DIURNAL MOVEMENT PATTERNS, HABITAT USE AND ENERGY COST OF LOCOMOTION BY SPOTTED HYENAS (*Crocuta crocuta*) IN THE MASAI MARA NATIONAL RESERVE, KENYA

By

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ABSTRACT

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Large carnivore population sizes are declining worldwide and this trend has been associated with habitat loss, diminishing prey availability, poaching, human-wildlife conflict and trade in their products. Large carnivores may feed on prey that are larger than themselves and are faced with challenges of meeting their daily food requirements. Here, I examined the diurnal (10am-4pm) movement patterns, habitat choice, and energy cost of locomotion by female spotted hyenas (*Crocuta crocuta*) in the Masai Mara National Reserve (MMNR) in Kenya. These patterns were investigated for a period of one year (2013). Two management regimes were employed in the MMNR throughout my study period, with intensive anthropogenic activity occurring on one side of the MMNR (disturbed) but not the other (undisturbed). I tested the hypothesis that the anthropogenic activity would be associated with differences in movement patterns, habitat choice and energy cost of locomotion between the two sides among groups of spotted hyenas fitted with GPS collars. I expected to see hyenas in the disturbed side of the MMNR travelling longer distances, using habitats characterized by denser vegetative cover, and using more energy in locomotion. As expected, my results showed hyenas in the disturbed side of MMNR travelled significantly longer distances than they did in the undisturbed side, and used habitats covered with more dense vegetation than expected. However, we saw hyenas in the undisturbed side of the Reserve using significantly more energy in locomotion than they did in the disturbed side.

This work is dedicated to my wife, daughter, parents, and siblings for being close to me despite the distance that kept us apart during my graduate studies at MSU.

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KEY TO ABBREVIATIONS

MSU - Michigan State University

NMNR - Masai Mara National Reserve

MHP - Mara Hyena Project

NCG – Narok County Government

TMC – The Mara Conservancy

MJ – Mega Joules

J – Joules

O_2 – Oxygen

Mm – Millimeters

Ml – Milliliters

Min’ – Minimum

Max’ Maximum

Temp’ – Temperature

^{0}C – Degree Celsius

SS – Serena South

SN – Serena North

TW – Talek West

No. – Number

Id. – Identity

NGO – Non-Governmental Organization

GPS – Global Positioning System

GCS – Geographic Coordinate System

UTM – Universal Transverse Mercator

WGS – World Geodetic System

GLM – Generalized Linear Model

UD – Utilization Distribution

Kg – Kilogram

M – Meters

Log – Logarithm

Fig. – Figure

Ldist – Log base 10 transformed distance

CO_2 – Carbon dioxide

H – High

L – Low

Yr – Year

IUCN – International Union for Conservation of Nature

Eqn – Equation

% - Percentage

USGS – United States Geological Society

v_o – Speed (m/s)

Mb – Body mass

V_O – Volume of Oxygen used

Hrs – Hours

Km – Kilometer

ESRI – Environmental Systems Research Institute

VHF – Very High Frequency

Std – Standardized

CHAPTER 1

GENERAL INTRODUCTION

Biodiversity is facing widespread competition with humanity for space and resources (Balmford et al., 2001). Many species, including large carnivores, are increasingly coming into conflict with people (Woodroffe and Ginsberg, 1998). Members of the mammalian order Carnivora, most of which are predators, number approximately 226 species, (Treves and Karanth, 2003) and feed on animals at lower trophic positions. Carnivores often regulate or limit the numbers of their prey, thereby influencing the structure and function of entire ecosystems (Estes et al. 1998; Berger et al. 2001; Terborgh et al., 2001). As a result, carnivore management remains a key concern to conservation biologists all over the world (Treves and Karanth, 2003).

The 31 largest carnivores (with body masses ≥ 15kg) belong to five families: Canidae, Felidae, Mustelidae, Ursidae, and Hyaenidae (Ripple at al., 2014). With the earth's terrestrial vertebrates feared to face a mass extinction of 30-96% (Rosenzweig et al., 2012), large carnivores are no exception. Large carnivores generally have small population sizes. The majority of these species (61%) are listed by the International Union for the Conservation of Nature (IUCN) as threatened (vulnerable, endangered, or critically endangered), and are at risk of local or total extinction (Ripple et al., 2014). In this thesis, I will be focusing on spotted hyenas (*Crocuta crocuta*), which belong to the Carnivore family Hyaenidae.

Populations of carnivores are declining around the globe, often with dramatic effects on lower trophic levels (Estes et al., 2011). These declines are most severe in large species, which require large areas with intact prey communities, and which are prone to killing livestock (Woodroffe, 2000). Large carnivores typically range over such wide areas that it can be difficult to maintain viable populations without some individuals coming into close proximity to humans, posing serious threats to human safety and domestic livestock (Packer et al., 2013). As a result, large carnivores are usually among the first species to disappear from landscapes, often with strong cascading effects on ecosystem structure and function (Estes et al., 2011). In the past century, carnivore populations have experienced drastic, global reductions due to increasing human population densities, habitat loss and fragmentation, reduced prey availability, and elevated rates of conflict (Gittleman et al., 2001). Conservationists have therefore sought methods to promote human–carnivore coexistence outside the confines of national parks and wilderness areas (Dickman et al., 2011).

Human-carnivore conflicts result from many factors including carnivores' protein-rich diet and large home ranges that draw them into recurrent competition with humans, who have very similar needs to those of the carnivores themselves. Indeed, many large carnivore species are specialized for ungulate predation; therefore some individuals readily kill domesticated ungulates when opportunities to do so arise (Karanth et al., 1999). This is a worldwide problem, exemplified by wolves (*Canis lupus*) and coyotes (*Canis latrans*) killing sheep in North America, pumas (*Puma concolor)* and jaguars (*Panthera onca*) taking cattle in South America, numerous carnivore genera preying on cattle and goats in Africa, and tigers (*Panthera tigris*) and leopards (*Panthera pardus*) killing livestock in Asia (Jackson & Nowell, 1996; Kaczensky, 1999). Between 1992 and 2001, black bears (*Ursus americanus)* killed 429 livestock in the state of Wisconsin (U.S.A.), whereas wolves (*Canis lupus*) killed 164 livestock (Treves et al., 2002). Under some conditions, individual carnivores attack humans, with tragic consequences for all (Treves & Naughton-Treves, 1999; Rajpurohit & Krausman, 2000). Because active persecution and accidental killing by local people remain the most important causes of mortality for many predators (Woodroffe & Ginsberg, 1998), carnivore declines are likely to roughly track the expansion of human populations in the future (Woodroffe, 2000). Regional and international trade in carnivore skins, bones and other body parts may also encourage local people to kill predators (Woodroffe, 2000).

In Africa, which is home to the last intact guild of large carnivores (Cozzi et al., 2012), large carnivore numbers have declined considerably over the last 30 years (Western et al., 2009). This decline is worrisome due to the fact that, in addition to their intrinsic value, Africa's large carnivores are important generators of income through tourism and hunting (e.g., Western & Henry, 1979). Conservation of large carnivores may therefore make economic sense, particularly in dry rangelands of limited value for agriculture (Ogada et al., 2003).

After lions (*Panthera leo*), spotted hyenas are the largest carnivores in Africa (Tilson and Henschel, 1986), and they are also by far the most abundant large carnivores on the continent. Spotted hyenas are opportunistic hunters, targeting whichever prey species are locally most abundant (Kruuk, 1972; Cooper, 1990; Holekamp et al., 1997b). These hyenas can survive in environments from which other large predators such as cheetahs (*Acinonyx jubatus*), lions, and African wild dogs (*Lycaon pictus*) have been extirpated; if hyenas also vanish, a particular habitat has most likely become very severely degraded (Mills and Hofer, 1998). It has become a conservation dictum in Africa that the survival of the continent's wildlife, and particularly of its ‘megafauna’, into the twenty-first century will depend on the goodwill of local communities (Lamprey and Reid, 2004) in order to avoid such extirpations.

Schuette et al., (2013) found that distance to active human settlements has the strongest influence on habitat occupancy by carnivore species in the southern Rift valley of Kenya indicating the likelihood of encounters between carnivores and people. This suggests that, at least in the southern rift valley of Kenya, carnivores adjust patterns of occupancy in reaction to human space use in quite a fine-scaled manner, rather than simply avoiding areas associated with high levels of human activity over the long term. Occupancies by lions, spotted hyenas, and baboons (*Papio* spp.), all potential high-conflict species, were high near active human settlements, whereas occupancies by striped hyenas (*Hyaena hyaena*) and black-backed jackals (*Canis mesomeles*), which are low-conflict species, were low near active human settlements. In general, Schuette et al., (2013) found that seasonal changes in land use by humans and livestock triggered seasonal changes in carnivore occupancy patterns.

In the study by Schuette et al. (2013), the probability of detecting lions was highest between 10:00 pm and 3:59 am, peaked between 12:00 am and 1:59 am, and was followed by a secondary peak at dawn from 6:00 to 7:59 am. This pattern is consistent with frequent nocturnal hunting, followed by movement into hiding cover around dawn. By contrast, spotted hyena detection probability was highest between 12:00 am and 5:59 am, with a peak between 12:00 am and 1:59 am and a secondary peak from 8:00 pm to 9:59 pm. This partial partitioning of time apparently allows for coexistence of large carnivores living in same ecosystem. Large carnivores including lions, spotted hyenas, and medium carnivores, including striped hyenas, and black-backed jackals, occurred at high rates in the community-run conservation area in which no people resided, but declined with increasing human utilization of the landscape (Schuette et al. 2013).

Dense vegetative cover appears to provide refuge to lions and spotted hyenas exposed to people and livestock (Boydston et al., 2003b; Kolowski and Holekamp, 2009). Selective harassment or killing of lions may happen if local pastoralists perceive lions as the most destructive, daring and aggressive large predators (Omondi, 1994) and thus respond to lion attacks by directing greater retaliative aggression toward them. This may also happen if lions remain closer to villages after attacks, are more reluctant to run away from people, or escape over shorter distances than other predators when detected by humans.

Due to habitat loss, poaching and other disturbances, resident wildlife populations have declined by more than 70% over the last 20 years in the Masai Mara National Reserve, Kenya (Ottichilo, 2000; Serneels & Lambin, 2001). Henceforth, I shall refer to this spectacular wildlife preserve as the “Reserve” or the “MMNR” or the “Mara”. Lion density in the MMNR ranks among the highest recorded in African savannas (Ogutu & Dublin, 2002) but is unusually low at the edge of the Reserve in areas adjoining pastoral ranches (Ogutu & Dublin, 2002, 2004), implicating possible negative impacts of pastoralism on lion density and distribution. Intensive and systematic searches for lions (Ogutu & Dublin, 2004; Reid et al., 2003) support the notion that lion numbers are lower in the pastoral areas than elsewhere, portending a severe threat to the long-term viability of the lion populations inhabiting such areas.

Like lions and African wild dogs, spotted hyenas are strongly dependent on protected areas or zones of low human density that contain sufficient numbers of suitable prey to support them (Mills and Hofer, 1998). Thus, the future of these species lies inside rather than outside large conservation areas. However, leopards and spotted hyenas appear better able to adapt to habitats modified by people (both may be sighted in some towns in East Africa) than do lions, wild dogs or cheetahs. This adaptability might reflect their avoidance of people by shifting from crepuscular to strictly nocturnal activity, and/or their ability to survive by scavenging when natural prey are depleted (Woodroffe, 2000).

Spotted hyenas from multiple social groups have been killed in villages near the Reserve during livestock depredation attempts (Kolowski and Holekamp, 2006). The Maasai people, who live near the Reserve, are pastoralists who often respond to livestock depredation by indiscriminately poisoning, snaring, or spearing the predators that were putatively responsible for livestock depredation (Rudnai, 1979; Omondi, 1994). Altered use of space, social behavior, circadian activity rhythms and demographic structure in spotted hyenas residing at the edge of the Reserve (Boydston et al., 2003b) have also been linked to increasing interference by livestock grazing within hyena clan territories. Indeed, herders sometimes harass or kill hyenas when they encountered them (K. E. Holekamp, unpubl. Data). Livestock grazing has been shown to be one of the key factors influencing behavioral plasticity of spotted hyenas in the MMNR (Kolowski et al., 2007; Boydston et al., 2003b; Kolowski and Holekamp, 2009), and hyenas have been reported to run away from pastoralists looking after their livestock on foot (Kolowski and Holekamp, 2009).

Patterns of activity are clearly variable in spotted hyenas, yet sources of this variation remain poorly understood. Kolowski et al. (2007) documented the influences of sex and social rank on activity patterns of spotted hyenas. They found that male spotted hyenas tended to be more active than females, particularly during the morning (0700–1100 h), and also tended to exhibit higher movement rates. Neither rates of activity nor movement varied with social rank, but low-ranking females spent more time feeding than did high-ranking females. Finally, female hyenas in territories with daily livestock grazing and high tourist visitation rates showed lower activity and less den use than did hyenas in an undisturbed territory during the times of day when human activity coincided with potential hyena activity. The specific times of day when hyena activity was reduced indicated that livestock grazing rather than tourist activity was most likely responsible for observed shifts in activity. However, to date no one has ever compared hyena activity or movement patterns between neighboring portions of any single protected area in which contrasting management policies were implemented, which is the primary purpose of this thesis research.

Boydston et al., (2003a) suggested that a better understanding of individual variation in space use patterns and the mechanisms by which edge effects can lead to extinction should aid in planning for the protection of wide ranging carnivores around the world. Therefore my own study investigated such effects by looking at the movement patterns, habitat usage, and energy costs of locomotion by spotted hyenas in the MMNR (Fig. 1.1), as these might be influenced by anthropogenic activities during the daytime (10am-4pm). The specific purpose of my thesis was to test the hypothesis that anthropogenic activities affect diurnal movement, habitat preferences, and energy use by spotted hyenas in the Reserve. 'Diurnal' here means the time between 10 am and 4 pm each day; this encompassed the time outside of the spotted hyena's primary active time (6pm-9am) (see Kolowski et al., 2007).

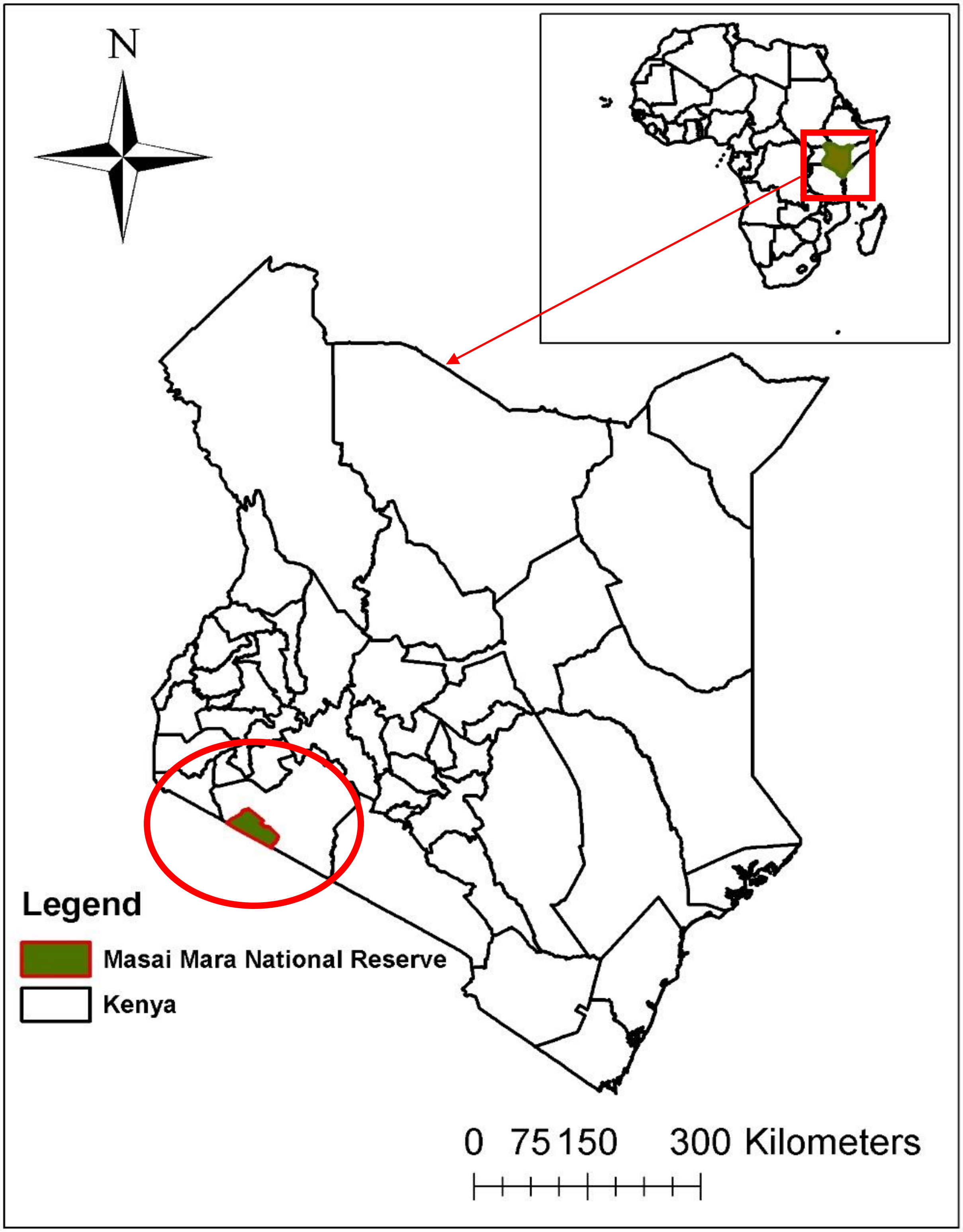

Figure 1.1: Map of Africa and Kenya showing location of the MMNR.

I investigated how social rank (high or low), time of day (am or pm) season (wet or dry), prey density (abundant or scarce), ambient temperature and local management regime within the Reserve (no livestock grazing allowed or livestock grazing allowed) influenced movement, habitat usage and energy expenditure by these hyenas. My work focused on 22 adult (> 3 years of age) female spotted hyenas in the Reserve by investigating their behavior patterns in three social groups, called ‘clans’ (Fig 1.2). I used Global Positioning System (GPS) technology deployed in radio collars (Fig. 1.3) on the hyenas to track their locations from January 1st to 31st December 2013. The Talek West (TW) clan was located near Talek town in an area (see Fig 1.2) where illegal intensive livestock grazing takes place on a daily basis from 9am-6pm (Kolowski et al., 2007). Livestock numbers in the Maasai homesteads <2km of the reserve’s north eastern border have been estimated as being over 12,000 for cattle and 16,500 for sheep and goats (Kolowski and Holekamp, 2006). By contrast, both the Serena South (SS) and Serena North (SN) clans were located in an area where livestock grazing was prohibited (Fig. 1.2).

The MMNR (1,500 km^2), which lies in southwestern Kenya ($1^0$40’S, $35^0$50’E), was established in 1961, bordering Tanzania’s Serengeti National Park (Singida, 1984) (Fig.1). The Reserve consists primarily of rolling grassland and scattered bushland (predominantly *Croton* and *Euclea* species), with riparian forest along the major watercourses. This habitat supports a large diversity of resident herbivores including both grazing and browsing species (Kolowski et al., 2007; Kolowski and Holekamp, 2009). It is bounded by the Serengeti National Park to the south, the Siria escarpment to the west and Maasai pastoral ranches to the north and east (Norton-Griffiths et al., 1975). The rangelands surrounding the MMNR contain year-round communities of resident wildlife, but migratory wildlife also spill out onto them during the dry season.

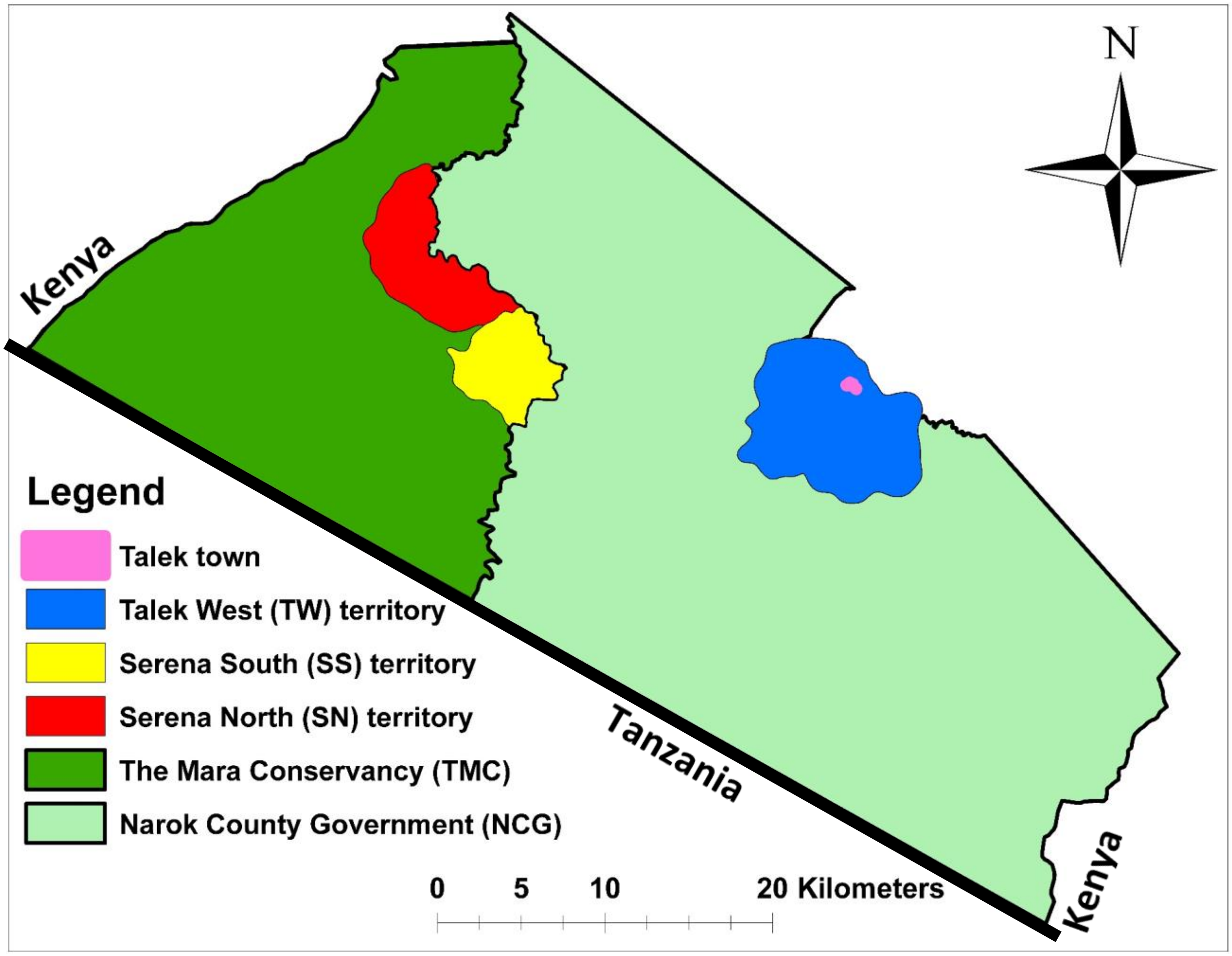

Figure 1.2: Map of the MMNR showing the territories of the three study clans.

Figure 1.3: A GPS collar like those applied to adult female hyenas in this study.

These dry-season grazing resources in the buffer zone surrounding the Reserve are important to the migrant wildebeest (*Connochaetes taurinus*) and to livestock alike (Singida, 1984). The land uses in the areas surrounding the MMNR include traditional pastoralism, wildlife conservation, tourism, subsistence maize cultivation and commercial wheat cultivation (Serneels et al., 2001). Wildlife conservation and tourism are the only land uses legally permitted within the Reserve. Wildebeest, common zebra (*Equus quagga*, formerly *Equus burchellii*) and Thomson's gazelles (*Eudorcas thomsonii*) migrate between MMNR and the Loita plains within the Masai group ranches to the north-east of MMNR (Norton- Griffiths et al., 1975). The Reserve is also the northernmost destination of the great migration of zebra and wildebeest from the southern portion of the Serengeti ecosystem. These migratory herbivores are usually present in the reserve from June or July through October each year (Ogutu et al., 2009). This “Great Migration” was named one of the new “7 Wonders of the World” in a global popularity poll contest in September 2007 by the international media (Ndegwa and Murayama, 2009).

The Sand, Talek and Mara rivers are the major watercourses draining the Reserve. Shrubs and trees fringe most permanent and seasonal watercourses, and bushes cover many slopes and hilltops (Ogutu et al., 2009). Rainfall in the ecosystem generally increases along a southeast to northwest gradient (Norton-Griffiths et al., 1975), varies strikingly in space and time within the Reserve, and is markedly bimodal during the year. Most rainfall occurs during 2 wet seasons: the ‘‘short rains’’ in November–December, and the ‘‘long rains’’ in March–May. Sunset and sunrise times take place around 18:45 and 06:30 hrs respectively, with little seasonal variation (Kolowski et al., 2007; Kolowski and Holekamp, 2009). The long dry season spans July–October (Norton- Griffiths et al., 1975). The MMNR is jointly managed by the Narok and Transmara County Governments on behalf of the government of Kenya. The Transmara County Government hires a management agency called The Mara Conservancy, hereafter referred to as ‘TMC,’ to manage the area of the Reserve located west of the Mara river (this area is called the ‘Mara Triangle’), whereas the Narok County Government, hereafter referred to as ‘NCG,’ manages the eastern portion of the Reserve with its own rangers (Fig. 1.2). The TW clan inhabits the area managed by the NCG, whereas the SN and SS clans defend territories in the Mara Triangle.

As has been shown in earlier research, the TW clan defends a territory along the northeastern Reserve border, in close proximity to a rapidly growing pastoralist population (Kolowski & Holekamp, 2006), and is subjected to intensive daily livestock grazing pressure (Kolowski and Holekamp, 2009). By contrast, livestock grazing is not allowed in the Mara Triangle. Previous research in the side of the Reserve managed by the NCG showed that 71% of all large carnivore attacks on livestock grazing illegally within the Reserve took place between 11am and 4pm (Kolowski and Holekamp, 2006).

All three of our study clans have been continuously monitored by Mara Hyena Project (MHP) personnel for many years, and the database from the entire history of the project was made available to me. GPS collars (Fig. 1.3) have been deployed on several female hyenas in each of these three clans since 2012, and they have been calibrated in such a way that the hyena locations are received at a central position within the MHP camp throughout each 24 hour cycle. Other data collected by MHP personnel include biweekly prey counts, daily minimum and maximum temperatures, reproductive states of the hyenas, and livestock & tourist counts done twice every month. All these data were available to me through the database maintained at Michigan State University (MSU), and it is on these data that my thesis is based.

I also utilized the seven elements of photo interpretation (size, shape, shadow, pattern, tone, texture and association), Google Earth and Landsat images to create random forests and thereafter classified the different vegetation cover types in the MMNR. As described by Bourgeau-Chavez et al., 2015, random forests were created within the Google Earth and Landsat TM 5 2009 by drawing polygons which corresponded to seven (7) different habitat types in the Masai Mara (Fig. 3.1). The polygons were converted into shape files using Environmental Systems Research Institute (ESRI) ArcMap software (v. 10.2.2). I used R statistical software (R core team, 2015) to convert the shape files into a classified habitat type image (raster for the MMNR). These seven habitat types were buildings, grassland, shrub land, bare ground, forest, river and wetland (Fig 3.1).

Chapter 2 of my thesis describes the diurnal movement patterns of collared female spotted hyenas in terms of linear distances travelled by these females, who rarely disperse from their natal territories (Smale et al., 1997). Chapter 3 of my thesis describes the usage patterns of female spotted hyenas in relation to the different habitat types in which they spend their time. My final chapter (Chapter 4) investigates the energetic costs to the hyenas of their movements and habitat usage, as described in Chapters 2 and 3. Each of these chapters will have Introduction, Methods, Results, and Discussion sections, as well as a brief Conclusion. Then finally, I will end my thesis with General conclusions at the end of Chapter 4.

Because this work was done collaboratively with my MHP colleagues, I will use 1st person plural in Chapters 2, 3, and 4.

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CHAPTER 2

DIURNAL MOVEMENT PATTERNS BY SPOTTED HYENAS (*Crocuta crocuta*) IN THE MASAI MARA NATIONAL RESERVE, KENYA

INTRODUCTION

Large carnivores are known to require large ranging areas with intact prey communities (Woodroffe, 2000), and they move across landscapes that are spatially heterogeneous (Kotliar and Wiens 1990). In fact, habitat heterogeneity plays a key role in determining animal movement patterns more generally, as well as such behavioral and ecological processes as feeding behavior (e.g. Etzenhouser et al. 1998; Bailey and Thompson, 2006). In their pursuit of food resources, large carnivores may come into conflict with livestock and humans thus causing serious threats to both (Packer et al., 2013). Human persecution has been shown to be one of the leading causes of carnivore mortality across the globe (Woodroffe and Ginsberg, 1998; Gittleman et al., 2001). Currently, 61% of largest carnivore species are listed as threatened by the International Union for Conservation of Nature (IUCN) (Ripple et al., 2014).

Large carnivores represent examples of elusive species that alter their daily movement patterns in response to environmental stimuli, and thus can be used as indicators of the degree of environmental stress caused by anthropogenic influence on ecosystems (Seryodkin et al., 2013). European brown bears (*Ursus arctos*) and wolves (*Canis lupus*) have been documented to show twilight or nocturnal activity periods to avoid humans (Theuerkauf et al., 2003; Ordiz et al., 2013). Mountain lions (*Puma concolor*) become more nocturnal when human activity increases (Van Dyke et al., 1986), and coyotes (*Canis latrans*) resume diurnality after human persecution ceases (Kitchen et al., 2000).

In Africa, large carnivores are faced with the same challenges as elsewhere in the world today, and they have undergone large population declines over the last 30 years (Western et al., 2009). In Tanzania, human respondents significantly viewed large carnivores as more problematic than other species because of the threats they pose to humans and livestock (Dickman, 2014). In Kenya, resident wildlife declines have been reported in such protected areas as Meru, Nairobi and the Tsavo National Parks (Western et al., 2009). Kenya is also an important international tourism destination. Kenya's tourism industry is heavily dependent on national parks and reserves, which comprise roughly 8% of the total land mass. These protected areas represent a key source of foreign exchange as well as a major source of employment for local people (Sindiga, 1996). One of the most important of Kenya's protected areas is the Masai Mara National Reserve, henceforth the "MMNR" or the "Reserve" or the "Mara." Livestock grazing and harassment of wildlife in the Mara is prohibited (Kenya Wildlife Act, 1989), but these regulations may rarely be enforced (Walpole et al., 2003).

In the Mara, livestock grazing has been documented to be one of the most important factors affecting space use patterns by the spotted hyena (*Crocuta crocuta*), the most abundant of the large carnivore species in the Reserve (Boydston et al., 2003b). Despite all the threats facing large carnivores, they are indicators of ecosystem health, and the spotted hyena has been documented to thrive in ecosystems where other species cannot survive. Thus, its disappearance from an ecosystem is an indication of particularly severe ecosystem degradation (Mills and Hofer, 1998; Woodroffe, 2000).

Here, we investigate the effects of anthropogenic activity on the diurnal movement patterns of the spotted hyena, which is found throughout most of sub-Saharan Africa (Kruuk, 1972). Spotted hyenas are strongly dependent on protected areas or zones with minimal human population densities and with adequate prey numbers (Mills and Hofer, 1998). Our study was carried out in the Mara located in south-western Kenya along the border with Tanzania to the South (Fig. 1.1). Details of our study area are as described in Chapter 1.

As mentioned in chapter 1, the MMNR is a protected area but it is managed by two different management agencies. The reserve is divided into two areas by the Mara River, and the area east of this river is managed by the Narok County Government (NCG); this management regime has been in place since the 1960s. The western side of the Reserve falls under the jurisdiction of the Trans-Mara County Government, and is managed by a non-governmental organization (NGO) called The Mara Conservancy (TMC); TMC has managed the western portion of the Reserve since 2001. Intensive livestock (cattle, sheep and goats) grazing takes place in the eastern side of the reserve, managed by the NCG, but no livestock grazing is allowed in the western side of the reserve, managed by TMC. Thus the eastern side of the Reserve is relatively heavily disturbed by anthropogenic activity but the western side is very pristine. Here we studied clans of spotted hyenas located on both sides of the Reserve. The members of the Talek West (TW) clan defend a group territory in the disturbed (livestock grazing allowed) side of the Reserve while the Serena South (SS) and Serena North (SN) clans defend territories in the undisturbed (livestock grazing prohibited) side of the Reserve (Fig. 1.2). This gave us the opportunity to make comparisons regarding distance travelled by hyenas living in these two environments. Specifically, we tested the hypothesis that anthropogenic activity affects hyena movements during daylight hours. We expected the daily movements of cattle and herders in the disturbed side of the Reserve to cause hyenas to change their locations more frequently and thus to travel longer distances than in the undisturbed area. Throughout this chapter, we will be using ‘TMC’ here to refer to the undisturbed side of the reserve and ‘NCG’ to refer to the disturbed side of the reserve (Fig. 1.2).

Methods

Study animals

Spotted hyenas live in fission-fusion social groups called clans, and each clan is composed of multiple adult females, their offspring, and one to several adult immigrant males (Kruuk, 1972; Holekamp et al., 1996). These hyenas may forage either singly or in small groups (Kruuk, 1972; Mills, 1984; Tilson & Henschel, 1986), and members of each clan defend a group territory (Hofer and East, 1993a). Here, all hyenas were known individually by their unique spots (Cooper, 1989). Sex was determined by the dimorphic glans morphology of the erect phallus (Frank et al., 1990). Females were considered adults when they reached three (3) years (yrs) of age or conceived their first litter, whichever came first (Boydston et al., 2003a). Social ranks of our study animals were known from their positions in a matrix of outcomes of dyadic agonistic interactions (Smale et al., 1993). High-ranking females were considered to be those in the top third of a clan’s dominance hierarchy, and low-ranking females were considered to be those in the bottom third (Green 2015). Between 1st January and 31st December 2013, 22 adult female spotted hyenas (>3yrs) were fitted with Global Positioning System (GPS) radio collars (see details below), and subsequently tracked to monitor their diurnal movement patterns in the MMNR (Fig. 2.1). Based on the outcomes of dyadic agonistic interactions between individual hyenas since birth, all hyenas’ social ranks (high-ranking or low-ranking) were individually known by the time we deployed GPS collars on them. In total, we collared 13 high-ranking (H) hyenas (TMC=9, NCG=4) and 9 low-ranking (L) hyenas (TMC=5, NCG=4) (Tables 2.1 and 2.2).

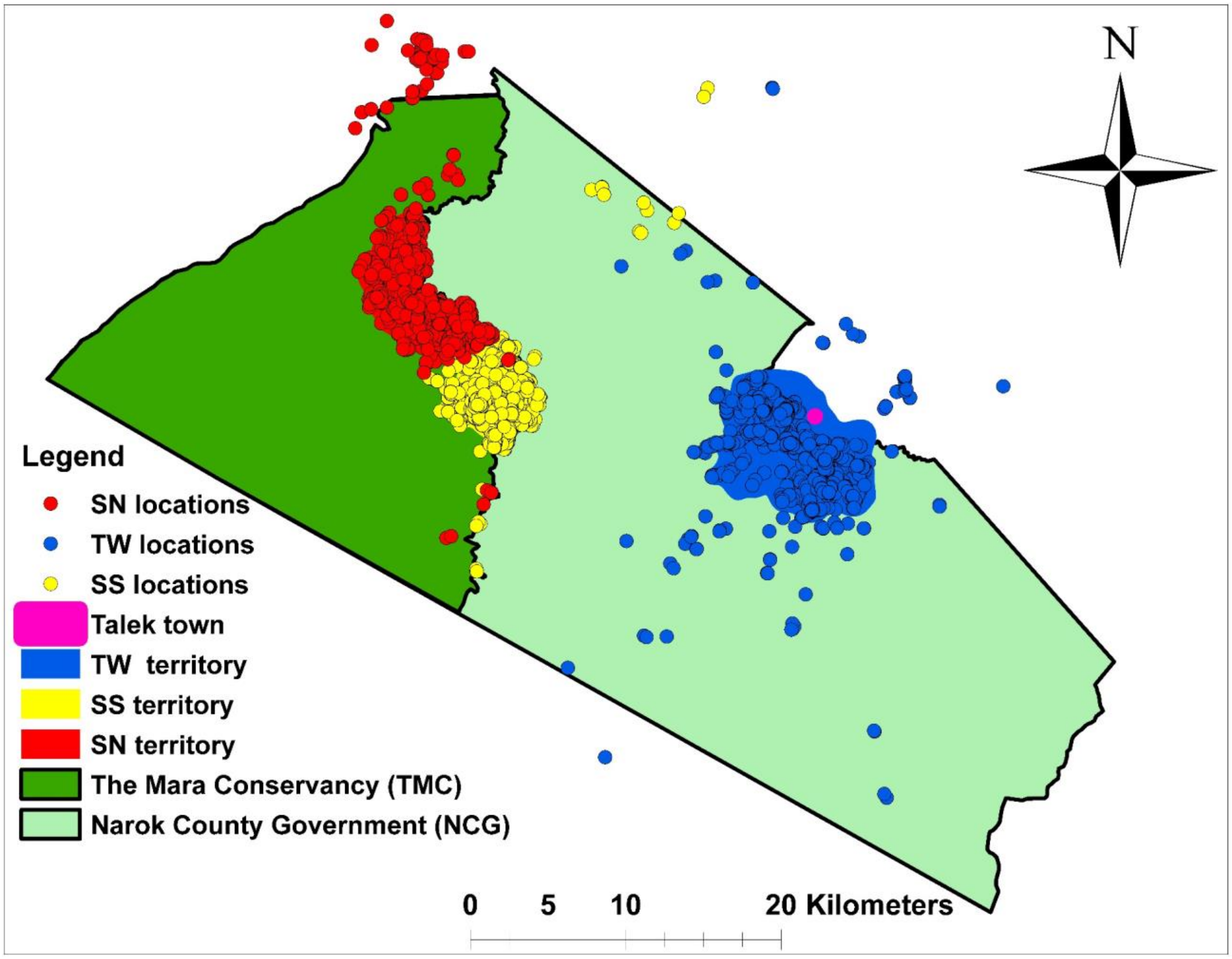

Figure 2.1: Hyena spatial movement patterns in the MMNR.

Name	**Collar Id**	**Rank**
Bart	11526	H
Clov	11528	H
Digs	11755	H
Ema	11530	L
Hndy	11522	L
Java	11757	H
Mtn	11523	L
Peep	11529	H
Shrm	11111	H
Slin	11520	H
Taj	11527	L
Tnsl	11525	L
Wafl	11521	H
Zoey	11524	H

Table 2.1: Hyenas studied in TMC.

Name	Collar Id	Rank
Baez	11414	L
Hel	11419	H
Hex	11417	L
Juno	11413	H
Mgta	11412	H
Pan	11416	H
Roos	12157	L
Tilt	11415	L

Table 2.2: Hyenas studied in NCG.

Collection of spatial data

Twenty two adult female spotted hyenas (TMC=14, NCG=8, see table 2.1 and 2.2) were immobilized using tiletamine-zolazepam (6.5 mg/kg; Telazol: W.A Butler Company, Brighton Michigan) administered in a plastic dart via a CO_2 –powered rifle (Telinject Inc., Saugus, California), and fitted with GPS collars (Vectronix Aerospace, Berlin, Germany). Collars were programmed to transmit their locations at 10am, 1 pm, and 4 pm every day. The GPS collar technology used here is very precise when compared to earlier studies, which used Very High Frequency (VHF) collars that could only be tracked from vehicles or airplanes. All locations here were digitized using ESRI ArcMap 10.2.2 software (Environmental Systems Research Institute, Redlands, CA, USA). We used a Geographic Coordinate System (GCS) of World Geodetic System of 1984 (WGS 84) then projected the shape files of the GPS coordinates into Universal

Transverse Mercator zone 36 South (WGS 84 UTM 36S) (Fig. 2.1). Finally, XY coordinates were added to the GPS coordinates to allow for linear distance calculations in meters (m); these calculations were done using R statistical software (R core team, 2015). Linear distances were then calculated between each two consecutive locations obtained during daylight hours. Territory sizes were estimated using fixed kernel utilization distributions (UDs) with 95% probabilities for all hyenas with collars in 2013 (Green, 2015).

Minimum and maximum temperatures

Earlier studies have shown that spotted hyenas reduce their activity with increases in ambient temperatures (Kruuk, 1972; Cooper, 1990). Therefore, we monitored daily minimum and maximum temperatures in 2013 at weather stations located in TMC and NCG. Our study area was situated very close to the equator, such that hours of daylight and darkness were roughly the same year-round. Sunrise and sunset hours at our study site take place between 6:18-6:48am and 6:28-6:48pm, respectively (Kolowski et al., 2007). Mean monthly daytime and nighttime temperatures in MMNR have been shown to average around 28.3^{0}C and 13.8^{0}C, respectively (Kolowski et al., 2007). We calculated the mean daily average minimum (min’) and maximum (max’) temperatures every month during our study period, and these were used as monthly means. We then calculated the 2013 mean monthly minimum and maximum temperatures to be 14.94^{0}C and 28.57^{0}C, respectively. Based on our temperature records taken in TMC and NCG, TMC was, on average, a bit warmer than NCG (Fig. 2.2). That is, the mean monthly minimum temperature in TMC was 15.19^{0}C, while in NCG it was 14.70^{0}C. The mean monthly maximum temperature in TMC was 30.22^{0}C, while in NCG it was 26.91^{0}C (Fig.2.2).

Prey counts

Throughout 2013, prey animals within each clan territory were counted in collaboration with Mara Hyena Project (MHP) personnel. Prey were counted twice every month within 100m (fixed widths) on either side of multiple, established 4-km transects in each territory. Prey counted were then averaged to obtain monthly means. The density of the prey per month (animals/km^2) was estimated by dividing the mean number of prey counted in the territories per month by the transect area (km^2). The monthly prey density totals were added together and divided by 12 to get the mean monthly prey density for 2013. All negative mean monthly prey density deviations from the overall mean for 2013 were referred to as “prey scarce” and all positive mean monthly prey density deviations were referred to as “prey abundant” in our statistical analysis (Fig. 2.3).

Seasons

Rainfall affects ungulate population dynamics in the Mara-Serengeti ecosystem through its effect on vegetation growth and water availability (Ogutu et al., 2008). Similar effects have also been observed in the Laikipia district in Kenya (Georgiadis et al., 2007). Rainfall in the MMNR has been shown to average between 800-1200mm annually. The longest dry period takes place between mid-June and mid-October, and a shorter dry season in January and February (Stelfox et al., 1986, Ndegwa and Murayama, 2009). In 2013, daily rainfall was recorded at our camps in TMC and NCG, using a standard metric rain-gauge, and added together to get monthly totals (Fig. 2.4). The monthly totals were added to get the total for the year (2013) which was estimated at 1231.45mm and 1275.5mm at TMC and NCG respectively. The total rainfall recorded in 2013 was divided by 12 to get the mean monthly total rainfall separately for TMC and NCG. All monthly rainfall deviations from the mean were referred to as 'wet' if positive and 'dry' if negative.

Reserve management regime

Previous studies carried out within the NCG side of the Reserve estimated that up to 6,000 livestock (cattle, sheep and goats) grazed daily within this area. This livestock space-use overlapped with the 95% Utility Distributions (UDs) of members of the Talek West (TW) clan (Boydston et al., 2003b). Nine (9) members of this clan (TW) were known to be killed at bomas next to the Reserve borders during livestock depredation in the period 2001-2005. Hyenas and other predators have also been reported to be killed indiscriminately by local community members in this area (e.g., 4 spotted hyenas and 1 lion were killed following livestock depredation) (Kolowski and Holekamp, 2006). In the NCG area, the value of livestock lost to depredation has been estimated to be about $6049 in 14 months in one earlier study (Kolowski and Holekamp, 2006).

Our study clan in the NCG area was the Talek West (TW) clan (Fig.1.2), which had a mean monthly clan size of 113 individuals in 2013. The TW territory size was approximately 77.04km^2. In TMC, we studied two clans, namely Serena North (SN) and Serena South (SS) (Fig. 1.2) with clan sizes averaging 51 and 39 individuals, respectively. Territory size for SN and SS was approximately 42.67km^2 and 28.29km^2 respectively. The TW clan defended a territory along the northeastern border of MMNR next to an area densely inhabited by Masai pastoralists (Kolowski & Holekamp, 2006). In addition to exposure to tour vehicles, these hyenas were also exposed to intensive daily livestock grazing pressure (Kolowski and Holekamp, 2009). The SN and SS clans defended territories near the western border of the MMNR, in TMC, where no human activities were allowed except wildlife viewing from tour vehicles.

Statistical analyses

R v.3.1.3 statistical software (R core team, 2015) was used for all statistical analysis. Linear distances were calculated between any hyena locations between 10am-1pm and 1pm-4pm. We used Generalized Linear Models (GLM) to model the distance travelled by hyenas as a function of eight predictor variables: 1) management regime (coded as 'TMC' or 'NCG'), 2) time of the day (coded as 'am' or 'pm'), 3) prey (coded as 'many' for prey abundant and 'few' for prey scarce), 4) social rank (coded as 'H' or 'L'), 5) season (coded as 'dry' or 'wet'), 6) interaction between management regime and rank (coded as rank*management), 7) interaction between management regime and prey (coded as prey*management) and 8) interaction between management regime and season (coded as season*management). Because the linear distances travelled by the hyenas were not normally distributed, data were log transformed (log base 10) to acquire normality before statistical analysis. Subsequently, our model was as follows:

Eqn 1: glm (ldist~rank+time+season+prey+management+rank*management+prey*management+season*management) where ldist was the Log transformed distances (log base 10).

In this model, all our fixed factors (rank, management, prey, season, and time) had two levels with "rank" being either high (H) or Low (L) (Table 2.1 and 2.2). "management" being 'TMC' or 'NCG') and "prey" had two levels (prey abundant i.e 'many' or prey scarce ie 'few'). "Season" had two levels ('dry' or 'wet'), and "time of day" had two levels as well ('am' or 'pm'). We also added the interactions between management regime and rank (rank*management),

management regime and prey (prey*management) and management regime and season (season*management) in our model. Other interactions were not included in this model since our primary focus was to describe spotted hyena movement patterns in the two sides of the Reserve under different management regimes.

In this chapter, sample sizes in our analyses were the daily distances calculated from the three daily locations in 2013 (total locations=6245; am=3164 locations, pm= 3081 locations). Two sample student t-tests were used to test for mean differences between TMC and NCG in total monthly rainfall. Since mean monthly prey density numbers estimated in TMC were not normally distributed, a Wilcoxon Rank Sum test was used to test for prey density differences between TMC and NCG. We presented our means with standard errors, and differences between groups were considered significant when *P* < 0.05.

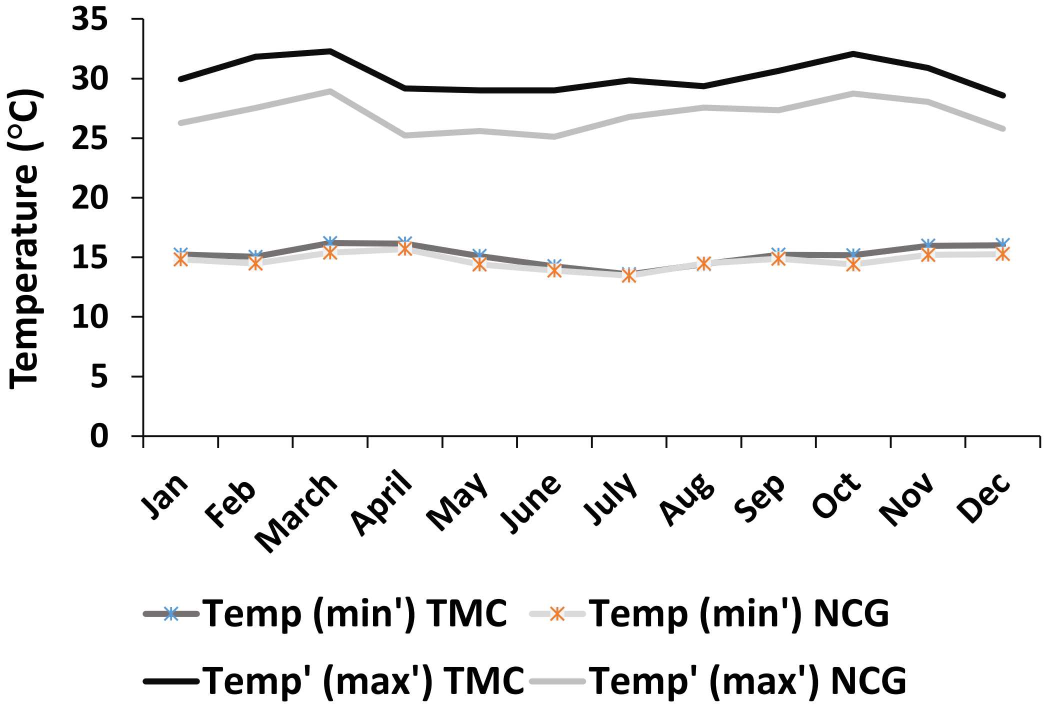

Figure 2.2: Mean monthly minimum and maximum temperatures in TMC and NCG.

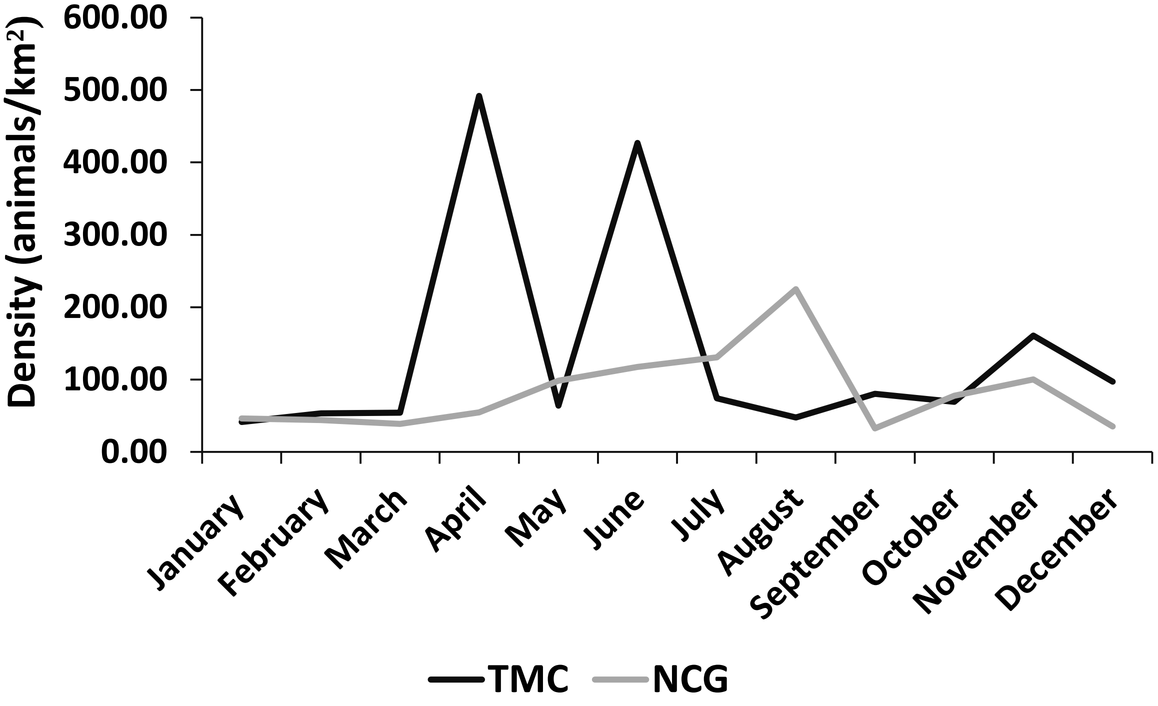

Figure 2.3: Prey density (animals/km^2) in TMC and NCG.

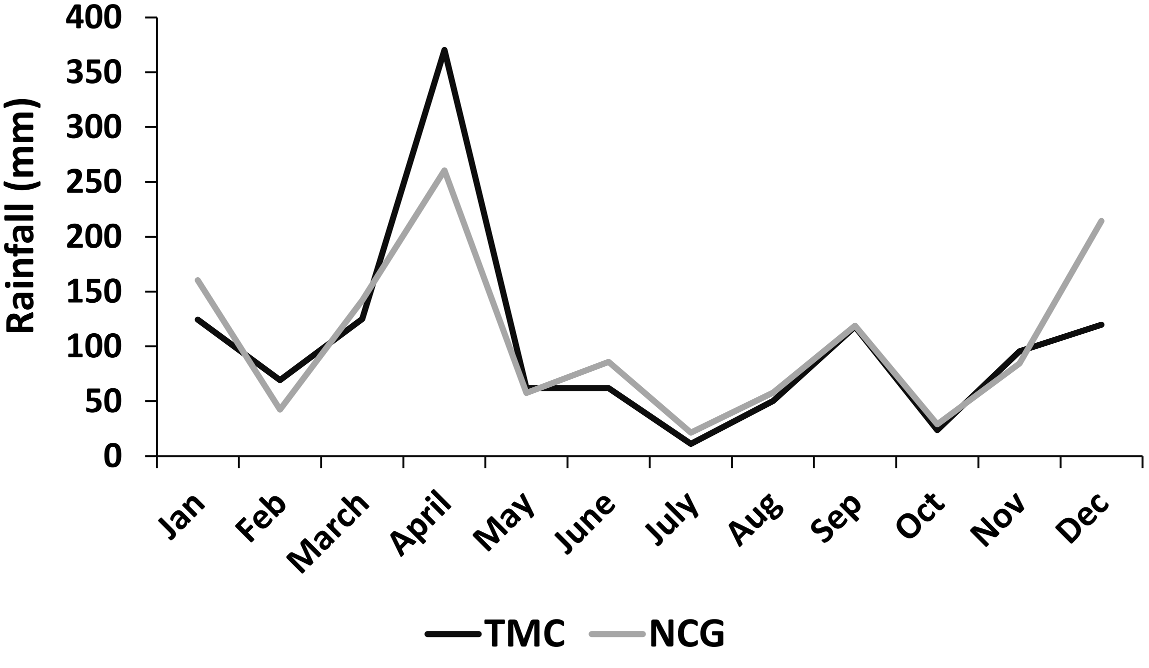

Figure 2.4: Total monthly rainfall recorded in the MMNR.

	Estimate Std.	Error	t value	Pr(>|t|)
(Intercept)	1.570892	0.045662	34.402	**<2e-16*** **
timepm	-0.326949	0.021200	-15.422	**<2e-16*** **
rankL	-0.069507	0.036700	-1.894	**0.058283**
managementtmc	-0.173692	0.049453	-3.512	**0.000447*** **
seasonwet	0.042689	0.049430	0.864	0.387827
preymany	0.034325	0.052001	0.660	0.509232
managementtmc:preymany	0.027157	0.059230	0.459	0.646608
managementtmc:rankL	0.201037	0.045149	4.453	**8.63e-06*** **
managementtmc:seasonwet	0.003157	0.056029	0.056	0.955070

Table 2.3: GLM table of results for distance moved. Distances have been transformed to log base 10. Bolded cells indicate significant effects.

Results

Reserve management regime and distance travelled

Our modeling showed that hyenas in the undisturbed side of the Reserve (TMC) travelled significantly shorter distances than did hyenas on the disturbed side (t= -3.512, p=0.0004) (Table 2.3, Fig. 2.5). In fact, some of the members of the clan defending their territory in the disturbed side of the reserve (TW) showed that they sometimes travelled all the way south into Tanzania (Kenya’s neighboring country), and northwards beyond the neighboring town of Talek (Fig.2.1). This result was consistent with our hypothesis that the anthropogenic activities (e.g., livestock grazing) in NCG were at least partially responsible for this unique behavior of hyenas. In TMC, hyenas appeared to behave more naturally, and with no disturbance allowed, they moved shorter distances.

Time of the day and distance travelled

Our results showed that time of day was important in determining how far the hyenas travelled. Hyenas were travelling significantly shorter distances in the afternoon (1pm-4pm) than in the morning (10am-1pm) (t= -15.422, p<0.0001) (Table 2.3, Fig. 2.6). This movement pattern was expected because mornings were a bit cooler than afternoons throughout 2013.

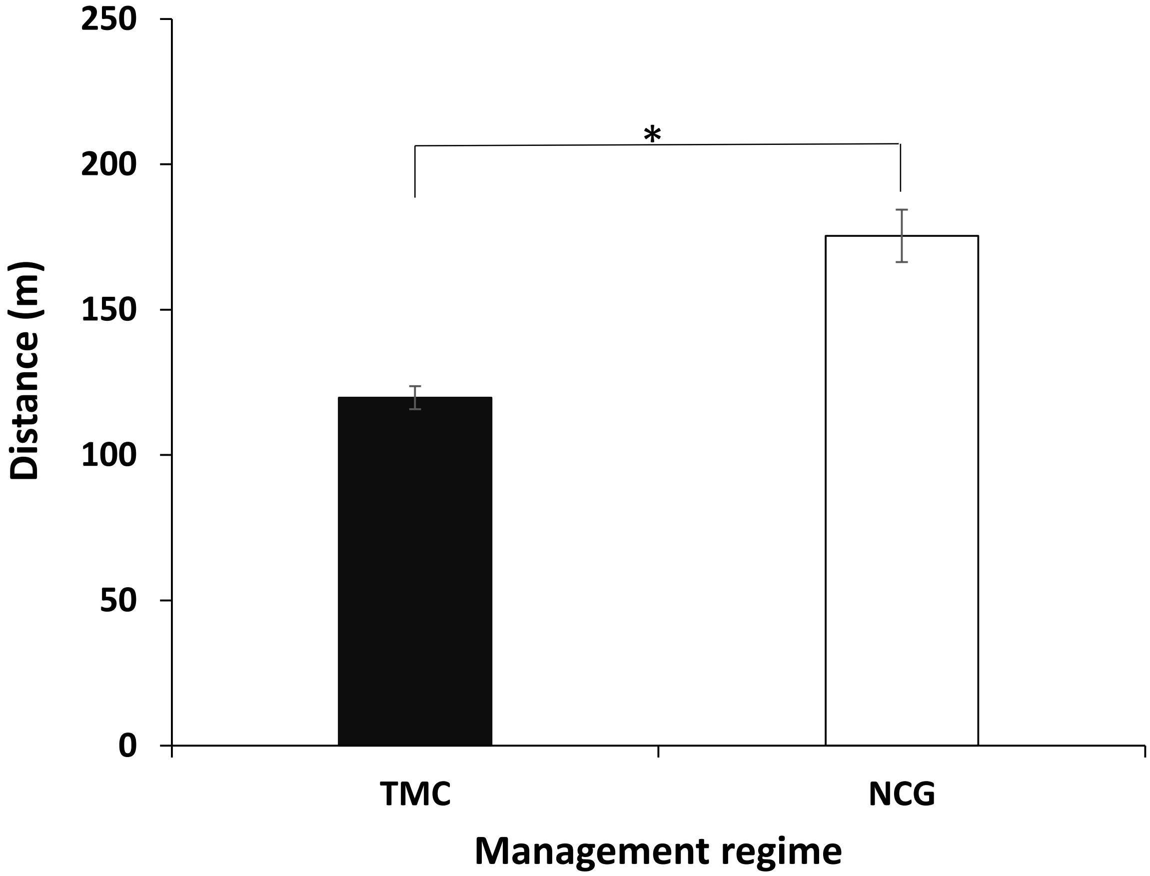

Figure 2.5: Management regime and average daily distance moved in TMC and NCG. Asterisk represents significant difference and error bars represent standard errors.

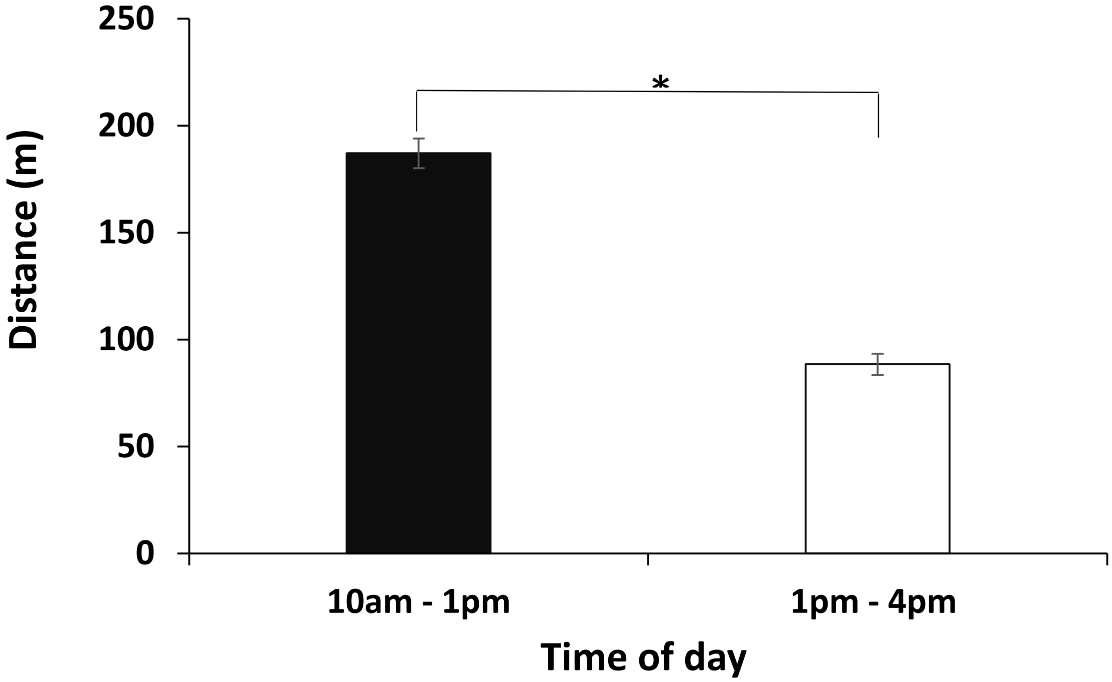

Figure 2.6: Time of day and average daily distance moved in the MMNR. Asterisk represents significant difference and error bars represent standard errors.

Social rank and distance traveled

Earlier studies have shown that low-ranking (L) spotted hyenas have little access to food compared to high-ranking (H) ones (Tilson & Hamilton, 1984; Frank, 1986*b*). Therefore, we expected to see significant differences between distances travelled by low- ranking hyenas when compared to the high-ranking ones. As expected, on average, low-ranking hyenas travelled longer distances than did high-ranking hyenas (Fig. 2.7) in 2013. However, our modeling revealed a marginally non-significant difference between the distances travelled by low-ranking and high-ranking hyenas (t= -1.894, p=0.0583) (Table 2.3). Moreover, our modeling showed that the low-ranking hyenas in TMC were moving significantly longer distances than were high-ranking hyenas (t=4.453, p<0.0001) (Table 2.3, Fig. 2.10) in this side of the reserve. However, we did not see the same rank-related variation in the NCG side of the Reserve. This might mean that in NCG, a hyena's high position in the hierarchy did not guarantee access to resources, as it does in pristine habitats.

Prey and distance travelled

Prey abundance has been documented as one of the factors affecting ranging patterns among large carnivores (Woodroffe, 2000). Therefore, we expected to see hyenas travelling significantly longer distances when prey were scarce than when prey were abundant. However, our results showed no difference in distances travelled during time of prey scarcity and abundance (t= -0.660; p=0.5092) (Table 2.3, Fig. 2.8). We also expected to see hyenas in the disturbed side of the Reserve travelling longer distances when prey were abundant due to anthropogenic activity. However, our modelling showed no significant difference between the distance travelled by hyenas in TMC and NCG when prey were abundant or scarce (t=0.459, p=0.6466) (Table 2.3, Fig. 2.11).

In order to investigate whether prey density recorded in TMC was different from that in NCG, we averaged prey density numbers in TMC recorded per month and compared those to the monthly averages recorded in NCG. Because the mean prey density numbers in TMC and NCG were not normally distributed (even after log transformation to base 10 and testing for normality with a Shapiro Wilk test), a Wilcoxon Rank Sum test was used to test for the difference in their means. Our results showed that there was no significance difference in the density of prey recorded in the two sides despite the fact that TMC had slightly higher mean prey density recorded (w=85, p=0.4776) (Fig. 2.3). Average monthly prey density in TMC was

138.45 (animals/km^2) while that of NCG was 83.42 (animals /km^2), but variance was high on both sides of the Reserve (Fig. 2.3).

Seasonality and distance travelled

Prey abundance has been shown to be higher in MMNR during the dry than wet season, as most ungulates concentrate during the dry season near watercourses within the Reserve (Ndegwa and Murayama, 2009). We therefore expected to see spotted hyenas travelling significantly shorter distances during the dry season than during the wet season. However, we found no significant differences between the distances moved by hyenas during the wet and dry seasons (t= 0.864, p=0.3878) (Table 2.3, Fig. 2.9). We also expected to see hyenas travelling longer distances during the wet season in NCG than TMC but our results showed no significant difference in this respect between the two sides of the Reserve (t=0.056, p=0.9551) (Table 2.3, Fig. 2.12)

In order to investigate whether total monthly rainfall received in TMC was different from that received in NCG, we compared the total monthly amount of rainfall that fell in the two areas. Data were log transformed to base 10 (tested normal with a Shapiro Wilk test) and tested with a (or with an independent) student t-test. Our results showed no significant difference between the total monthly rainfall received in TMC and NCG (t=0.3079, df=22, p=0.761) (Fig. 2.4). Our results showed NCG received slightly higher rainfall than TMC throughout 2013, total rainfall received was 1275.5mm and 1231.45mm in NCG and TMC, respectively.

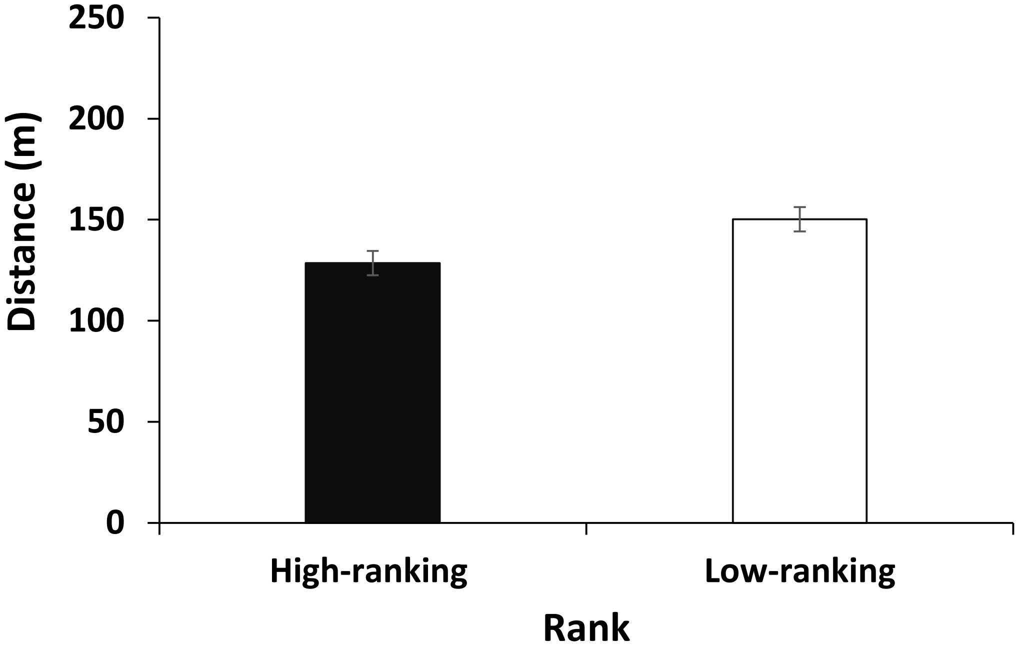

Figure 2.7: Social rank and average daily distance moved in the MMNR. Error bars represent standard errors.

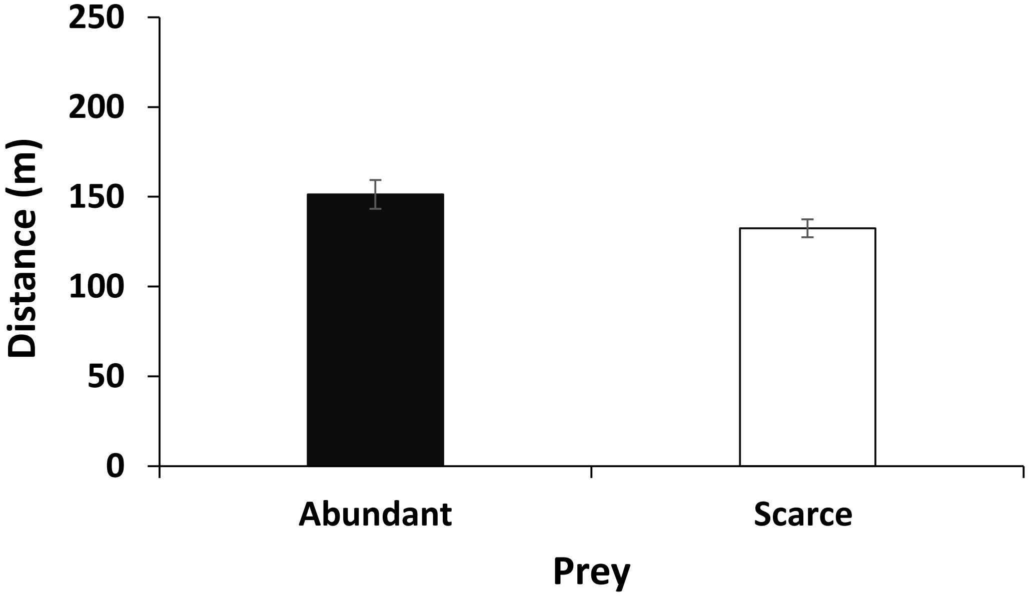

Figure 2.8: Prey availability and average daily distance moved in the MMNR. Error bars represent standard errors.

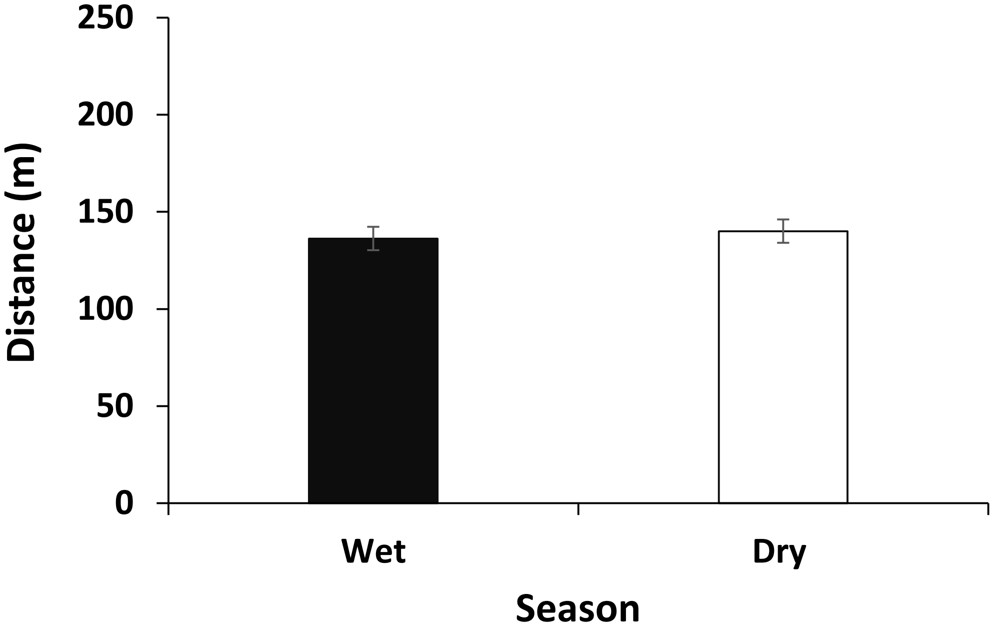

Figure 2.9 Seasonality and average daily distance moved in the MMNR. Error bars represent standard errors.

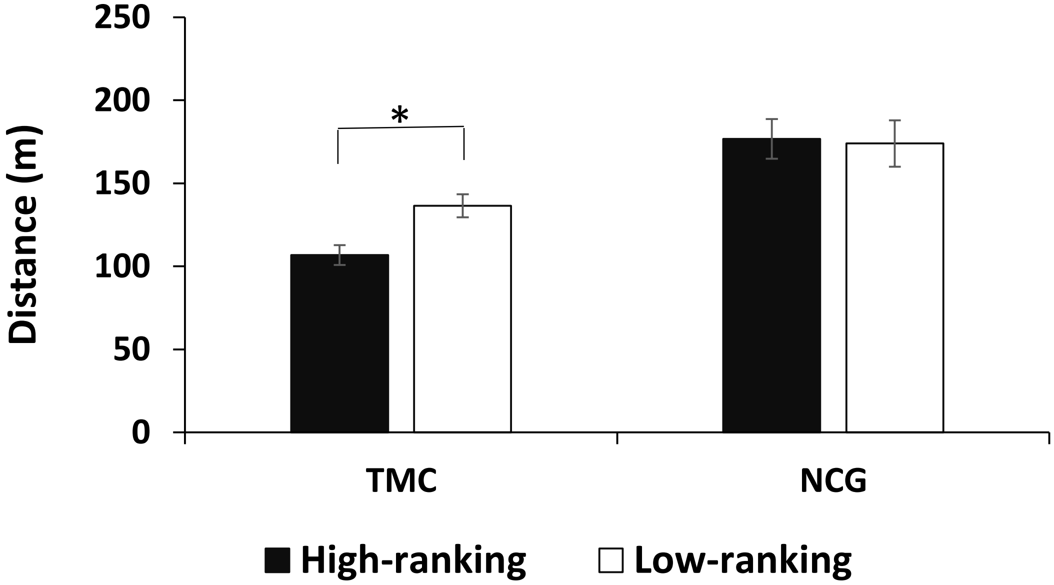

Figure 2.10: Social rank and average daily distance moved in TMC and NCG. Asterisk represents significant difference, and error bars represent standard errors.

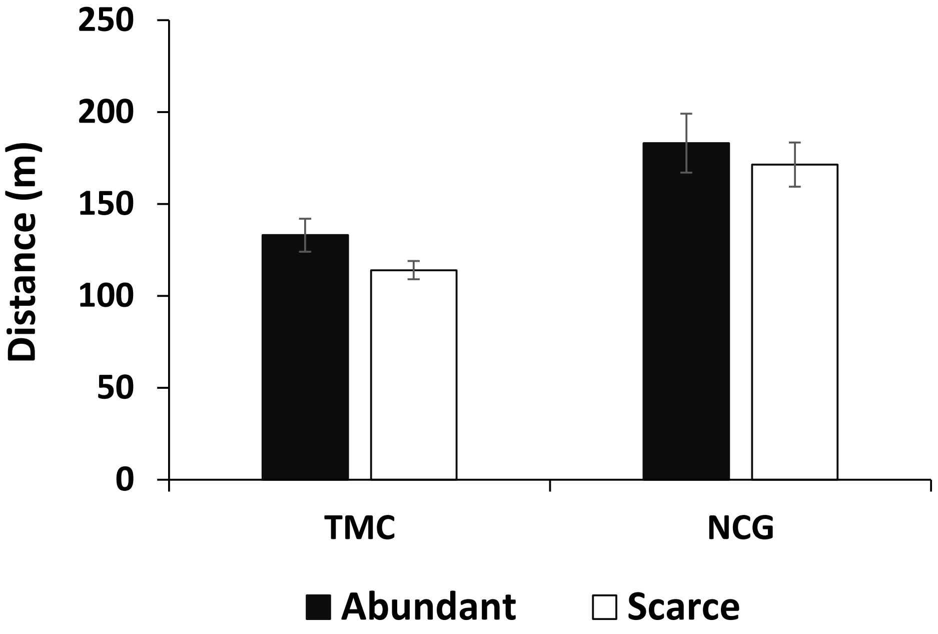

Figure 2.11: Prey availability and average daily distance moved in TMC and NCG. Error bars represent standard errors.

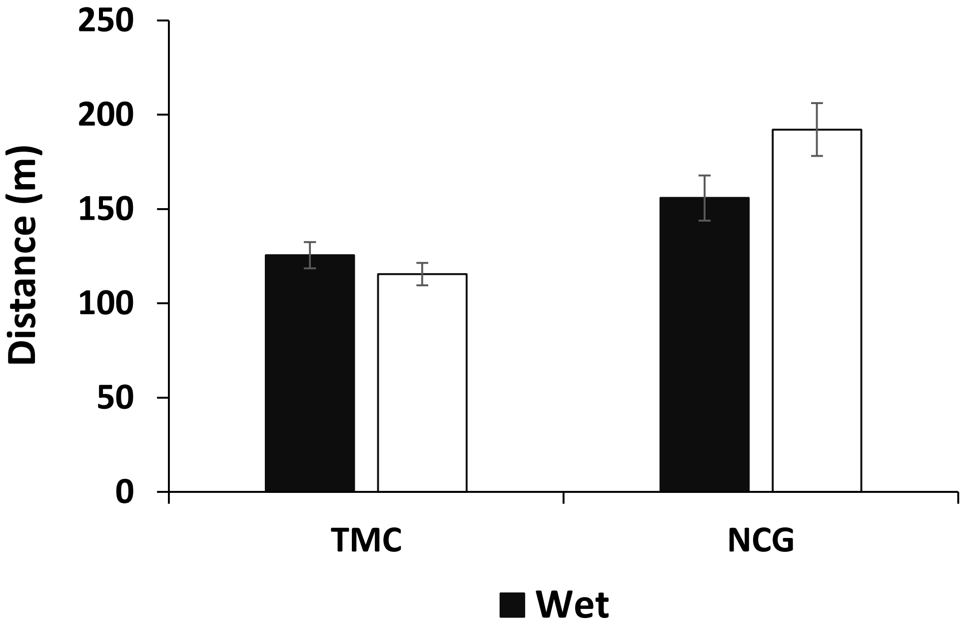

Figure 2.12: Seasonal variation and average daily distance moved in TMC and NCG. Error bars represent standard errors.

Frequency of movement

Our results showed decreasing frequency of hyenas movement as distance increased. >80% of the distances moved during the day were less than 200m and only ~7% of the distances moved were more than 500m (Figure 2.13). See also table 2.14 for average monthly distances moved by hyenas in the year 2013.

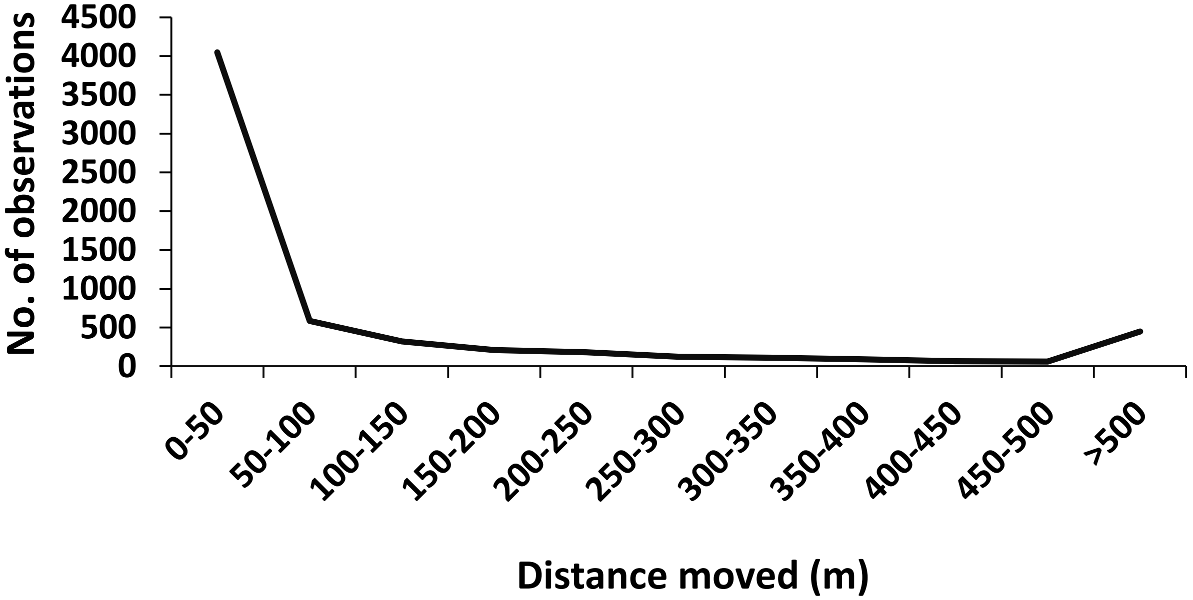

Figure 2.13: Diurnal frequency of movement by spotted hyenas in the MMNR.

Month	Average distance moved (m) in TMC	Average distance moved (m) in NCG
Jan	99.64	113.53
Feb	106.06	111.52
March	106.83	181
April	126.92	111.72
May	141.33	135.64
June	123.79	132.69
July	86.21	158.12
Aug	85.77	222.47
Sep	132.41	184
Oct	118.67	281.22
Nov	141.44	219.55
Dec	147.56	175.73

Table 2.4: Table of average diurnal monthly distances travelled by hyenas in 2013 in the MMNR.

Discussion

Management regime and movement patterns

Previous research in NCG has shown that female spotted hyenas defending their territory in an area with intensive livestock grazing remained active during the morning hours more than did hyenas defending their territory in an area with no livestock grazing allowed (Kolowski et al., 2007). Our results were thus consistent with this study because we did find hyenas travelling significantly shorter distances in the undisturbed area than in the disturbed area (Fig. 2.5). This finding was similar to other previous studies showing that large carnivores alter their activity patterns in response to anthropogenic activities (e.g. Kitchen, Gese & Schauster, 2000); in the MMNR it was during the day when intensive livestock grazing occurred in 2013 within NCG. Our finding that hyenas were traveling longer distances in the morning was consistent with that of Kolowski et al., (2007) (mentioned above).

Social rank and distance moved

Earlier studies indicated that hyenas of low social rank have low priority of access to resources (Kolowski et al., 2007, Holekamp et al., 2012). Each individual's position in the hierarchy in the clan determines its priority of access to food (Tilson & Hamilton, 1984; Frank, 1986b). Earlier studies done in NCG have shown that low-ranking female hyenas with no den-dwelling cubs travelled longer distances than did high-ranking female hyenas with no den-dwelling cubs (Boydston et al., 2003a). Another study in Tanzania also found that low-ranking hyenas travelled longer distances in search of food than did high-ranking hyenas during times of low prey abundance (Hofer and East, 1993a). Therefore, we expected significant differences between the distances travelled by low-ranking hyenas and those travelled by high-ranking ones. However, our results showed no significant difference between the distances travelled by low and high-ranking hyenas. This result was consistent with those of Kolowski et al., (2007) who found no significant difference between the percent of time high-ranking females spent while travelling when compared to the low-ranking females over a 24-h period in TW clan. Consistent with our prediction and with results from the studies mentioned above, our results revealed a significant difference in distance travelled between low and high-ranking hyenas in the undisturbed side of the reserve (TMC). It may be that we saw no significant effects of rank on the NCG side of the Reserve because hyenas of all ranks on that side are affected similarly by human activity (Fig. 2.7). This hypothesis is also supported by our finding that high rank individuals from the east side travel further than low rank individuals on the west side.

Time of day and movement patterns

Earlier studies have shown that spotted hyenas tend to become almost entirely nocturnal in their daily activities in hot, dry habitats (Tilson & Hamilton, 1984; Cooper, 1990). This was consistent with our finding that hyenas were moving longer distances during the cooler morning hours (10am-1pm) than during the warmer afternoon hours (1pm-4pm) (Fig. 2.6). Other than temperature differences, our finding may also be due to reduced anthropogenic activity, and thus less disturbance, in TMC. Unfortunately we cannot distinguish between these hypotheses. The implementation of a strict management plan in TMC may be benefiting the hyenas living there. In NCG, livestock grazing takes place (despite being illegal in the country; Kenya Wildlife Act, 1989; Walpole et al., 2003) on a daily basis, and this may be causing the local hyenas to move longer distances.

Our results are consistent with those of earlier researchers who have shown that daily trends in temperature do affect the optimal activity patterns of terrestrial carnivores (Avenant and Nel, 1998). Normally the onset of activities for spotted hyenas is observed to resume around sunset and end early in the morning (Kolowski et al., 2007; Kruuk, 1972). By contrast, here we find the hyenas traveling even in the afternoon (1pm-4pm) when temperatures are high. Despite having been shown to be nocturnal hunters (Cooper, 1990), here we also find spotted hyenas moving about during the daytime, which signifies a change in their normal behavior.

Prey availability and movement patterns

Prey abundance has been shown to affect space use of large carnivores (Macdonald, 1983). Large carnivores feed on animals at lower trophic levels than themselves (Treves and Karanth, 2003). Large carnivores regulate numbers of their prey through predation (Estes et al. 1998; Berger et al., 2001; Terborgh et al. 2001). Lions were found to increase their attacks on humans in areas with few prey except bush pigs *(Potamochoerus larvatus)* (Packer et al., 2005). Distribution and densities of spotted hyenas were also found to be prey-dependent throughout Africa (Hayward et al., 2009; Hofer and East 1993b; Mills 1989; Trinkel et al., 2004). Reproductive success in female spotted hyenas is directly correlated with priority of access to food (Holekamp et al., 1996). In east Africa, the diet of spotted hyenas is composed mainly of medium to large-sized ungulates (Kruuk, 1972).

In the MMNR, the resident wildlife are joined annually from July to at least October (Ogutu et al., 2005) by large migratory herds of herbivores from the Serengeti National Park, and this affects prey availability in the Reserve . Therefore, we expected that hyenas would travel longer distances when prey were scarce than when prey were abundant. In contrast to our expectation, our results showed do difference in distance travelled during times of prey scarcity nor during times of prey abundance. We also did not see significant differences in distance travelled on either side of the Reserve when prey were scarce or when prey were abundant (Figs. 2.8 and 2.11). These results were similar to those from a study by Boydston et al., (2003a), who found that prey availability did not significantly affect space use patterns of female hyenas with den-dwelling cubs in NCG. Earlier studies with the TW clan found that hyenas were actually avoiding prey rich areas, as these were the same areas utilized most heavily by livestock. Hyenas have also been shown to be scared by the herders who guarded their livestock in NCG area (Boydston et al., 2003a; Kolowski and Holekamp, 2009; KE Holekamp unpublished data). In fact, Boydston et al., (2003b) in her study on TW clan did observe hyenas being displaced from their resting places by cattle, and also observed hyenas emerging from bushy cover immediately after livestock herds passed through an area.

Seasonal variation in movement

Desert hyenas have been documented to disperse from their territories when their water supply failed (Tilson and Henschel, 1986). Hyenas in the Savuti area of Botswana were observed to travel longer distances in search of drinking water during the dry season (Cooper, 1989). Another study done in Ruaha National Park, Tanzania, revealed a positive correlation between large carnivore distributions and water availability (Abade et al., 2014). Lions were also found to select areas that were within 2km of a waterhole, and they also covered shorter distances than when they were farther from a waterhole (Valeix et al., 2010). However, the MMNR has reliable water sources throughout the year in both TMC and NCG, and water availability seems not to be limited in the Reserve even in the dry season. Therefore we predicted that hyenas would be travelling longer distances during the wet season than they would do during the dry season. This is because it is during the wet season when some prey move out of the Reserve into the surrounding ranches, but then move back into the Reserve during the dry season (Ndegwa and Murayama, 2009). Here we found that distances travelled by collared MMNR hyenas during daylight hours did not differ significantly between the wet and dry season (Fig. 2.9). We expected to see hyenas travelling shorter distances during the dry season than during the wet season but we found no seasonal differences in daytime movements. Earlier studies have documented that prey are sparsely distributed in MMNR during the wet season (Ndegwa and Murayama, 2009), forcing hyenas to travel further. However we found no significant seasonal variation in daytime movements.

Conclusion

Human wildlife conflict can lead to species extinctions (Woodroffe and Ginsberg, 1998). Our results suggest that hyenas in the undisturbed side of the Reserve were travelling significantly shorter distances than were hyenas in the disturbed side (Fig. 2.5). We also noted that collared hyenas in the disturbed side of the Reserve were travelling past the nearby town of Talek and into Tanzania (Fig. 2.1). This can be expected to bring them into conflict with humans living around the Reserve (see Kolowski et al., 2006). This situation jeopardizes the survival of this species in this important ecosystem. Therefore, we are concerned that these could be warning signs of drastic negative changes to this ecosystem in the near future. We suggest that a good management system should be put in place to safeguard the future of hyenas and other large carnivores.

Our findings also showed that hyenas were travelling significantly longer distances in the mornings than they were in the afternoons (Fig. 2.6). This concerns us since the movement patterns investigated here occurred during the time interval each day when spotted hyenas are generally inactive (Kolowski et al., 2007). Hyenas should be using their inactive time resting or nursing their young ones; so we worry that the patterns seen here could in the long run affect the welfare of hyenas in NCG.

We found that there was a greater difference in distances traveled between high and low-ranking hyenas in the undisturbed side than the disturbed side of the Reserve (Fig. 2.10). This result in the undisturbed side of the reserve was expected, but we were surprised to find that high-ranking hyenas in the disturbed side of the Reserve were actually traveling longer distances than were low-ranking hyenas (Fig. 2.10). We suggest that the differences in rank-related variation in movements revealed by our findings could potentially serve as early warning signs that the effects of social rank in spotted hyenas are being superseded by effects of anthropogenic disturbance. Clearly we need empirical conservation policies to ensure long-term survival of this and other large carnivore species in the MMNR. The current situation is only expected to become worse, as suggested by previous studies which showed declining trends in resident herbivores in the MMNR (Ottichilo et al., 2000, 2001). These herbivores serve as the prey base for hyenas and other predators in the reserve.

Just as it has been suggested that protected areas attract human settlement (Wittemyer et al., 2008), human population round the MMNR has been observed to be increasing (Ndegwa and Murayama, 2009). Increased rates of human-wildlife conflict are expected, especially around NCG, just as spotted hyenas have been observed to attack more livestock at villages closer to Reserve borders (see Kolowski et al., 2006). Therefore we suggest an all-inclusive management strategy that could serve as a way forward for the survival of man and wildlife in this ecosystem. Such management strategies would work towards involving local community members to discuss matters of wildlife conservation in and around MMNR, review land tenure and use systems, consider benefit sharing with the locals and educating them on matters of wildlife conservation.

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CHAPTER 3

HABITAT USE PATTERNS BY SPOTTED HYENAS (*Crocuta crocuta*) IN THE MASAI MARA NATIONAL RESERVE, KENYA

INTRODUCTION

Habitat heterogeneity plays a key role in determining animal movement patterns as well as behavioral and ecological processes, such as feeding behavior (e.g. Etzenhouser et al. 1998; Bailey and Thompson 2006). Behavioral changes in habitat use, are often the first measurable reactions exhibited by animals to human-induced environmental changes (Tuomainen and Candolin, 2011). Animals seldom range randomly (Duncan, 1983), and use certain types of space disproportionally (Samuel et al., 1985). Land cover change is thus an important component of wildlife habitat, as its alteration has important implications for animal species distribution (Balmford et al., 2001; Brooks et al., 2002). Habitat loss and fragmentation have been shown to be among the drivers of declining populations of large carnivores in the world over the last 100 years (Gittleman et al., 2001). Habitat loss also leads to species extinction or causes species to be threatened with extinction (Brooks et al., 2002). Habitat loss has also been shown to influence animal population dynamics (Ogutu et al., 2009). Large carnivore distribution and habitat selection are mostly determined by prey availability (Hayward et al., 2009; Valeix et al., 2010). Prey availability in turn is affected by vegetation cover, water availability and elevation (Valeix et al., 2010; Pita et al., 2009; Schadt et al., 2002).

The majority (61%) of largest carnivore species are currently listed as threatened by the International Union for Conservation of Nature (IUCN) (Ripple et al., 2014). In Africa, the spotted hyena (*Crocuta crocuta*) has been shown to have altered its space use patterns due to competition for space with livestock (Boydston et al., 2003b). This change in behavior has occurred in the Masai Mara National Reserve (hereafter referred to as the ‘Reserve’, the ‘Mara’ or the ‘MMNR’) in southwestern Kenya (Fig. 1.1). Dense vegetative cover, which serves as a food source for herbivores in the MMNR, also provides refuges to lions and spotted hyenas exposed to people and livestock (Boydston et al., 2003b; Kolowski and Holekamp, 2009). Vegetative cover in general near the MMNR has declined over the last two decades (e.g. Homewood et al., 2001; Serneels, Said & Lambin, 2001; Ndegwa and Murayama, 2009). This is due to significant expansion in farmland, which now occupies areas that were previously natural grasslands, and were used by wildlife for dispersal, breeding and or calving areas (Ndegwa and Murayama, 2009).

Although spotted hyenas have been shown to occupy habitats ranging from deserts, through grasslands to wooded savannas (Cooper, 1989), their survival is currently faced with many challenges that need to be addressed. With more land expected to be converted into grazing land for livestock, given the global demand for meat (McAlpine, 2009), we fear that survival of this iconic species in the Mara may be jeopardized in the near future.

Although three prior studies investigated habitat preferences by spotted hyenas in relation to anthropogenic activities in the MMNR (e.g., Boydston et al., 2003a, Boydston et al., 2003b, Kolowski and Holekamp, 2009), none of these studies focused specifically on diurnal habitat use patterns, nor did they compare space use between spotted hyena clans inhabiting the same protected area but experiencing different management regimes. Therefore, in this chapter we investigate daytime habitat use patterns in the MMNR by adult female spotted hyenas living in three different clans (Fig. 1.2). One of the clans defended a territory in an area where intensive livestock grazing took place (‘NCG’) while the other two study clans defended territories in an area where livestock grazing was not allowed (‘TMC’). We used telemetry technology to track the adult female hyenas with Global Positioning System (GPS) collars (as described in Chapter 2). Here we compared habitat usage between TMC and NCG by investigating patterns of habitat use by 22 adult female spotted hyenas in the MMNR for a period of one year, Jan 1 - Dec 31, 2013. We tested hypotheses suggesting that the two different management styles in TMC and NCG would be associated with different patterns of vegetative cover, and that hyenas in TMC and NCG would use the available habitat types differently. Due to the high levels of anthropogenic activities in NCG, we expected to see hyenas avoiding habitats where livestock grazing took place but we did not expect to see such behavior in TMC.

Methods

Study site and study animals

Details of our study area and study animals are as described in Chapters 1 and 2.

Generating a classified vegetation map of the Masai Mara National Reserve (MMNR), Kenya

We used ESRI ArcMap v. 10.2.2 and R v.3.1.3 statistical software (R core team, 2015) to create a classified land cover raster map for the Mara from Google Earth and Landsat images (Landsat 5 TM June 2009). The Landsat image was downloaded from the United States Geological Society (USGS) and we maintained our pixels at a 30m resolution. Landsat images were selected after consideration of cloud cover and other features that might have influenced our final classified image (map). We utilized the seven elements of photo interpretation (shape, pattern, tone, association, size, texture and shadow) in our creation of random forests within the selected

Landsat and Google Earth images (see Bourgeau-Chavez et al., 2015). We generated polygons that met our criteria to represent different land cover types and these served as our training data.

The polygons were then converted into shape files using ESRI ArcMap v. 10.2.2, and assigned different numbers to represent specific land cover classes. We made sure that our training data had a representative sample of each vegetation class, and was well distributed within our study clan territories in 2013 (Fig. 1.2). The territories were generated from Kernel density 95% utility distributions (UDS) using all hyenas that had radio collars in the year 2013 (Green, 2015). We then assigned same numbers to similar land cover types, and our classification was as follows; 1 represented buildings, 2 represented grasslands, 3 represented shrub lands, 4 represented bare ground, 5 represented forests, 6 represented rivers, and 7 represented wetlands.

All the shape files were assigned a Geographic Coordinate System (GCS) of WGS 84 and projected in Transverse Mercator UTM Zone 36S, which is the projection system used in the Masai Mara National Reserve. We then used the statistical software R v.3.1.3 (R core team, 2015) to generate the final raster image representing the classified and combined vegetation cover maps for the Mara using the already assigned vegetation classes (Figs. 3.1, 3.2). Because most of our training data were concentrated within the territories of our study clans, we suggest that our final classified image may not be a perfect fit for use in the entire MMNR, but it is valid within our clan territories, and it is for this reason that our habitat analysis was carried out within the territories defended by our study animals.

Statistical analyses

R v.3.1.3 statistical software (R core team, 2015) and ESRI ArcMap v.10.2.2 were used in all our statistical analysis. We projected hyenas' locations onto the final classified vegetation cover map for MMNR (Fig. 3.3; see methods above), ran queries on the projected data, and subsequently used Chi-squared tests in our analysis. A Chi-squared test for independence was used to test whether habitat use in either side of the reserve differed significantly from what was available. Both use and availability were determined from counts of pixels. We also used Chi-square tests to compare habitat availability in either side of the Reserve, and habitat use by collared spotted hyenas within and outside of their defended territories (although here we only used the hyena locations).

Although we initially classified habitats as 7 different types (Fig. 3.1), we later combined some cover classes in our final habitat analysis. Buildings, which represented only 2% of the total habitat in both TMC and NCG, were excluded in our final analysis. Cover classes that were combined were 1) 'grasslands' and 'wetlands'; together these were simply called 'grasslands', and 2) 'forest' and 'river' were combined and referred to as 'riparian'; due to the fact that most forests occurred along the rivers . Therefore, we used grasslands, shrub lands, bare ground and riparian vegetation classes in our final analysis (Table 3.1 and 3.2). We also ran queries on the projected data to estimate the number of hyena locations that fell outside of their defended territories (Fig. 3.4).

Results

Habitat types availability in TMC and NCG

Our results showed different habitat types available to hyenas in TMC and NCG. In TMC, grassland dominated the ecosystem (81.48% of the total pixels), shrub land represented 7.02%, while riparian and bare ground represented 6.17% and 5.36%, respectively. In NCG, grassland covered 48.82% of the total pixels, bare ground covered 28.11%, while shrub land and riparian covered 21.34% and 1.72%, respectively. As predicted by our hypothesis, our results showed different habitat types available for hyenas in TMC and NCG. Chi-square test of independence results showed that available habitats differed significantly between TMC and NCG (χ^2=26628.21, df =3, p = 0.0001) (Tables 3.1, 3.2, and 3.3).

Habitat use relative to availability in TMC and NCG

Habitat use relative to availability differed between TMC and NCG. Out of the total habitats used in TMC, 82.59% was grassland, 6.96% was shrub land, 6% was bare ground and 4.45% was riparian. Out of the total habitats used in NCG, 25.57% was grassland, 45.55% was shrub land, 13.05% was bare ground and 15.82% was riparian (Tables 3.1 and 3.2). Results from Chi-square tests of independence showed that hyenas in TMC were using habitats in proportion to their availability (χ^2=0.3236, df=3, p = 0.9555) while habitat use by hyenas in NCG differed significantly from habitat availability (χ^2=32.8575, df =3, p = 0.0001) (Tables 3.4 and 3.5).

Grassland habitat use

Our results showed that hyenas in TMC were using grassland habitat in proportion to its availability while hyenas in NCG used far less of grassland habitat than was available (χ^2=1603.246, df =1, $p < 0.0001$) (Table 3.6).

Shrub land habitat use

Shrub land habitat use relative to availability did not differ significantly between TMC and NCG (χ^2= 1.2114, df =1, p = 0.271), although NCG hyenas used shrub land habitat slightly more than expected (Table 3.6).

Bare ground habitat use

Our results showed bare ground habitat use relative to availability differed significantly between TMC and NCG. While hyenas in TMC were using bare ground as expected based on its availability, hyenas in NCG used significantly less bare ground habitat than was available to them (χ^2= 599.3769, df =1, p <0.0001) (Table 3.6). We recognize that the greater abundance of bare ground in NCG (28.11%) than TMC (5.36%) is most likely due to intensive trampling and removal of vegetation by cattle while grazing or traveling to grazing sites.

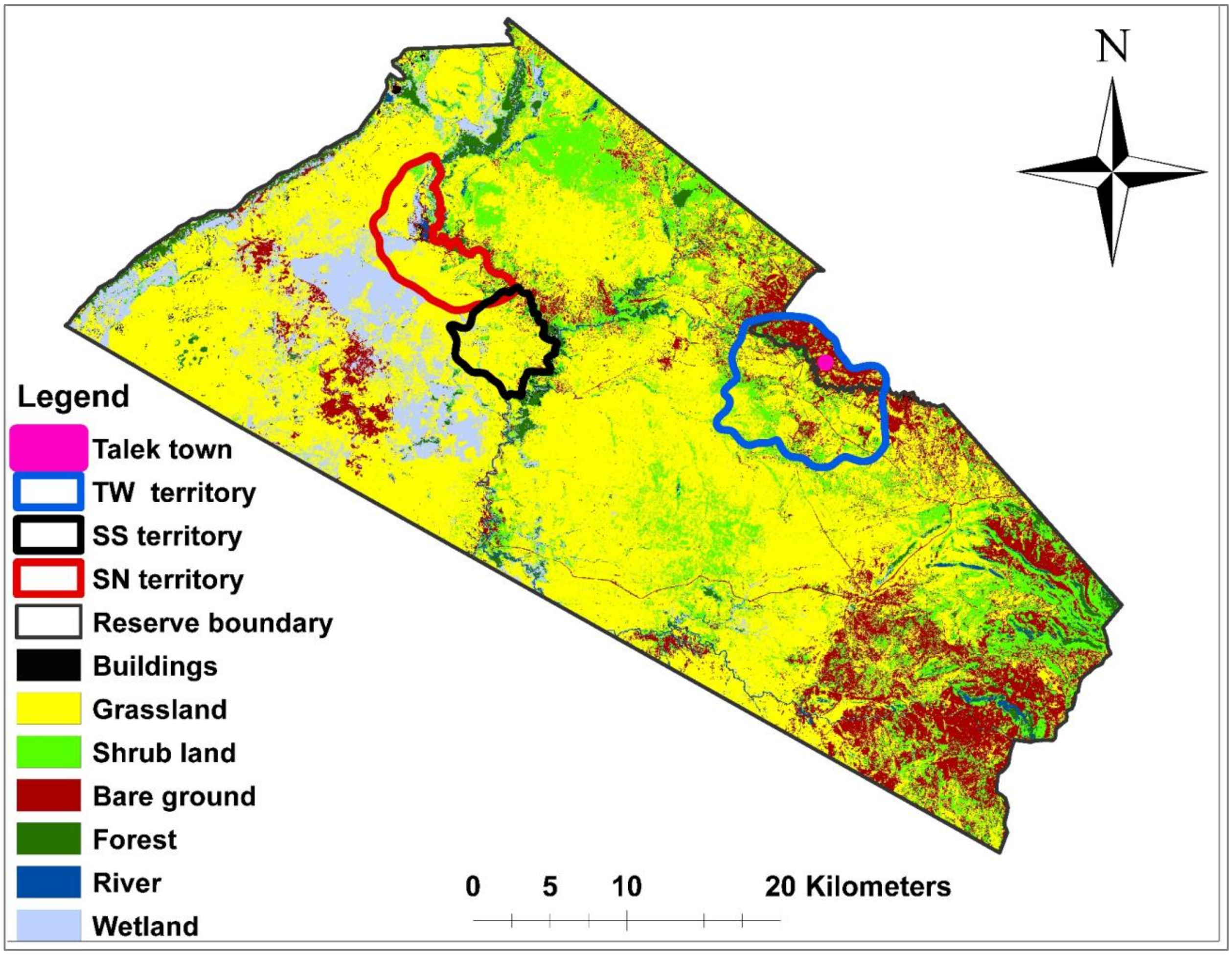

Figure 3.1: Classified habitat map of the MMNR showing the 7 habitat types.

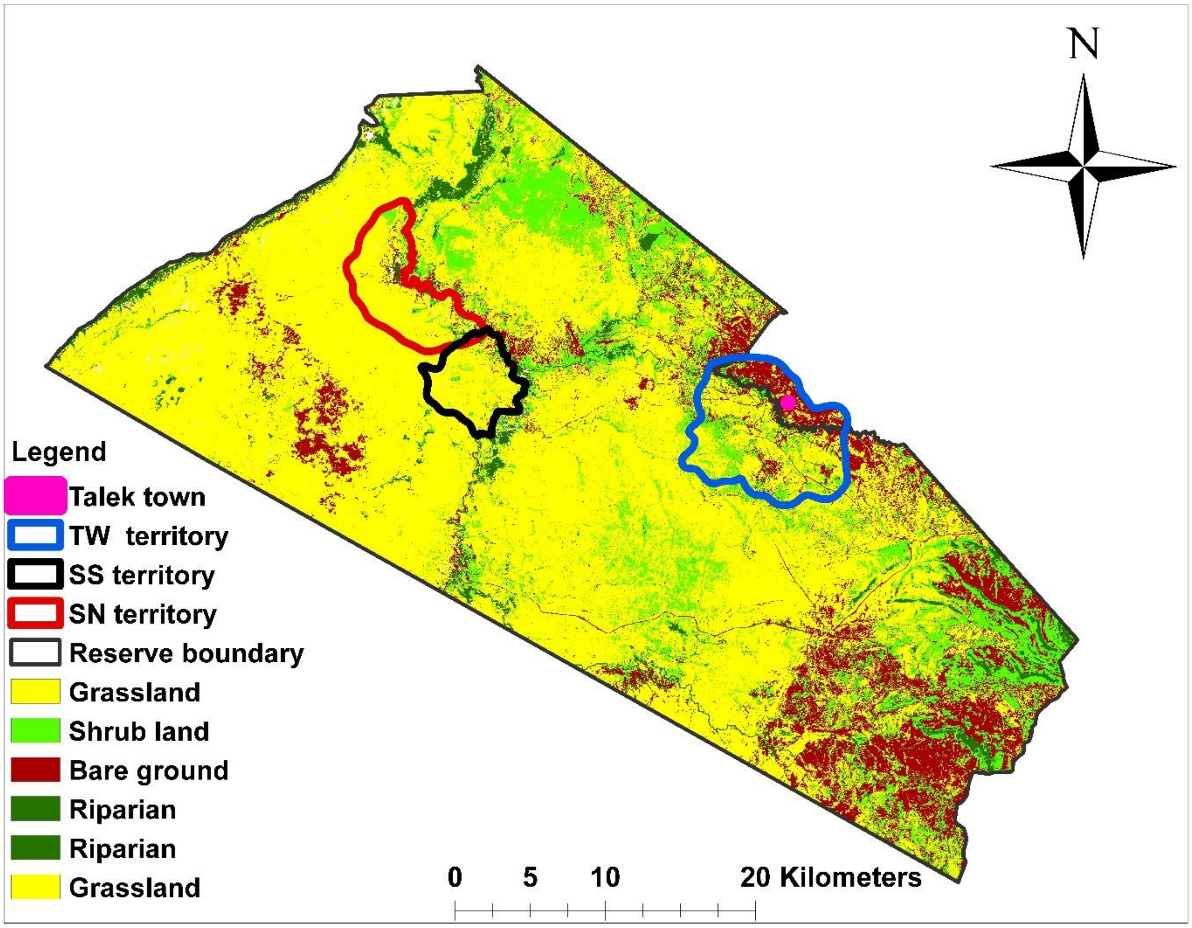

Figure 3.2: Classified habitat map of the MMNR showing the combined habitats.

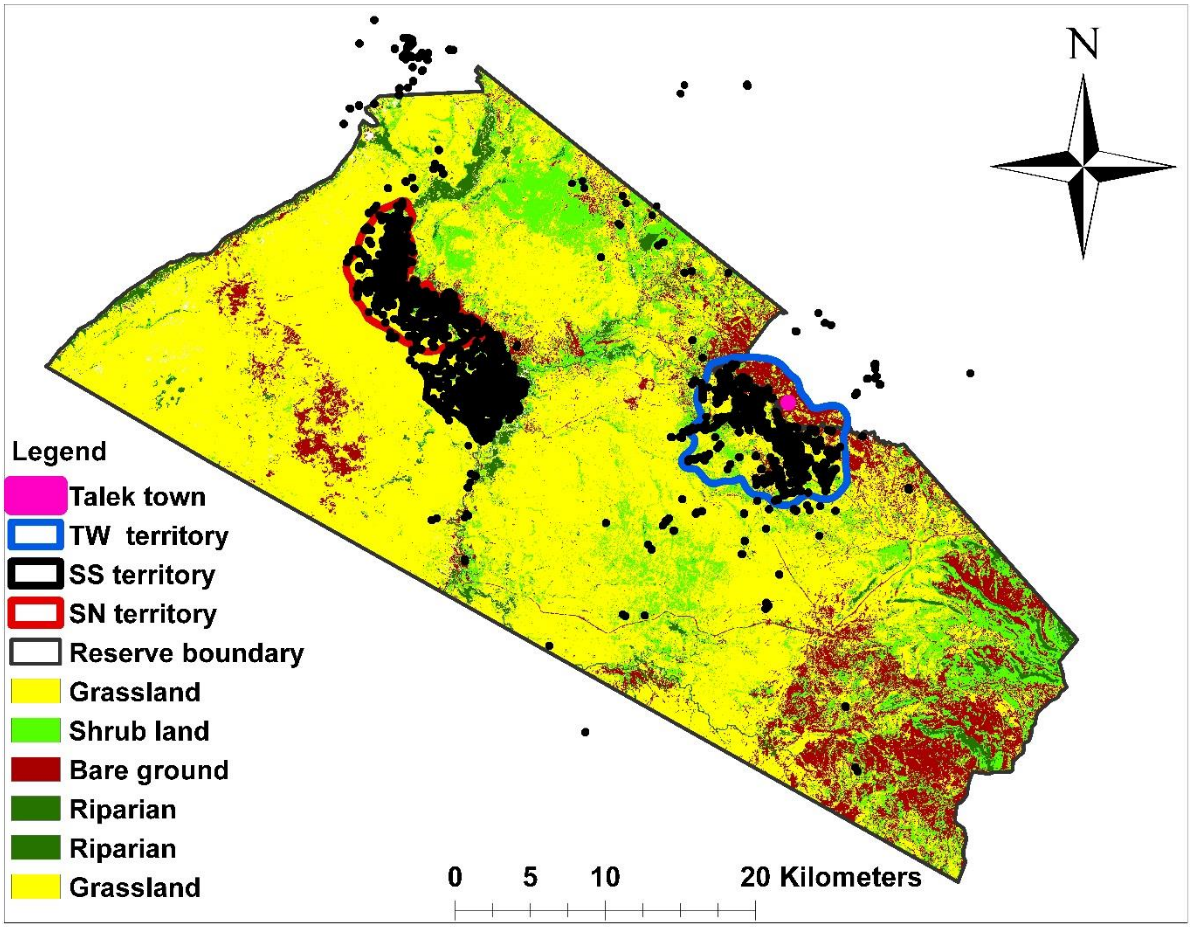

Figure 3.3: Classified habitat map of the MMNR showing hyena locations.

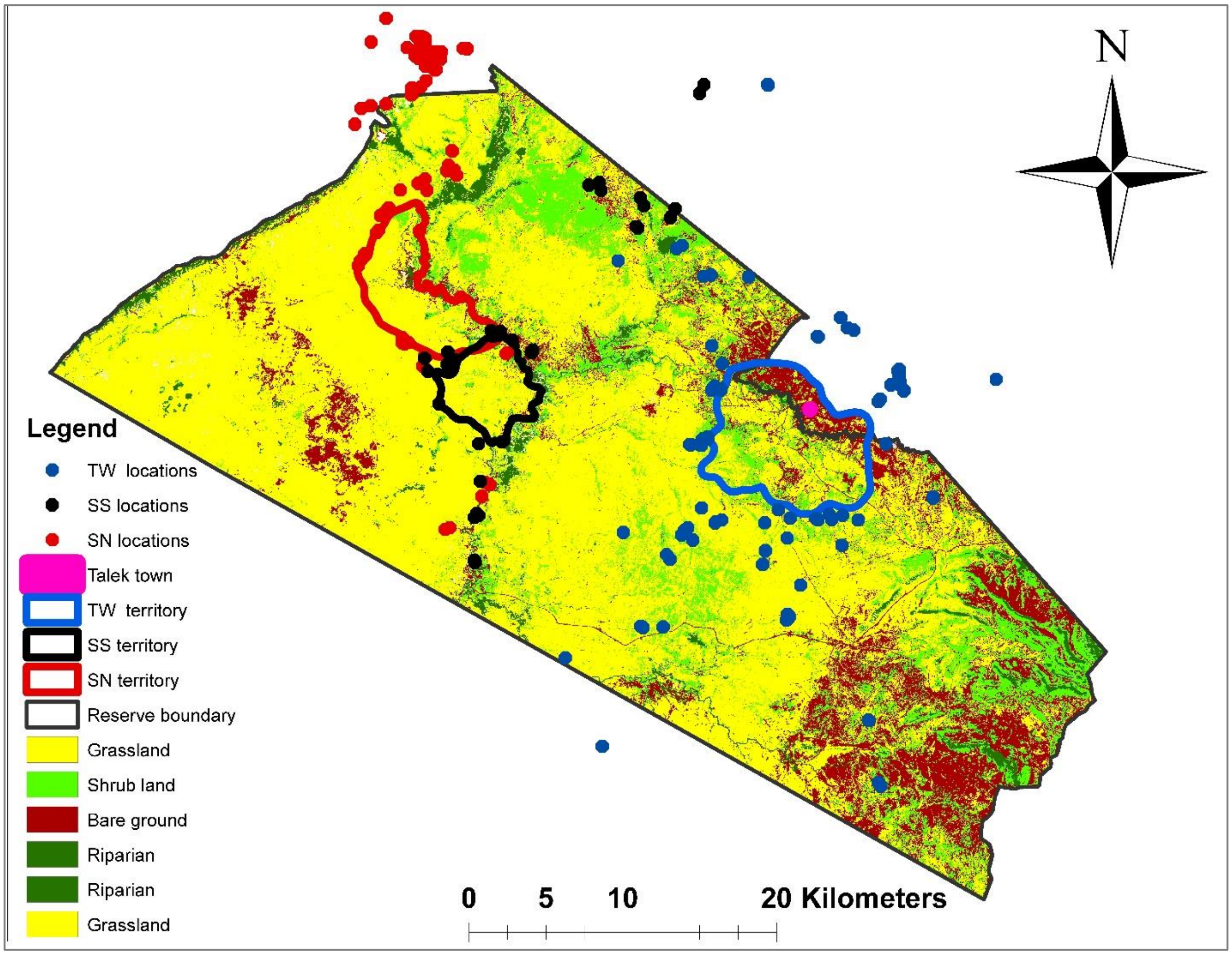

Figure 3.4: Classified habitat map of the MMNR showing habitat use outside defended territories.

Riparian habitat use

Our results showed that riparian habitat use relative to availability differed significantly between TMC and NCG. While hyenas in TMC used riparian habitat in proportion to its availability, NCG hyenas significantly used riparian habitat more than it was available (χ^2= 654.8744, df =1, p <0.0001) (Table 3.6).

Habitat use outside the clan territories

Habitat use by hyenas outside of their defended territories differed between TMC and NCG. External habitat use represented 2.82% and 3.72% of all hyena locations in TMC and NCG respectively (Tables 3.7, 3.8, and 3.9; Fig. 3.4). Results of a Chi-square test of independence showed that NCG hyenas used habitats outside of their defended territory significantly more than did TMC hyenas (χ^2= 6.2353, df =1, p = 0.0125) (Table 3.9, Fig.3.4).

Habitat	Available pixels	Used pixels	% available	% used
Grassland	62860	5350	81.48%	82.59%
Shrub land	5418	451	7.02%	6.96%
Bare ground	4135	389	5.36%	6%
Riparian	4758	288	6.17%	4.45%

Table 3.1: Habitat classification in TMC hyena territories.

Habitat	Available pixels	Used pixels	% available	% used
Grassland	41603	905	48.82%	25.57%
Shrub land	18191	1612	21.34%	45.55%
Bare ground	23961	462	28.11%	13.05%
Riparian	1470	560	1.72%	15.82%

Table 3.2: Habitat classification in NCG hyena territory.

Habitat availability	TMC	NCG	Chi-square
Grassland available pixels	62860	41603	χ^2= 26628.21, df = 3, **p<0.0001**
Shrub land available pixels	5418	18191	
Bare ground available pixels	4135	23961	
Riparian available pixels	4758	1470	

Table 3.3: Chi-square test results for differences in available habitats in TMC and NCG. Bolded cells represent significant effects.

Habitat	% habitat available	% habitat used	Chi-square
Grassland	81.455469 (82.021344)	82.587218 (82.021344)	χ^2= 0.3236, df = 3, p= 0.9555
Shrub land	7.020772 (6.991399)	6.962025 (6.991399)	
Bare ground	5.358230 (5.681585)	6.004940 (5.681585)	
Riparian	6.165529 (5.305673)	4.445817 (5.305673)	

Table 3.4: Chi-square test results for habitat use in TMC. Expected values are presented in parenthesis.

Habitat	% habitat available	% habitat used	Chi-square
Grassland	48.815488 (37.193842)	25.57220 (37.193842)	χ^2= 32.8575, df = 3, **p= 0.0001**
Shrub land	21.344676 (33.447133)	45.54959 (33.447133)	
Bare ground	28.114990 (20.584762)	13.05454 (20.584762)	
Riparian	1.724846 (8.774263)	15.82368 (8.774263)	

Table 3.5: Chi-square test results for habitat use in NCG. Expected values are presented in parenthesis. Bolded cells represent significant effects.

Habitat	TMC	NCG	Chi-square
Grassland available pixels	62860 (64356.484)	41603 (40106.516)	χ 2= 1603.246, df = 1, **p<0.0001**
Grassland used pixels	5350 (3853.516)	905 (2401.486)	
Shrub land available pixels	5418 (5397.3676)	18191 (18211.632)	χ 2= 1.2114, df = 1, p=0.271
Shrub land used pixels	452 (471.6324)	1612 (1591.368)	
Bare ground available pixels	4135 (4391.0009)	23961 (23704.9991)	χ 2= 599.3769, df = 1, **p<0.0001**
Bare ground used pixels	389 (132.9991)	462 (718.0009)	
Riparian available pixels	4758 (4441.2787)	1470 (1786.7213)	χ 2= 654.8744, df = 1, **p<0.0001**
Riparian used pixels	288 (604.7231)	560 (243.2787)	

Table 3.6: Chi-square test results for differences in habitat use compared to available habitats in TMC and NCG. Expected values are presented in parenthesis. Bolded cells represent significant effects.

Name	Inside territory locations	Outside territory locations	Total locations
Bart	316	1	317
Clov	387	0	387
Digs	542	8	550
Ema	816	119	935
Hndy	307	6	313
Java	947	1	948
Mtn	368	16	384
Peep	108	0	108
Shrm	938	6	944
Slin	317	7	324
Taj	1005	19	1024
Tnsl	369	5	374
Wafl	290	7	297
Zoey	18	0	18

Table 3.7: Hyena locations inside and outside their defended territories in TMC.

Name	Inside territory locations	Outside territory locations	Total locations
Baez	357	29	386
Hel	957	0	957
Hex	195	8	203
Juno	358	1	359
Mgta	319	0	319
Pan	237	3	240
Roos	263	35	298
Tilt	883	62	945

Table 3.8: Hyena locations inside and outside their defended territory in NCG.

	TMC	NCG	Chi-square
Outside locations	195 (216.8729)	138 (116.1271)	χ^2= 6.2353, df = 1, **p=0.0125**
Inside locations	6728 (6706.1271)	3569 (3590.8729)	

Table 3.9: Chi-square test results for habitat use within and outside defended territories in TMC and NCG. Expected values are presented in parenthesis. Bolded cells represent significant effects.

Discussion

Non-uniform use of habitat has been demonstrated amongst a number of terrestrial mammal species (Gates, 1979; Duncan, 1983; Samuel et al., 1985). Habitat use studies have also been shown to guide management policies (Ingram and Rogan, 2002). Successful management of predator and prey populations requires detailed knowledge of regulatory factors within populations (Cooper, 1990). The wildebeest migration into the MMNR from the Serengeti National Park has been shown to be influenced by the vegetation conditions in the Reserve (Ottichilo, 2000). Here we found that habitat use by spotted hyenas differed a great deal between parts of the Reserve managed by TMC and NCG. Clearly the anthropogenic disturbance and intensive grazing on the NCG side of the Reserve are having strong effects, both on the types of habitat that are available for use by the hyenas and on their choice of habitat types in which to spend their time.

Grassland habitat use

Most livestock (especially cattle) prefer grassland habitats in the Reserve and this may increase conflict with hyenas in NCG. Even though grassland was the most abundant habitat in the TW clan territory covering 48.82% (Table 3.2), our results showed hyenas used significantly less of this habitat than was available. This result was consistent with that of Boydston et al., (2003b), who showed female hyenas in the TW clan avoiding the prey rich central short grass plains due to intensive use by livestock. Our results were also consistent with those of Kolowski and Holekamp (2009) who found TW hyenas avoiding open grasslands more than was expected based on availability.

Shrub land habitat use

Shrub land was the third most abundant habitat type available in NCG (21.34%), but hyenas there used this habitat more than expected. We suggest this pattern may result from livestock grazing and potential harassment by herders. This condition is therefore forcing hyenas to spend much of their time in the limited available shrub land habitats on this side of the Reserve. Our results were consistent with those of Kolowski and Holekamp, (2009) who found TW hyenas having a greater preference for shrub land vegetation than was expected based on availability. Vegetation class was also found to be one of the most important variables determining space use by spotted hyenas during the daily livestock grazing period in this area (Kolowski and Holekamp, 2009). Shrub land use in TMC showed no difference from expected values, so we suggest the strict management plan observed in the TMC side of the reserve is favoring the welfare of hyenas there.

Bare ground habitat use

Although there was far more bare ground available to hyenas in NCG (28.11%) than TMC (5.36%), NCG hyenas used significantly less of the available bare ground habitat than expected there. We suggest that bare ground areas in NCG are just not particularly useful to hyenas because the livestock that graze daily inside the Reserve have ruined the vegetation in those areas so no natural prey for the hyenas occur there. Habitat loss has been shown to lead to the decline of endangered Africa wild dogs (*Lycaon pictus*) (Gorman et al., 1998). Therefore, the high percentage of bare ground we found in this side of the Reserve was of grave concern to us.

Riparian habitat use

Riparian habitat was the least represented in NCG (1.72%), yet we see hyenas there using significantly more of this habitat than expected. Our results suggest that, as with shrub land habitat, hyenas in NCG may prefer riparian habitats, which are characterized by dense vegetative cover, to avoid harassment by humans attending their cattle.

Habitat use outside defended territories

As hyenas in NCG have been shown to avoid areas where grazing occurs within the clan territories (see Boydston et al., 2003b), we expected to see significant differences between NCG and TMC with respect to the proportion of hyena locations found outside defended territories. Anthropogenic activities have been shown to have direct effects on wildlife (See Sinclair et al., 2007). Thus, our observation was expected that hyenas in NCG were using habitats outside their defended territories significantly more than were TMC hyenas. We suggest that the anthropogenic activities occurring in NCG may be driving hyenas outside their territories more than is the case in TMC.

Conclusion

Concerted conservation efforts are required to avoid species extinctions (Brooks et al., 2002). Human population increase has also been shown to be one of the greatest drivers of global environmental change (Tilman et al., 2001). Therefore there is urgent need to balance wildlife protection with the welfare of local people. Such efforts are proposed here including removal of grazing pressure if sound management practices are to be employed in this important ecosystem. Such practices are known to aid in recovery of overgrazed or over-browsed habitats. Similar studies in other parts of the world have shown positive correlations between plant species composition and palatable plant cover recovery following cessation of grazing pressure (Frank et al., 2014). Although balancing the economic development of local people and wildlife conservation remains a big challenge (Tosun, 2001), we suggest that, if good management policies are implemented. Such management policies would involve strict law enforcement to ensure no livestock grazing in NCG, and raising awareness amongst local communities regarding the importance of wildlife conservation. Through such policies and many others, we could ensure that wildlife protection is enhanced while promoting the welfare of local people. Just as other studies have suggested, we need to promote habitat conservation so as to ensure coexistence of man and wildlife. Tourists pay a considerable amount of money to see wildlife in the MMNR. Therefore, if the patterns of habitat use observed here in NCG by spotted hyenas are similar to those of other large carnivores, then cattle grazing in the Reserve may be negatively affecting tourism in this ecosystem by forcing the predators into thick vegetative cover, out of sight of tourists.

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CHAPTER 4

ENERGY COST OF LOCOMOTION BY SPOTTED HYENAS (*Crocuta crocuta*) IN THE MASAI MARA NATIONAL RESERVE, KENYA

INTRODUCTION

Animals may travel for several reasons but foraging is one of the most basic activities that mammals undertake (Garland, 1983). Predators, in particular, have to overcome enormous energetic constraints that strongly affect their ecology and evolution (Van Valkenburgh et al., 2004; Gorman et al., 1998; Carbone et al., 1999; Gittleman, 1985). The energetic cost of transport has been expressed as a function of body mass in various vertebrates (Schmidt-Nielson, 1972). Large carnivores range widely (Woodroffe, 2000; Packer et al., 2013) and their energy requirements while moving are expected to be high compared to those of many other mammals. Large carnivores specialize on feeding on medium and large-sized vertebrates (Carbone et al., 2007). Garland (1983) found that carnivores have greater daily movement distances than do other mammals, and their costs of movement are expected to be higher as well. Members of the order Carnivora move an average of 4.4 times farther than other mammals on a daily basis (Garland, 1983) so their energy expenditure should be relatively high. In nature, many animals move at speeds that climax at their maximum rate of oxygen consumption (VO_2max) (see Kruuk, 1972; Seeherman et al., 1981; Thompson, 1980; Taylor et al., 1981). Because VO_2max is in most cases 10 times greater than the resting metabolic rate in mammals (Taylor et al., 1981), locomotion can be a costly activity.

Taylor et al. (1981) pointed out that it is only in Africa where one can currently find a diversity of large wild animals. One place in Africa where animal diversity is extraordinarily high is the Masai Mara National Reserve (hereafter the ‘Reserve’ or the ‘MMNR’ or the ‘Mara’) in Kenya. Here we estimated daytime energy use during locomotion by 22 adult female spotted hyenas (*Crocuta crocuta*) in the Mara in 2013 (see methods below). Spotted hyenas may scavenge on carrion (Kruuk, 1972; Cooper, 1990), which is less energetically costly than hunting live prey, but most of their food (roughly 3/4) is obtained from hunting (Cooper, 1990). Spotted hyenas generally prefer medium to large size prey (Henschel and Skinner, 1990, Kruuk, 1972). This preference for large prey maximizes their energy gain but also requires extra energy to pursue and subdue large prey (Carbone et al., 2007). As previous research has shown, dietary requirements are key determinants of animal energetics (Altmann, 1987). Here we asked whether management regime also affects the energy expenditure by wild spotted hyenas. As we explained in Chapter 1 (recall the undisturbed side of the Reserve ‘’TMC’’ and the disturbed side of the Reserve ‘’NCG’’), we expected to see hyenas in the disturbed side of the Reserve using more energy during locomotion than hyenas in the undisturbed side of the Reserve during the daytime (10am-4pm).

Methods

Study area, and study animals

Details of our study area and study animals are as explained Chapters 1 and 2.

Estimating the energy cost of locomotion

Hyena energy use during locomotion was determined by using GPS collar technology to monitor movement patterns of twenty two adult female spotted hyenas in the MMNR (TMC=14, NCG=8, see tables 2.1 and 2.2). The hyenas were immobilized using tiletamine-zolazepam (6.5 mg/kg; Telazol: W.A Butler Company, Brighton Michigan) administered in a plastic dart via a CO_2 –powered rifle (Telinject Inc., Saugus, California), and fitted them with GPS collars (Vectronix Aerospace, Berlin, Germany) (Fig. 1.3). Each GPS collar was fitted with a temperature sensor to record the ambient temperature corresponding to hyena locations. The daily temperatures recorded by the sensors in the GPS collars were averaged each month separately for TMC and NCG (Table 4.1).

Using the local Kenyan cell phone network, which is handy for acquiring the locations of the hyenas, movement patterns across space and time were recorded daily. The GPS locations were received at a central point using the local cell phone network, and then downloaded into computers. Collars were programmed to transmit their locations at 10am, 1 pm, and 4 pm every day. All locations were digitized using ESRI ArcMap 10.2.2 software (Environmental Systems Research Institute, Redlands, CA, USA). Shape files of the downloaded GPS coordinates (locations) were given a Geographic Coordinate System (GCS) of World Geodetic System of 1984 (WGS 84) then projected into Universal Transverse Mercator zone 36 South (WGS 84 UTM 36S). Finally XY coordinates were added to allow for linear distance calculations in meters (m) which were done using R v. 3.1.3 statistical software (R core team, 2015). Linear distances in meters (m) were calculated between each two consecutive locations. Territory sizes were estimated using fixed kernel utilization distributions with 95% probabilities for all hyenas with collars in 2013 (Green, 2015).

During immobilization, body mass (kg) for each hyena was recorded, and the body mass was used to estimate their energy expenditure (Tables 4.2 and 4.3). If a single hyena was darted twice during our study period (2013) or earlier during adulthood, her body mass (kg) as used in the energy calculation was the latest weight recorded (Table 4.3). Distance travelled in meters

(m) and time taken in seconds (s) between any two locations at the three time-points each day (10am, 1pm, and 4pm) were calculated in R statistical software (R core team, 2015). The cost of locomotion has been shown to be a function of body mass (Taylor et al., 1982), so we calculated energy spent in locomotion as a function of body mass (kg) and speed of movement (v_o) expressed in m/s. The distance travelled, time taken, speed of movement, and body mass of each animal were used to determine the energy used by that animal during locomotion via the formula $Vo_2/Mb = 0.533Mb^{-0.316}.v_o+0.300\ Mb^{-0.303}$ (Taylor et al., 1982). Here, Mb represents body mass, and Vo_2/Mb is the energy use per kg of body mass expressed in units $mlO_2/s/kg$. v_o (speed) was expressed in m/s, Mb was in kg, and Vo_2/Mb was converted to Joules (J) by using the energetic equivalent $1mlo_2$=20.1 Joules (J) (Taylor et al. 1982).

The energy in Joules (J) was then multiplied by the total time (seconds) and total weight (kg) of each hyena to determine her total energy use during locomotion and thereafter converted into mega joules (MJ). This conversion was done by dividing the calculated energy (J) by 1,000,000. Energy units (MJ) were calculated per day and thereafter averaged per month to get monthly estimates (Table 4.2). Throughout this Chapter (as we also did in Chapter 2), we will be using morning to refer to the time between 10am-1pm and afternoon to refer to the time between 1pm-4pm.

Month	TMC temperature (°C)	NCG temperature (°C)
Jan	36.83	32.99
Feb	37.64	32.14
March	36.11	32.43
April	37.55	31.97
May	33.99	31.43
June	33.48	31.1
July	32.99	31.14
Aug	34.03	32.7
Sep	36.07	33.42
Oct	37.12	33.68
Nov	36.32	33.51
Dec	36.93	32.19

Table 4.1: Table of mean monthly temperatures in TMC and NCG. Temperatures were recorded daily by sensors fitted on GPS collars and thereafter averaged into monthly records.

Month	Average monthly energy cost of locomotion (MJ) in TMC	Average monthly energy cost of locomotion (MJ) in NCG
Jan	1.157	1.133
Feb	1.162	1.131
March	1.171	1.142
April	1.169	1.108
May	1.174	1.101
June	1.169	1.098
July	1.143	1.111
Aug	1.142	1.121
Sep	1.148	1.113
Oct	1.140	1.117
Nov	1.142	1.115
Dec	1.143	1.104

Table 4.2: Table of average diurnal monthly energy cost of locomotion by hyenas in TMC and NCG.

TMC hyenas	TMC hyenas' body mass (kg)	NCG hyenas	NCG hyenas' body mass (kg)
Bart	56.2	Baez	55.2
Clov	63.6	Hel	55.2
Digs	50.3	Hex	60.4
Ema	61.4	Juno	48.6
Hndy	56.2	Mgta	64.8
Java	66.3	Pan	63.4
Mtn	54.6	Roos	53.8
Peep	55.6	Tilt	57.8
Shrm	57.6	-	-
Slin	47.8	-	-
Taj	68.8	-	-
Tnsl	55.6	-	-
Wafl	64.9	-	-
Zoey	57.6	-	-

Table 4.3: Table of hyenas' body masses in TMC and NCG.

Statistical analyses

R v.3.1.3 statistical software (R core team, 2015) was used for all statistical analysis. Linear distances were calculated between any two given sets of coordinates between 10am-1pm and 1pm-4pm. We used Generalized Linear Models (GLM) to model the energy used by hyenas as a function of ten predictor variables: 1) management regime referred to as “management” (coded as ‘TMC’ or ‘NCG’), 2) time of the day (coded as ‘am’ or ‘pm’), 3) prey (coded as ‘many’ referring to abundant prey and ‘few’ referring to scarce prey), 4) social rank (coded as ‘H’ or ‘L’), 5), season (coded as ‘dry’ or ‘wet’) and 6) standardized temperature (‘tempstd’ recorded by the collars) was also added in the model. We also added 7) an interaction between management regime and rank (coded as management*rank), 8) interaction between management regime and prey (coded as management*prey), 9) an interaction between management regime and season (coded as management*season) and 10) an interaction between standardized temperature and management regime (coded as management*tempstd). Subsequently, our model was as follows:

Eq1:

glm(LMJ~time+rank+management+season+prey+tempstd+prey*management+rank*management+season*management+tempstd*management). Where, LMJ refers to the log transformed (base10) energy cost of locomotion in Mega Joules (MJ).

In this model, five of our main factors (rank, management, prey, season and time) had two levels with rank being either high (H) or Low (L) (Table 2.1 and 2.2). Management regime had two levels (TMC or NCG). “Prey” had two levels (‘many’ for abundant prey or ‘few’ for scarce prey), season had two levels (‘dry’ or ‘wet’) while “time of day” had two levels as well (‘am’ or ‘pm’). Standardized temperature (6th main factor) was treated as a continuous variable and the standardization was done from the mean of all the temperature values recorded by the 22 hyenas (Table 2.1 and 2.2) in the MMNR in 2013. We also included the interactions between management regime and rank (management*rank), management regime and prey (management*prey), management regime and season (management*season) and management regime and standardized temperature (management*tempstd) in our model.

Speed of movement (v_o) was calculated by dividing the linear distance traveled in meters by time spent doing so in seconds; we thus expressed speed (v_o) in m/s. The body mass (kg) measured during immobilization (Table 4.2) and the calculated speed (m/s) were then used to calculate the energy spent in locomotion using the method above (recall; $Vo_2/Mb = 0.533Mb^{-0.316}.v_o+0.300\ Mb^{-0.303}$). We presented our means with standard errors, and differences between groups were considered significant when $P < 0.05$.

Results

Reserve management regime and energy use

Our results showed that hyenas in the undisturbed side of the Reserve significantly used more energy than did hyenas in the disturbed side (t=2.775, p=0.0055) (Table 4.4, Fig. 4.2). This result was shocking to us because our results based on movement data showed hyenas in NCG travelled significantly longer distances than did hyenas in TMC.

Time of day and energy use

Our results showed hyenas were using significantly less energy in the afternoon (1pm-4pm) than in the morning (10am-1pm) (t= -10.668, p<0.0001) (Table, 4.4, Fig. 4.2). This result was expected, as our movement results showed hyenas moving significantly shorter distances in the afternoon than in the morning.

Social rank and energy use

Although our results showed low-ranking (L) hyenas used slightly more energy than did high-ranking (H) hyenas (Fig.4.3), this difference was not statistically significant (t= 1.298, p=0.1945) (Table 4.4). This result was not surprising, as we found no significant difference in distance moved between low-ranking hyenas and high-ranking hyenas in our movement modeling results. However, low-ranking hyenas in TMC used significantly more energy than did high-ranking hyenas in TMC (t=8.681, p<0.0001). Surprisingly, such a difference was not observed in NCG. (Table 4.4, Fig. 4.6).

Prey availability and energy use

Our results showed hyenas were using significantly less energy when prey were abundant than when prey were scarce (t= -2.121, p=0.0339) (Table 4.4, Fig. 4.4). This result was expected, as predators are expected to need less energy in acquiring food when prey are abundant. However we did not see significant differences between energy use in locomotion by hyenas in TMC and NCG when prey was abundant or scarce (t= -1.501, p=0.1334), (Table 4.4, Fig. 4.7).

Seasonality and energy use

Our results showed no significant difference in energy use between wet and dry seasons (t= -0.399, p =0.6897) (Table 4.4, Fig. 4.5). This result was expected, as we also found no significant difference in the distance moved by hyenas between dry and wet seasons. We did not find significant differences between energy use in locomotion when comparing hyenas living in TMC and NCG during the wet and dry seasons (t=0.550, p=0.5827) (Table 4.4, Fig. 4.8). This result was expected because we got similar results with our movement modeling.

Standardized temperature and energy use

Our results showed hyenas were using significantly more energy in locomotion as the temperature increased (t=2.728, p=0.0064). This result was expected, as increases in temperature have been shown to increase metabolic energy so animals are expected to use more energy as ambient temperatures increase (Knut, 1997). Our results also showed no difference in energy cost of locomotion between the undisturbed side of the Reserve (TMC) and the disturbed side of the Reserve (NCG) (t= -0.475, p=0.6347) with increase in temperature. This result was somewhat surprising to us because we expected to see hyenas using significantly higher amounts of energy in the warmer TMC side than the cooler NCG side of the Reserve.

Discussion

Management regime and energy use

We suspect our finding that hyenas in TMC were using significantly more energy in locomotion than NCG hyenas might have been due to differences in their body masses (Fig. 4.9). On average, TMC hyenas weighed more than NCG hyenas but moved shorter distances. The average weight for TMC hyenas was ~60.2kg while that of NCG hyenas was ~56.77kg (Table 4.3). Since our energy calculation was expressed as a function of body mass, the bias we observed here may be due to body mass differences. . .

Social rank and energy use

We were somewhat surprised by our finding that the difference in energy use between low-ranking and high-ranking hyenas in TMC was significantly more than was the difference in NCG (Fig. 4.6). This means that both high-ranking and low-ranking hyenas in NCG are spending similar amounts of energy in locomotion (Fig. 4.6). We fear that the high stress levels that hyenas in this side of the Reserve seem to be facing may have negative fitness consequences in the long run.

Prey and energy use

Our results showed that spotted hyenas used significantly more energy in locomotion when prey were scarce than when they were abundant. This result was consistent with our expectation that hyenas should be using more energy while looking for prey when prey density is low in the Reserve. However, we did not see the same patterns of energy use in relation to prey availability in TMC and NCG. This result was not consistent with our expectation that hyenas in NCG should be using more energy during locomotion due to extra movement resulting from livestock grazing within their territories. We are concerned that the decreasing ungulate population trends in the MMNR (Ottichilo et al., 2000, Serneels and Lambin, 2001) and its environs may continue to impose further energetic costs on hyenas.

Season and energy use

We did not find significant differences in the energy costs of locomotion to hyenas between dry and wet seasons. This was not consistent with our expectation that hyenas should be using less energy in locomotion during the dry period. This result may have been due to the fact that it is during the dry season that most prey concentrate in the greener pastures near water courses in the Reserve as opposed to during the wet season when they may even move out of the Reserve onto the neighboring group ranches. We also found no significant differences in energy use between hyenas in TMC and those in NCG in locomotion during the dry and wet seasons. Other factors like distribution of the prey may play a part here since we did not look at prey distribution in this research. Other prey also develop defensive mechanisms when they are in groups, so hyenas may be forced to move around the Reserve looking for easy prey to catch despite the fact that lots of prey may be present during the dry period.

Standardized temperature and energy use

Our results were consistent with earlier findings that energy use increases with ambient temperature (Knut, 1997). However, our finding that there was no difference in energy use in locomotion between hyenas in TMC and NCG hyenas was unexpected because we saw hyenas traveling significantly shorter distances in TMC than they did in NCG.

Conclusion

Our results were surprising in light of the greater anthropogenic disturbance in NCG than TMC. Based on this, we had expected to see more costly locomotion in NCG than TMC, but we observed the opposite. We suggest this pattern might be due either to differences in body mass between hyenas in TMC and NCG. Our results also showed that the differences we observed in energy cost of locomotion was due to differences in management regimes but not differences in temperatures.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.132751	0.005040	224.740	**<2e-16*** **
timepm	-0.0104763	0.0009821	-10.668	**<2e-16*** **
rankL	0.0019274	0.0014853	1.298	0.19447
managementtmc	0.0056330	0.0020298	2.775	**0.00553** **
seasonwet	-0.0007992	0.0020013	-0.399	0.68967
preymanyp	-0.0044752	0.0021097	-2.121	**0.03394***
tempstd	0.0030949	0.0011346	2.728	**0.00639** **
managementtmc:preymany	-0.0036071	0.0024031	-1.501	0.13341
rankL: managementtmc	0.0158660	0.0018277	8.681	**<2e-16*** **
managementtmc:seasonwet	0.0012487	0.0022724	0.550	0.58268
managementtmc:tempstd	-0.0005673	0.0011939	-0.475	0.63468

Table 4.4: GLM table of results for energy cost of locomotion. Energy values have been transformed to log base 10. Bolded cells represent significant effects.

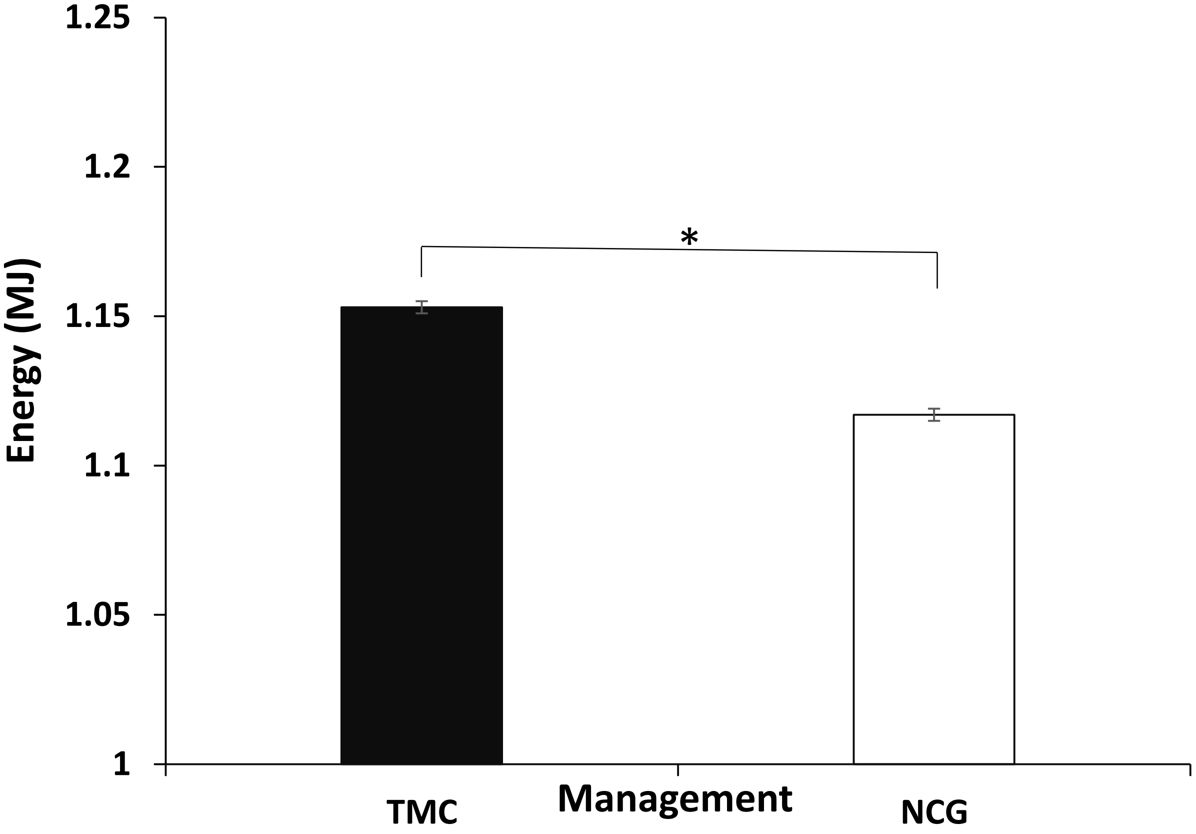

Figure 4.1: Management regime and average daily energy cost of locomotion in TMC and NCG. Asterisk represents significant difference, and error bars represent standard errors.

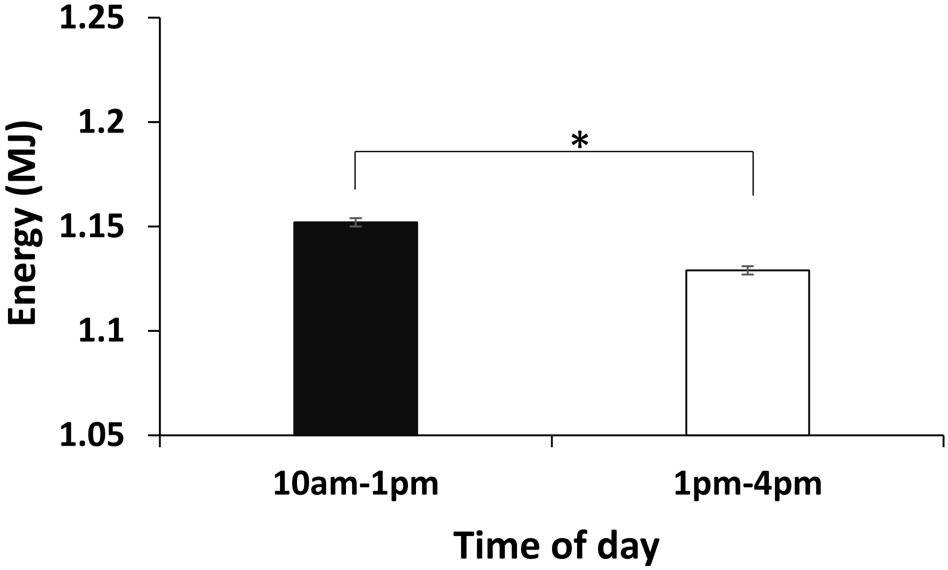

Figure 4.2: Time of day and average daily energy cost of locomotion in the MMNR. Asterisk represents significant difference, and error bars represent standard errors.

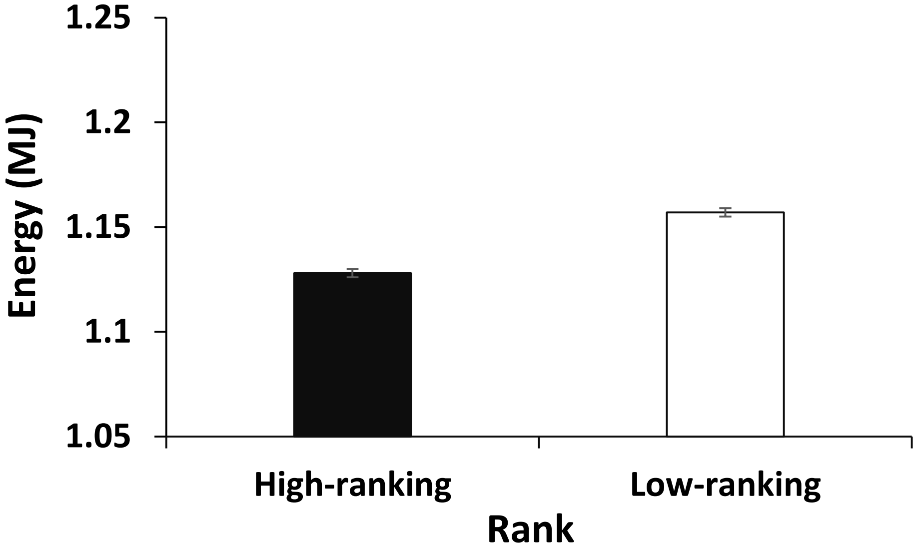

Figure 4.3: Social rank and average daily energy cost of locomotion in the MMNR. Error bars represent standard errors

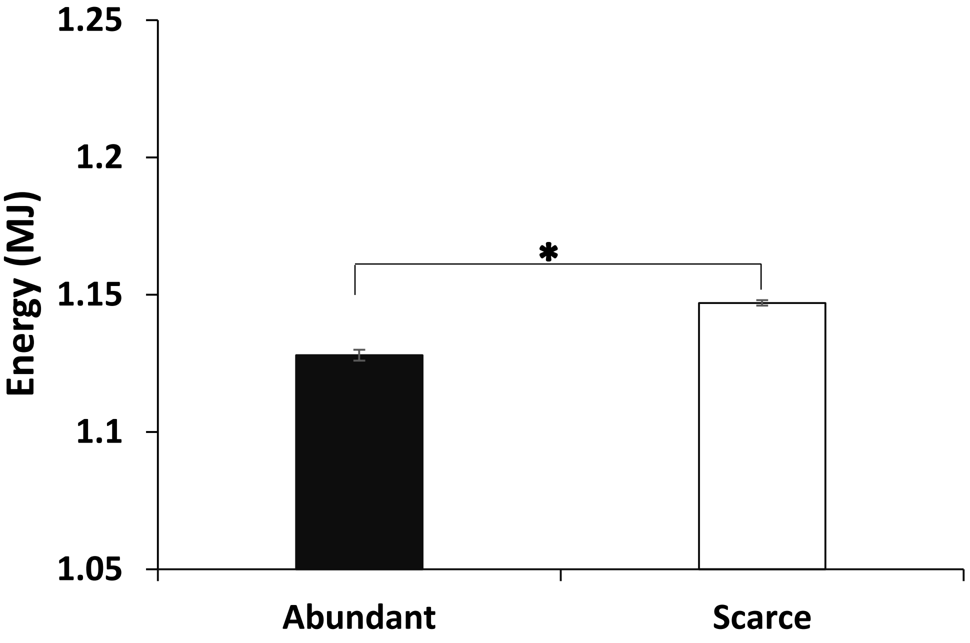

Figure 4.4: Prey availability and average daily energy cost of locomotion in the MMNR. Asterisk represent significant difference, and error bars represent standard errors.

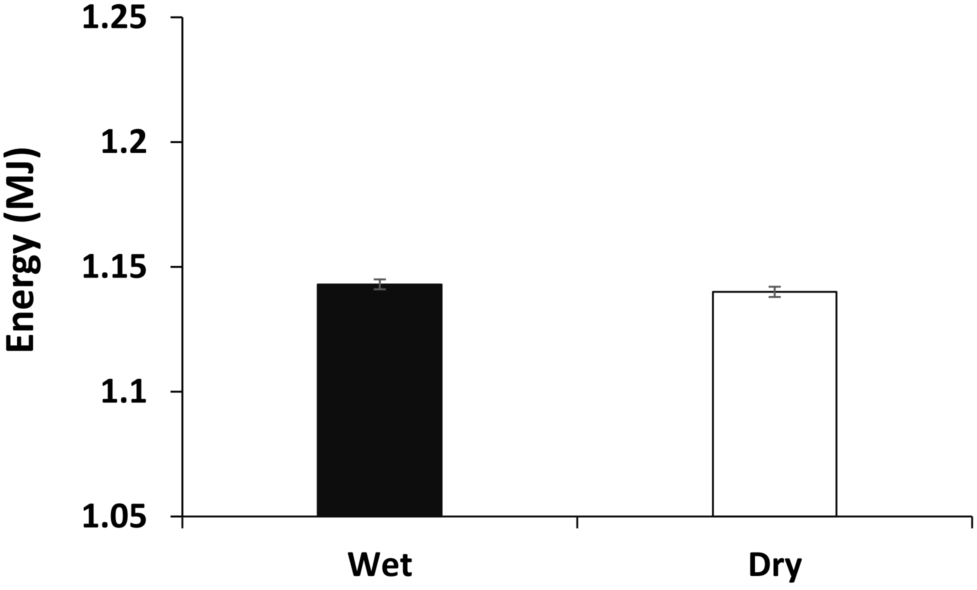

Figure 4.5: Seasonality and average daily energy cost of locomotion in the MMNR. Error bars represent standard errors.

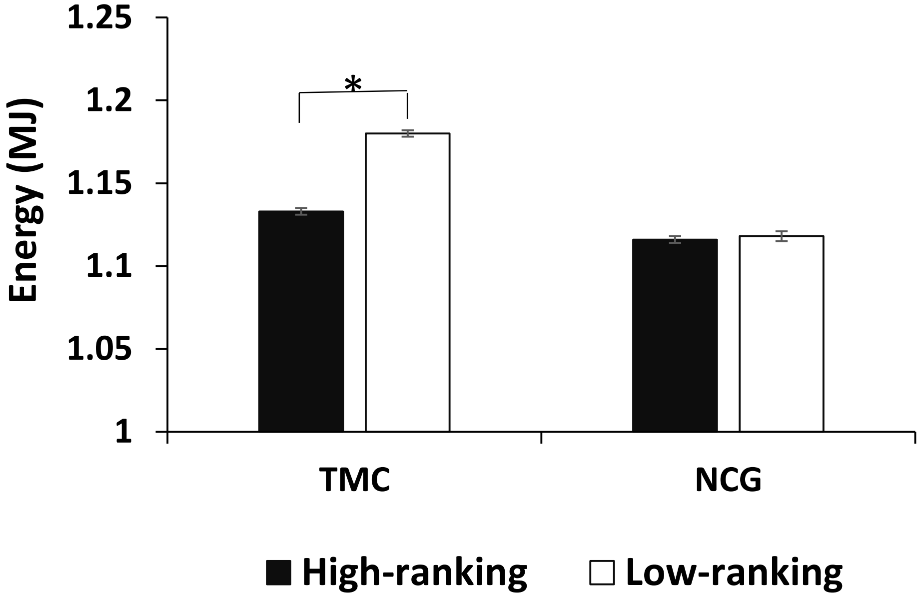

Figure 4.6: Social rank and average daily energy cost of locomotion in TMC and NCG. Asterisk represents significant difference, and error bars represent standard errors.

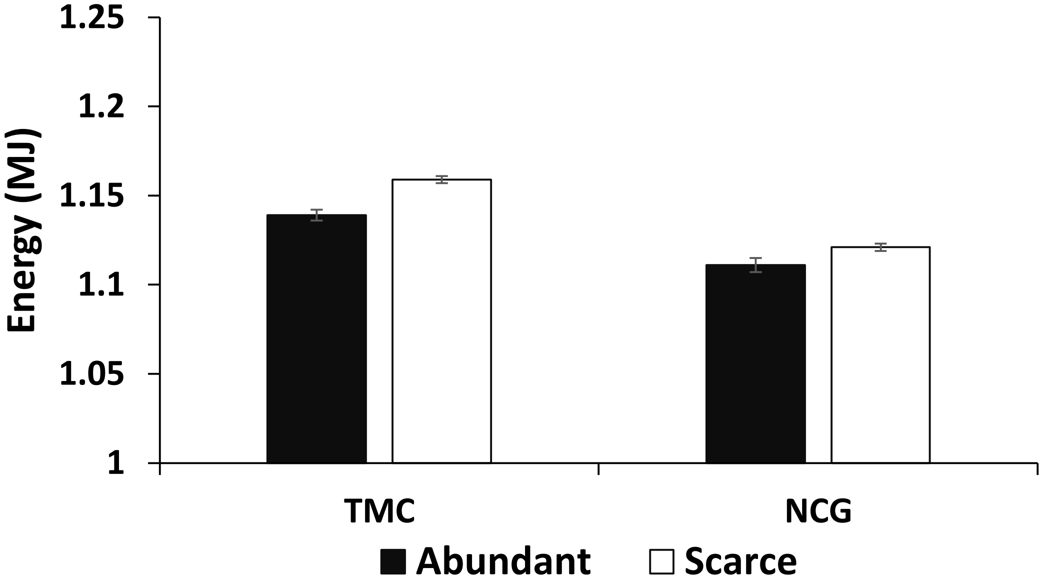

Figure 4.7: Prey availability and average daily energy cost of locomotion in TMC and NCG. Error bars represent standard errors.

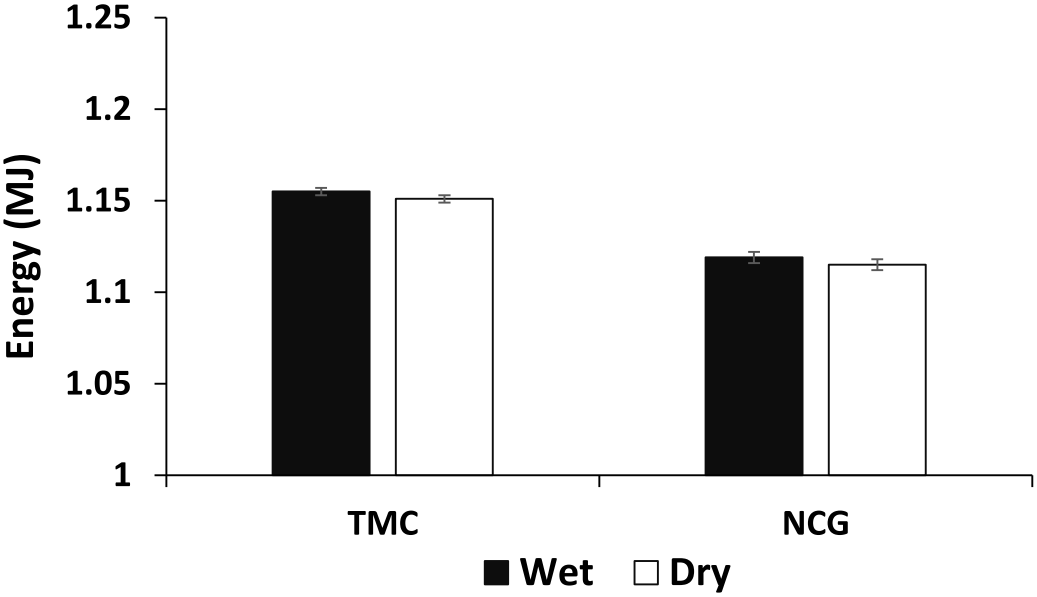

Figure 4.8: Seasonality and average energy cost of locomotion in TMC and NCG. Error bars represent standard errors.

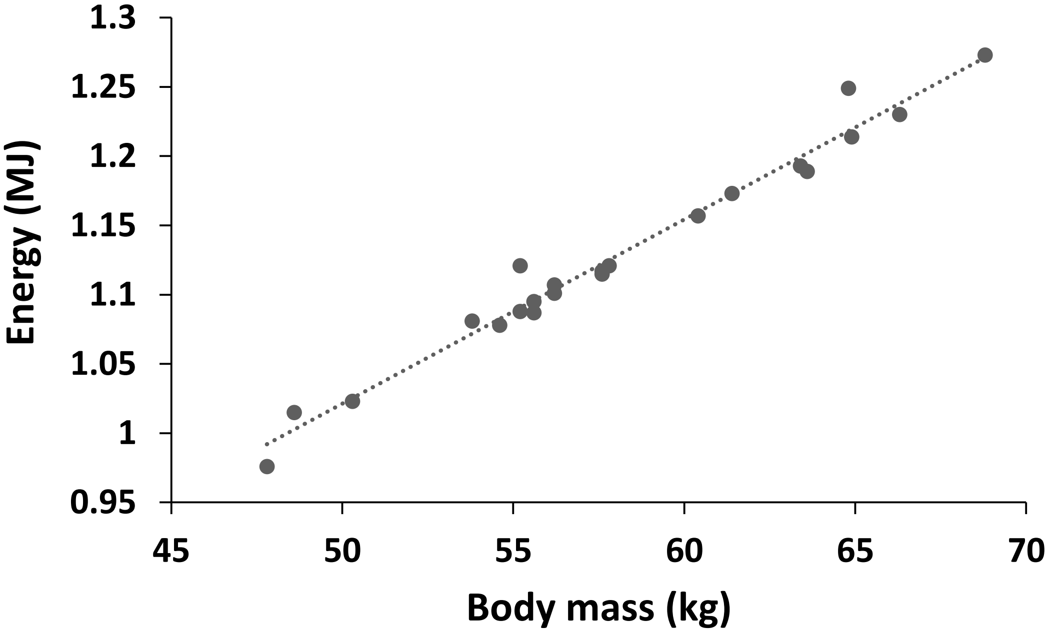

Figure 4.9: The relationship between hyena body mass (kg) and energy cost of locomotion (MJ).

GENERAL CONCLUSIONS FROM THIS THESIS

This study has shown that during the daytime, hyenas were moving significantly longer distances in the morning (10am-1pm) than they did in the afternoon (1pm-4pm). We have also seen that hyenas inhabiting the disturbed side of the Reserve (NCG) were moving significantly longer distances than were hyenas in the undisturbed side of the reserve (TMC). We also saw differences between TMC and NCG with respect to the effects of social rank on hyenas' movement patterns. In addition we found that hyenas in the undisturbed side of the Reserve were travelling significantly shorter distances than they did in the disturbed side of the Reserve as temperatures increased. Hyenas in the disturbed side of the Reserve may be forced to move about more as temperatures increase while trying to look for dense vegetation which is scarcely available. Through this study, we have shown that the anthropogenic activities that take place in NCG may be causing serious behavioral change in hyenas during the daytime, and we believe these effects should be addressed very soon by Reserve managers.

In our study of habitat use we found that hyenas in TMC significantly preferred open vegetation (grassland and bare ground) whereas hyenas in NCG preferred habitat characterized by dense vegetative cover (shrub land and riparian). Our habitat results also showed that hyenas in NCG were found significantly outside their defended territory than expected. We suggest that the livestock grazing that takes place in this side of the Reserve may be forcing the hyenas here to seek alternative resources outside their defended territory.

Finally, in Chapter 4 we obtained the surprising result that TMC hyenas spend more energy on locomotion than do NCG hyenas despite that fact that NCG hyenas travelled significantly longer distances. We found here that hyenas experienced significantly higher energetic costs in the morning than they did in the afternoon. Our results also showed that seasonal variation in rainfall (dry or wet) does not lead to significant differences in the cost of locomotion in NCG as well as in TMC. We also saw that one's social rank in the clan has significantly fewer benefits in NCG than is the case in TMC. We found that movement was less costly energetically to hyenas when prey were abundant than when prey were scarce. Finally, our results showed that differences in temperatures between TMC and NCG do not lead to significant differences in energy cost of locomotion. . We conclude by suggesting that addressing the anthropogenic activities in NCG in a better way will not only benefit he hyenas but also other animals in this key ecosystem for biodiversity conservation.

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