1500km^2) in southwestern Kenya (Figure 4.1). The portion of the study area outside the Reserve was situated in sections of the Koyake and Siana group ranches, which share their southern borders with the northern border of the Reserve. The study focused on three adjacent locales within these ranches: Talek, Ntipilikwani, and Olosogon. These were chosen for their accessibility, and their relatively high density of settlements near the Reserve. The Talek region supports the highest density of settlements along the entire northern border of the Reserve (Reid et al. 2003). The dominant land uses on the group ranches are subsistence pastoralism and wildlife tourism. Most of the annual rainfall in this region falls during one of two wet seasons: the "short rains" in November–December, and the "long rains" in March–May. During 2003, total rainfall in our study area was 1223 mm.

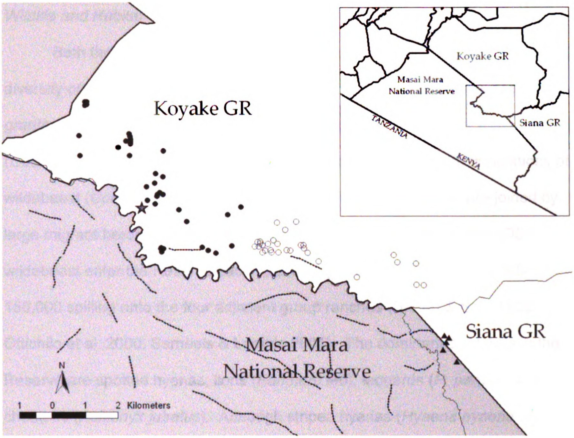

Figure 4.1. Locations of Maasai bomas (villages) of the Talek (filled circles), Ntipilikwani (open circles), and Olosogon (triangles) locales from which information on livestock depredation by large carnivores was collected from March 2003 to April 2004. Only bomas that contained livestock and were located within 2 km of the Reserve border are included. Dashed lines indicate prey transects and the town of Talek is indicated with a star.

Wildlife and Habitat

Both the Reserve and the surrounding group ranches support a large diversity of resident ungulates including gazelles (*Gazella thomsonii* and *G. granti*), impala (*Aepyceros melampus*), topi (*Damaliscus lunatus*), and giraffe (*Giraffa camelopardalis*). From August to October small resident populations of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) are joined by large migrant herds from Tanzania. It is estimated that 300,000–750,000 wildebeest enter the Reserve each year during the migration, with 50,000–150,000 spilling onto the four adjacent group ranches (Broten & Said 1995; Ottichilo et al. 2000; Serneels & Lambin 2001). The dominant predators in the Reserve are spotted hyenas, lions (*Panthera leo*), leopards (*P. pardus*) and cheetahs (*Acinonyx jubatus*). Although striped hyenas (*Hyaena hyaena*) also occur in this region, they are rare and were not known to attack any livestock during the study period. Therefore, discussions of hyenas below refer exclusively to spotted hyenas.

The Reserve consists primarily of rolling grassland habitat and scattered bushland (predominantly *Croton* and *Euclea* species), with riparian forest along the major watercourses. The Koyake and Siana group ranch property in our study area is grazed year-round by livestock, and includes habitat similar to that of the Reserve, with somewhat reduced woody vegetative cover. The Talek River and its tributaries support the majority of the vegetative cover in the study area.

The Maasai Village

The traditional Maasai village, or boma, in this region consists of a collection of huts, constructed from wooden frames covered with mud and dung, surrounding a central cattle enclosure (Figure 4.2). Although sometimes used to mean "fence", the term boma here will refer to an entire village or settlement, which may include numerous households and livestock enclosures (Burnsilver et al. 2003; Homewood & Rodgers 1991). Typically a number of household heads reside at a boma with their personal dwellings built in distinct sections of the boma. Each household head keeps his cattle in the shared central enclosure at night and maintains a separate personal enclosure among his huts, in which his own sheep and goats are kept at night. Of the 78 bomas identified within our study area, 64 (82.1%) of these contained a single cattle enclosure with < 2 sheep/goat enclosures. The remaining bomas contained one cattle enclosure and, on average, three separate sheep/goat enclosures, roughly approximating the number of resident livestock owners.

In our study area, livestock enclosures were constructed of local bush (often thorned), or tall (1.5–2 m) pieces of split timber (referred to as poles), spaced up to 0.25 m apart, and sometimes fortified by chain link or barbed wire. Enclosures for sheep and goats were always more sturdy and complete than those for cattle. A small peripheral and often poorly maintained fence of bush was often constructed around the entire boma compound (Figure 4.2). However, this peripheral fence was always fortified where it comprised part of an individual

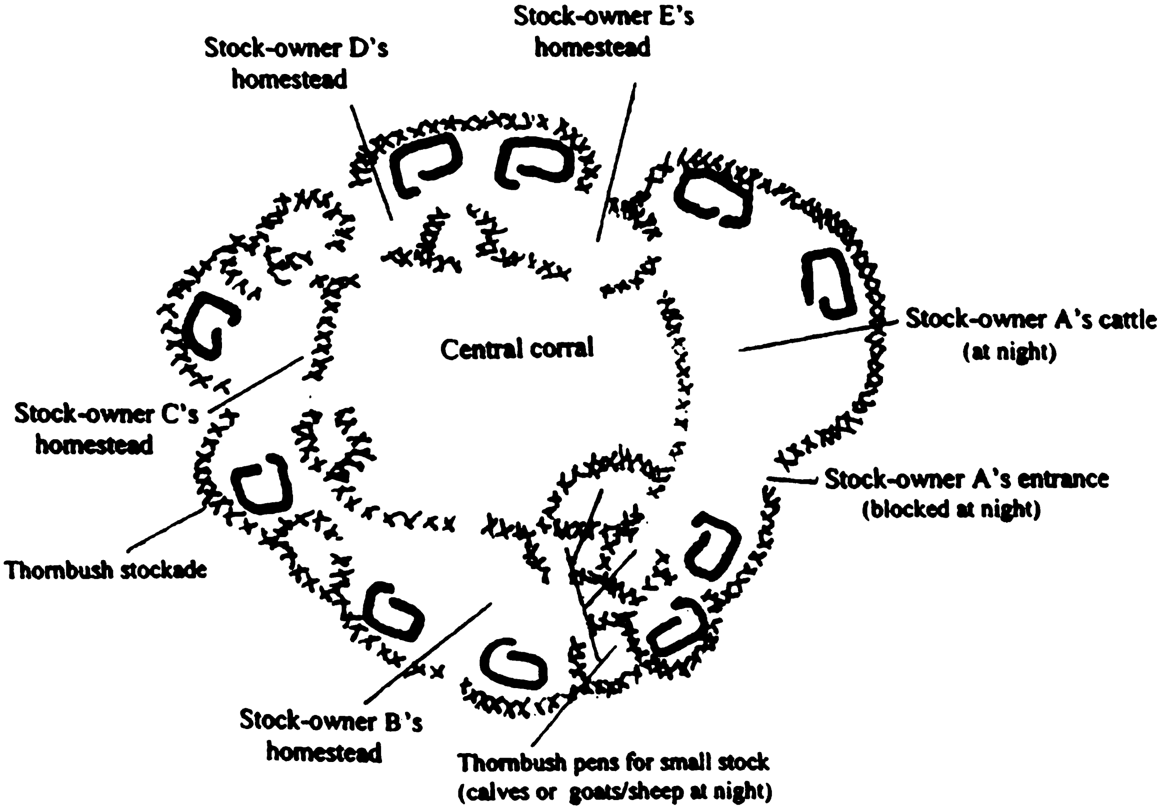

Figure 4.2. Configuration of a typical Maasai village (boma). Cattle from all household heads are housed together in the shared central corral. Individual homesteads maintain separate enclosures for their own small stock. Figure adapted with permission from Spencer (2003) pg 45.

livestock enclosure. Donkeys were rare in the region, but when present were usually kept at night within the peripheral boma fence.

Livestock were typically driven out of the boma between 0800–0900 h for grazing, and returned to the boma just before sunset. All herds outside of the boma are referred to here as grazing herds. Cattle typically traveled 2–5 km from the boma during the day, but sheep and goat herds generally remained < 2 km from the boma. Grazing herds were always monitored by one to several herders and all livestock were kept within their enclosures when not grazing. Illegal livestock grazing occurred within the Reserve, and sometimes occurred at night, when Reserve rangers rarely patrolled.

Collection of conflict data

In February 2003, we trained three Maasai scouts, one from each of the study locales, to complete a one-page report when notified of any injury or death of livestock deemed to have been caused by carnivores. During the same month, we held meetings with elders from each locale to discuss our project goals and request their cooperation and assistance. We asked landowners to inform their local scout of depredation events occurring either at the boma or during grazing, as soon as possible after they occurred. Scouts visited each attacked boma or herd owner to collect data. It was widely known by local villagers that our research was not affiliated with the government or other political entities, and that we offered no compensation for depredated livestock. There was thus no apparent incentive for exaggerating or fabricating claims, yet scouts made every effort to confirm all incidents based on available evidence. Bomas more than 2 km from the Reserve were excluded to maximize efficient monitoring of the area by scouts. A few settlements that contained no livestock of any type were also excluded from the study. Conflict reports were collected from March 2003 through April 2004.

Based on available evidence and witness accounts, scouts recorded the estimated time of day of each attack, the number and species of all livestock killed or injured in the attack, the predator species involved, and the nature of the interaction, if any, between villagers and the predator. In addition, a narrative account of each event was recorded, as well as the evidence used to identify the predator species. We documented the number of cattle held in the central enclosure as well as the number of sheep and goats held in the owner's small stock enclosure. With the exception of the enclosures themselves, village residents and their domestic dogs are the only deterrents to predator attack at Maasai bomas. Neither firearms nor night watchmen are used in this region. We therefore recorded the number of dogs associated with each affected household as well as the total number of dogs at the boma. As an indicator of the number of residents and the corresponding levels of human activity in attacked bomas, the number of household huts and the total number of huts in the boma were recorded. Finally, we categorized the type of enclosure used to protect small stock and cattle as pole fence, bush fence, or other. All of the above variables were recorded within 1–3 days of the incident. These same variables were also recorded for all bomas and enclosures that did not suffer any depredation losses during the study. A single observer (JMK) assessed the strength (strong vs. weak) of attacked and unattacked enclosure fences based on their relative levels of maintenance, reinforcement, and overall sturdiness.

The spatial locations of all study bomas and enclosures were recorded using a hand-held GPS unit. We measured the distance from each boma and enclosure to the nearest vegetative cover adequate to conceal a predator in daylight, because predators may be less willing to attack livestock further from cover. Because densities of some large predators are likely lower outside than inside protected areas (Caro 1999b; Mills & Hofer 1998; Ogutu et al. 2005), bomas further from the Reserve may be less vulnerable to attack. We therefore measured the distance to the Reserve border for each study boma and enclosure using ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, CA, USA). Finally, the isolation of bomas relative to other bomas may also influence their vulnerability to attack. We therefore recorded the distance to the nearest boma, and the density of bomas within a 200 m radius of each boma. The same analysis was repeated using enclosure locations to characterize the relative isolation of individual sheep/goat enclosures. Accurate locational data were unavailable for attacks on grazing herds.

Ecological conditions

Previous research has suggested natural prey abundance may influence depredation rates (Polisar et al. 2003; Woodroffe et al. 2005), and that rainfall may be an indirect measure of prey abundance and observed variation in depredation frequency (Patterson et al. 2004; Woodroffe & Frank 2005). We therefore examined relationships between temporal variation in depredation frequency and both rainfall and prey abundance. Total monthly rainfall was measured using a standard metric rain-gauge located along the Talek River. We assessed the availability of natural prey to large predators by counting all prey occurring along 29 1-km road transects, two of which were located on group ranch property (Figure 4.1). We counted all wild ungulates within 100 m of each transect 2–4 times per month for 13 of 14 months during the study period. An average number of total ungulates counted per census was then calculated as an index of local prey abundance in each month.

Predator movements

We monitored radiocollared adult spotted hyenas throughout the study period to determine whether predator movements were associated with temporal variation in depredation behavior. Spotted hyenas live in social groups called clans and cooperatively defend a stable group territory. Monitored hyenas were members of a single clan whose northern territory boundary extended into the Talek and Ntipilikwani locales outside the Reserve, and whose 47–55 members were known to be involved in local depredation events. Between 2001 and 2005, at least nine individuals from this clan were killed at bomas within the study region during livestock attacks.

We documented hyena space use with two different monitoring techniques. The first method utilized frequent (~ 1 location per hyena every 2–3 days) telemetry locations collected at all times of day and night, with the majority of monitoring effort occurring near dusk and dawn. Three individual home-ranges (HRs) were constructed for each of 8 hyenas (4F, 4M) based on a minimum of 35 locations per hyena ($\bar{x}$ = 57 locations) collected during months in each of 3 depredation categories. Months having < 4 hyena attacks were classified as "low" depredation periods, between 4 and 7 as "mid", and > 7 as "high". We then associated each depredation category with the proportion of each individual's corresponding HR situated outside the Reserve. All home-ranges were calculated with Animal Movement Analyst (Hooge & Eichenlaub 2000) as 95% fixed-kernel utilization contours with smoothing factors (*h*) determined using least-squares cross-validation (Seaman & Powell 1996; Worton 1989).

Our second method utilized long-term (2–15 hr) follows of nine radiocollared hyenas (6F, 3M) conducted at all times of day and night. During follows, locations of the focal hyena were collected every 10 min using telemetry, often with visual confirmation, to assess the frequency of use by hyenas of the group ranch properties outside the Reserve. The average proportion of locations per follow on ranch property was compared to the proportion of the clan territory extending into the ranches. The clan territory boundary was based on a 95% fixed-kernel utilization contour constructed using 4763 locations of 11 adult female hyenas collected from May 2002–April 2004. Infrared spotlights and night-vision goggles were used to observe hyenas at night with minimal disturbance. Special attention was paid to the behavior of followed hyenas in close proximity to bomas or humans. For both follow-based and tracking-based analyses, all locations collected within 200m of the communal den were excluded from consideration to control for the influence of this location. Cubs less than approximately 9 months of age, from all mothers in the clan, reside at the communal den and it serves as a center of social activity for clan members.

Statistical analysis

Much of the data involving livestock losses and characteristics of attacks were summarized using proportions, which were compared between two groups using Fisher exact tests (Zar 1999). Relationships between monthly mean values for ecological variables and monthly attack frequencies were first investigated using Pearson's correlation coefficients (r_p). Data on monthly prey abundance were log-transformed to obtain normality. We then modeled both rainfall and prey abundance in a multiple regression analysis, with monthly attack frequency as the dependent variable. The relative influence of these two variables on attack frequency was examined using partial correlation coefficients (Bart et al. 1998). To identify whether hyena movements were associated with specific ecological conditions, we used these same independent variables in a regression model with % of HR outside the Reserve as the dependent variable. For this model, locations from all monitored hyenas were pooled by month ($\bar{x}$ = 120 locations per month, minimum = 74) to obtain a continuous monthly measure of clan space use. To associate hyena depredation behavior with hyena space use, average % HR outside the Reserve for individual hyenas was compared among the three hyena depredation categories using the non-parametric Friedman test for repeated measures.

We used univariate analyses to compare characteristics of bomas and enclosures containing livestock that were attacked by predators with those of bomas and enclosures that were not attacked. Most data describing boma and enclosure characteristics were not normally distributed, so we used Mann–Whitney U-tests to compare continuous variables between groups.

We next used these descriptive variables in multivariate logistic regression analyses to determine which were useful in predicting probabilities of hyena and leopard attacks on both bomas and individual sheep/goat enclosures for a total of four model-building progressions. The set of predictor variables was initially reduced by eliminating highly correlated continuous variables from consideration using Spearman rank order correlation coefficients (r_s). One of the variables in each correlated ($r_s > 0.70$) pair was excluded based on the results of exploratory univariate tests. All possible logistic regression models for each of the four dependent variables, utilizing all combinations of the remaining predictor variables, were then analyzed and compared using Akaike's Information Criterion (AICc) values corrected for low sample sizes. Relative to the model with the lowest AICc value, models with a difference in AICc > 2.0 are considered to have substantially lower empirical support (Burnham & Anderson 2002). We therefore considered all models within 2.0 AICc points of the lowest AICc model. The significance of individual logistic regression models was assessed using a likelihood-ratio χ^2 test, while significance of model parameters was assessed using Wald's χ^2 test. All tests were considered statistically significant at $\alpha = 0.05$, and all statistical analyses were conducted using the software package STATISTICA (StatSoft 2002).

RESULTS

Losses of livestock and carnivores

A total of 130 depredation events were recorded from March 2003 through April 2004. Of the 104 monitored livestock enclosures, 48% suffered loss or injury of stock due to predators during our study period. Every incident was attributed to a specific predator, with 71% based on visual confirmation of the predator, and the rest based on tracks, claw marks, or the condition of the livestock carcass. Hyenas were involved in 69 of the 130 reported incidents (53%), with leopards and lions involved in 32% and 15%, respectively. There were no reported depredation events involving other predators.

During attacks, carnivores killed 147 stock animals; 115 sheep and goats (78%), 30 cattle (20%) and two donkeys. Hyenas, leopards and lions were responsible for 50% ($n = 74$), 37% ($n = 55$) and 12% ($n = 18$) of the livestock deaths, respectively (Figure 4.3). Non-fatal attacks injured an additional 32 sheep and goats, 12 cattle, and one donkey. Leopards accounted for 48% of all sheep and goats killed, but never attacked cattle (Figure 4.3). Lions killed only one goat, but accounted for 57% ($n = 17$) of all cattle kills. Sheep and goats comprised 80% of all livestock kills by hyenas. Hyenas were responsible for 51% and 43% of all sheep/goat and cattle depredation respectively (Figure 4.3).

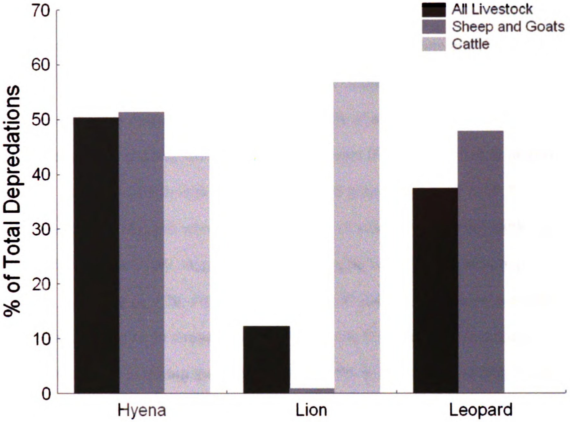

Figure 4.3. The percent of the total losses of sheep and goats, cattle, and all livestock species that were attributed to spotted hyena, lion, and leopard depredation. Percentages shown are out of a total of 147 livestock killed during a 14-month period along the northeast border of the Masai Mara National Reserve. Kenya.

Seventy-five (58%) of the 130 recorded attacks occurred inside bomas, with the remaining attacks directed at grazing animals. Hyenas attacked grazing herds as often as corralled herds (45% and 55% respectively; Fisher exact test $p = 0.336$) and were responsible for more than 80% of attacks both on cattle within the boma, and on grazing herds of sheep and goats (Figure 4.4). Lions attacked corralled livestock ($n = 2$) less than they attacked grazing herds ($n = 18$; Fisher exact test $p = 0.014$), and were involved in 74% of attacks on grazing cattle herds (Figure 4.4). Conversely, leopards attacked grazing herds ($n = 5$) less than livestock in bomas ($n = 36$; Fisher exact test, $p = 0.0003$) and were responsible for 56% of all attacks on sheep and goats in bomas (Figure 4.4). All attacks at the boma took place during the night whereas 71% of attacks on grazing herds took place between 11:00 and 16:00 h.

Of 109 fatal attacks, 81% resulted in the death of only one stock animal, and 8% in the death of 3 or more. Although leopards tended to kill more livestock per attack (1.34) than hyenas (1.06) and lions (0.9), the difference was not significant (Kruskal-Wallis test $H_{2,130} = 2.27$, $p = 0.322$). Most (76%) of the attacks on livestock in bomas were detected in progress, often resulting in the predator being chased from the scene. Undetected boma attacks were more likely than detected attacks to result in the death of livestock (100% vs. 79%, Fisher exact test, one-tailed $p = 0.027$). Although one of the assumed benefits of the presence of dogs is their ability to alert residents to the presence of predators, locations at which predators were detected during attacks were not characterized by more dogs either at the attacked enclosure ($U = 505.0$, $p =$

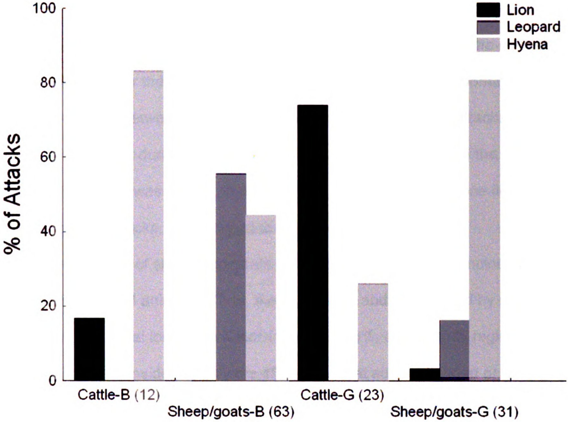

Figure 4.4. Involvement of lion, leopard and hyena in 4 categories of livestock depredation incidents along the northeast border of the Masai Mara National Reserve during a 14-month study period. Total numbers of attacks of each type are listed in parentheses after category headings. "B" indicates attacks at the boma; "G" indicates attacks while grazing.

0.921) or at the boma (U = 457.5, p = 0.984) than were locations where attacking predators went undetected. In addition, there was no difference in the number of houses within either the homestead (U = 415.0, p = 0.982) or the boma (U = 418.5, p = 0.380) between locations of detected and undetected attacks. Only one reported attack during the study period resulted in the death of the intruding carnivore (a hyena was killed). In other cases, three hyenas and one lion were speared during attacks, but escaped to unknown fates.

The number of sheep and goats reported for 99 individual enclosures was estimated at 16,523 animals. Thus, the 115 sheep and goats killed by predators resulted in an annual loss of 98.4 individuals, or 0.6%, of the study region's small stock holdings. Considering only the 48 owners that suffered sheep or goat losses to predators, each suffered an average annual loss of 1.8% of his stock (range: 0.2–8.6%). Given an estimated 11,864 cattle at the 78 study bomas, we recorded an annual loss to predators of 25.7 cattle, or 0.2% of the total cattle holding.

Based on local information from numerous sources, adult cows were priced at 10,000 Kenya shillings (KSh), adult goats and sheep at 2,000 KSh, calves at 6,000 KSh, and juvenile goats and sheep at 1,000 KSh. An exchange rate of 76.04 to USD was used, based on the average exchange rate during the study period (www.centralbank.go.ke – accessed 6 Apr 2005). Over a 14-month period, livestock depredation by predators resulted in a loss of 6,049 USD (460,000 KSh) to the study region. Hyenas were responsible for 45% of this monetary loss, lions for 36%, and leopards for 19%.

Temporal patterns of attacks and relationship to predator movements

There was substantial monthly variation in the number of depredation events, with attack frequency highest from March – May and lowest in October (Figure 4.5). Monthly attack frequency was positively correlated with total monthly rainfall ($r_p = 0.66$, $p = 0.010$, $n = 14$; Figure 4.6), and the two months during which depredations reached their highest levels were the only months in the study period during which rainfall exceeded 200mm. In addition, monthly prey levels were weakly correlated with attack frequencies ($r_p = -0.47$ $p = 0.103$; $n = 13$ months). However, despite occurring during the influx of migratory wildebeest and zebra from the Serengeti, October 2003 prey counts failed to reflect this super-abundance of prey and indicated below-average prey numbers. With this outlier month excluded, prey abundance showed a strong negative correlation with attack frequency ($r_p = -0.67$, $p = 0.018$; $n = 12$). Although both variables were related to attack frequency, total monthly rainfall and average monthly prey abundance were not correlated ($r_p = -0.44$, $p = 0.149$; outlier excluded).

It was the belief of local livestock owners that not only was the rainy season a time of increased predator conflict, but also that predators specifically preferred to attack bomas during rainfall events. To investigate whether the above correlations were driven by seasonal or nightly factors, we documented the proportion of attacks that occurred on night when rainfall was recorded. There was no difference between the proportion of nights during the study period

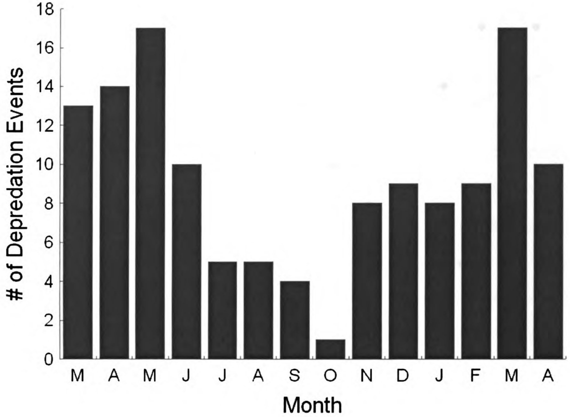

Figure 4.5. Total monthly livestock attacks by predators recorded within 2 km of the northeastern border of the Masai Mara National Reserve, Kenya, from March 2003 to April 2004. Conflicts included attacks by lions, leopards, and hyenas that resulted in either death or injury of livestock.

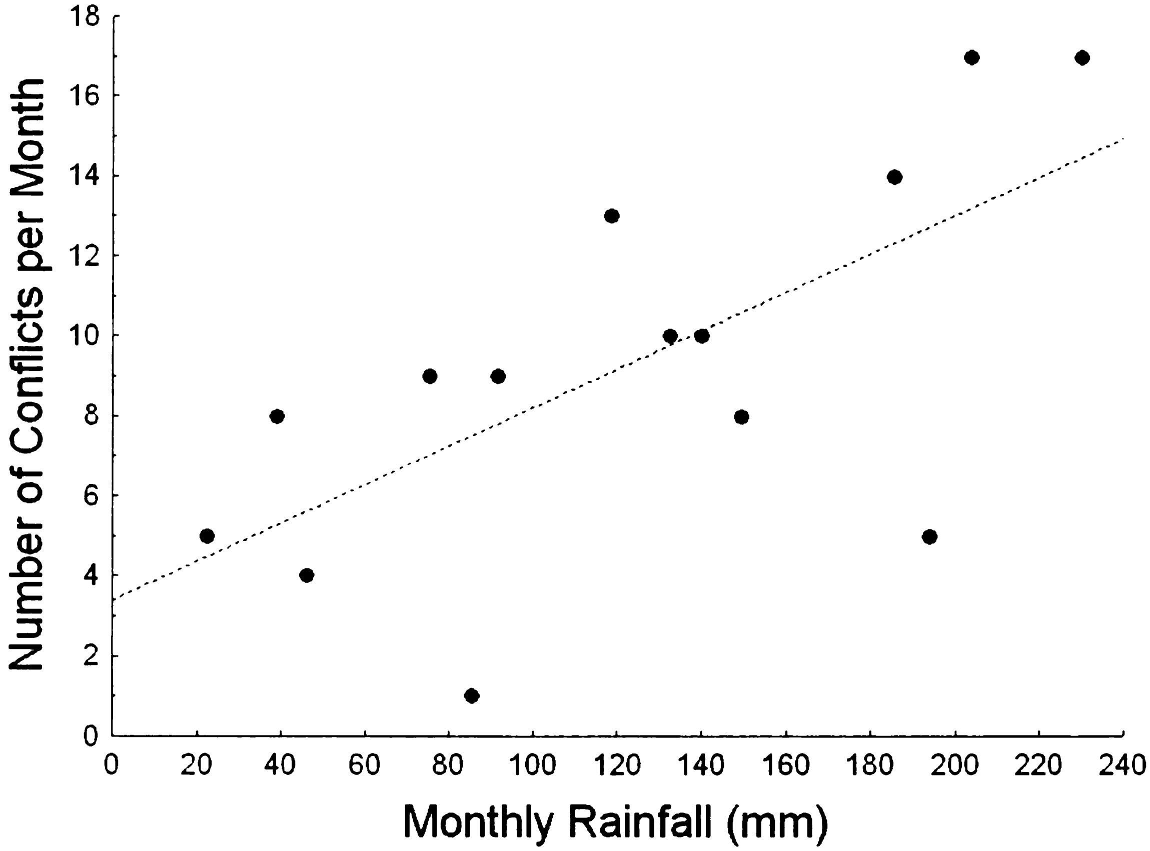

Figure 4.6. Correlation ($r_p = 0.66$, $p = 0.010$) between monthly rainfall (mm) and total predator incident reports collected each month during a 14-month study period.

on which it rained (30.1%), and the proportion of attack nights on which it rained (39.4%, $\chi^2 = 2.692$, $p = 0.102$). Thus, the correlation between monthly conflict frequency and rainfall patterns does not appear to be driven by a predator preference for raiding bomas on rainy nights.

Using multiple regression analysis, we compared the relative influence of rainfall and prey abundance on attack frequency. The two-variable regression model explained a significant amount of the variation in monthly attack frequency ($F_{(2,10)} = 4.84$, $R^2 = 0.492$, $p = 0.034$), yet prey abundance explained only 9.1% of the variance beyond that explained by rainfall. Thus, although both independent variables were useful in predicting monthly attack rate, rainfall was a slightly better predictor than local prey abundance.

Space use by radiocollared hyenas was related to hyena depredation behavior. We found that the % of each hyena's HR falling outside the Reserve border was significantly higher in mid- (n = 5 months) and high-level (n = 4 months) depredation periods than in low-level (n = 5 months) periods (Friedman $\chi^2 = 12.0$, $p < 0.003$; Figure 4.7). This variation was not likely to have resulted from changes in natural prey abundance outside the Reserve, as group ranch prey transects showed negligible prey numbers throughout the year. On average, 2.4 ± 3.4 (*SD*) prey were counted per transect on group ranches each month, compared to 40.6 ± 31.2 prey per transect inside the Reserve. Neither rainfall nor prey abundance was useful in predicting the % of monthly clan HR outside the Reserve ($F_{(2,10)} = 1.19$, $R^2 = 0.192$, $p = 0.344$).

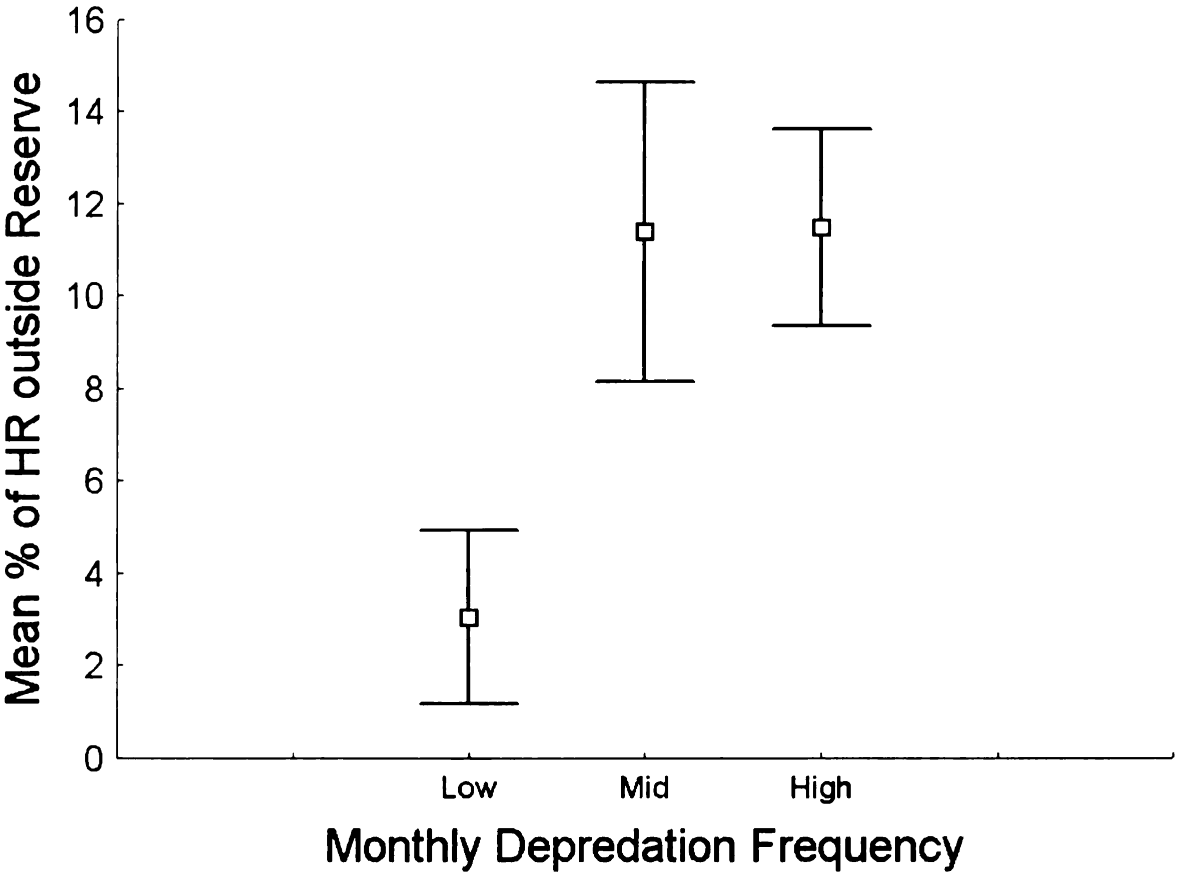

Figure 4.7. Mean percent of individual hyena home ranges (95% fixed-kernel) that were located outside the Masai Mara National Reserve based on locations collected during months of low, medium and high frequencies of livestock depredation events involving hyenas from March 2003–April 2004. Whiskers indicate 95% confidence intervals.

We collected 1754 locations (*n* = 811 night, 943 daylight) during multiple follows on each of 9 different hyenas. Both nighttime (*n* = 33) and daytime follows (*n* = 39) provided an average of 24 locations per follow. Followed hyenas frequently used of lands outside the Reserve. Although 9% of the clan territory lay outside the Reserve, an average of 17% of locations per nighttime follow were collected outside the Reserve. However, on average, only 0.4% of locations per daytime follow were outside the Reserve. Of 130 locations recorded outside the Reserve during all follows, 23% were within 200 m of a boma. When outside the Reserve, followed hyenas were often seen foraging in close proximity to bomas, but making no attempts to enter them. In addition, our observations suggest that, at least during hours of darkness, hyenas do not appear to be concerned about humans. For example, groups of hyenas sometimes slept for extended periods within 150 m of large bomas. In addition, hyenas were seen to walk calmly within 50 meters of humans, only fleeing from those carrying flashlights.

Characteristics of bomas and enclosures

Univariate Comparisons

Bomas that suffered at least one hyena attack differed from those that did not with respect to five of nine variables (Table 4.1). Bomas attacked by hyenas contained larger numbers of cattle, sheep and goats, sheep/goat enclosures, dogs and houses than did bomas not attacked by hyenas. All significant variables with the exception of the number of cows at the boma were

Table 4.1.Univariate comparisons between mean values ± standard error of nine independent variables recorded at attacked and unattacked Maasai bomas (villages) within 2 km of the northeastern border of the Masai Mara National Reserve, Kenya. *P*-values are based on Mann-Whitney *U* tests. Variables indicated by asterisks are intercorrelated.

		Hyena Boma Attack			Leopard Boma Attack		
	N	Yes	No	*p*-value	Yes	No	*p*-value
Cows	68	222.0(42.1)	127.4(118.7)	0.039[a]	189.6(44.1)	152.7(22.4)	0.420
Sheep/goats*	69	349.0(65.3)	171.9(19.0)	0.010[a]	322.9(66.8)	206.6 ± 28.6	0.108
Dogs*	67	6.6(1.0)	4.1 ± 0.4	0.016[a]	6.3 ± 1.2	4.5 ± 0.4	0.308
Houses*	69	9.9(1.2)	5.2 ± 0.4	0.000[a]	8.2 ± 1.6	6.2 ± 0.5	0.299
Dist. to Reserve (m)	69	731.7(102.5)	915.1 ± 57.7	0.075	790.7 ± 114.8	890.7 ± 57.1	0.286
Sheep/goat enclsrs.*	71	1.8(0.3)	1.0 ± 0.0	0.022[a]	1.7 ± 0.4	1.2 ± 0.1	0.355
Dist. to cover (m)	66	253.9(39.3)	306.5 ± 47.3	0.969	312.8 ± 69.2	280.1 ± 39.1	0.757
Bomas in 200 m	69	1.8(0.4)	1.6 ± 0.3	0.795	0.4 ± 0.2	2.1 ± 0.3	0.003[a]
Closest boma (m)	69	230.1 ± 53.7	222.4 ± 25.9	0.651	314.7 ± 40.2	192.8 ± 29.9	0.001[a]

(*) intercorrelated variables

([a]) significant at $\alpha = 0.05$

intercorrelated ($r_s > 0.70$; Table 4.1). Bomas suffering at least one leopard attack on livestock had fewer other bomas within a 200 m radius, and were further from the closest boma than those suffering no leopard attacks (Table 4.1).

Few differences were identified between attacked and unattacked sheep/goat enclosures (Table 4.2). Enclosures attacked by hyenas were closer to the next enclosure and were more frequently constructed of local bush material than were unattacked enclosures (Table 4.2). Enclosures suffering leopard attacks only differed from unattacked enclosures with respect to fence type, with attacked enclosures more likely to be made from pole fencing than were unattacked enclosures (Table 4.2).

There was no difference between the proportion of pole (43%) and bush fences (36%) present in the study area that were attacked by predators (Fisher exact test, $p = 0.656$). However, sheep and goats enclosed by pole fences were more likely to be attacked by leopards than were those enclosed by bush fences (Fisher exact test, $p = 0.002$), whereas small stock within bush fences were more likely to be attacked by hyenas than were those in pole enclosures (Fisher exact test, $p = 0.003$; Figure 4.8). Livestock held under strong, well-maintained pole fences were no less likely to be attacked by leopards (Fisher exact test, $p = 0.752$) or hyenas ($p = 0.286$) than were those within weak pole fences. Similarly, relative strength of bush fences did not affect probability of attack by either hyenas (Fisher exact test, $p = 0.757$) or leopards ($p = 1.0$).

Table 4.2. Univariate comparisons between mean values ± standard error of seven independent variables recorded at attacked and unattacked sheep/goat enclosures within 2 km of the northeastern border of the Masai Mara National Reserve, Kenya. *P*-values are based on Mann-Whitney *U* tests for continuous variables and Fisher exact tests for proportions. None of the variables examined here were intercorrelated.

		Hyena Sheep/Goat Attack			Leopard Sheep/Goat Attack		
	N	Yes	No	*p*-value	Yes	No	*p*-value
Sheep/goats inside (#)	99	196.3 ± 27.8	158.0 ± 14.1	0.189	205.0 ± 34.4	155.4 ± 12.7	0.281
Dogs at enclosure (#)	96	4.0 ± 0.3	3.7 ± 0.3	0.363	4.0 ± 0.5	3.7 ± 0.3	0.488
Houses at enclosure (#)	90	4.6 ± 0.4	4.9 ± 0.3	0.809	4.6 ± 0.6	4.9 ± 0.3	0.669
Enclosures in 200 m (#)	96	3.7 ± 0.6	2.9 ± 0.4	0.200	2.7 ± 0.8	3.2 ± 0.3	0.092
Closest enclosure (m)	96	116.7 ± 55.9	156.5 ± 18.6	0.013[a]	201.6 ± 41.4	131.2 ± 21.4	0.178
Pole enclosure (%)	93	18.2	50.7	0.007[a]	77.3	32.4	0.000[a]
Bush enclosure (%)	93	77.3	38.0	0.002[a]	22.7	54.9	0.014[a]

([a]) significant at $\alpha = 0.05$

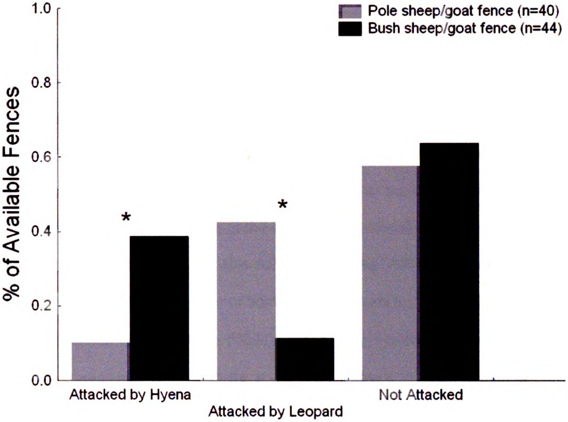

Figure 4.8. Relative attack rates by leopard and hyena on the two most common types of sheep/goat enclosures within 2 km of the northeastern Reserve border. Significant differences (Fisher exact test for comparison of proportions; $p < 0.05$) are indicated by an asterisk.

Multivariate Analyses

Nine variables were initially considered for estimation of hyena and leopard attack probability at Maasai bomas (Table 4.1). The most significant of all intercorrelated variables, number of boma houses, was retained, but numbers of sheep and goats, sheep/goat enclosures, and boma dogs were excluded from further analysis. With occurrence of a hyena attack as the dependent variable, all possible model combinations of the six remaining variables were compared based on model AICc values (Table A.20). The lowest AICc value was assigned to a model including the number of boma houses (Wald's χ^2 = 13.52; $p < 0.001$) and the distance to the Reserve (Wald's χ^2 = 3.92; $p = 0.048$) as predictive variables (Log-likelihood χ^2 = 22.54, $p < 0.0001$; Table 4.3). Two additional models were supported by the data, both of which combined these first two variables with an additional third variable (distance to the closest boma or number of bomas within 200 m). However, none of the variables other than distance to the Reserve and the number of bomas houses were significant parameters in the two additional models. Model selection procedures thus indicated that likelihood of hyena attack on bomas increased as number of houses increased and distance to the Reserve decreased.

Considering all possible models with the same six variables predicting boma attack by leopards (Table A.21), the lowest AICc value was assigned to a model including only the number of bomas within a 200 m radius (Wald's χ^2 = 7.38, $p = 0.007$; Log-likelihood χ^2 = 12.17, $p < 0.001$; Table 4.3). Two additional models were included in the optimal subset of models; both included the number

Table 4.3. Logistic regression models predicting the probability that a Maasai boma (village) will be attacked by large carnivores. Presented models were selected based on the minimum AIC value of all model combinations using 6 uncorrelated continuous variables.

	Estimate	St. Error	Wald Stat.	*p*-value
Hyena				
Intercept	- 2.0664	0.8505	5.9027	0.0151
Boma houses (#)	+0.3955	0.1075	13.5264	0.0002
Distance to Reserve (m)	- 0.0016	0.0008	3.9226	0.0476
Leopard				
Intercept	- 0.2393	0.3438	0.4847	0.4863
Bomas within 200 m (#)	- 0.7476	0.2753	7.3760	0.0066

of bomas within 200 m, and added a single variable (distance to the Reserve or the number of boma houses). However, none of these other models included significant parameter estimates additional to the number of bomas within 200 m (Table A.21). Therefore modeling procedures indicated that a decrease in the density of surrounding bomas was the most important factor increasing the probability of a leopard attack.

Finally, we attempted to identify variables most important in estimating the probability of leopard and hyena attacks at the level of individual sheep/goat enclosures. Both logistic regression models initially considered five continuous variables and one categorical variable representing fence type. Model-building for hyena enclosure attack probability indicated a set of eight optimal models (Table A.22). The lowest AICc value was assigned to a model that included only fence type (Wald's χ^2 = 9.64; p = 0.002) as an independent variable (Log-likelihood χ^2 = 6.42, p = 0.011; Table 4.4). No additional variables in the other seven models were significant model parameters (Table A.22). The odds ratio for fence type indicated that the presence of a bush fence increased the probability of hyena attack by 2.43 times. With leopard enclosure attack as the dependent variable, we identified three optimal models (Table A.23). The model with the lowest AICc only included fence type (Wald's χ^2 = 11.88; p = 0.001) as a model variable (Log-likelihood χ^2 = 11.49, p = 0.001; Table 4.4), and no additional variables in the other two models were significant model parameters (Table A.23). The odds ratio for fence type indicated that the presence of a pole fence increased the probability of leopard attack by 2.67 times.

Table 4.4. Logistic regression models predicting the probability that a Maasai sheep/goat enclosure will be attacked by large carnivores. Presented models were selected based on the minimum AIC value of all model combinations using five uncorrelated continuous variables and one categorical variable.

	Estimate	St. Error	Wald Stat.	*p*-value
Hyena				
Intercept	+0.7403	0.5737	1.6653	0.1969
Bush fence?	+0.8875	0.2858	9.6408	0.0019
Leopard				
Intercept	+1.2820	0.2842	20.3456	0.0000
Pole fence?	+0.9797	0.2842	11.8823	0.0006

DISCUSSION

Predator Involvement and Livestock Losses

Our study was designed, in part, to complement and expand on recent work on livestock depredation by carnivores on rangelands in eastern Africa. Patterson et al. (2004), who conducted their study on commercial ranches in southeastern Kenya, found lions to be responsible for 86% of attacks on livestock, with hyenas involved in <10%. They reported no leopard attacks on livestock. A study conducted on primarily commercial ranches in northern Kenya, found that lions accounted for approximately 63% of all livestock kills, with hyenas and leopards accounting for only 15% and 11% of kills, respectively (Ogada et al. 2003). In an earlier study conducted on group ranches near our own study site, Karani (1994) found that leopards were the most serious livestock predators (50% of livestock attacks), with lions and hyenas responsible for 31% and 19% of recorded attacks respectively. Thus, although multiple earlier studies on Kenyan rangelands concluded that the lion is the most serious livestock predator, and that hyena predation is relatively infrequent (Frank 2000; Ogada et al. 2003; Patterson et al. 2004), we found relatively little involvement by lions in livestock attacks, particularly at Maasai bomas, with leopards and hyenas responsible for most attacks.

Regional variation in relative livestock depredation by these large predators may be attributed to differences in relative densities of large carnivores, husbandry practices, and relative abundance of different stock species. Although some researchers have been unable to associate predator density with livestock depredation rates (Connor et al. 1998; Graham et al. 2005), others have clearly documented increases in depredation with increases in carnivore density (Sagor et al. 1997; Stahl et al. 2001; Stoddart et al. 2001). Recent surveys on the Koyake group ranch have indicated that lion densities there may be very low (Ogutu et al. 2005). However we assumed at least some of our depredation events involved lions from inside the Reserve, where lion density was relatively high (0.369 lions/km^2; Ogutu et al. 2005). Hyena density in the northeastern portion of the Reserve was estimated to be 0.86/km^2 (Frank 1986a), one of the highest densities reported in Africa. Unfortunately predator densities are not reported in most studies, preventing direct comparisons.

Husbandry practices on commercial ranches may reduce the relative involvement of hyenas in livestock depredation. Various researchers have concluded that rates of livestock loss to predators in Kenya, particularly hyenas, could be reduced through construction of sturdier boma fences (Frank 2000; Kruuk 1981), and bush fences for livestock corrals on commercial ranches are often sturdier than those built in pastoral bomas (Ogada et al. 2003). However, Ogata et al. (2003) found no effect of boma height or thickness on depredation rates. Our data support the conclusion that improved fencing, at least on pastoral ranches, is not necessarily an effective solution to livestock depredation.

Finally, relative availability of small and large stock animals is also likely to influence involvement of predators in livestock depredation. The Patterson et al. (2004) study, which reported low hyena depredation, included ranches on which the majority of stock animals were cattle (Patterson et al. 2004). The low frequency of hyena and leopard depredation in some areas may thus result from the rarity of their preferred livestock prey, sheep and goats.

Hyenas attacked bomas approximately once every 11 nights. Although densities of both lions and hyenas inside the Reserve appear to be high, lions rarely attacked livestock in bomas outside the Reserve. Perhaps lions prefer to remain in their defended territories within the Reserve even when prey abundance there is relatively low, as even at these times natural prey abundance inside the Reserve is far greater than on our study group ranches.

The annual loss of 0.6% and 0.2% of the total small stock and cattle holdings respectively for our study region falls within the range reported for a large subset of depredation studies from around the globe (0.02% to 2.6% of local livestock holdings Graham et al. (2005)). Within Kenya, reported annual livestock losses to predators range from 0.7% to 5.5% (Frank 1998; Karani 1994; Kruuk 1981; Patterson et al. 2004), indicating that our observed depredation rates are relatively low for Kenyan rangelands. In contrast to Ogada et al. (2003), who found cheetah to be a significant predator of sheep and goats (49% of 195 sheep and goat kills away from the boma), we found no cheetah predation on livestock. This, together with the relatively small impact of lions on livestock, particularly sheep and goats, may account for our low depredation rates. However, these low annual stock losses to predators fail to represent the significance and costs of depredation events to individual owners, who have been known, in our study area, to lose up to 70 sheep and goats in a single attack by hyenas. Such a loss to an individual livestock owner is catastrophic and can also result in devastating retaliatory attacks. For example, in 1990, at least 16 hyenas were killed in a single poisoning event, following a depredation event in our study area (Holekamp & Smale 1992). Our study documented very few carnivore deaths during livestock attacks; however, the loss of even single carnivore individuals can have important economic impacts on areas benefiting from wildlife tourism (Sillero-Zubiri & Laurenson 2001). And, although Kenyans are legally permitted to kill carnivores in defense of their livestock, these events are generally underreported due to fears of government fines or penalties and likely resulted in an underestimation of carnivore losses during our study period.

Attacks on grazing herds

Attacks on grazing herds here were equally as common as were attacks at bomas. While previous studies on commercial ranches have found approximately 25% of livestock attacks to occur on grazing herds (Ogada et al. 2003; Patterson et al. 2004), pastoral ranches have documented up to 90% of predator attacks on livestock to be directed at grazing herds (Kruuk 1981). Attacks on grazing herds are probably more frequent on pastoral group ranches than on commercial ranches due to differences in herdsman behavior. In the case of commercial ranches, herders are paid for their work, may be fired for inadequate herd attendance, and work in groups large enough to discourage stock theft (Ogada et al. 2003). Larger groups of herders appear to be effective at limiting attacks on grazing herds (Ikanda 2005; Ogada et al. 2003). Herds on pastoral ranches however, such as those included in our study, are often accompanied only by small groups of young boys who vary considerably in their level of attendance to the herd.

Notably all three livestock predators in this study are primarily nocturnal, yet many of the attacks on grazing herds took place during the middle of the day. This indicates that not only are all three predator species bold enough to attack livestock herds accompanied by herdsmen, but also that they are willing to attack during periods when visibility of herdsmen is high. The preponderance of attacks during midday may represent predatory behavior that capitalizes on a reduction in herdsmen attentiveness and a corresponding increase in the spatial dispersion of the herd that are likely to occur near the heat of midday. Hyenas in particular have been shown to recognize and capitalize on similar behavior changes by their willingness to attack sleeping topi during midday (Rainy & Rainy 1989). Accounts of attacks on grazing herds in our study often described predators rapidly emerging from vegetative cover to attack. We therefore suggest that herdsmen avoid densely vegetated areas, where possible, particularly during the rains when attacks are most frequent and vegetation is thickest. Studies that investigate the spatial location of attacks on grazing herds in combination with herdsmen behavior, herdsmen numbers, as well as herd size and composition for attacked and unattacked herds are required to determine the effectiveness of various husbandry techniques in minimizing depredation losses.

Temporal patterns of attacks and relationship to predator movements

Monthly rates of carnivore attacks on livestock were related to both rainfall and natural prey abundance. Although Maasai pastoralists in some areas recognize rainy seasons as periods of increased carnivore conflict (Patterson et al. 2004; Rudnai 1979), some previous researchers have been unable to associate rainfall with depredation frequency (Rudnai 1979), while others have found the highest rates of depredation in the dry season (Butler 2000; Ikanda 2005). However, elevated rates of lion-human conflict have been associated with the monsoon rains in India, and recent studies have documented increases in livestock depredation during the rains in Africa (Patterson et al. 2004; Woodroffe & Frank 2005). Our data further support the importance of this relationship. Both Patterson et al. (2004) and Woodroffe and Frank (2005) suggest this trend may be ultimately driven by seasonal variation in local availability of natural prey, which is dictated by rainfall patterns. Whether the wet or dry season brings increased livestock depredation is likely ultimately dictated by the regional relationship between rainfall and natural prey. Whereas the dry season in some areas is associated with increased natural prey and reduced livestock depredations, the inverse has been shown in areas where prey levels peak in the wet season (e.g. southern Serengeti; Ikanda (2005)). Although our data failed to directly relate prey abundance with rainfall, prey abundance clearly influenced depredation rates. Many studies have documented relatively high rates of carnivore predation on livestock in areas occupied by few natural prey (Meriggi & Lovari 1996; Mishra 1997; Polisar et al. 2003; Vos 2000; Woodroffe et al. 2005), while others, including this study, have shown depredation rates to increase as natural prey abundance decreases over time (Stoddart et al. 2001).

Temporal variation in depredation behavior by hyenas was associated with changes in space utilization by monitored hyenas. As expected, hyenas used group ranch property more during months when hyena attacks on livestock were most frequent. However, the ecological conditions associated with this spatial shift were less obvious. We anticipated hyena movements would shift toward the group ranches when rainfall increased and natural prey abundance decreased. However, no correlation was identified between either of these variables and HR shifts. Tracking data suggested that hyenas spent more time outside the Reserve than expected, based on the small proportion of the clan's territory lying outside the Reserve, and that hyenas outside the Reserve were often near bomas.

Boma and enclosure vulnerability

Both univariate and multivariate analyses indicated that, contrary to previous findings (Ogada et al. 2003), increased human activity was associated with an increased probability of hyena attack. Based on these and follow data, we suspect that hyenas, as opportunistic feeders, are making regular visits to bomas not for livestock primarily, but rather for discarded food and other edible items. Large bomas, with more enclosures and houses, would thus be most attractive to hyenas interested in exploiting refuse and opportunistic attacks on livestock should therefore be more likely to occur at these bomas. Given the attractiveness of these sites to foraging hyenas, secure refuse disposal at bomas may reduce hyena attack frequency.

Unlike hyenas, leopards preferred to attack bomas that were relatively isolated on the landscape. In contrast to hyenas, leopards generally only consume fresh meat and are not known to frequent open spaces, such as those surrounding most bomas in our study area, as they rely heavily on stealth and ambush while hunting. Therefore, a leopard approaching a boma is much more likely than a hyena to be searching specifically for livestock prey. While our findings suggest that leopards avoid dense aggregations of human settlements, they do not indicate leopards specifically select smaller bomas, as did the results of Ogada et al. (2003). Our results may therefore suggest a trade-off in boma selection by leopards. While isolated bomas offer a reduced level of human activity and likely reduced probability of predator detection, bomas with fewer enclosures or livestock offer reduced opportunities to access appropriately vulnerable prey. As demonstrated by Ogada et al. (2003), dogs in our study area did not seem effective in deterring leopard or hyena attacks. This is further supported by reports from villagers suggesting that dogs were killed and eaten by both predators with some frequency.

Surprisingly we found no effect of distance to cover on probability of attack at a boma by either hyena or leopard. Ogada et al (2003) also found no influence of cover on leopard and lion depredation rates at bomas, but did see a trend for hyenas to attack bomas closer to cover more frequently. In general, very few of the bomas in our study region were close to dense vegetative cover with distances to cover averaging more than 250m. Predators in this region then, may simply be used to crossing open space at night to approach villages. Indeed, hyenas were observed to casually and slowly travel across large open plains between villages without apparent distress.

The only variable effective in estimating the vulnerability of sheep/goat enclosures was fence type. Overall, fences made from bush and pole material were equally susceptible to predator attack. Given that material used to make pole fences is expensive and not obtained locally, this was a surprising finding. Pole fences offer certain advantages over bush fences in that they require less maintenance and appear to be effective deterrents against hyena attack. However, the use of pole material in enclosure construction more than doubled the likelihood of a leopard attack. Although many villagers reinforced the pole fences with iron sheeting, barbed wire or thorn bush to close gaps and remove possible footholds, leopards appeared capable of capitalizing on small weaknesses in these reinforcements. Bush fences however, seemed effective at limiting leopard attacks, probably because they are often built at an outward angle and provide few sturdy footholds for climbing. Unfortunately, the use of bush material in enclosure construction more than doubled the likelihood of a hyena attack, as hyenas proved highly adept at pushing through even the densest of bush fences.

Given the absence of a relationship between predator attack frequency and fence quality, and the time, labor, and depletion of local vegetation involved in maintaining a strong fence (Kruuk 1981), it may be more effective for livestock owners to concentrate efforts on developing novel methods of detection and interruption of carnivore attacks, than on improving fences to minimize losses. Our data further indicate that increased human activity not specifically designed to deter predators, may be ineffective in reducing the probability of attack. However, actively guarding bomas (e.g. posting night guards, sleeping in huts within enclosures), particularly with the help of lights, may prove effective. Investment of major effort in guarding enclosures, a practice rarely utilized in our study area, may be most worthwhile during the rainy season, when attacks are most common, and could potentially be relaxed when migratory herds are present. Selection of fence type, however, is clearly important. Pole enclosures are effective at minimizing losses to hyenas and should therefore be used, when affordable, at larger bomas, particularly those built in close proximity to other bomas, which our data indicate are more susceptible to hyena attack. Bush fences, though still permeable to persistent leopards, seem to provide superior leopard exclusion and should therefore be favored at isolated bomas, which appear more vulnerable to leopard attacks. With respect to our finding that boma isolation and size can play an important role in vulnerability to predator attack, similar findings in North America regarding wolf depredation on cattle farms (Mech et al. 2000) indicate that these factors may be important spatial predictors of attacks on livestock not only by African predators, but by predators worldwide. Our study has demonstrated that monitoring of both socio-ecological and environmental variables, together with collection of detailed depredation information, can be useful in generating practical recommendations for conflict mitigation. In addition, knowledge of the movements and behavior of predators involved in livestock depredation can offer important insight into the effectiveness of prevention measures as well as the factors affecting temporal variation in depredation rates.

APPENDIX

Table A.1. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for all Mara River modeling periods based on hyena locations collected during all times of day and night. Final selected models are in bold. Only one model was identified for MR2 and MR3.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR1-Model #1	Dist to Den	- 0.0009	243.10	<0.0001	2161.48
	Dist to Stream	- 0.0032	87.89	<0.0001	
	Prey Value	+0.0508	30.06	<0.0001	
	Dist to Perm	+0.0005	10.66	0.0011	
	Habitat		9.96	0.0069	
	Shrubland	+0.3688	7.97	0.0048	
	Riparian F.	- 0.4533	8.57	0.0034	
MR1-Model #2	Dist to Den	- 0.0009	231.58	<0.0001	2162.42
	Dist to Stream	- 0.0033	80.95	<0.0001	
	Prey Value	+0.0481	25.28	<0.0001	
	Habitat		10.01	0.0067	
	Shrubland	+0.3809	8.41	0.0037	
	Riparian F.	- 0.4426	8.10	0.0044	
	Dist to Perm	+0.0005	8.29	0.0040	
	Dist to Cover	+0.0003	1.08	0.2997	
MR2	Dist to Den	- 0.0007	190.56	<0.0001	–
	Dist to Cover	- 0.0017	38.03	<0.0001	
	Prey Value	+0.0245	22.71	<0.0001	
	Dist to Stream	- 0.0015	19.88	<0.0001	
	Habitat		15.00	0.0006	
	Shrubland	+0.2337	5.50	0.0190	
	Riparian F.	+0.1179	1.35	0.2459	
	Dist to Perm	+0.0004	9.72	0.0018	
MR3	Dist to Den	- 0.0009	596.97	<0.0001	–
	Dist to Perm	+0.0010	139.23	<0.0001	
	Dist to Cover	- 0.0016	51.79	<0.0001	
	Dist to Stream	+0.0017	44.78	<0.0001	
	Prey Value	+0.0259	24.91	<0.0001	
	Habitat		19.97	0.0005	
	Shrubland	- 0.0480	0.34	0.5582	
	Riparian F.	+0.3147	14.93	0.0001	

Table A.2. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the first Talek West modeling period (TKW1) based on hyena locations collected during all times of day and night. The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW1-Model #1	Dist to Den	- 0.0014	201.27	<0.0001	3239.48
	Habitat		123.15	<0.0001	
	Shrubland	+0.6059	36.35	<0.0001	
	Riparian F.	- 0.0439	0.07	0.7968	
	Dist to Perm	+0.0006	22.94	<0.0001	
	Prey Value	- 0.0430	22.17	<0.0001	
	LUV	- 0.0162	9.22	0.0024	
TKW1-Model #2	Dist to Den	- 0.0014	198.34	<0.0001	3239.94
	Habitat		96.97	<0.0001	
	Shrubland	+0.6381	37.70	<0.0001	
	Riparian F.	- 0.0201	0.01	0.9067	
	Prey Value	- 0.0424	21.59	<0.0001	
	Dist to Perm	+0.0006	21.16	<0.0001	
	LUV	- 0.0149	7.59	0.0059	
	Dist to Cover	+0.0004	1.56	0.2122	
TKW1-Model #3	Dist to Den	- 0.0014	176.83	<0.0001	3240.75
	Habitat		97.69	<0.0001	
	Shrubland	+0.6587	38.69	<0.0001	
	Riparian F.	- 0.0583	0.11	0.7402	
	Dist to Perm	+0.0006	22.14	<0.0001	
	Prey Value	- 0.0428	21.97	<0.0001	
	LUV	- 0.0164	8.58	0.0034	
	Dist to Cover	+0.0004	2.19	0.1391	
	Dist to Stream	- 0.0002	1.19	0.2762	
TKW1-Model #4	Dist to Den	- 0.0014	174.54	<0.0001	3240.92
	Habitat		119.21	<0.0001	
	Shrubland	+0.6149	36.77	<0.0001	
	Riparian F.	- 0.0727	0.17	0.6782	
	Dist to Perm	+0.0006	22.82	<0.0001	
	Prey Value	- 0.0434	22.44	<0.0001	
	LUV	- 0.0174	9.72	0.0018	
	Dist to Stream	- 0.0001	0.56	0.4535	

Table A.3. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the second Talek West modeling period (TKW2) based on hyena locations collected during all times of day and night. The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW2-Model #1	Prey Value	+0.0733	153.21	<0.0001	2009.42
	Habitat		152.46	<0.0001	
	Shrubland	+0.8041	39.53	<0.0001	
	Riparian F.	+0.0489	0.05	0.8300	
	Dist to Den	- 0.0009	57.76	<0.0001	
	Dist to Stream	- 0.0023	40.11	<0.0001	
	Dist to Perm	+0.0005	10.91	0.0010	
TKW2-Model #2	Prey Value	+0.0737	143.61	<0.0001	2011.37
	Habitat		110.65	<0.0001	
	Shrubland	+0.8105	38.15	<0.0001	
	Riparian F.	+0.0553	0.06	0.8099	
	Dist to Den	- 0.0009	57.11	<0.0001	
	Dist to Stream	- 0.0023	36.11	<0.0001	
	Dist to Perm	+0.0005	10.95	0.0009	
	Dist to Cover	+0.0002	0.05	0.8246	
TKW2-Model #3	Habitat		151.62	<0.0001	2011.41
	Shrubland	+0.8049	39.22	<0.0001	
	Riparian F.	+0.0480	0.04	0.8336	
	Prey Value	+0.0734	151.27	<0.0001	
	Dist to Den	- 0.0009	55.81	<0.0001	
	Dist to Stream	- 0.0023	40.03	<0.0001	
	Dist to Perm	+0.0005	10.62	0.0011	
	LUV	- 0.0002	0.00	0.9515	

Table A.4. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the third Talek West modeling period (TKW3) based on hyena locations collected during all times of day and night. The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW3-Model #1	Dist to Den	- 0.0007	40.35	<0.0001	1591.85
	Habitat		34.73	<0.0001	
	Shrubland	+0.7352	14.42	0.0001	
	Riparian F.	- 0.4564	1.66	0.1976	
	Dist to Cover	- 0.0025	17.48	<0.0001	
	Dist to Perm	- 0.0004	14.02	0.0002	
	Dist to Stream	+0.0010	9.67	0.0019	
	Prey Value	+0.0214	2.10	0.1471	
TKW3-Model #2	Dist to Den	- 0.0008	50.10	<0.0001	1591.89
	Habitat		35.63	<0.0001	
	Shrubland	+0.7688	15.69	<0.0001	
	Riparian F.	- 0.5149	2.11	0.1462	
	Dist to Perm	- 0.0005	24.06	<0.0001	
	Dist to Cover	- 0.0026	19.15	<0.0001	
	Dist to Stream	+0.0010	9.13	0.0025	
	LUV	- 0.0072	1.86	0.1725	
TKW3-Model #3	Dist to Den	- 0.0007	48.79	<0.0001	1591.89
	Habitat		34.75	<0.0001	
	Shrubland	+0.7455	14.84	0.0001	
	Riparian F.	- 0.4801	1.84	0.1748	
	Dist to Perm	- 0.0005	21.94	<0.0001	
	Dist to Cover	- 0.0025	18.58	<0.0001	
	Dist to Stream	+0.0011	10.62	0.0011	
TKW3-Model #4	Dist to Den	- 0.0007	41.56	<0.0001	1592.50
	Habitat		35.43	<0.0001	
	Shrubland	+0.7564	15.14	0.0001	
	Riparian F.	- 0.4896	1.90	0.1680	
	Dist to Cover	- 0.0025	17.99	<0.0001	
	Dist to Perm	- 0.0005	15.50	<0.0001	
	Dist to Stream	+0.0010	8.56	0.0034	
	Prey Value	+0.0180	1.42	0.2339	
	LUV	- 0.0061	1.27	0.2601	

Table A.5. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the fourth Talek West modeling period (TKW4) based on hyena locations collected during all times of day and night. The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW4-Model #1	Habitat		113.72	<0.0001	2729.17
	Shrubland	+1.1725	73.13	<0.0001	
	Riparian F.	- 0.9631	16.12	<0.0001	
	Dist to Den	- 0.0004	91.82	<0.0001	
	Dist to Perm	- 0.0007	66.92	<0.0001	
	Dist to Cover	+0.0020	34.78	<0.0001	
	Dist to Stream	- 0.0005	3.18	0.0746	
TKW4-Model #2	Habitat		116.15	<0.0001	2730.45
	Shrubland	+1.1694	72.78	<0.0001	
	Riparian F.	- 0.9341	15.22	<0.0001	
	Dist to Den	- 0.0004	88.47	<0.0001	
	Dist to Perm	- 0.0008	77.15	<0.0001	
	Dist to Cover	+0.0018	32.13	<0.0001	
TKW4-Model #3	Habitat		112.73	<0.0001	2730.63
	Shrubland	+1.1673	72.33	<0.0001	
	Riparian F.	- 0.9562	15.87	<0.0001	
	Dist to Den	- 0.0004	87.05	<0.0001	
	Dist to Perm	- 0.0007	59.97	<0.0001	
	Dist to Cover	+0.0020	35.27	<0.0001	
	Dist to Stream	- 0.0005	3.29	0.0695	
	LUV	+0.0029	0.55	0.4575	
TKW4-Model #4	Habitat		113.27	<0.0001	2731.14
	Shrubland	+1.1723	73.09	<0.0001	
	Riparian F.	- 0.9593	15.87	<0.0001	
	Dist to Perm	- 0.0007	64.88	<0.0001	
	Dist to Den	- 0.0004	34.66	<0.0001	
	Dist to Cover	+0.0020	31.27	<0.0001	
	Dist to Stream	- 0.0005	3.08	0.0794	
	Prey Value	+0.0009	0.03	0.8530	

Table A.6. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the first Mara River modeling period (MR1) based on hyena locations collected during grazing hours (0900–1800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR1-Model #1	Dist to Stream	- 0.0070	72.18	<0.0001	725.18
	Dist to Den	- 0.0011	67.65	<0.0001	
	Dist to Perm	+0.0011	13.08	0.0003	
	Habitat		11.69	0.0029	
	Shrubland	+0.7354	11.20	0.0008	
	Riparian F.	- 0.5324	2.91	0.0878	
	Dist to Cover	+0.0009	3.44	0.0635	
	Prey Value	+0.0332	2.17	0.1404	
MR1-Model #2	Dist to Den	- 0.0012	81.98	<0.0001	725.33
	Dist to Stream	- 0.0070	71.66	<0.0001	
	Dist to Perm	+0.0012	17.40	<0.0001	
	Habitat		11.74	0.0028	
	Shrubland	+0.7316	10.99	0.0009	
	Riparian F.	- 0.4866	2.47	0.1163	
	Dist to Cover	+0.0011	6.25	0.0125	
MR1-Model #3	Dist to Den	- 0.0010	73.53	<0.0001	726.44
	Dist to Stream	- 0.0064	71.85	<0.0001	
	Dist to Perm	+0.0011	15.74	<0.0001	
	Habitat		10.55	0.0051	
	Shrubland	+0.7001	10.36	0.0013	
	Riparian F.	- 0.5886	3.64	0.0564	
	Prey Value	+0.0466	4.73	0.0296	
MR1-Model #4	Dist to Den	- 0.0011	86.48	<0.0001	728.99
	Dist to Stream	- 0.0061	67.67	<0.0001	
	Dist to Perm	+0.0013	23.66	<0.0001	
	Habitat		10.03	0.0066	
	Shrubland	+0.6803	9.74	0.0018	
	Riparian F.	- 0.5435	3.15	0.0760	

Table A.7. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the first Mara River modeling period (MR1) based on hyena locations collected during livestock-free hours (1900–0800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR1-Model #1	Dist to Den	- 0.0011	159.48	<0.0001	1338.23
	Prey Value	+0.0521	19.39	<0.0001	
	Dist to Stream	- 0.0015	14.86	0.0001	
MR1-Model #2	Dist to Den	- 0.0011	154.92	<0.0001	1338.77
	Dist to Stream	- 0.0018	14.37	0.0002	
	Prey Value	+0.0470	14.24	0.0002	
	Dist to Cover	+0.0004	1.49	0.2224	
MR1-Model #3	Dist to Den	- 0.0011	147.58	<0.0001	1339.06
	Prey Value	+0.0485	15.65	<0.0001	
	Dist to Stream	- 0.0017	14.62	0.0001	
	Dist to Perm	+0.0011	15.74	<0.0001	
MR1-Model #4	Dist to Den	- 0.0011	156.82	<0.0001	1339.38
	Prey Value	+0.0524	19.56	<0.0001	
	Dist to Stream	- 0.0016	16.02	<0.0001	
	Habitat		2.61	0.2711	
	Shrubland	+0.1403	0.56	0.4536	
	Riparian F.	- 0.2927	2.36	0.1248	

Table A.8. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the second Mara River modeling period (MR2) based on hyena locations collected during grazing hours (0900–1800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR2-Model #1	Dist to Den	- 0.0010	76.81	<0.0001	982.09
	Habitat		25.93	<0.0001	
	Shrubland	+0.7639	22.74	<0.0001	
	Riparian F.	- 0.1866	0.97	0.3251	
	Prey Value	+0.0250	10.56	0.0012	
	Dist to Stream	- 0.0019	7.91	0.0049	
	Dist to Cover	- 0.0015	7.71	0.0055	
MR2-Model #2	Dist to Den	- 0.0010	71.10	<0.0001	983.57
	Habitat		26.17	<0.0001	
	Shrubland	+0.7678	22.76	<0.0001	
	Riparian F.	- 0.1531	0.61	0.4338	
	Dist to Stream	- 0.0021	8.42	0.0037	
	Dist to Cover	- 0.0016	8.15	0.0043	
	Prey Value	+0.0214	5.51	0.0190	

Table A.9. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the second Mara River modeling period (MR2) based on hyena locations collected during livestock-free hours (1900–0800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR2-Model #1	Dist to Den	- 0.0006	99.95	<0.0001	1922.18
	Dist to Cover	- 0.0012	15.55	<0.0001	
	Dist to Stream	- 0.0017	15.47	<0.0001	
	Prey Value	+0.0171	6.95	0.0084	
	Dist to Perm	+0.0003	4.04	0.0443	
MR2-Model #2	Dist to Den	- 0.0006	103.32	<0.0001	1924.05
	Prey Value	+0.0238	18.53	<0.0001	
	Dist to Cover	- 0.0010	12.28	0.0005	
	Dist to Stream	- 0.0014	12.00	0.0005	

Table A.10. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model, as well as the final selected model (in bold), for the third Mara River modeling period (MR3). Models are based on hyena locations collected during grazing hours (0900–1800 h).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR3-Model #1	Dist to Den	- 0.0014	238.75	<0.0001	1782.50
	Dist to Stream	- 0.0056	167.97	<0.0001	
	Dist to Perm	+0.0018	107.15	<0.0001	
	Habitat		12.01	0.0025	
	Shrubland	+0.2840	4.28	0.0386	
	Riparian F.	+0.1254	0.59	0.4407	
	Prey Value	+0.0206	5.01	0.0252	
MR3-Model #2	Dist to Den	- 0.0014	235.70	<0.0001	1784.41
	Dist to Stream	- 0.0055	116.05	<0.0001	
	Dist to Perm	+0.0018	103.16	<0.0001	
	Habitat		10.38	0.0056	
	Shrubland	+0.2771	3.97	0.0462	
	Riparian F.	+0.1206	0.55	0.4602	
	Prey Value	+0.0194	3.80	0.0514	
	Dist to Cover	- 0.0001	0.09	0.7600	
MR3-Model #3	Dist to Den	- 0.0014	238.91	<0.0001	1785.45
	Dist to Stream	- 0.0060	231.23	<0.0001	
	Dist to Perm	+0.0019	125.94	<0.0001	
	Habitat		11.18	0.0037	
	Shrubland	+0.2694	3.90	0.0483	
	Riparian F.	+0.1266	0.61	0.4356	

Table A.11. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the third Mara River modeling period (MR3) based on hyena locations collected during livestock-free hours (1900–0800 h). Only one model was identified.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
MR3-Model #1	Dist to Den	- 0.0008	353.32	<0.0001	3306.75
	Dist to Cover	- 0.0017	33.33	<0.0001	
	Dist to Perm	+0.0006	31.52	<0.0001	
	Prey Value	+0.0325	26.16	<0.0001	
	Habitat		19.59	<0.0001	
	Shrubland	- 0.0811	0.67	0.4123	
	Riparian F.	+0.3711	15.89	<0.0001	
	Dist to Stream	- 0.0008	7.13	0.0076	

Table A.12. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model, as well as the final selected model (in bold), for the first Talek West modeling period (TKW1). Models are based on hyena locations collected during grazing hours (0900–1800 h).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW1-Model #1	Habitat		58.97	<0.0001	1041.97
	Shrubland	+0.9545	25.72	<0.0001	
	Riparian F.	+0.2456	0.64	0.4243	
	Dist to Den	- 0.0012	32.78	<0.0001	
	Dist to Stream	- 0.0013	8.24	0.0041	
	Prey Value	- 0.0535	8.13	0.0044	
	Dist to Perm	+0.0006	7.39	0.0066	
	LUV	- 0.0206	3.47	0.0623	
	Dist to Cover	+0.0011	2.36	0.1246	
TKW1-Model #2	Habitat		82.76	<0.0001	1042.78
	Shrubland	+0.8496	23.98	<0.0001	
	Riparian F.	+0.1888	0.39	0.5340	
	Dist to Den	- 0.0012	31.69	<0.0001	
	Prey Value	- 0.0569	9.12	0.0025	
	Dist to Perm	+0.0006	7.13	0.0076	
	Dist to Stream	- 0.0011	6.81	0.0091	
	LUV	- 0.0220	3.95	0.0469	
TKW1-Model #3	Habitat		57.63	<0.0001	1043.69
	Shrubland	+0.8679	22.55	<0.0001	
	Riparian F.	+0.3812	1.61	0.2047	
	Dist to Den	- 0.0011	30.27	<0.0001	
	Dist to Perm	+0.0007	9.59	0.0020	
	Prey Value	- 0.0488	6.61	0.0101	
	Dist to Stream	- 0.0011	6.54	0.0106	
	Dist to Cover	+0.0012	2.90	0.0881	
TKW1-Model #4	Habitat		79.73	<0.0001	1044.52
	Shrubland	+0.7471	20.12	<0.0001	
	Riparian F.	+0.3288	1.22	0.2687	
	Dist to Den	- 0.0010	28.68	<0.0001	
	Dist to Perm	+0.0007	9.26	0.0023	
	Prey Value	- 0.0526	7.55	0.0060	
	Dist to Stream	- 0.0009	4.86	0.0274	

Table A.13. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model, as well as the final selected model (in bold), for the first Talek West modeling period (TKW1). Models are based on hyena locations collected during livestock-free hours (1900–0800 h).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW1-Model #1	Dist to Den	- 0.0013	87.34	<0.0001	1995.57
	Habitat		21.96	<0.0001	
	Shrubland	+0.3464	6.60	0.0102	
	Riparian F.	+0.0131	0.00	0.9532	
	Prey Value	- 0.0387	10.35	0.0013	
	Dist to Stream	+0.0007	7.23	0.0072	
	LUV	- 0.0141	3.65	0.0562	
	Dist to Perm	+0.0003	2.38	0.1231	
TKW1-Model #2	Dist to Den	- 0.0012	137.42	<0.0001	1996.01
	Habitat		20.32	<0.0001	
	Shrubland	+0.3546	7.06	0.0079	
	Riparian F.	- 0.0369	0.03	0.8658	
	Prey Value	- 0.0462	17.99	<0.0001	
	Dist to Stream	+0.0009	12.18	0.0005	
	LUV	- 0.0159	4.86	0.0275	
TKW1-Model #3	Dist to Den	- 0.0013	87.28	<0.0001	1997.41
	Habitat		20.46	<0.0001	
	Shrubland	+0.2763	4.51	0.0338	
	Riparian F.	+0.1171	0.29	0.5896	
	Dist to Stream	+0.0009	12.52	0.0004	
	Prey Value	- 0.0345	8.35	0.0039	
	Dist to Perm	+0.0003	3.70	0.0545	

Table A.13. (cont'd).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW1-Model #4	Dist to Den	- 0.0013	87.78	<0.0001	1997.42
	Habitat		17.83	0.0001	
	Shrubland	+0.3610	6.63	0.0100	
	Riparian F.	+0.0174	0.01	0.9378	
	Prey Value	- 0.0387	10.39	0.0013	
	Dist to Stream	+0.0007	6.65	0.0099	
	LUV	- 0.0138	3.43	0.0642	
	Dist to Perm	+0.0003	2.23	0.1356	
	Dist to Cover	+0.0002	0.15	0.7029	
TKW1-Model #7	Dist to Den	- 0.0011	151.17	<0.0001	1999.25
	Habitat		18.19	0.0001	
	Shrubland	+0.2800	4.70	0.0302	
	Riparian F.	+0.0680	0.10	0.7500	
	Dist to Stream	+0.0011	24.20	<0.0001	
	Prey Value	- 0.0434	15.93	0.0001	

Table A.14. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model, as well as the final selected model (in bold), for the second Talek West modeling period (TKW2). Models are based on hyena locations collected during grazing hours (0900–1800 h).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW2-Model #1	Habitat		59.91	<0.0001	679.00
	Shrubland	+1.4724	16.46	<0.0001	
	Riparian F.	- 0.6361	0.85	0.3568	
	Prey Value	+0.0569	27.09	<0.0001	
	Dist to Stream	- 0.0025	12.91	0.0003	
	Dist to Den	- 0.0003	6.50	0.0108	
TKW2-Model #2	Habitat		59.30	<0.0001	679.78
	Shrubland	+1.4558	16.04	<0.0001	
	Riparian F.	- 0.6092	0.78	0.3777	
	Prey Value	+0.0552	24.53	<0.0001	
	Dist to Stream	- 0.0025	12.40	0.0004	
	Dist to Den	- 0.0003	2.78	0.0956	
	LUV	+0.0054	1.26	0.2623	
TKW2-Model #3	Habitat		45.17	<0.0001	679.88
	Shrubland	+1.5525	17.37	<0.0001	
	Riparian F.	- 0.5576	0.64	0.4225	
	Prey Value	+0.0594	27.49	<0.0001	
	Dist to Stream	- 0.0028	13.23	0.0003	
	Dist to Den	- 0.0004	7.18	0.0074	
	Dist to Cover	+0.0017	1.22	0.2688	
TKW2-Model #4	Habitat		76.43	<0.0001	680.57
	Shrubland	+1.4458	15.83	<0.0001	
	Riparian F.	- 0.2912	0.18	0.6714	
	Prey Value	+0.0591	29.58	<0.0001	
	Dist to Den	- 0.0002	2.59	0.1074	
	LUV	+0.0065	1.96	0.1616	
TKW2-Model #5	Habitat		44.87	<0.0001	680.67
	Shrubland	+1.5344	16.93	<0.0001	
	Riparian F.	- 0.5310	0.58	0.4453	
	Prey Value	+0.0577	25.01	<0.0001	
	Dist to Stream	- 0.0027	12.75	0.0004	
	Dist to Den	- 0.0003	3.22	0.0728	
	LUV	+0.0054	1.24	0.2645	
	Dist to Cover	+0.0016	1.21	0.2709	

Table A.14. (cont'd).

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW2-Model #6	Habitat		63.40	<0.0001	680.77
	Shrubland	+1.4999	17.06	<0.0001	
	Riparian F.	- 0.6269	0.83	0.3636	
	Prey Value	+0.0591	28.21	<0.0001	
	Dist to Stream	- 0.0022	9.07	0.0026	
	Dist to Perm	- 0.0004	4.46	0.0346	
TKW2-Model #7	Habitat		61.87	<0.0001	680.77
	Shrubland	+1.4704	16.30	<0.0001	
	Riparian F.	- 0.5922	0.74	0.3913	
	Prey Value	+0.0562	24.26	<0.0001	
	Dist to Stream	- 0.0022	9.56	0.0020	
	LUV	+0.0067	2.07	0.1502	
	Dist to Perm	- 0.0002	1.73	0.1887	
TKW2-Model #8	Habitat		59.97	<0.0001	680.80
	Shrubland	+1.4829	16.64	<0.0001	
	Riparian F.	- 0.6537	0.90	0.3441	
	Prey Value	+0.0578	26.76	<0.0001	
	Dist to Stream	- 0.0024	10.69	0.0011	
	Dist to Den	- 0.0003	1.89	0.1695	
	Dist to Perm	- 0.0001	0.20	0.6554	
TKW2-Model #15	Habitat		66.29	<0.0001	683.60
	Shrubland	+1.4369	15.71	<0.0001	
	Riparian F.	- 0.4341	0.40	0.5266	
	Prey Value	+0.0546	27.32	<0.0001	
	Dist to Stream	- 0.0025	12.39	0.0004	

Table A.15. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the second Talek West modeling period (TKW2) based on hyena locations collected during livestock-free hours (1900–0800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW2-Model #1	Prey Value	+0.0866	91.80	<0.0001	1168.82
	Habitat		53.96	<0.0001	
	Shrubland	+0.4893	10.63	0.0011	
	Riparian F.	+0.3499	1.94	0.1640	
	Dist to Den	- 0.0013	49.36	<0.0001	
	Dist to Stream	- 0.0020	14.96	0.0001	
	Dist to Perm	+0.0004	3.32	0.0685	
TKW2-Model #2	Prey Value	+0.0891	87.27	<0.0001	1170.06
	Dist to Den	- 0.0013	50.15	<0.0001	
	Habitat		43.62	<0.0001	
	Shrubland	+0.5207	11.28	0.0008	
	Riparian F.	+0.3859	2.28	0.1309	
	Dist to Stream	- 0.0021	14.96	0.0001	
	Dist to Perm	+0.0004	3.33	0.0682	
	Dist to Cover	+0.0009	0.79	0.3739	
TKW2-Model #3	Prey Value	+0.0892	95.97	<0.0001	1170.24
	Dist to Den	- 0.0011	87.58	<0.0001	
	Habitat		54.82	<0.0001	
	Shrubland	+0.5155	12.19	0.0004	
	Riparian F.	+0.3117	1.59	0.2070	
	Dist to Stream	- 0.0016	11.44	0.0007	
TKW2-Model #4	Prey Value	+0.0857	87.95	<0.0001	1170.35
	Habitat		52.98	<0.0001	
	Shrubland	+0.4767	9.92	0.0016	
	Riparian F.	+0.3646	2.09	0.1486	
	Dist to Den	- 0.0013	46.98	<0.0001	
	Dist to Stream	- 0.0020	14.65	0.0001	
	Dist to Perm	+0.0005	3.66	0.0556	
	LUV	+0.0023	0.48	0.4906	

Table A.16. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the third Talek West modeling period (TKW3) based on hyena locations collected during grazing hours (0900–1800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW3-Model #1	Dist to Den	- 0.0009	33.32	<0.0001	512.76
	Habitat		23.75	<0.0001	
	Shrubland	+1.0656	23.75	<0.0001	
	Dist to Cover	- 0.0043	4.68	0.0305	
TKW3-Model #2	Dist to Den	- 0.0009	33.89	<0.0001	514.16
	Habitat		23.95	<0.0001	
	Shrubland	+1.0723	23.95	<0.0001	
	Dist to Cover	- 0.0044	4.87	0.0273	
	LUV	- 0.0064	0.55	0.4571	
TKW3-Model #3	Habitat		23.80	<0.0001	514.45
	Shrubland	+1.0686	23.80	<0.0001	
	Dist to Den	- 0.0008	17.33	<0.0001	
	Dist to Cover	- 0.0044	4.88	0.0272	
	Dist to Stream	+0.0003	0.31	0.5752	
TKW3-Model #4	Dist to Den	- 0.0009	32.94	<0.0001	514.57
	Habitat		23.84	<0.0001	
	Shrubland	+1.0689	23.84	<0.0001	
	Dist to Cover	- 0.0044	4.82	0.0281	
	Dist to Perm	+0.0001	0.19	0.6594	
TKW3-Model #5	Dist to Den	- 0.0009	26.49	<0.0001	514.62
	Habitat		23.76	<0.0001	
	Shrubland	+1.0667	23.76	<0.0001	
	Dist to Cover	- 0.0044	4.78	0.0288	
	Prey Value	- 0.0102	0.14	0.7074	

Table A.17. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the third Talek West modeling period (TKW3) based on hyena locations collected during livestock-free hours (1900–0800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW3-Model #1	Dist to Perm	- 0.0010	29.13	<0.0001	930.82
	Dist to Den	- 0.0004	10.57	0.0011	
	Dist to Stream	+0.0014	7.62	0.0058	
	Dist to Cover	- 0.0016	5.53	0.0187	
	Prey Value	+0.0358	3.49	0.0616	
TKW3-Model #2	Dist to Perm	- 0.0010	25.82	<0.0001	931.55
	Dist to Den	- 0.0004	9.42	0.0021	
	Dist to Stream	+0.0015	8.22	0.0041	
	Dist to Cover	- 0.0015	4.90	0.0268	
	Prey Value	+0.0395	4.20	0.0404	
	LUV	+0.0075	1.38	0.2407	
TKW3-Model #3	Dist to Perm	- 0.0011	38.88	<0.0001	932.13
	Dist to Den	- 0.0005	12.10	0.0005	
	Dist to Stream	+0.0016	9.95	0.0016	
	Dist to Cover	- 0.0017	6.26	0.0123	

Table A.18. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the fourth Talek West modeling period (TKW4). Using only hyena locations collected during grazing hours (0900–1800 h), only one model was identified.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW4-Model #1	Habitat		75.93	<0.0001	–
	Shrubland	+1.6213	75.93	<0.0001	
	Prey Value	+0.0553	29.90	<0.0001	
	Dist to Den	- 0.0005	14.48	0.0001	
	Dist to Cover	- 0.0028	12.58	0.0004	
	Dist to Perm	- 0.0006	8.78	0.0030	
	LUV	+0.0139	4.25	0.0392	

Table A.19. Logistic regression results showing all models within 2.0 AIC points of the lowest AIC model for the fourth Talek West modeling period (TKW4) based on hyena locations collected during livestock-free hours (1900–0800 h). The final selected model is in bold.

Model	Variable	Estimate	Wald Stat.	*P*	AIC
TKW4-Model #1	Habitat		45.04	<0.0001	1469.91
	Shrubland	+1.3926	28.96	<0.0001	
	Riparian F.	- 1.6321	11.40	0.0007	
	Dist to Perm	- 0.0009	38.71	<0.0001	
	Dist to Den	- 0.0007	38.43	<0.0001	
	Dist to Cover	+0.0026	21.31	<0.0001	
	Prey Value	- 0.0201	6.26	0.0124	
	Dist to Stream	- 0.0011	6.00	0.0143	
TKW4-Model #2	Habitat		45.46	<0.0001	1470.57
	Shrubland	+1.4036	29.37	<0.0001	
	Riparian F.	- 1.6521	11.66	0.0006	
	Dist to Perm	- 0.0009	39.77	<0.0001	
	Dist to Den	- 0.0007	38.05	<0.0001	
	Dist to Cover	+0.0026	21.02	<0.0001	
	Prey Value	- 0.0221	7.15	0.0075	
	Dist to Stream	- 0.0011	5.76	0.0164	
	LUV	- 0.0072	1.22	0.2686	

Table A.20. Results from all logistic regression models considered for the prediction of the probability of hyena attack on livestock within Maasai bomas (villages). Results shown are from all models within 2.0 AICc points of the optimal model (considered Model #1, also shown in Table 4.3).

	Estimate	Wald Stat.	*p*-value	AICc
Model #1				69.74
Boma houses (#)	+0.39553	13.5264	0.0002	
Distance to Reserve (m)	- 0.00164	3.9226	0.0476	
Model #2				70.19
Boma houses (#)	+0.4300	13.3083	0.0003	
Distance to Reserve (m)	- 0.0019	4.3936	0.0361	
Bomas within 200 m (#)	+0.2033	1.5798	0.2088	
Model #3				71.64
Boma houses (#)	+0.4066	13.2797	0.0003	
Distance to Reserve	- 0.0017	3.8971	0.0484	
Distance to closest boma (m)	- 0.0007	0.2605	0.6098	

Table A.21. Results from all logistic regression models considered for the prediction of the probability of leopard attack on livestock within Maasai bomas (villages). Results shown are from all models within 2.0 AICc points of the optimal model (considered Model #1, also shown in Table 4.3).

	Estimate	Wald Stat.	*p*-value	AICc
Model #1				68.28
Bomas within 200 m (#)	- 0.7476	7.3760	0.0066	
Model #2				68.40
Bomas within 200 m (#)	- 0.8845	7.8145	0.0052	
Distance to Reserve (m)	- 0.0011	2.1717	0.1406	
Model #3				69.87
Bomas within 200m (#)	- 0.7262	6.8753	0.0087	
Boma houses (#)	+0.0650	1.0791	0.2989	
Model #4				70.34
Bomas within 200m (#)	- 0.8455	7.1457	0.0075	
Boma houses (#)	+0.0561	0.7316	0.3924	
Distance to Reserve	- 0.0010	1.8109	0.1784	
Model #5				70.35
Bomas within 200 m (#)	- 0.7262	7.0435	0.0080	
Distance to bush (m)	- 0.0004	0.1457	0.7027	

Table A.22. Results from all logistic regression models considered for the prediction of the probability of hyena attack on livestock within sheep/goat (shoat) enclosures. Results shown are from all models within 2.0 AICc points of the optimal model (considered Model #1, also shown in Table 4.4).

	Estimate	Wald Stat.	*p*-value	AICc
Model #1				83.20
Bush fence?	+0.8561	9.2012	0.0024	
Model #2				83.46
Bush fence?	+0.9439	9.6430	0.0019	
Sheep and goats inside (#)	+0.0038	2.9695	0.0848	
Model #3				84.14
Bush Fence?	+0.8825	9.3716	0.0022	
Dogs of owner (#)	+0.1011	0.7680	0.3809	
Model #4				84.47
Bush fence?	+0.8122	6.6553	0.0099	
Sheep and goats inside (#)	+0.0037	2.2622	0.1326	
Houses of owner (#)	- 0.1355	1.3159	0.2513	
Model #5				84.84
Bush fence?	+0.7148	5.9064	0.0151	
Houses of owner (#)	- 0.0946	0.6966	0.4039	
Model #6				84.97
Bush fence?	+0.7686	6.4912	0.0108	
Dogs of owner (#)	+0.1768	1.7483	0.1861	
Houses of owner (#)	- 0.1330	1.2689	0.2600	
Model #7				85.07
Bush Fence?	+0.9915	10.0447	0.0015	
Sheep and Goats inside (#)	+0.0040	2.9951	0.0835	
Dogs of owner (#)	+0.0753	0.3825	0.5363	
Model #8				85.20
Bush fence?	+0.9182	8.3833	0.0038	
Distance to closest enclosure (m)	+0.0007	0.1803	0.6711	

Table A.23. Results from all logistic regression models considered for the prediction of the probability of leopard attack on livestock within sheep/goat (shoat) enclosures. Results shown are from all models within 2.0 AICc points of the optimal model (considered Model #1, also shown in Table 4.4).

	Estimate	Wald Stat.	*p*-value	AICc
Model #1				84.93
Pole fence?	+0.9797	11.8824	0.0006	
Model #2				85.89
Pole fence?	+0.9304	9.9706	0.0016	
Sheep and goats inside (#)	+0.0008	0.1303	0.7181	
Model #3				86.82
Pole Fence?	+0.8825	9.3716	0.0022	
Distance to closest enclosure (m)	+0.0010	0.5557	0.4560	

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