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THREAT-SENSITIVE BEHAVIOR AND ITS ONTOGENETIC DEVELOPMENT IN TOP MAMMALIAN CARNIVORES

By

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ABSTRACT

THREAT-SENSITIVE BEHAVIOR AND ITS ONTOGENETIC DEVELOPMENT IN TOP MAMMALIAN CARNIVORES

By

Wiline Mallory Pangle

Animals have evolved behaviors to both detect and respond to threats in order to maximize survivorship. In my dissertation, I describe four studies that focused on inter- and intra-specific variation in threat-sensitive behaviors, with special attention to vigilance, among East African mammalian carnivores.

I first evaluated the functions of vigilance behavior in adult and juvenile spotted hyenas (*Crocuta crocuta*) by observing them in various behavioral contexts and over gradients of risk. The results indicated that the main function of vigilance in hyenas is to detect inter-specific rather than intra-specific threats, as vigilance was lower when hyenas were in large than small groups, and was not affected by social rank. Vigilance was also highly context-specific, with hyenas most vigilant when nursing a young litter, and least vigilant when consuming food of high quality. Adult hyenas exhibited pronounced individual variation in vigilance. Juvenile hyenas were less vigilant than adults in all contexts and showed less consistency in their vigilance behavior.

I then further explored the ontogenetic variation in vigilance apparent in the first study. I used playback experiments to evaluate age-related variation in responses by spotted hyenas to roars of their main natural predators, lions (*Panthera leo*). Both juvenile and adult hyenas moved in response to lion roars, but not to control sounds. Juveniles showed a stronger response to lion sounds than did adults. Both juvenile and

adult hyenas also had stronger reactions to roars emitted by male than female lions. Thus, juvenile hyenas appear to associate certain signals with dangers, and respond accordingly. However, during ontogeny, young hyenas may need experience with danger to learn the specific environmental circumstances under which they need to be vigilant when no threat is immediately apparent.

The third study assessed the lethal and non-lethal effects of anthropogenic activities by comparing vigilance in an undisturbed population of hyenas to that in one experiencing human disturbance. Proportions of deaths of known causes that were attributable to humans increased between 1988 and 2006 in the disturbed population. In addition, hyenas from the disturbed population were more vigilant during rest than hyenas from the undisturbed population, especially on days during which livestock were grazing in their territory. I assessed this livestock effect using playback experiments of cow bells. I found that hyenas from the disturbed population responded more strongly to these bells, but also to control sounds, than did hyenas from the undisturbed populations, indicating a heightened responsiveness to all unnatural sounds.

The last study placed the findings from the previous studies in a comparative perspective by examining vigilance by adult members of eight sympatric East African carnivore species. Vigilance varied strongly among the eight species, and this could be attributed to variation in body size, mortality rate and sociality. In addition, each carnivore species spent about the same amount of time vigilant during rest as when feeding, but vigilance strategies differed between these activities in a way that was consistent among species. Animals generally exhibited long, infrequent vigilance bouts during rest, and short, frequent vigilance bouts when feeding.

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GENERAL INTRODUCTION

The objectives of this general introduction are threefold. First, I will review the study of threat-sensitive behaviors, and specifically vigilance behavior. Second, I will explain why East African carnivores, and particularly spotted hyenas (*Crocuta crocuta*), are excellent model organisms in which to further extend the study of threat-sensitive behaviors to carnivores. Finally, I will present an overview of each chapter of my dissertation.

Threat-sensitive behaviors can be broadly defined as behaviors used by animals to assess risk and adjust their behavioral responses accordingly (Helfman 1989, Helfman and Winkelman 1997). Studies of threat-sensitive behaviors have been instrumental to understanding the risks that animals perceive and the costs they incur to avoid predation. These costs can be substantial and have been shown to have effects on fitness as strong or even stronger than direct, lethal predation (Lima 1998; Preissier et al. 2005; Creel and Christianson 2008). Because of the ubiquitous nature of threat-sensitive behaviors, their study offers opportunities for comparisons among populations or species as well as for answering fundamental questions in both basic and applied biology.

Many studies of threat-sensitive behaviors in mammals and birds focus on vigilance (reviewed by Caro 2005a). Vigilance can be broadly defined as any behavior that increases the likelihood that an animal will detect a given stimulus at a given time (Dimond and Lazarus 1974), and is often operationally defined in birds and mammals as any raising of the head above a certain level (Caro 2005a). Vigilance is typically studied in animals that are engaged in fitness-dependent activities such as foraging; under these circumstances, animals must trade off benefits gained from their current activity against their ability to perceive information about the surrounding environment (e.g. Arenz and Leger 1999, 2000; reviewed in Lima and Dill 1990). Variation in vigilance during fitness-dependent activities can inform us about animals' perceptions of risk, and about the decision-making processes germane to these risks.

Several general patterns have emerged from the myriad past studies of vigilance behavior in mammals and birds (reviewed by Quenette 1990 and Caro 2005a). First, as body size increases, vigilance generally decreases; body size appears to be a good proxy for the number of different predators that prey on a focal species (Quenette 1990). Second, vigilance typically decreases with increasing group size; this is often referred to as the "group-size effect" (reviewed in Elgar 1989). This group-size effect may be driven by an increased number of eyes, allowing individuals to reduce their vigilance (Pulliam 1973), or by dilution of predation risk among larger numbers of individuals (Hamilton 1971; Bednekoff and Lima 1998; Krause and Ruxton 2002; Fairbanks and Dobson 2007). Third, many studies have provided direct and indirect evidence that vigilance functions to detect approaching predators (termed "antipredator vigilance"; e.g. Lima 1987; Hunter and Skinner 1998; Lima and Bednekoff 1999; Treves 2000), but individuals can also direct their vigilance toward conspecific group members (termed "social vigilance"; e.g. Treves 2000; Hirsch 2002; Cameron and du Toit 2005; Lung and Childress 2007). Many additional factors related to predation risk, such as age of the focal animal, and distance to cover, have also been examined in studies of vigilance but no consensus has been reached (Caro 2005a). Thus, it appears that some risk-related factors may be species- or context-dependent.

Most earlier studies of vigilance behavior have focused on species that occupy low trophic positions in food webs, such as passerine birds, rodents and ungulates (e.g. Lima 1987; Hunter and Skinner 1998; Blumstein et al. 2001; Ebensperger et al. 2006). Studies of species at higher trophic levels generally focus on their roles as predators (e.g. Mills and Shenk 1992; Murray et al. 1995; Cooper et al. 2007). Little research has been done on vigilance by predators, and this has resulted in a lack of understanding of the mechanisms these animals possess for coping with danger. Mammalian carnivores confront many natural threats, including both intraguild predation and kleptoparasitism by members of their own and other species (Caro and Stoner 2003). The few existing studies on antipredator behavior exhibited by carnivorous mammals suggest that vigilance behavior might be important for predators as well as for prey (Caro 1987; Rasa 1989; Clutton-Brock et al. 1999; Switalski 2003; Di Blanco and Hirsch 2006; Hunter et al. 2007; Atwood and Gese 2008). Nevertheless, general trends in vigilance behavior among mammalian predators remain largely unexplored.

I focused most of my dissertation research specifically on threat-sensitive behaviors of spotted hyenas. The spotted hyena offers several advantages as a model organism in which to examine threat-sensitive behaviors. First, in contrast to most other predators, hyenas occur in large numbers (Mills and Hofer 1998), they are easily observable in the savannahs of sub-Saharan Africa, and they are active around dawn and dusk (Kruuk 1972; Kolowski et al. 2007). Spotted hyenas are keystone predators in most sub-Saharan ecosystems (Hofer and East 1995). Their social organization in large fission-fusion societies (Kruuk 1972; Smith et al. 2008), called clans, allows for collection of repeated measures from multiple known individuals in each of several clans. Relative to other carnivores, spotted hyenas are extraordinarily flexible in their behavior and ecology. For instance, they breed throughout the year, they may be either diurnal or nocturnal, they occupy a vast array of habitat types, and they eat carrion as well as live prey ranging in size from termites to elephants (Kruuk 1972; Mills 1990; Sillero-Zubiri and Gottelli 1992; Holekamp et al. 1997; Holekamp et al. 1999). Therefore, their responses to dangers presented by natural and human-related stimuli may represent conservative indicators of how other top predators, including those that are rare and endangered, are likely to respond to specific threats (Arcese and Sinclair 1997).

Spotted hyenas are also particularly well-suited for studies of ontogenetic variation in behavior (e.g. Holekamp and Smale 1993). In contrast to many other mammals, hyenas have a life history characterized by discrete stages, each of which begins and ends with observable milestones (Holekamp and Smale 1998). Although hyenas are top predators in the food webs of many African ecosystems, they encounter a number of serious threats, particularly during early developmental stages, and most die violent deaths (Kruuk 1972; Watts 2007). Indeed, fewer than 50% of cubs born survive to adulthood, and mortality rates diminish rapidly after spotted hyenas reach reproductive maturity (Frank et al. 1995; Watts 2007). This pattern suggests that juveniles might be more vulnerable than adults to negative effects of competition and intraguild predation.

Here my primary objectives were to better understand vigilance, its functions and its development, in spotted hyenas. I used a combination of field observations and playback experiments on wild hyenas in the Masai Mara National Reserve, Kenya (hereafter the Reserve). I conducted a total of four studies focused on inter- and intra-specific variation in threat-sensitive behaviors in spotted hyenas and other carnivores of

East Africa. Throughout this dissertation, I use the term "we" instead of "I", which reflects the true collaborative nature of my work and the fact that all chapters were prepared in manuscript format.

Overview of Chapters

In the first chapter, we used natural patterns of vigilance behavior by spotted hyenas to determine functions and key predictors of vigilance. Repeated observations in multiple behavioral contexts were collected from individual members of one clan of hyenas over a one-year period. We examined variation in hyena vigilance attributable to age, group size, social rank, and factors related to predation risk. We also compared vigilance behavior exhibited by hyenas engaged in one of three different types of activities at the time of observation: resting, feeding or nursing. Our results indicated that: 1) the primary function of vigilance in hyenas is to detect inter-specific rather than intra-specific threats; 2) vigilance is highly context-specific; (3) adults were more vigilant than juveniles in all contexts sampled; and 4) adult hyenas, but not juveniles, exhibited pronounced individual variation in vigilance within behavioral contexts. These findings shed light on the relative importance of different risks in shaping hyena behavior, and provide general insights into context-dependence and group-size effects on vigilance.

In the second chapter, we further explored the age-related variation in vigilance behavior described in the first chapter. First, we compared naturally-occurring vigilance between age groups when hyenas were resting alone, and we found that juveniles were less vigilant than adults when no immediate threat was present. Second, we performed playback experiments to test predictions of a hypothesis suggesting that hyenas in different life history stages are differentially competent to deal with danger. Because juvenile hyenas are more vulnerable than adults to mortality caused by lions, we expected that juveniles would respond to lion roars with much more caution than adults. We also inquired whether responses by hyenas varied with the sex of the lions, as male lions are the leading natural mortality source for both juvenile and adults hyenas (Cooper 1991; Frank et al. 1995). Our results indicated that both adult and juvenile hyenas responded to lion roars more vigorously than to the control sounds (baboon "wahoo" calls), but that juveniles showed a stronger response than adults. Both age classes also showed stronger reactions to roars emitted by male than female lions. Thus, like adults, juvenile hyenas appear to recognize certain signals as dangerous and respond accordingly. However, during ontogeny, young hyenas may need experiences with danger to learn the environmental circumstances under which they need to be vigilant when no threat is immediately apparent.

In the third chapter, we evaluated the lethal and non-lethal effects of anthropogenic activities on wild spotted hyenas by comparing vigilance in an undisturbed population of hyenas to that in one experiencing human disturbance. We used three different approaches: 1) we examined the proportion of all hyena deaths of known causes that could be attributed to humans between 1988 and 2006; 2) we made field observations of naturally-occurring vigilance among hyenas; and 3) we performed an experiment to test predictions of a hypothesis suggesting that vigilance behavior in hyenas is influenced by livestock grazing. We expected members of a clan living beside the border of the Reserve, and experiencing frequent human disturbance in the form of livestock and herders, would spend more time vigilant in natural contexts of resting, nursing and feeding than hyenas living in a clan far from the Reserve boundaries and experiencing little human disturbance. The proportions of all known deaths that could be attributed to humans increased dramatically in the disturbed population between 1988 and 2006. In addition, resting hyenas living in close proximity to humans were more vigilant than hyenas from the undisturbed population, especially on days when livestock were grazing in their territory. In southern Kenya, local pastoralists fit their livestock with metal cow bells, so we made recordings of these sounds, and compared hyena responses to them in playback experiments with their responses to control sounds of church bells. In these experiments, we found that hyenas from the disturbed population responded more strongly to these bells, but also to control sounds, than did hyenas from the undisturbed populations, indicating a heightened responsiveness to all unnatural sounds.

In the fourth study, we broadened our approach by examining vigilance in multiple species of mammalian carnivores. We focused on eight sympatric species that occupy an East African savannah habitat in the northern part of the Serengeti ecosystem. These eight species represent four different families in the mammalian order Carnivora: Herpestidae, including dwarf mongooses (*Helogale parvula*) and banded mongooses (*Mungos mungos*); Felidae, including cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), and lions; Hyaenidae, including spotted hyenas; and Canidae, including black-backed jackals (*Canis mesomelas*) and wild dogs (*Lycaon pictus*). These species vary considerably in body size, in the intensity of the intra- and interspecific feeding competition they experience, and in their social behavior. Our goals were to identify variables that predict patterns of vigilance in carnivores, and to compare patterns of vigilance among species. Vigilance varied strongly among the different species, and this variation could be attributed to differences in body size, mortality rate and sociality. Vigilance also varied within each species, and this could be attributed to different factors for each species. The carnivores studied were similarly vigilant while resting and feeding. However, they adopted alternative vigilance strategies depending on the activity in which they were engaged: they exhibited long, infrequent vigilance bouts during rest, and short, frequent vigilance bouts while feeding.

CHAPTER ONE

FUNCTIONS OF VIGILANCE BEHAVIOR IN A SOCIAL CARNIVORE, THE SPOTTED HYENA

INTRODUCTION

Many studies of threat-sensitive behavior in mammals and birds focus on vigilance because it can have important consequences for survivorship (e.g. FitzGibbon 1989), and because it is easily quantifiable. Vigilance has been defined by Dimond and Lazarus (1974) as any behavior that increases the likelihood that an animal will detect a given stimulus at a given time. This stimulus might be an approaching predator (e.g. Boland 2003) or an alarm call emitted by a conspecific (e.g. Shriner 1998; Baack and Switzer 2000), but it might also be an approaching competitor or a potential mate (e.g. Roberts 1988; Burger and Gochfield 1994). Vigilance is typically studied in animals that are engaged in fitness-dependent activities such as feeding; under these circumstances, the animal must trade off benefits gained from its current activity against its ability to perceive information about the surrounding environment (e.g. Arenz and Leger 1999, 2000; reviewed in Lima and Dill 1990). Variations in vigilance during fitness-dependent activities can inform us about animals' perceptions of risks, and the decision-making processes germane to these risks.

Here we studied natural patterns of vigilance behavior exhibited by spotted hyenas (*Crocuta crocuta*). Hyenas live in complex, social groups, called clans, containing up to 80 individuals; clans are rigidly structured by dominance hierarchies, and an individual's social rank determines its priority of access to food (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986; Mills 1990). Hyenas feed primarily on ungulates they kill themselves, and carcasses can be monopolized by only one or a few individuals (Cooper et al. 1999). Competition at carcasses can be fierce and kleptoparasitism among clan members is a common event; individuals of low social rank are at particular high risk of kleptoparasitism (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986). Thus, hyenas may need to be frequently vigilant against theft of food by conspecifics. Furthermore, hyenas rarely die of old age, but instead succumb most often to predation by lions and humans (Cooper 1991; Frank et al. 1995; Watts 2007). Hyenas may therefore need to be vigilant against intraguild or human predators. The relative importance of these intra- and inter-specific threats faced by hyenas can be best understood by relating hyena vigilance to risk-modifying factors such as group size.

One of the most pervasive ideas in the study of vigilance is that animals reduce their vigilance as the number of individuals per group increases (Elgar 1989). This group-size effect may be driven by an increased number of eyes, allowing individuals to reduce their vigilance (Pulliam 1973), or by dilution of predation risk among larger numbers of individuals (Hamilton 1971; Krause and Ruxton 2002; Bednekoff and Lima 1998). However, this effect can be masked or reversed if substantial threats also come from members of the group itself. Internal threats should increase with increasing group size, counterbalancing the usual effect of increasing group size on antipredator vigilance (e.g. Treves 2000; Hirsch 2002; Kutsukake 2006, 2007). Studies of primates have shown that individuals direct a large part of their total vigilance toward monitoring conspecifics (reviewed by Treves 2000). This behavior has been termed "social vigilance", as opposed to antipredator vigilance, and recent studies have also reported such vigilance in various non-primate species (e.g., Waite 1987; Cameron and du Toit 2005; Lung and Childress 2007; Pays and Jarman 2008). Comparing time spent vigilant among individuals that vary in social rank, but that also occur in subgroups of varying sizes, can provide information about the relative importance of intra- and inter-specific threats to spotted hyenas.

The function and level of vigilance may also depend on the particular behavior in which animals are engaged. Previous studies of vigilance have focused heavily on animals engaged in foraging, and on the factors that influence the tradeoff between food intake and information acquisition (reviewed in Caro 2005a). Recently, there has been a call for research that addresses factors important to animals engaged in other behaviors, such as resting (Arenz 2003; Roberts 2003; Lima et al. 2005), to better understand the selection pressures operating in these contexts. Increasing the number of contexts in which vigilance is studied also enables us to validate ideas derived from observations of foraging animals, and to tease apart confounding factors that have been identified with foraging animals. For instance, if the group-size effect occurs in contexts other than foraging, this would suggest that the primary mechanism driving the group-size effect is more likely predation risk than food competition or kleptoparasitism (Arenz 2003; Beauchamp 2003). Because the function of rest remains poorly understood, tradeoffs animals might experience while resting are less clear than those experienced while foraging, but animals may nevertheless be at high risk during these and other activities (Caro 2005a). In contrast to many boreal carnivores, spotted hyenas inhabiting African savannahs are easily observable while they are engaged in several different types of activities.

To identify the primary functions of vigilance in spotted hyenas, we examined hyena vigilance behavior with field observations made over gradients of group size, social rank, and factors related to predation risk (i.e. age of subject, time of day, and distance to nearest bushes). We also compared vigilance among hyenas engaged in three behavioral contexts (resting, feeding and nursing), and between two age groups (juveniles and adults). All else being equal, we expected that hyenas would be more vigilant during rest than while feeding or nursing, as we assumed rest to be the behavioral context in which the cost of vigilance would be smallest. If vigilance functions as a means to detect intra-specific threats, we expected hyenas to be more vigilant (1) in larger than smaller groups; (2) when they are low- rather than high-ranking; (3) when they are found on the edge of their territory than in its center; and (4) when they are closer than further from their nearest conspecific neighbor. If vigilance functions as a means to detect inter-specific threats, we expected hyenas to be more vigilant (1) in smaller than larger groups; (2) when further than closer from their nearest conspecific neighbor; (3) when they are feeding than during rest, as their likelihood of encountering lions when food is present is much higher than when food is absent; (4) when they are nursing younger than older offspring; and (5) when they are closer to bushes that could potentially conceal lions. In addition to detecting threats, vigilance may also be used to find mates or prey (e.g. Caro 1987; Quenette 1990; Pays and Jarman 2008), so these functions must be considered as well. If vigilance functions as a means to detect potential prey, we expected hyenas to be more vigilant (1) during rest than while feeding, and (2) during times of the year when prey are scarce. Lastly, if vigilance functions as a means of detecting potential mates, we expected to detect (1) sex differences in vigilance, and (2) variation based on the sex ratio of the current group. Although all four of these functions may apply to adult hyenas, we expected the function of vigilance among juveniles might differ from that among adults.

For example, juveniles neither hunt nor mate so vigilance would not function in either of these capacities among youngsters.

Our observations focused on one clan of hyenas for over a year, and we obtained repeated measures within and between behavioral contexts for given individuals in the clan. This allowed us to ask questions about individual variation within and between behavioral contexts. Our results thus shed light on the context-dependence and group-size effects on vigilance among large carnivores.

METHODS

Study site and study animals:

This study took place in the Masai Mara National Reserve (the Reserve – 1,500 km^2) in southwestern Kenya (1°40 S, 35°50 E) between June 2005 and July 2006. The Reserve is an area of open, rolling grassland inhabited by large numbers of resident ungulates (Sinclair and Norton-Griffiths 1979) that support high densities of large carnivores (Ogutu and Dublin 2002; Dloniak 2006). Every year between June and September, large migratory herds of wildebeest (*Connochaetes taurinus)* and zebra (*Equus burchelli*) join resident ungulates, leading to a superabundance of prey during these months (Sinclair and Norton-Griffiths 1979).

We monitored one clan, the Talek West clan, which contained 52 to 63 individuals during the study period, including 11 to 15 adult females, their young, and 10 to 13 immigrant males. All hyenas in the clan were known individually by their unique spots. Ages (± 7 days) of all natal hyenas were determined using previously described methods (Holekamp et al. 1996). The sex of each hyena was known based on the dimorphic shape of its erect phallus (Frank et al. 1990). Reproductive maturity in spotted hyenas occurs at approximately 24 months of age (Matthews 1939; Glickman et al. 1992). Females give birth to litters of 1 or 2 cubs (rarely 3) in an isolated natal den, and they move their cubs to a communal den when their cubs reach 2 to 5 weeks of age (Kruuk 1972; East et al. 1989). Talek cubs reside at the communal den until about 9 months of age (Boydston et al. 2005). Juveniles were considered to be den-independent once we observed them further than 200 m from the communal den on four consecutive occasions. Mothers nurse their litters until cubs are approximately 14 months of age (Holekamp et al. 1996), although cubs start feeding on meat opportunistically when they are only a few months old (Kruuk 1972; Holekamp and Smale 1990). No allonursing occurs in this species (Mills 1985). Here, we assigned sampled individuals to one of two age groups: juveniles were hyenas younger than 24 months of age, and adults were hyenas older than 24 months of age. Other than observations of mothers nursing their litters, all subjects (both juveniles and adults) were den-independent.

We determined social ranks of hyenas in the study clan based on wins and losses in dyadic agonistic interactions (described in Holekamp and Smale 1993; Smale et al. 1993). Cubs 'inherit' their social rank from their mothers (Engh et al. 2000). A clan contains multiple matrilines of adult females and their offspring, and members of each matriline cluster along the social rank continuum. The highest-ranking matriline was the alpha matriline, the second through fourth were considered the mid-ranking matrilines, and the bottom three were considered here to be the low-ranking matrilines. Each of these three categories represented roughly a third of the females and their young in the clan. After puberty, virtually all natal males disperse from their natal clan; when they join a new clan as immigrant males, they assume rank positions at the very bottom of the social hierarchy, below all other immigrant males already present (Smale et al. 1997; East and Hofer 2001). Thus all natal animals (philopatric females and their young) are socially dominant to all immigrant males. We ranked individual adult hyenas from highest (the alpha female) to lowest (the immigrant male that had most recently joined the clan) as a single hierarchy.

Observations of naturally-occurring vigilance:

Individual hyenas were videotaped in the field to document their vigilance behavior. Daily observations of the study animals took place during daylight hours between 0600 - 1200 h (the AM period) and 1200 - 1920 h (the PM period). During these observation periods, we videotaped hyenas engaged three behavioral contexts, resting, feeding or nursing, from a field vehicle that served as a mobile blind. During these observations, the field vehicle was parked no closer than 15 m from each focal hyena. All monitored hyenas were well habituated to our vehicle. Hyenas were considered to be resting when they were lying down in the absence of food for at least five minutes (and usually for several hours), alone or with other conspecifics, and not interacting with other conspecifics; the eyes of resting hyenas were usually shut. Hyenas were considered to be feeding if they were actively involved in consuming a food item for at least two minutes. Food items were categorized as high- or low-quality, depending on whether or not they included fresh meat. A female hyena was considered to be nursing if a litter suckled from her for more than two minutes. Upon finding a suitable subject, we set up a Sony DCR

H65 video camera mounted on a window tripod, and videotaped the focal hyena for 2 - 7 min ($\overline{X} = 4.01 \pm 0.02$ min).

In conjunction with each filmed sequence, we also recorded several variables that may affect vigilance (e.g. Elgar 1989; Devereux et al. 2006; Liley and Creel 2008; reviewed in Caro 2005a). These variables included Julian date (used as a proxy for prey abundance), time of day, the location of the trial (on the edge or in the center of the clan's territory), the strength of the wind at the time of filming (categorized from 0 if there was no wind, up to 6 if winds were very strong), the distance in meters between the focal individual and the closest patch of bushes (using a Bushnell range finder), and the height of the grass where the focal individual was filmed. Grass height was evaluated relative to the head of the focal individual, and was ranked as 0 if there was no grass and up to 6 if the grass was higher than the raised head of the focal individual. Wind strength and grass height are both factors that may impair hyenas' ability to detect danger. Social variables included the number of conspecifics present within 100 m of the focal individual (referred to hereafter as "group size"), the distance between the focal individual and its nearest conspecific neighbor, and the group's sex ratio (only adults were included in this sex ratio as this factor was recorded to inquire whether vigilance was directed to detect potential mates). Age of the suckling litter was also recorded for nursing females.

Data extraction from video tapes:

We reviewed videotaped observations using a Sony DRC TRV900 digital camcorder that superimposed a time code on the screen with a precision of 0.33 s, with each video frame uniquely labeled. We extracted information on all vigilance events that occurred during filming. We defined vigilance behavior as occurring whenever the focal individual lifted its head. The onset of a vigilance bout was considered the point at which the animal lifted its head (halfway through the raising of the head), and the end was considered the point at which the animal lowered its head again (halfway through the lowering of the head). From the video footage, we extracted the duration of each vigilance bout, summed all bouts, divided this sum by the total length of the filmed sequence, and multiplied by 100 to obtain a percent time spent vigilant. We also divided the total sum of bout durations by the number of bouts in the filmed sequence to obtain an average bout duration for each trial. Finally, we divided the number of bouts in a sequence by the length of the filmed sequence to obtain a rate of head raises. These three aspects of vigilance were the response variables used in our data analyses.

Data analysis

We tested assumptions of normality and homogeneity of variance using the Wilks-Shapiro Test and the Levene's Test, respectively. All three response variables met both assumptions once they were log-10 transformed. We used general linear mixed-effect models (GLMMs) to identify the variables that best explained vigilance. We considered each response variable separately, and we also analyzed data from adults and juveniles separately. We ran GLMMs for each of the three behavioral contexts in which vigilance was sampled (resting, feeding and nursing). In these models, we initially included all measured independent variables, and removed these terms sequentially according to the Akaike's Information Criterion (AIC; Burnham and Anderson 1998) until each model included only terms for which inclusion would significantly decrease the AIC of the model. In all models, hyena identity was entered as a random effect, because random terms allow for repeated sampling for the same focal individuals to avoid pseudo-replication (Pinheiro and Bates 2000). The final variables included in each model were not correlated with each other (highest correlation coefficient was 0.2). We used restricted maximum likelihood (REML) methods for model estimation. We present F and p values for the final models. Significance of random effects was evaluated using likelihood ratio tests by comparing models with and without random effects (Pinheiro and Bates 2000).

To compare vigilance among behavioral contexts, we averaged values for response variables recorded multiple times from each hyena engaged in a given activity, and analyzed these averages using an analysis of variance (ANOVA). We identified differences among the three activities with Tukey post-hoc tests. Similarly, to compare vigilance between juveniles and adults, we averaged the response variables for each hyena within a given age group (juveniles vs. adults) and a given activity (resting, feeding or nursing), and compared averages for each activity separately using t-tests. All analyses were performed in the statistical software package R, v.2.1.1 (R Development Core Team 2005), using two-tailed tests with an alpha level of 0.05. The GLMMs were done using the R library 'nlme' (Pinheiro et al. 2005). Unless otherwise indicated, response values are reported as means ± 1 standard error.

RESULTS

The number of observations collected and the number of individuals sampled in each behavioral context are reported in Table 1.1. We first describe differences in

Table 1.1. Sample sizes and average number of observations for individual juvenile and adult hyenas in the three behavioral contexts observed (resting, feeding and nursing).

	Juveniles				Adults			
Context	# of obs	# indiv. sampled	$\overline{X}$ (± SE) # obs / ind	Range of obs / ind	# of obs	# indiv. sampled	$\overline{X}$ (± SE) # obs / ind	Range of obs / ind
Resting	168	16	10.62 ± 1.32	1 to 18	409	35	11.88 ± 1.20	1 to 29
Feeding	101	18	5.42 ± 0.72	1 to 12	129	35	3. 71 ± 0.38	1 to 9
Nursing	43	15	2.87 ± 0.69	1 to 11	40	9	4. 67 ± 1.72	1 to 14
Totals	312				578			

vigilance among the three behavioral contexts, and then present results within each context. Regardless of the behavioral context, the following variables had no effect on any vigilance variables and were therefore removed from the models: Julian date, distance to nearest bushes, distance to nearest neighbor, strength of wind, grass height, location within the territory, sex, sex ratio of the group, and social rank.

Vigilance in different behavioral contexts

The time dedicated to vigilance by adult hyenas varied among behavioral contexts ($F_{2,76} = 13.26, p < 0.001, r^2 = 0.26$; Figure 1.1 a-c). Adults spent significantly more time vigilant while nursing than while feeding or resting (post-hoc tests, both $p < 0.001$; Figure 1.1a), but vigilance did not differ significantly between feeding and resting (post-hoc test, $p = 0.15$; Figure 1.1a). Rates and durations of head raises also varied significantly among activities (rates: $F_{2,76} = 83.71, p < 0.001, r^2 = 0.69$, Figure 1b; durations: $F_{2,76} = 90.50, p < 0.001, r^2 = 0.70$, Figure 1.1c), but in different ways. The highest rates were observed among feeding individuals, the lowest among resting individuals, and intermediate rates among nursing individuals (post-hoc tests, all $p < 0.01$; Figure 1.1b). The shortest durations were observed while feeding (post-hoc tests, $p < 0.001$), but durations did not differ significantly between nursing and resting (post-hoc test, $p = 0.89$; Figure 1.1c).

As was true among adults, the time spent vigilant by juvenile hyenas varied among behavioral contexts ($F_{2,47} = 62.81, p < 0.001; r^2 = 0.73$; Figure 1.1d-f). Juveniles spent significantly less time vigilant while nursing than while feeding or resting (post-hoc tests, both $p < 0.001$; Figure 1d), and behavior in the latter contexts did not differ

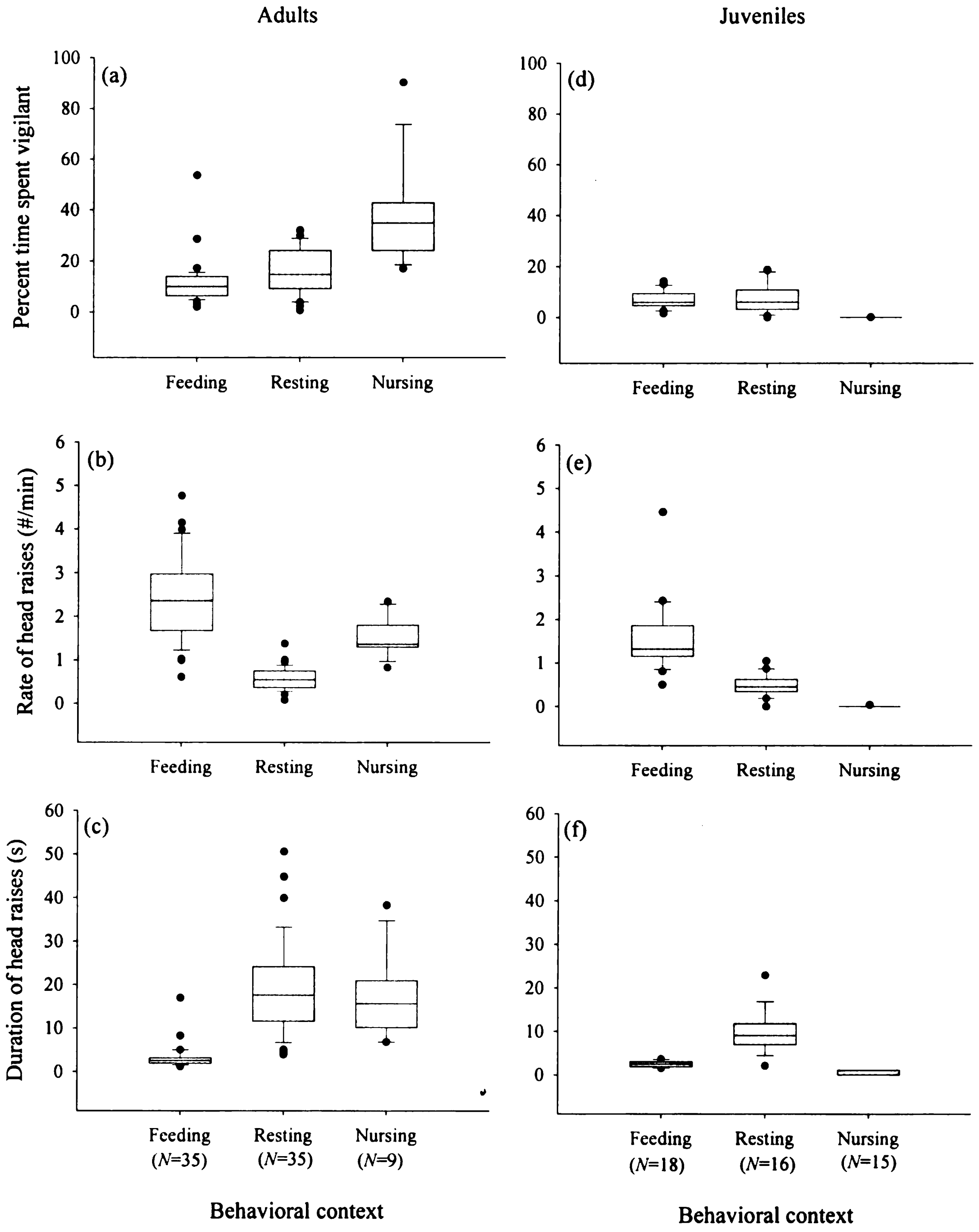

Figure 1.1. Effect of behavioral context on vigilance measures in adult (a - c) and juvenile hyenas (d - f). The line in each box represents the median, and the box encompasses the 25th percentile (lower limit) and the 75th percentile (upper limit); whiskers represent the 10th and 90th percentile, and data points outside the whiskers represent outliers. *N* represents the number of individual hyenas sampled in each context. Statistics for full models are available in the text.

significantly (post-hoc Tukey test, $p = 0.94$; Figure 1.1d). Rates and durations of head raises also varied significantly among contexts ($F_{2,47} = 90.47$, $p < 0.001$; Figure 1.1), but in different ways. As in adults, the highest rates were observed among juveniles engaged in feeding. Rates were the lowest among nursing juveniles, and intermediate rates were observed among juveniles at rest (post-hoc tests, all $p < 0.001$; Figure 1.1e). Resting individuals kept their heads elevated longer than did feeding individuals ($t_{33} = 8.43$; $p < 0.001$; Figure 1.1f). We did not compare durations of head raises when nursing to those during other contexts due to the low number of these observations; only 2 of the 15 juveniles sampled while nursing actually ever interrupted their nursing to scan the environment.

Juveniles spent significantly less time vigilant than adults in all behavioral contexts sampled. While resting, juveniles were less vigilant than adults ($\overline{X}_{\text{juveniles}} = 7.66 \pm 1.41$ %; $\overline{X}_{\text{adults}} = 16.17 \pm 1.55$ %; $t_{49} = 3.29$; $p = 0.002$; Figure 1.1a and d), which was driven by juveniles having shorter head raises than adults ($\overline{X}_{\text{juveniles}} = 10.01 \pm 1.28$ s; $\overline{X}_{\text{adults}} = 19.08 \pm 1.85$ s; $t_{49} = 3.28$; $p = 0.001$; Figure 1.1c and f). Rates of head raises did not differ significantly between juveniles and adults ($\overline{X}_{\text{juveniles}} = 0.48 \pm 0.07$ head raise/min; $\overline{X}_{\text{adults}} = 0.58 \pm 0.04$ head raise/min; $t_{49} = 1.20$, $p = 0.24$; Figure 1.1b and e). Juveniles spent significantly less time vigilant when feeding than did adults ($\overline{X}_{\text{juveniles}} = 6.78 \pm 0.86$ %; $\overline{X}_{\text{adults}} = 11.50 \pm 1.51$ %; $t_{51} = 2.75$; $p = 0.008$; Figure 1.1a and d); this difference was driven by juveniles raising their heads less frequently than adults ($\overline{X}_{\text{juveniles}} = 1.63 \pm 0.20$ head raise/min; $\overline{X}_{\text{adults}} = 2.43 \pm 0.17$ head raise/min; $t_{51} = 3.00$;

$p = 0.004$; Figure 1.1b and e). Durations of head raises were similar between juveniles and adults ($\overline{X}_{\text{juveniles}} = 2.49 \pm 0.16$ s; $\overline{X}_{\text{adults}} = 3.11 \pm 0.46$ s; $t_{51} = 0.74, p = 0.46$; Figure 1.1c and f). Juvenile hyenas also spent significantly less time vigilant than their mothers when nursing ($\overline{X}_{\text{juveniles}} = 0.01 \pm 0.01$ %; $\overline{X}_{\text{mothers}} = 38.40 \pm 7.28$ %; $t_{22} = 29.04; p < 0.001$; Figure 1.1a and d); in contrast to cubs, mothers raised their heads frequently while nursing their litters ($\overline{X}_{\text{juveniles}} = 0.002 \pm 0.0006$ head raise/min; $\overline{X}_{\text{mothers}} = 1.52 \pm 0.16$ head raise/min; $t_{22} = 19.09; p < 0.001$; Figure 1.1b and e).

Determinants of vigilance within each behavioral context

Three explanatory factors remained in the final model for vigilance among resting adult hyenas: group size, time of day, and hyena identity. Adult hyenas spent less time vigilant when resting in large than small groups ($F_{1,372} = 9.88, p = 0.002$; Figure 1.2a) and more time vigilant in the AM period than in the PM period ($\overline{X}_{\text{AM}} = 18.29 \pm 1.71$ %, $N = 196$; $\overline{X}_{\text{PM}} = 11.36 \pm 0.89$ %, $N = 213$; $F_{1,372} = 19.67, p < 0.0001$). Hyena identity was also a strong predictor of the percent time spent vigilant while resting (likelihood ratio test statistic distributed as $\chi^2 = 22.78, p < 0.0001$; Figure 1.3). In other words, individual hyenas exhibited either consistently high or low vigilance over multiple observations in which they were resting. We inquired whether the same individuals that were highly vigilant in one behavioral context were also highly vigilant in other contexts, but we found no statistically significant correlations (all $p > 0.3$). Among juveniles, we did not detect any effect of time of day ($F_{1,149} = 0.38, p = 0.54$) or identity ($\chi^2 = 1.34, p = 0.25$) on vigilance, so these variables were removed from the model. Like adults,

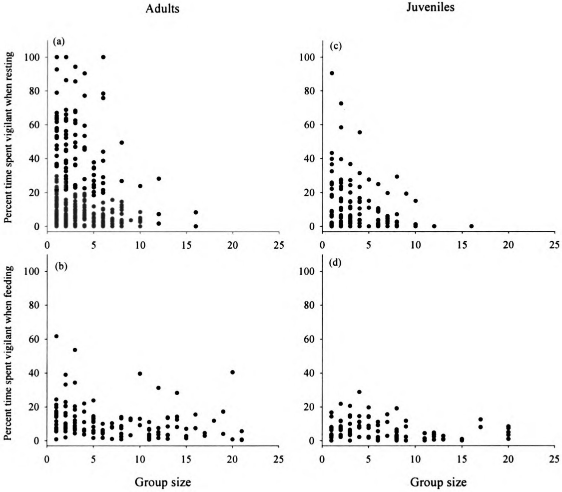

Figure 1.2. Effect of group size on the percent time spent vigilant by adults (a and b) and juveniles (c and d) when resting (top row, panels a and c) and when feeding (bottom row, panels b and d). Group size represents the number of hyenas resting or feeding at a given location. Each data point represents an observation of an individual hyena. Group size was a significant factor in all four cases (mixed-effect models, all *p*s < 0.05).

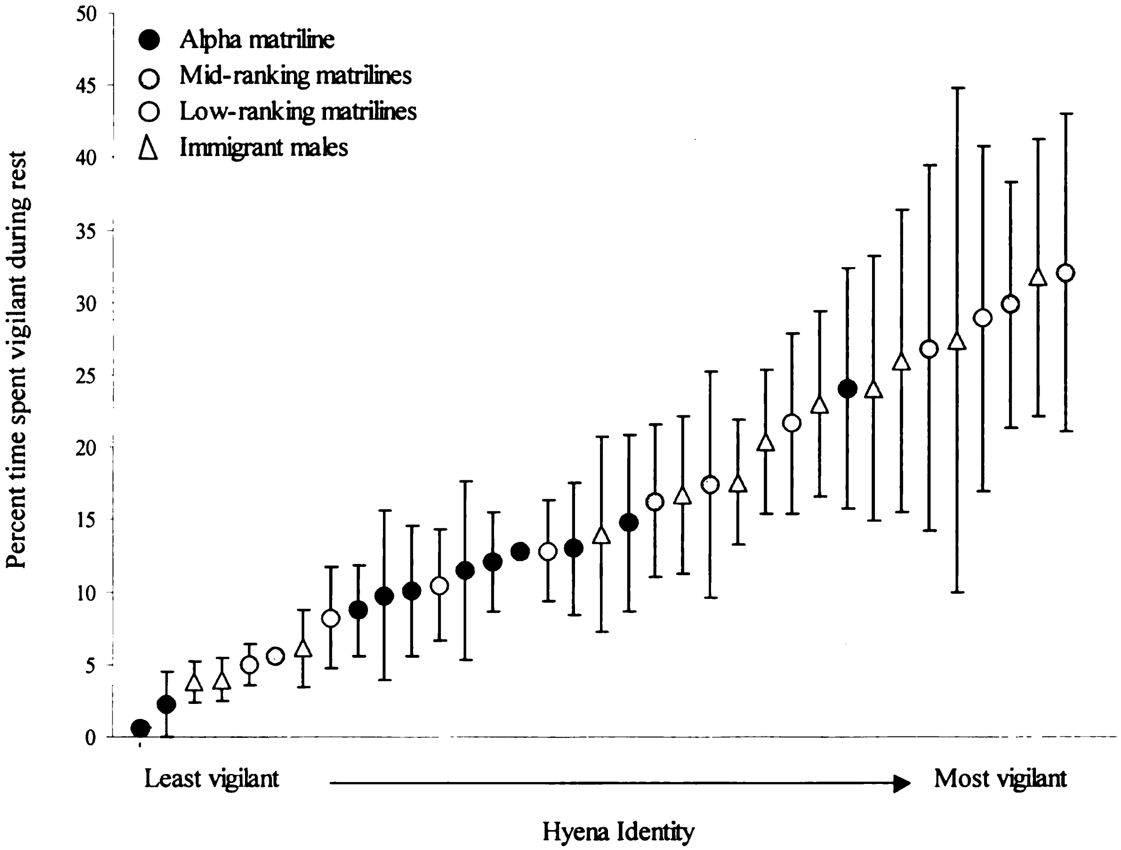

Figure 1.3. Average percent time spent vigilant during rest (± SE) by each adult focal hyena ($N = 35$) ranked from least to most vigilant. Symbols indicate social rank categories, with filled circles representing the alpha matriline, gray circles the middle-ranking matrilines, empty circles the lowest-ranking matrilines, and empty triangles the immigrant males. Identity was a significant predictor of vigilance ($p < 0.0001$), whereas social rank was not ($p > 0.05$). Statistics are from a multivariate mixed-effect model in which group size was also included. Statistics for the whole model are available in the text.

juveniles spent less time vigilant while resting in large than small groups ($F_{1,151} = 10.69$, $p = 0.0013$; Figure 1.2c).

Three explanatory factors remained in the final model for the percent time spent vigilant while feeding among adult hyenas: group size, food quality and hyena identity. Adult hyenas spent less time vigilant when feeding in large than small groups ($F_{1,92} = 16.03$, $p = 0.0001$; Figure 1.2b) and when feeding on food of high- than low-quality ($F_{1,92} = 6.19$, $p = 0.01$; Figure 1.4). Hyena identity was also a good predictor of the percent time spent vigilant while feeding ($\chi^2 = 4.96$, $p = 0.026$). We did not detect any effect of hyena identity on juvenile vigilance ($\chi^2 = 0.10$, $p = 0.75$). Like adults, juveniles spent less time vigilant when feeding in large than small groups ($F_{1,81} = 6.38$, $p = 0.01$; Figure 1.2d) and when feeding on food of high- than low-quality ($F_{1,81} = 5.82$, $p = 0.02$; Figure 1.4).

Only one factor remained in the final model explaining variation in vigilance of adult female hyenas nursing their cubs: age of the litter being nursed. As the litter being suckled grew older, mothers spent less time vigilant when nursing ($F_{1,30} = 9.98$, $p = 0.004$; Figure 1.5). In contrast to results obtained when adult females were engaged in other behaviors, adult female identity was not a significant predictor of vigilance while nursing ($\chi^2 = 0.002$, $p = 0.97$). In contrast to adults, juvenile hyenas were seldom vigilant while suckling from their mothers: juveniles raised their heads during only 2 of the 43 trials, resulting in very low percent time spent vigilant ($\overline{X} = 0.01 \pm 0.001$ %).

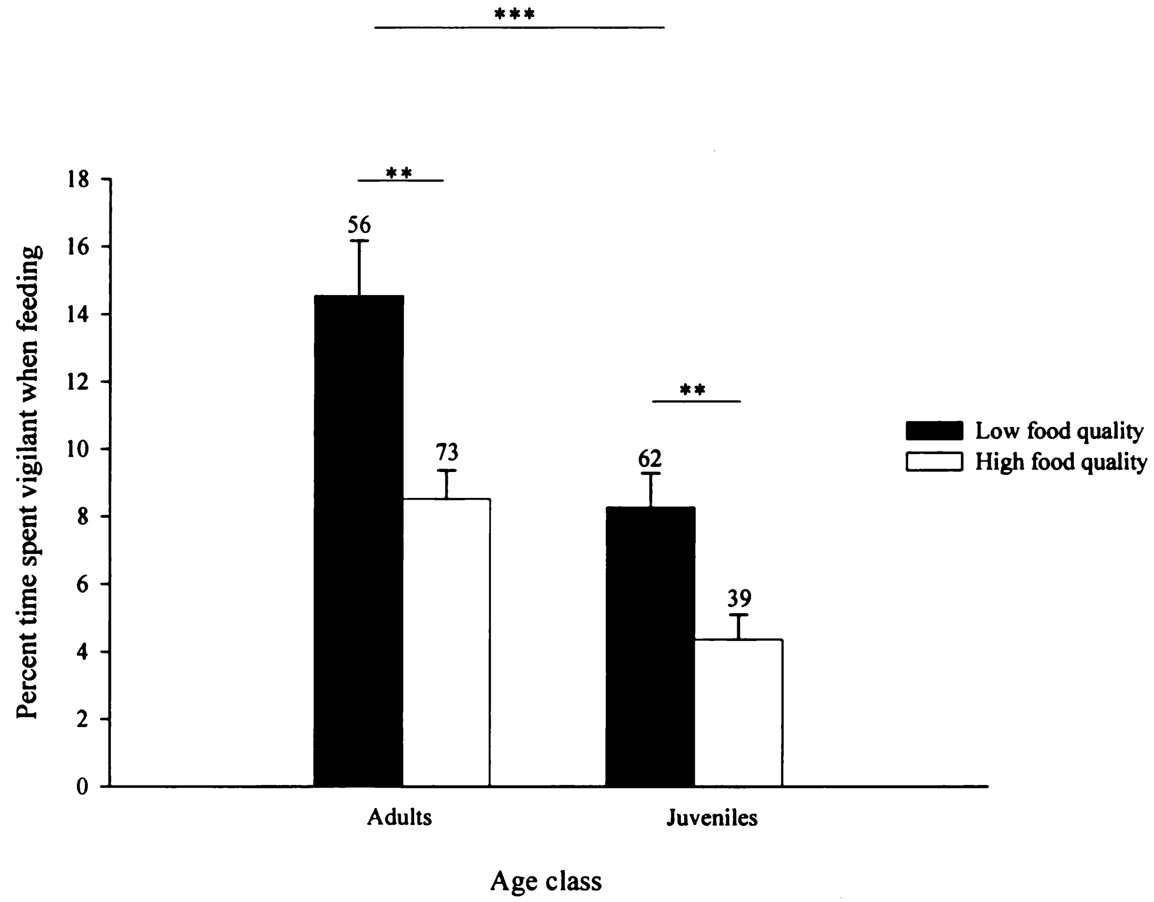

Figure 1.4. Effect of food quality (low quality: black bars; high quality: white bars) on the percent time spent vigilant by adult and juvenile hyenas. Means (± SE) are represented, with the number of feeding observations indicated above each bar. Quality of food was assigned as high if it was fresh meat, or low in other cases. Asterisks represent a statistically significant difference (mixed-effect model, in which group size and identity were included; $^{**}p < 0.01$; $^{***}p < 0.001$). Statistics for the full models are available in the text.

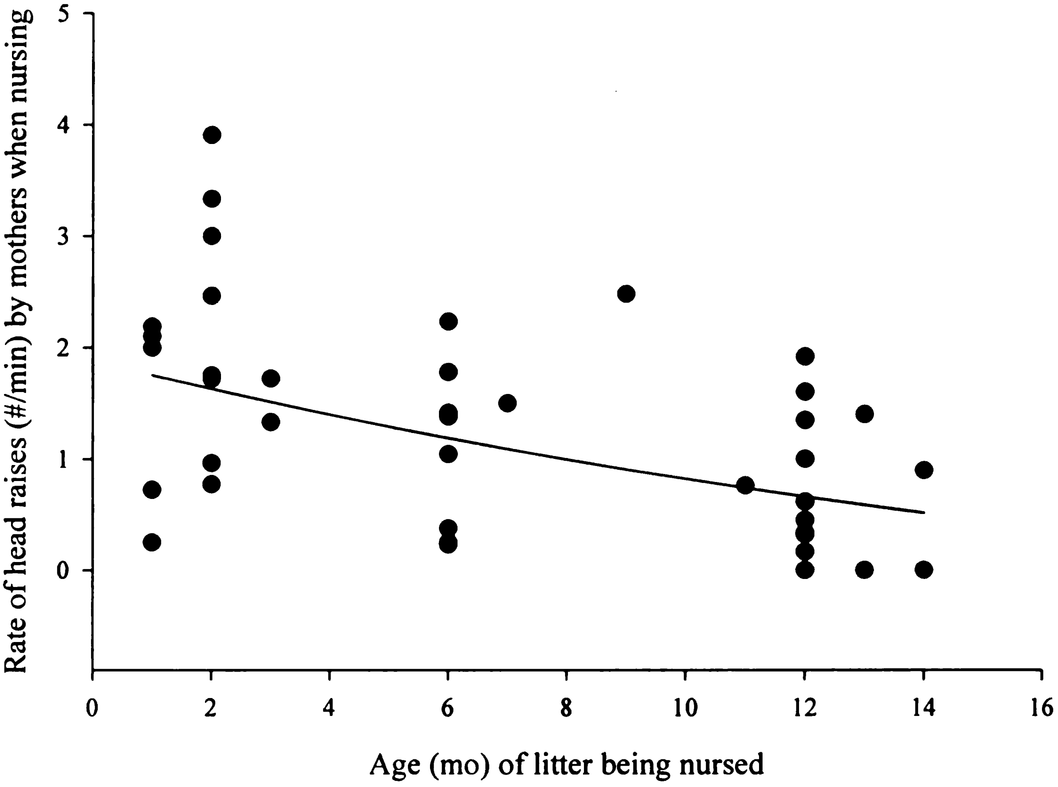

Figure 1.5. Effect of age of the suckling litter on the rate of head raises by adult female hyenas during nursing. Each data point represents a single nursing event (*N* = 40), and 9 different females are represented in this figure. The line represents a linear regression performed on transformed data and plotted on untransformed data. There was a significant effect of litter age on the rate of head raises by mothers (mixed-effect model, $p = 0.001$).

DISCUSSION

Our results supported the hypothesis that hyena vigilance functions more importantly to detect inter-specific than intra-specific threats. One line of evidence supporting this idea was that hyenas were more vigilant in small than large groups regardless of the behavioral activity in which they were engaged. If hyenas were directing their vigilance toward potential intra-specific threats as when avoiding aggression, we would not expect to see such a decrease in vigilance as group size increases. Another line of evidence was that we observed the same group-size effect among both feeding and resting individuals, indicating that vigilance was not used as a means to detect potential foraging competition or kleptoparasitism (Lendrem 1983; Arenz 2003; Beauchamp 2003; Roberts 2003). Other lines of evidence confirmed that vigilance was not used to detect intra-specific threats: there were no effects of social rank on vigilance, nor were hyenas more vigilant on the edge than in the center of their territory, or when closer than further to conspecific neighbors. Hyenas were also more vigilant when nursing younger than older litters, but this may be a response to either inter- or intraspecific threats, as infanticide, although rare, is known to occur in this species (Kruuk 1972; East and Hofer 2002; White 2005).

We found no support for the idea that vigilance functions as a means to detect potential mates in spotted hyenas. We did not detect any differences in vigilance between sexes, nor any effect of sex-ratio in the current group. Thus, adults were similarly vigilant whether they were resting with only members of their sex, or with varying combinations of male and female adult hyenas. Similarly, we did not find any support for the hypothesis that vigilance by hyenas may function to detect potential prey, as vigilance was not affected by Julian date, and hyenas were equally vigilant during rest and while feeding. It is not surprising that hyenas did not use vigilance to monitor prey, as spotted hyenas are not stalking predators; instead, they are coursing predators (Kruuk 1972) that rely on endurance. Hyenas looking for animals to hunt typically run toward a herd of ungulates, then stop to watch the prey animals running before picking a specific individual to chase (Kruuk 1972; Holekamp et al. 1997).

Although vigilance has been reported to detect inter-specific threats in many species (reviewed in Elgar 1989; Caro 2005a), we were surprised to witness this effect in hyenas because of the very high levels of intra-specific competition observed in this species (Kruuk 1972; Frank 1986). Many social species, including primates, are known to use vigilance to monitor conspecifics (e.g. Waite 1987; Treves 2000; Hirsch 2002; Cameron and du Toit 2005; Nutsukake 2006; Lung and Childress 2007; Pays and Jarman 2008). It is interesting to note that, although hyena society resembles those of cercopithecine primates more than those of other carnivores (Drea and Frank 2003; Holekamp et al. 2007), hyenas still displayed a group-size effect, whereas many primates do not (reviewed by Treves 2000). In addition, the group-size effect we observed was similar for adult and juvenile hyenas. We are only aware of two studies, both of birds, that have evaluated the group-size effect for adults and juveniles in a single species (Boukhriss et al. 2007; Avilés and Bednekoff 2007). Contrary to our results, in these studies, a group-size effect was detected for adults but not for juveniles when birds were foraging in mixed-age flocks.

We did not detect any evidence for social vigilance in hyenas; however, hyenas may be monitoring conspecifics without adjusting vigilance time, or by using modalities other than sight. Indeed, we noticed that resting hyenas exhibited multiple ear-twitching movements even in the absence of insects, suggesting that they are using auditory cues to monitor the environment. In addition, it has been suggested in studies of birds (Bednekoff and Lima 2005; Fernandez-Juricic et al. 2005) that animals might be using peripheral vigilance to monitor conspecifics, and overt vigilance to monitor predatory threats. The avian species used in such studies have broad fields of vision (e.g. Guillemain et al. 2002), allowing individuals to be vigilant even with their heads down. However, it is unlikely that spotted hyenas could monitor conspecifics with such peripheral vigilance. In contrast to birds, rodents or ungulates, hyenas rely heavily on binocular vision, and their eyes are located on the front rather than the sides of the head (Bradbury and Wehrencamp 1998), so their fields of view are much more restricted. Further, contrary to recent studies showing that animals can be vigilant while handling food (e.g. Lima and Bednekoff 1999, Makowska and Kramer 2007), the behavioral contexts in which we sampled hyenas restricted their visual fields: hyenas often had their heads deep in a carcass while feeding, or had their eyes closed while resting and nursing. Thus, it is unlikely that hyenas used peripheral vigilance while engaged in the behavioral activities we observed.

Spotted hyenas varied their vigilance based on the behaviors in which they were currently engaged, indicating that different activities may involve different tradeoffs. We assume that hyenas should attempt to optimize the relationship between the benefits of a given activity and its perceived risk. This was suggested, for instance, by our observation that hyenas were less vigilant when feeding on high- than low-quality meat; when feeding on high-quality meat, the cost of vigilance would rise by limiting intake of richer food. Similarly, female hyenas spent the most time vigilant when they were nursing the youngest cubs: young cubs are more vulnerable to predation than older cubs, resulting in a enhanced need for the mother to monitor the environment against threats (Caro 1987). We expected adult hyenas to be most vigilant when resting, a behavioral activity in which we assumed the cost of vigilance would be minimal. However, vigilance did not differ significantly between feeding and resting hyenas, indicating that either vigilance while resting has a higher cost than we expected, or resting is as risky a behavior as feeding. It is interesting to note that, although hyenas spent similar time vigilant during both feeding and resting, this was obtained by using different strategies: resting hyenas exhibited infrequent long vigilance bouts, whereas feeding hyenas exhibited frequent short vigilance bouts. This was true for both adult and juvenile hyenas in our study, and this has also been documented in other carnivore species (Chapter 4). The use of different strategies may be due to varying tradeoffs associated with resting and feeding, or to individuals monitoring different aspects of their environment when engaged in these two activities.

Few previous studies, all done on primates, have compared vigilance in a single species across several behavioral contexts (Cords 1995; Cowlishaw 1998; Treves et al. 2001; Hirtch 2002; Kutsukake 2006), although some studies have focused specifically on sleeping birds (Lendrem 1983; Lendrem 1984; Gauthier-Clerc et al. 1994, 1998, 2002; Gauthier-Clerc and Tamisier 2000). Contrary to the hyenas observed here, primates were found to be less vigilant while foraging than while resting in all these studies. It is difficult to assess whether this difference is based on biological differences between carnivores and primates, or whether it is based on methodological differences regarding what is considered 'resting behavior': hyenas were considered to be resting in this study when lying down with their eyes closed, whereas primates were often considered to be resting when not actively engaged in any specific activity.

We found a strong effect of individual hyena identity on adult vigilance during rest and feeding. Other studies have included the identity of focal individuals in statistical models as a random factor (e.g. Treves et al. 2001; Kutsukake 2007; Atwood and Gese 2008), but the results regarding this identity effect were not reported or discussed; its inclusion in statistical models was used strictly to control for individual variation. Our results indicate that some adult hyenas were consistently 'relaxed' while others were consistently 'worried' about their environments. This finding is similar to those from studies examining animals that vary along the shy-bold continuum (e.g. Coleman and Wilson 1988; López et al. 2005; Quinn and Cresswell 2005; van Oers et al. 2005; Réale et al. 2007). We did not find that trends in hyena vigilance were consistent between behavioral contexts; for example, hyenas that were consistently vigilant while resting were not necessarily those that were consistently vigilant while feeding. Such variation should caution against generalizing results from one behavioral context to another. Interestingly, we did not find any effect of hyena identity among juveniles, suggesting that experience may play a role in determining the extent to which a particular individual is vigilant as an adult.

Juvenile hyenas were less vigilant than adults, regardless of the activity in which they were engaged. Similar results regarding variation among age classes have been found in other animals including birds (e.g. Avilés and Bednekoff 2007), ungulates (e.g. Alados 1985; Burger and Gochfeld 1994), rodents (e.g. Loughry 1993; Arenz and Leger 1997; Monclús et al. 2006) and primates (e.g. De Ruiter 1986; Fragaszy 1990). However, a few studies have reported mixed effects or no effects of age on vigilance (e.g. Alberts 1994; McDonough and Loughry 1995; Blumstein 1996). The lower vigilance we observed among juvenile than adult hyenas can be explained by several hypotheses that are not mutually exclusive. Juvenile hyenas might require more rest or higher food ration than adults, they might rely on nearby adults to detect approaching threats, or they might need more time during ontogeny to correctly identify circumstances under which they need to be vigilant (Caro 2005a).

Ecological factors that have been found to affect vigilance in many species of prey were not found to affect vigilance in hyenas (Caro 2005a). For instance, despite large sample sizes and high resolution, we did not detect any effect of distance to nearest bushes on vigilance, nor of grass height or wind strength. This might be due to differences in tradeoffs experienced by prey and predators. However, resting adult hyenas were more vigilant in the morning than in the afternoon in all seasons. Hyenas resting in the morning may be more alert after the night of activities, whereas hyenas sampled in the afternoon, which have just spent the majority of the day resting, may be less diligent. Another possibility is that hyenas perceive their environment as riskier in the morning.

In conclusion, we have shown that spotted hyenas relied on vigilance to detect inter-specific threats as demonstrated by group-size effects in adults and juveniles, that vigilance varied among behavioral context, that adult hyenas exhibited consistent vigilance across multiple trials within a given context, but not between contexts, and that juveniles exhibited less vigilance than adults. Our study thus sheds light on the relative importance of ecological functions of vigilance in a large, gregarious carnivore.

CHAPTER TWO

DEVELOPMENT OF THREAT-SENSITIVE BEHAVIORS IN SPOTTED HYENAS: OBSERVATIONAL AND EXPERIMENTAL APPROACHES

INTRODUCTION

Compared to adults, juvenile mammals appear poorly equipped to deal with danger (Janson and van Schaik 1993). Juveniles often fail to recognize or detect dangers as rapidly as adults do, and juveniles sometimes respond inappropriately to alarm signals produced by conspecifics (e.g., Seyfarth and Cheney 1986; Janson and van Schaik 1993; Hollén and Manser 2006). Perhaps because juveniles are often tacitly assumed to be imperfect adults, they are often ignored in studies of threat-sensitive behaviors. Indeed, most such studies focus exclusively on adult responses to threat stimuli (reviewed in Caro 2005a). However, as noted by Janson and van Schaik (1993), juvenile and adult conspecifics may confront different sets of selection pressures, and juvenile behavior may therefore reflect responses to age-specific challenges (e.g. Holmes 1984; Janson and van Schaik 1993; Hoogland et al. 2006; Boukriss et al. 2007). Thus, juveniles might be expected to adopt different strategies for dealing with danger than do adults. Indeed, age-specific adaptive strategies in antipredator behavior have now been documented in primates, ground squirrels, lizards and birds (e.g. Janson and van Schaik 1993; Hersek and Owings 1994; Mateo 1996; Ramakrishnan and Coss 2000; McCowan et al. 2001; Martin and López 2003; Platzen and Magrath 2004; Stone 2007). One of our goals here was to extend our knowledge about the ontogeny of threat-sensitive behaviors to include large mammalian carnivores. We focused specifically on spotted hyenas (*Crocuta crocuta*).

Spotted hyenas are particularly well-suited for studies of ontogenetic variation in behavior (e.g. Holekamp and Smale 1993). In contrast to many other mammals, hyenas have a life history characterized by discrete stages, each of which begins and ends with observable milestones (Holekamp and Smale 1998). Although hyenas are top predators in the food webs of many African ecosystems, they encounter a number of serious threats, particularly during early developmental stages, and most die violent deaths (Kruuk 1972; Watts 2007). Indeed, fewer than 50 % of cubs born survive to adulthood, and mortality rates diminish rapidly after spotted hyenas reach reproductive maturity (Frank et al. 1995; Watts 2007). This pattern suggests that juvenile hyenas might be more vulnerable than adults to negative effects of competition and intraguild predation.

Most hyena mortality is caused by lions, especially male lions (Cooper 1991; Frank et al. 1995; Trinkel and Kastberger 2005). Furthermore, young hyenas are substantially more vulnerable to lion-caused mortality than adults, particularly after they become independent of dens (Kruuk 1972; Frank et al. 1995; Watts 2007). Interestingly, however, in addition to representing a potential source of injury or mortality for hyenas, lions may also offer benefits by providing hyenas with opportunities to acquire food by scavenging (Kruuk 1972; Cooper 1991; Watts and Holekamp 2008). Hyenas have been shown to be highly successful at scavenging from kills abandoned by lions, and at stealing kills from lions if the hyenas are present together in sufficient numbers (Kruuk 1972; Cooper 1991; Höner et al. 2002). Thus, hyenas might potentially either avoid lions to minimize risk of injury and death, or approach them to explore the possibility of acquiring food. Furthermore, the nature of the relationship betweeen lions and hyenas might be expected to change during ontogenetic development as hyenas gain motor coordination, strength and experience. Previous work on carnivores has examined inter-specific competition, intra-specific threats, and avoidance of intraguild competitors (e.g. McComb et al. 1993, 1994; Durant 1998, 2000), but age-specific variation in stimulus valence has not, to our knowledge, previously been explored in studies of threat-sensitive behaviors in carnivores.

Here we used two different approaches to evaluate ontogenetic variation in the threat-sensitive behavior of spotted hyenas. First, we evaluated naturally-occurring vigilance in the absence of any immediate threats when hyenas were resting alone. We expected that juvenile hyenas would be less vigilant than adults, because juveniles may need more rest than adults, or because they are relatively naïve about how to correctly identify circumstances under which to be vigilant (Kruuk 1971; Caro 2005a). Second, we performed playback experiments of lion roars to juvenile and adult hyenas. Because juvenile hyenas are more vulnerable than adults to mortality caused by lions, and because juvenile hyenas usually have poorer motor coordination as well as shorter limbs and thus more limited escape capabilities than adult hyenas (Frank et al. 1991), we expected that juveniles would respond to lions with much more caution than adults. Finally we inquired whether responses by hyenas varied with the sex of the lions producing acoustic stimuli. Male lions are the leading natural mortality source for both juvenile and adults hyenas (Cooper 1991; Frank et al. 1995). Therefore, we expected adult hyenas to respond differently to acoustic stimuli produced by male and female lions, but we expected that juvenile hyenas would be unable to make this discrimination if the distinction between male and female lions was learned during the juvenile period.

METHODS

Study site and study animals

All work was conducted in the Masai Mara National Reserve (henceforth the Reserve – 1,500 km^2) in southwestern Kenya (1°40′ S, 35°50′ E) between August 2005 and June 2006. The Reserve is an area of open, rolling grasslands inhabited by large numbers of ungulates (Sinclair and Norton-Griffiths 1979); this habitat therefore supports high densities of both lions and hyenas (0.439 lions / km^2, Ogutu and Dublin 2002; and 0.95 hyenas / km^2, Watts 2007).

Spotted hyenas are gregarious carnivores that live in social groups, called clans, containing up to 80 individuals (Kruuk 1972). Three clans that inhabit the Reserve were monitored during data collection here, and playback experiments were carried out on individuals from all three clans. All hyenas were known individually by their unique spots. Birth dates (± 7 days) and ages of all studied hyenas were determined using previously described methods (Holekamp et al. 1996). Reproductive maturity in spotted hyenas occurs at approximately 24 months of age (Glickman et al. 1992). Here, juvenile subjects were those between 9 and 24 months of age, and subjects older than 24 months were considered to be adults. All tested or observed subjects were independent of dens. Social ranks were known for all hyenas based on wins and losses in dyadic agonistic interactions (described in Holekamp et al. 1996). We classified individuals as high-ranking if they were in the upper half of the social dominance hierarchy, and as low-ranking if they were in the lower half of the hierarchy. Note that juveniles were assigned the same ranks as their mothers.

Naturalistic observations of vigilance in the absence of threats

Hyenas were videotaped in the field to document their natural vigilance behavior. Daily observations of the study animals took place between 0600 - 1000 h and 1600 - 1900 h from a field vehicle that served as a mobile blind. During these observations, the field vehicle was parked no closer than 15 m from the focal hyena. Hyenas were well habituated to our vehicle as all natal animals were exposed to it since infancy. Vigilance data were only taken when we found a solitary hyena resting, defined as lying down in the absence of food for at least five minutes, and at least 400 m from the nearest conspecific. Upon finding a suitable subject, we set up a Sony DCR H65 video camera mounted on a window tripod, and videotaped the focal hyena for 2 - 7 min ($\overline{X} = 4.00 \pm 0.07$ min). We divided hyenas into 4 age groups: 8 - 16 months, 17 - 24 months, 25 - 48 months, and more than 48 months. If the same hyena was sampled repeatedly within an age group, we averaged the data points for that individual and used this average in subsequent analyses.

Playback stimuli

Hyenas were exposed to two types of sounds during playback experiments: lion roars were treatment sounds, and baboon contest 'wahoos' were used as control sounds. Lion roars should signal potential danger to hyenas and, because lions often roar at their kills (C. Packer, pers. com.), they should also potentially indicate the presence of food. Baboons (*Papio anubis*) abound in the Reserve and their contest wahoo calls are similar in intensity and frequency to lion roars (Fischer et al. 2002, 2004; Kitchen et al. 2003).

Male baboons produce these calls during aggressive interactions with conspecifics (Fischer et al. 2002). Baboons represent no threat to hyenas, nor do hyenas from the Reserve hunt baboons. Wahoos therefore represent sounds with which hyenas are familiar, but which should neither attract nor repel them.

Prior to the start of our study, we created a library of sound stimuli for use in the playback experiments. Recordings of lion roars were obtained from Craig Packer ($N = 8$) and from the Borror Laboratory of Bioacoustics ($N = 5$). Each recording consisted of a single bout of roars ($\overline{X}_{\text{number of roars per bout}} = 19$; $\overline{X}_{\text{roar duration}} = 39.23$ s) emitted by a single adult female ($N = 5$) or male ($N = 8$) lion. Roars produced by male lions are acoustically different from roars produced by females in that males produce roars of lower pitch than females (Pferfferle et al. 2007). Lion sounds were not manipulated here. Recordings of baboon wahoos ($N = 15$) were obtained from A. L. Engh. Each wahoo recording consisted of a series of ‘wahoos’ ($\overline{X}_{\text{number of wahoos per bout}} = 8.53$; $\overline{X}_{\text{duration of the stimulus}} = 25.3$ s) emitted by a single adult male. Six of the fifteen wahoo recordings were manipulated using the software Pratt either to lengthen or shorten the call, or to remove vocalizations produced by additional baboons.

Playback experiment set-up

Experimental and control sounds were played back from our research vehicle to solitary hyenas resting on open savannah. Here, a hyena was considered to be resting if it was lying down for more than ten minutes. All hyenas were tested under similar conditions, near the centers of their clan territories. Upon finding a suitable subject, the car was positioned approximately 100 m (range: 73 to 130 m; $\overline{X}_{\text{distance}} = 91 \pm 2.01$ m) from the subject hyena, at an angle of approximately 45 degrees to the plane formed by a straight line between the subject and the observer, who was videotaping the hyena's response.

Recordings used in the field were picked randomly from the sound library, but no recording was used more than three times to minimize pseudo-replication (McGregor et al. 1992). The recordings were played from a Creative Nomad Jukebox 3 linked to two loud speakers (Fender Passport P-150) placed on window mounts facing away from the focal hyena, and thus hidden by the car. The two speakers were separated only by about 20 cm. Both roars and wahoos are loud, low frequency calls (Fischer et al. 2002; Pferfferle et al. 2007), requiring large speakers and high amplification when played back. Sound amplitude was calibrated by ear to match natural sounds. The playbacks were carried out between 0600 - 0900 hours and 1700 - 1900 hours when both lion roars and baboon wahoos are heard naturally in this environment.

Before playing back any sound, all equipment was set-up and turned on, and a window-mounted digital video camera aimed at the focal hyena. The observer (WMP) started filming at least three minutes before sound onset; filming continued throughout the duration of the playback, and for at least five minutes after sound onset. Once sound onset occurred, a second observer in the same vehicle recorded the distance between the focal hyena and the car every five seconds using a Bushnell laser range finder.

Most hyenas were exposed to both a lion roar and a baboon wahoo in random order, with playbacks to any given hyena separated by at least two weeks (and, on average, by 67 ± 10 days) to avoid habituation (McGregor et al. 1992). Not all hyenas were exposed to both sounds due to lack of opportunities in the field. We obtained data for both types of playbacks from 18 hyenas, but 11 other hyenas were exposed to only one of the two sound stimuli.

Data extraction from video tapes

We reviewed videotapes using a Sony DRC TRV900 digital camcorder that superimposed a time code on the screen with a precision of 0.33 s, with each video frame uniquely labeled. From tapes of naturally-occurring vigilance, we extracted information on all vigilance events that occurred during filming. We defined vigilance behavior as occurring whenever the focal individual lifted its head. The onset of a vigilance bout was considered the point at which the animal lifted its head (halfway through the raising of the head), and the end was considered the point at which the animal lowered its head again (halfway through the lowering of the head). From the video footage, we extracted the duration of each vigilance bout, summed all bouts, divided this sum by the total length of the filmed sequence, and multiplied by 100 to obtain a percent time spent vigilant. In our experimental work, we extracted the following data from each video tape for both pre- and post-playback periods: 1) seconds spent orienting toward the speakers; 2) seconds spent resting (when individuals were lying motionless with their heads down); 3) seconds spent approaching the speakers, avoiding the speakers, or not moving in relation to the speakers; and 4) the rate of movement (in meters per minute) of the focal hyena. We also extracted the latency to first movement by the hyena after sound onset. This included such events as the hyena standing up, but we did not count grooming behavior as a first movement. Hyenas that never moved toward or away from the speakers were assigned a latency to first movement of five minutes, as filming usually stopped five minutes after sound onset.

Data analysis

We tested assumptions of normality and homogeneity of variance in our observational data using the Wilks-Shapiro Test and the Levene's Test, respectively. The percent time spent vigilant while resting alone met both assumptions once it was square-root transformed. We used a one-way ANOVA to test the effect of age group on the percent time spent vigilant, and we assessed differences between age groups using a post-hoc Tukey test. To compare overall juvenile vigilance to adult vigilance, we used a Student t-test on the transformed percent time spent vigilant. In addition, we used linear regressions to examine the effect of social rank on hyena vigilance.

We tested assumptions of normality and homogeneity of variance in our experimental playback data. Only latency to first movement met both assumptions once it was log-10 transformed. All other variables were non-normal, even after transformations. Therefore, we used non-parametric tests in the analyses of all variables except latency to first movement. In addition, we used linear regressions to examine the effect of age on responses to playbacks within juvenile and adult age groups separately. We examined the effect of social rank on all response variables, first among all individuals using linear regression, and second among juveniles or adults separately, using a Fisher exact probability test to compare low- and high-ranking individuals.

We then evaluated the effect of age group (juveniles vs. adults) and playback type (baboon or lion) on hyena responses. We began by comparing the percent time hyenas spent resting, orienting and moving before and after each playback, using Wilcoxon signed rank tests for paired samples. We then compared responses between lions roars and baboon wahoos within each age group using Wilcoxon-Mann-Whitney tests for non-paired data (Siegel and Castellan 1988). In the remainder of our analyses, we only considered responses to lion roars. In this subset, we used chi-square tests, applying Yates' correction for small sample sizes as necessary, to examine the effect of age group on whether or not subjects moved in response to playback sounds (Zar 1999). We then compared juveniles and adults with respect to the percent time spent avoiding, not moving, or approaching the sound source after a lion roar using Wilcoxon-Mann-Whitney tests for non-paired data. Here, we used a one-tailed test, as the hypothesis being tested predicted that juveniles would react more negatively than adults to a lion roar. We used a two-way ANOVA to test the effects of the sex of the lion roaring, and the age group of the responding hyena, on latency to first movement. Finally, we compared rates of movement made by hyenas after roars emitted by male and female lions using a Wilcoxon-Mann-Whitney test. Here again we used a one-tailed test, as the hypothesis being tested predicted that hyenas would move at higher rates after hearing roars emitted by male than female lions. We performed retrospective power analysis if we found no significant differences between juveniles and adults after roar onset to determine the effect size detectable by our design (Thomas 1997; Orrock et al. 2004).

All analyses were performed in the statistical software package R, v.2.1.0 (R Development Core Team 2005), using an alpha level of 0.05. All tests were two-tailed except the two indicated above. Unless otherwise indicated, means ± 1 standard error are represented.

RESULTS

Naturalistic observations of vigilance in the absence of immediate threat

We obtained vigilance observations for 9 hyenas between 8 and 16 months of age, 12 hyenas between 17 and 24 months, 17 hyenas between 25 and 48 months, and 15 hyenas 49 months and older. When resting alone in open savannah, age groups varied in the percent time spent vigilant ($F_{3,\ 49} = 4.14$, $r^2 = 0.20$, $p = 0.01$; Figure 2.1), with the youngest age group showing less vigilance than the oldest age group (post-hoc test, $p = 0.012$). The youngest hyenas sampled (between 8 and 16 months of age) spent an average of 5.88 ± 3.0 % of their time vigilant, whereas adults older than 48 months of age spent an average of 18.16 ± 3.52 % of their time vigilant. Hyenas in the two age groups older than 24 months showed nearly identical levels of vigilance, but hyenas in the 17 – 24 months age group showed intermediate values between the two older groups and the youngest group (Figure 2.1). Overall, we observed that hyenas younger than 25 months differed from those 25 months and older ($t_{51} = 3.12$, $p = 0.003$). Thus, it appears that hyenas reach adult-like vigilance after 24 months of age. There were no effects of hyena's social rank on the percent time spent vigilant ($p > 0.1$).

Common responses to playbacks

We carried out a total of 22 playbacks on juvenile hyenas (10 baboon playbacks and 12 lion roar playbacks), and a total of 25 playbacks on adult hyena (12 baboon playbacks and 13 lion roar playbacks). Although juveniles tested here included hyenas from 9 to 24 months of age, age did not significantly affect any of the response variables

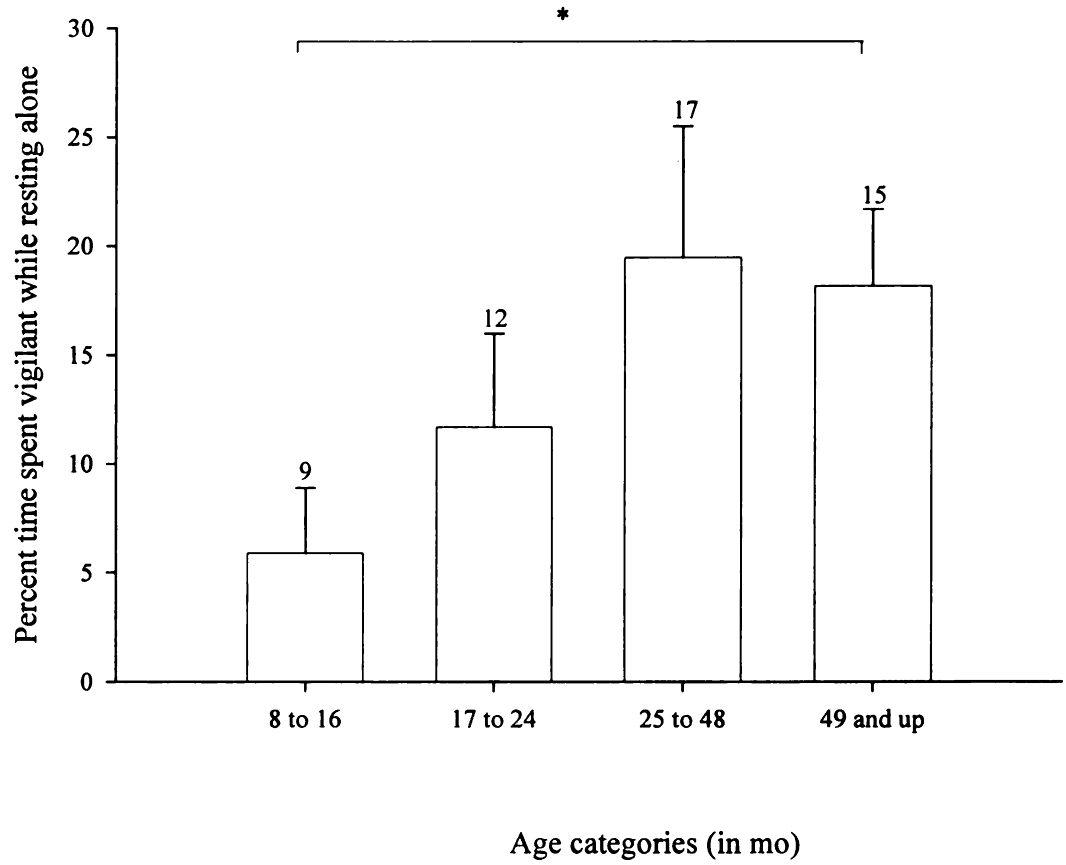

Figure 2.1. Variation in vigilance throughout ontogeny observed among hyenas resting alone on open savannah. Means (± SE) are represented for each age category, and numbers of individuals sampled are indicated above each bar. The asterisk (*) indicates $p < 0.05$.

documented among juveniles (all $R^2 < 0.1$, all $p > 0.05$), and the same was true among animals classified as adults. There was also no detectable effect of clan membership on any of the dependent variables (Krustal-Wallis tests, all $p > 0.05$), so we combined data from all clans. There were no effects of the focal hyena's social rank on its reaction to the playback stimulus, regardless of the response variable examined (all $r^2 < 0.06$, all $p > 0.25$).

The behavior of hyenas observed before sound onset differed significantly from that observed after sound onset, and this was true for both juveniles and adults (Figure 2.2). Before sound onset, hyenas spent the majority of their time resting, which was occasionally interrupted by bouts of vigilance oriented in various directions, but never involved movement to a new location. After sound onset, hyenas increased their time spent orienting directly toward the hidden speakers by an average of 27.4 ± 3.2 %, regardless of which sound was played back (Figure 2.2). This increase in time spent orienting after sound onset was statistically significant for both juveniles (wahoo: $Z = 2.09$, $p = 0.037$; roar: $Z = 3.06$, $p = 0.002$; Figure 2.2a) and adults (wahoo: $Z = 2.84$, $p = 0.004$; roar: $Z = 2.97$, $p = 0.003$; Figure 2.2b). This increase in orientation was not significantly different between control sounds and lion roars, regardless of whether we looked at juveniles ($W = 81$, $p = 0.166$) or adults ($W = 70$, $p = 0.663$). Juveniles only decreased their time spent resting after roar onset (wahoo: $Z = 2.09$, $p = 0.37$; roar: $Z = -3.06$, $p = 0.002$; Figure 2.2a), whereas adult hyenas significantly decreased their time spent resting after onset of both wahoo and roar sounds (wahoo: $Z = 0.2.84$, $p = 0.004$; roar: $Z = 3.18$, $p = 0.001$; Figure 2.2b).

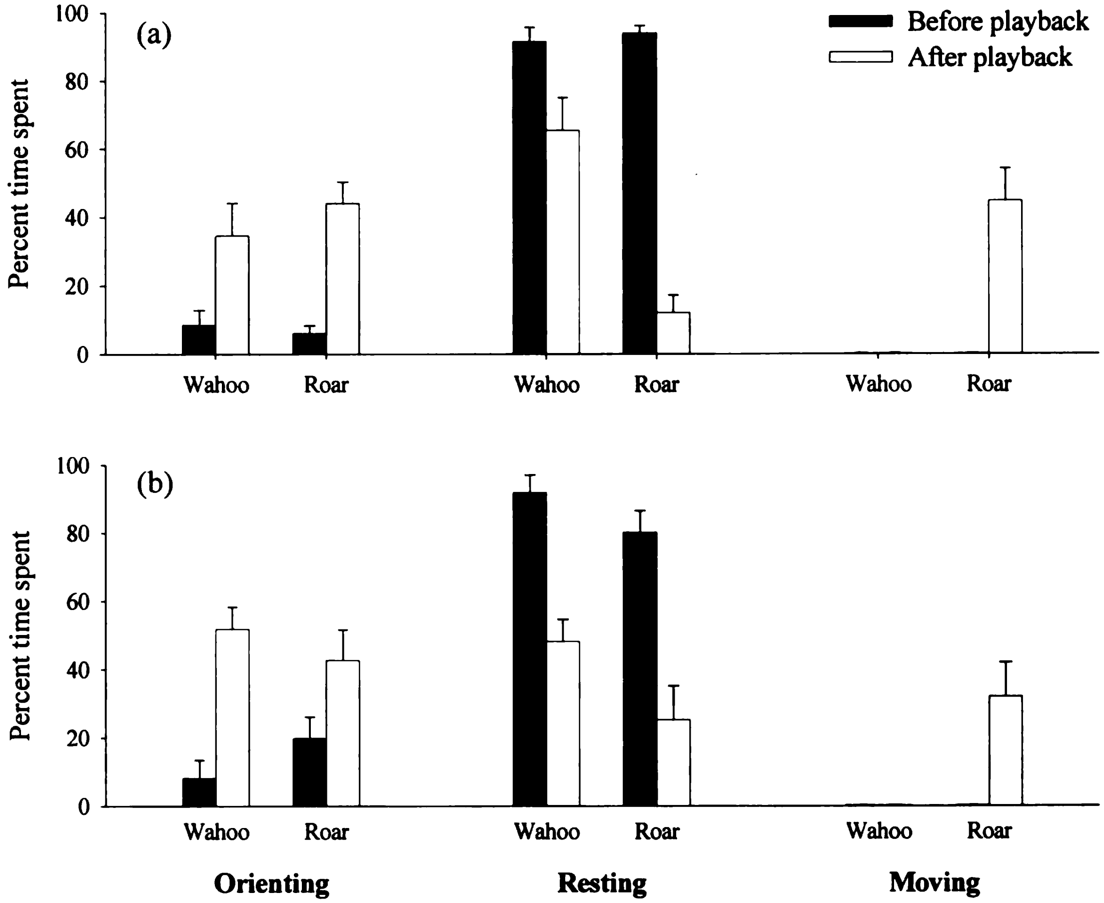

Figure 2.2. Behaviors exhibited by (a) juvenile ($N = 10$ for wahoos, $N = 12$ for roars), and (b) adult hyenas ($N = 12$ for wahoos, $N = 13$ for roars) before (black bars) and after (white bars) sound onset during playback. The sound played was either a baboon wahoo (control sound) or a lion roar (treatment sound). Means (± SE) are represented.

Among both juvenile and adult hyenas, movement away from the animal's original location only occurred after lion roars (Figure 2.2). Most hyenas initiated movement after hearing lion roars (83 % of juveniles and 54 % of adults), regardless of age (percent hyenas that moved after sound onset, Fisher exact test: juveniles: $p < 0.001$; adults: $p = 0.005$). After hearing a baboon wahoo, hyenas never moved, and always continued to lie in their original positions (Figure 2.2).

Differences between juveniles and adults exposed to lion roars

Differences between juveniles and adults in their responses to playbacks of lion roars were surprisingly subtle. Juveniles and adults spent about the same percent time motionless (Figure 3: around 30 %; $W = 59$; $p = 0.16$), and moved at similar rates after lion roar playbacks ($\overline{X}_{\text{juveniles}} = 38.2 \pm 8.4$ m / min; $\overline{X}_{\text{adults}} = 25.2 \pm 7.9$ m / min; $W = 60.5$; $p = 0.17$). However, more juveniles (10 out of 12) than adults (7 out of 13) initiated movement after roar onset, although this age difference was not statistically significant (Yates' $\chi^2 = 1.32$, $p = 0.25$). Out of the 10 juvenile hyenas that initiated movement, 8 moved away from the sound source. In contrast, 3 adult hyenas approached the sound source, while 4 avoided it. When considering the percent time spent moving in specific directions, juveniles were significantly more likely than adults to avoid speakers after roars (percent time spent avoiding speakers: $\overline{X}_{\text{juveniles}} = 42 \pm 9.7$ %; $\overline{X}_{\text{adults}} = 12.7 \pm 5.0$ %; $W = 44$; $p = 0.03$; Figure 2.3). In contrast, adults tended to approach the speakers slightly more than juveniles (percent time spent approaching speakers: $\overline{X}_{\text{juveniles}} = 2.7 \pm 1.8$ %; $\overline{X}_{\text{adults}} = 13.8 \pm 6.8$ %; Figure 2.3), but this trend was not statistically significant

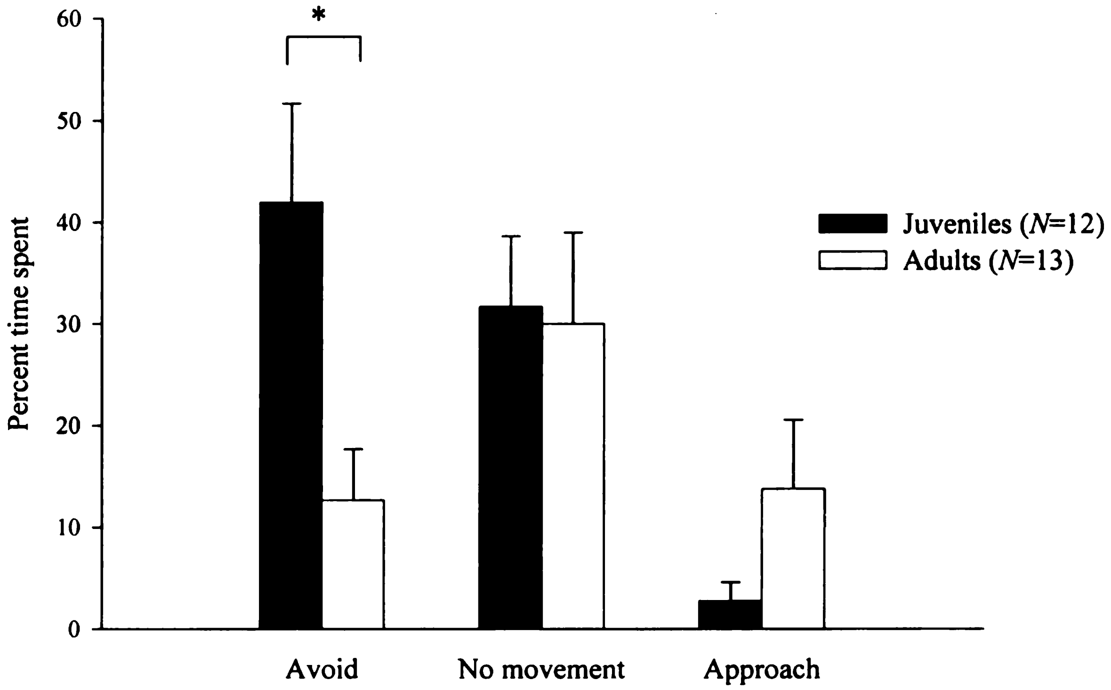

Figure 2.3. Mean (± SE) percent time spent avoiding, approaching or remaining motionless in relation to the speakers by the focal hyena following a lion roar playback. Adult responses (white bars) are compared to juvenile responses (black bars). The asterisk (*) indicates $p < 0.05$.

($W = 87.5$; $p = 0.27$). Juveniles exhibited a shorter latency to first response after roars than did adults, although this difference was not significant ($\overline{X}_{\text{juveniles}} = 108.2 \pm 34.6$ s; $\overline{X}_{\text{adults}} = 189.54 \pm 33.8$ s; $F_{1,22} = 2.69$; $p = 0.11$; Figure 2.4). Thus, of the six variables used to compare responses of juvenile and adult hyenas, only one (percent time spent avoiding speakers) was statistically significant. However, five of these six variables show relatively large effect sizes that are in the direction predicted by our hypothesis (Table 2.1). Results from our power analyses showed that sample sizes of 29 to 64 (instead of the 12 and 13 we obtained) would have been required to statistically detect differences between juveniles and adults. Thus, it appears that differences in responses to roars between adults and juveniles are subtle, but may nonetheless have biological significance.

Differential responses to roars emitted by male and female lions

We found that hyenas reacted more strongly to roars emitted by male than female lions. Hyenas exhibited a lower mean latency to first movement after male than female roars that was marginally significant ($\overline{X}_{\text{male roars}} = 108.94 \pm 27.44$ s; $\overline{X}_{\text{female roars}} = 238.75 \pm 38.27$ s; $F_{1,22} = 3.83$; $p = 0.06$; Figure 2.4), and this response did not differ between juvenile and adult hyenas (non-significant age x roar type interaction). In contrast to our expectation based on hyena mortality patterns, no hyena ever approached speakers after female roars, whereas adults spent 12.5 % of their time, on average, approaching speakers after roars emitted by male lions ($U = 40$; $p = 0.04$). Hyenas also exhibited a higher mean rate of movement after male than female roars ($U = 36.5$; $p =$

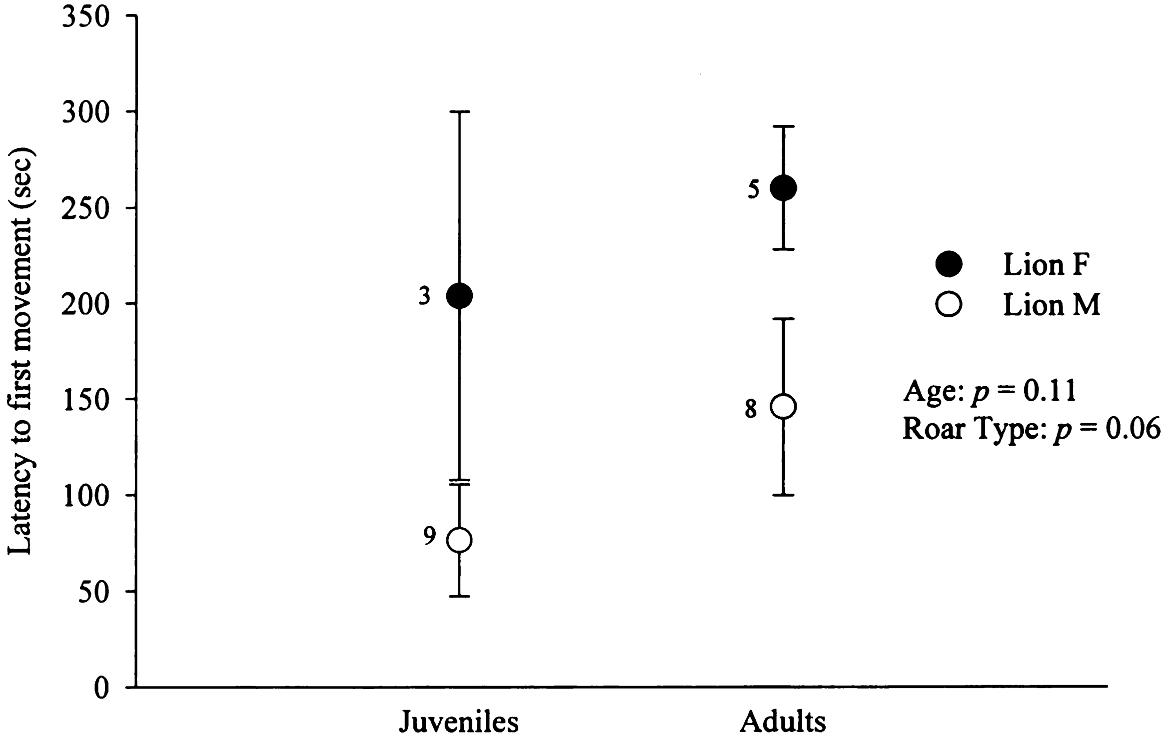

Figure 2.4. Mean (± SE) latency to first movement of hyenas following sound onset. The playback sound was a roar produced either by a female lion (open circles) or a male lion (filled circles). Numbers next to each mean represent the number of individuals that received a given treatment. The statistics shown are results from a 2-way ANOVA.

Table 2.1. Effect sizes for the results of the playback experiment. All variables are comparing the responses of juveniles ("juvs") to those of adults after a lion roar was played. Sample sizes represent the number of individuals tested.

Response variable	**Direction predicted***	**Mean juvs ($N = 12$)**	**Mean adults ($N = 13$)**	**Relative Effect size****	**Statistical results**
Percent time avoiding speakers (%)	juvs > adults	42.0	12.7	230.7 %	$W = 44$ $P = 0.03$
Percent time not moving (%)	juvs < adults	31.67	29.99	5.6 %	$W = 59$ $P = 0.16$
Percent time approaching speakers (%)	juvs < adults	2.75	13.75	80.0 %	$W = 87.5$ $P = 0.27$
Rate of movement (m/min)	juvs > adults	38.22	25.22	51.55 %	$W = 60.5$ $P = 0.17$
Latency to 1st movement (s)	juvs < adults	108.17	189.54	42.93 %	$F_{1,22} = 2.58$ $P = 0.1$
Percent hyenas that moved (%)	juvs > adults	83	54	53.7 %	$\chi^2 = 1.32$ $P = 0.25$

* This is the direction predicted by an hypothesis suggesting that hyenas in different life history stages are differentially competent to deal with dangers; because juvenile hyenas are more vulnerable than adults to mortality by lions, we expected that juveniles would respond to lions with more caution than adults.

** The relative effect size was calculated as: Abs(Mean juvs – Mean adults) / (Mean adults) * 100 and is thus a percentage (LeBlanc 2004).

0.03; Figure 2.5), regardless of the direction in which they were moving. There were no effects of sex of the roaring lion on the percent time after playback during which hyenas oriented, remained motionless, or avoided speakers (all $U > 50$, all $p > 0.3$).

DISCUSSION

Our results indicate that hyenas exhibit age-related variation in threat-sensitive behaviors. First, young hyenas exhibited less naturally-occurring vigilance than adults when resting alone, and they reached adult-like levels after puberty, which occurs at around 24 months of age. Second, juvenile hyenas responded more strongly than adults in response to lion roars in experimental playback. This was indicated by the fact that juveniles started to move more quickly than adults after sound onset, and spent more time avoiding the speakers than did adults. In addition, there were several suggestive, but not significant, trends in the data: juveniles moved away from speakers at slightly higher rates than adults, and spent slightly less time approaching the sound source after sound onset. Some adults also spent time avoiding the sound source, but adults showed much more variability in their responses to the roars than did juveniles; whereas most juveniles (8 out of 10) that changed positions after sound onset moved away from the hidden speakers, some adults did not move at all and some moved toward the speakers.

Young hyenas exhibited low vigilance when resting alone in the absence of any imminent threats, a pattern also observed in other species in which both juveniles and adults were studied (e.g. Fragaszy 1990; Loughry and McDonough 1999; Monclús et al. 2006; Avilés and Bednekoff 2007). This pattern of low vigilance among juveniles can be

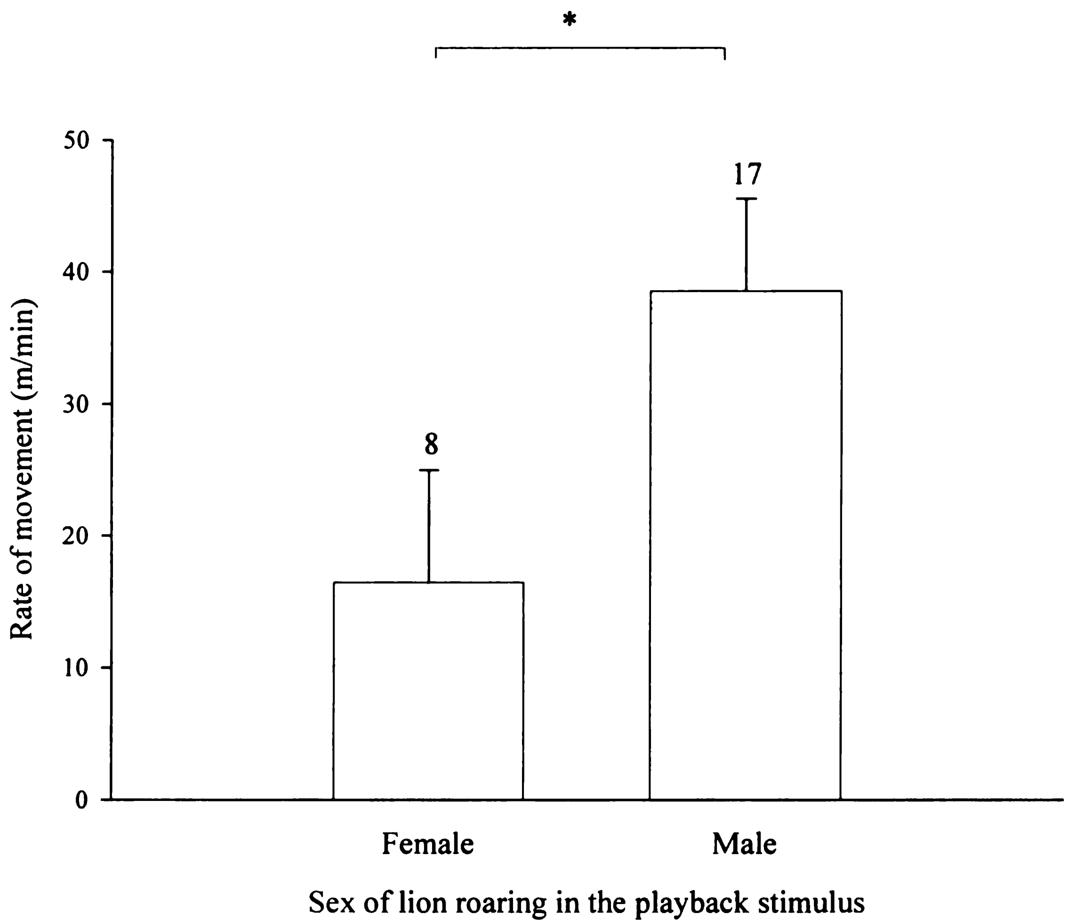

Figure 2.5. Mean (± SE) rate of movement by the focal hyena following exposure to a lion roar playback made by either a female or a male lion. Both directions of movement (approaching and avoiding the sound source) are included here. Sample sizes are located above each mean and indicate the numbers of hyenas tested. There was no effect of age on the movement rate, so juveniles and adults were combined here. The asterisk (*) indicates $p < 0.05$.

explained by several hypotheses that are not mutually exclusive. Young animals may need more rest than do adults due to growth requirements (e.g. Arenz and Leger 2000). Earlier studies (e.g. Avilés and Bednekoff 2007) have proposed that young may rely on nearby adults to compensate for their lower vigilance behavior, although in our case, juvenile hyenas were sampled alone. In addition, young animals might need time during ontogeny to learn to identify the circumstances under which they should be vigilant.

In the presence of an immediate threat indicated by lion roars, juvenile hyenas showed slightly stronger negative responses than did adults. As the escape capabilities of juveniles may be limited relative to those of adults, lions might represent a larger threat for juveniles than for adults. Indeed, this notion is supported by the observation that juveniles experience much higher rates of lion-induced mortality (Watts 2007). That juveniles react more strongly to threats than do adults has also been shown in a number of other species (e.g. Ramakrishnan and Coss 2000; Pongrácz and Altbäcker 2000), and our results suggest that juvenile hyenas appear to be somewhat less naïve than juvenilesof many other species (e.g. Hollén and Manser 2006; Hanson and Coss 1997).

Our study is quite simplistic compared to those done on primates in which more complex arrays of threat stimuli were presented to juveniles (e.g. vervet monkeys, *Cercopithecus aethiops*: Seyfarth et al. 1980). Nevertheless, we observed differences between juvenile and adult hyenas, albeit not as strong as those reported in monkeys. This suggests that perhaps certain antipredator responses emitted by hyenas require less learning than do those of monkeys. This idea is supported by an anecdotal observation reported by Kruuk (1972) regarding a hand-reared juvenile hyena who showed a very strong antipredator response to lion odor before having ever been exposed to any lions.

Although this response was elicited via a different sensory modality, it may indicate nonetheless that hyenas need little or no direct experience with lions in order to respond to them appropriately.

We found that both juvenile and adult hyenas responded more strongly to roars emitted by male than female lions, suggesting that both age groups of hyenas can distinguish lion sex based on roars. Lions have acoustically different roars based on their sex, which can be entirely explained by their large size dimorphism (Pferfferle et al. 2007). However, these differences are not readily audible to naïve human observers. Nevertheless, hyenas responded to roars emitted by males and females in accordance with our predictions, in that they showed higher rates of movement after male than female roars. However, contrary to our expectations, all occasions on which adult hyenas approached the hidden speakers occurred after male roars. This might be either because male roars provide a stronger indication of scavenging opportunities, or because they induce a heightened need to acquire information about the potential threat. In general, studies of threat-sensitive behavior do not evaluate the effect of the predator's sex because the two sexes are assumed to represent similar risks to prey. The fact that we found several response variables to vary with lion sex suggests perhaps that prey animals may be more sensitive than we had previously assumed, and able to make finer discriminations than anticipated.

We did not find an effect of hyena social rank on the response to lion roars, although our small sample sizes might be responsible for this. Indeed, two of the three adult hyenas that spent time approaching the speakers after lion roars were low-ranking hyenas. These hyenas might have been looking for opportunities to scavenge food from lions, and lions may have appeared more attractive to low- than high-ranking hyenas. Similar results, in which low-ranking individuals were willing to take more risks than high-ranking individuals after exposure to a threat, have been obtained in studies of a number of different types of animals (e.g. Reinhardt 1999; Hegner 1985; Slotow and Paxinos 1997). For instance, subordinate blue tits (*Parus caeruleus*) returned sooner to a food patch than did dominant individuals after exposure to a threat stimulus (Hegner 1985). To more fully explore the effect of social rank on the behavior of hyenas in response to lions, more extensive experimental work will be necessary with larger samples of adults holding various rank positions.

In conclusion, our results suggest that hyenas early in life appear to recognize certain signals (in our case, lion roars) as dangerous, and respond adaptively by avoiding the source of potential danger. Nevertheless, juvenile hyenas appear to be learning about the environmental circumstances under which they need to be vigilant, and they appear to require many months to fine tune their behavior. Our study extends our knowledge about the ontogeny of threat sensitive behaviors to include a large, gregarious carnivore. Such ontogenetic studies can provide useful insights into the potential variability among selective forces acting on animals during different stages of their life history.

CHAPTER THREE

LETHAL AND NON-LETHAL ANTHROPOGENIC EFFECTS ON SPOTTED HYENAS IN THE MASAI MARA NATIONAL RESERVE

INTRODUCTION

Persecution by humans often represents a leading source of mortality for wild carnivores, even inside protected areas (Woodroffe and Ginsberg 1998, 2000), and contributes to reduced population size (Woodroffe 2000, 2001; Creel and Creel 2002). This mortality is frequently associated with human-carnivore conflicts in areas where carnivores persist but human populations are expanding (Woodroffe 2000; Ogutu et al. 2005; Johnson et al. 2006). In addition to such lethal effects, humans can potentially also have non-lethal effects on carnivores by modifying their behavior and physiology (Lima 1998; Creel et al. 2002). Recent studies have shown that carnivores display both spatial and temporal avoidance in response to increasing human activity (e.g. Boydston et al. 2003; Kolowski et al. 2007), and they also undergo changes in their stress physiology (Van Meter et al., in review). Anthropogenic activity has also been linked to elevated concentrations of excreted stress hormones, reduced time spent feeding, and more time spent alert in various other carnivores (e.g. Creel et al. 2002; Dyck and Baydack 2004; Nevin and Gilbert 2005; reviewed by Frid and Dill 2002). Such findings have led to a call for a better understanding of both lethal and non-lethal effects of human activity on large mammalian carnivores in order to conserve them (e.g., Caro and Durant 1995; Berger 1998, 2000; Gittleman et al. 2001).

Threat-sensitive behaviors, such as vigilance, are of particular significance to conservation in that they have the potential to influence foraging and time-budgets (Lima and Dill 1990; Caro 1999), which in turn can affect population growth rates (Dobson and

Poole 1998). Currently, most studies on mammalian carnivores focus on the roles played by these animals as predators rather than prey (e.g. Mills and Shenk 1992; Murray et al. 1995; Cooper et al. 2007), resulting in a lack of understanding of the mechanisms these animals possess for coping with danger. Only a few studies have examined threat-sensitive behaviors in mammalian carnivores (Caro 1987; Rasa 1989; Clutton-Brock et al. 1999; Switalski 2003; Di Blanco and Hirsch 2006; Hunter et al. 2007; Atwood and Gese 2008). Because vigilance is ubiquitous and easily quantifiable, it may provide a non-invasive indicator of how much risk a given animal perceives, especially in populations disturbed by human activity. Indeed, vigilance has been used as such a tool with polar bears (*Ursus maritimus*), which increase their vigilance and energetic costs in the presence of wildlife-viewing vehicles (Dyck and Baydack 2004).

Conducting behavioral studies on most carnivores can be quite challenging because they occur at low densities, they are generally nocturnal, and they are wary of humans (Sargeant et al. 1998). However, spotted hyenas (*Crocuta crocuta*) are well-suited for such investigations because they are easily observable in the open habitats of sub-Saharan Africa, and they are active around dawn and dusk (Kruuk 1972; Kolowski et al. 2007). Their social organization in large fission-fusion societies, called clans, containing up to 80 individuals (Kruuk 1972; Mills 1990), allows for repeated observations of many known individuals. Furthermore, although spotted hyenas are currently considered a species of Lower Risk by the World Conservation Union (IUCN 2006), they may represent conservative indicators of how threatened and endangered carnivores inhabiting the same ecosystems might react to human disturbance. In contrast to most other carnivores, spotted hyenas breed year-round, can be active day or night, occur in a diverse array of habitat types, and can survive on food ranging from insects to elephants (Kruuk 1972; Mills 1990; Sillero-Zubiri and Gottelli 1992; Cooper et al.1999). In parts of the Masai Mara National Reserve (henceforth the Reserve), spotted hyenas must cope not only with lions (*Panthera leo*), which are their only natural predators (Cooper 1991; Frank et al. 2005), but also with intensive disturbance by humans, particularly along Reserve borders (Boydston et al. 2003; Kolowski 2007).

Here we compared two hyena clans that differed dramatically in their exposure to anthropogenic disturbance in order to evaluate the effects of human activity. We compared behavior of hyenas in the Mara River clan, which was located in the center of the Reserve, with that of hyenas in the Talek West clan, which was located at the edge of the Reserve. The hyenas in these clans experienced different levels of human disturbance from both tourists in vehicles and pastoralists on foot guarding livestock inside the Reserve (Kolowski et al. 2007). We used three different approaches in this study. First, we assessed long-term trends in human-caused mortality among hyenas in the two clans. Second, we documented naturally-occurring vigilance behavior exhibited by wild hyenas in three different behavioral contexts, both when lions were present with hyenas and when lions were absent. Finally, we performed an experiment to test predictions of an hypothesis suggesting that vigilance behavior in hyenas is influenced by the presence of livestock and herders. Because of their frequent exposure to human disturbance, we expected that Talek West hyenas would spend more time vigilant than Mara River hyenas. In southern Kenya, local pastoralists always accompany their livestock, which wear metal cow bells; herders sometimes kill or harass indigenous wildlife while watching their herds, suggesting that hyenas might associate the sound of cow bells with danger. In playback experiments, we compared responses of hyenas in both study clans to cow bells (treatment sounds) and church bells (control sounds). We predicted that hyenas from the clan experiencing little human disturbance would react similarly to sounds of cow bells and church bells, as both should represent novel sounds, whereas we expected that hyenas from the clan experiencing cow bell sounds daily would show greater vigilance in response to these sounds than to sounds of church bells.

METHODS

Study site and study animals:

The Reserve (1,500km^2) is located in southwestern Kenya (1°40 S, 35°50 E), in an area of open, rolling grasslands. The Reserve is inhabited by large numbers of ungulates (Sinclair and Norton-Griffiths 1979) and high densities of the various large carnivores that prey on them (Ogutu and Dublin 2002; Dloniak 2006).

The two clans monitored in the Reserve, the Talek West and the Mara River clans, are ecologically very similar except for exposure to human activity (Kolowski 2007). Both clans experience similar rainfall, prey density, lion density and vegetation cover (Table 3.1; Dloniak 2006; Kolowski et al. 2007). Because their territory lies along the border of the Reserve, Talk West hyenas live in close proximity to Masai villages, and experience daily human disturbances in the forms of livestock herds guarded by herdsmen, and in the form of vehicles carrying tourists engaged in wildlife viewing. In contrast, the territory defended by the Mara River clan is located over 6 km from the nearest Reserve border, which is too deep in the Reserve for livestock to travel for daily

Table 3.1. Salient characteristics of the two study clans, Talek West and Mara River clans. Unless otherwise indicated, all information from this table was obtained from Kolowski (2007).

	Talek West Clan	**Mara River Clan**
Clan size (# hyenas)	47 – 55	28 - 43
Territory size (km^2)	28.4	31.0
Number of lion prides using territory*	3	3
Mean lion pride size ± SE*	15.33 ± 2.73	18 ± 2.08
Mean lion sub group size (# lions) ± SE	3.9 ± 0.26	3.4 ± 0.30
Prey density (# / km^2)	210.8	196.6
Mean number of livestock grazing daily on the territory ± SE	1386 ± 181	0
Distance to Reserve border (km)	0	6.5
Number of tour vehicles approaching hyenas per hour	0.87	0.18

* Dloniak 2006

grazing; Mara River hyenas experience some visitation by tourists, but no livestock herds or pastoralists (Table 3.1). All hyenas from both study clans were known individually by their unique spots. Ages (± 7 days) of all hyenas were determined using previously described methods (Holekamp et al. 1996). Only adults (older than 2 years old; Matthews 1939; Glickman et al. 1992) were included in this study.

Determination of causes of death:

The Talek West clan was observed between July 1^{st}, 1988 and September 1^{st}, 2006 as part of a long-term monitoring program. During this period, we recorded all known deaths, and attributed a cause of death when this could be reliably determined from observer reports or marks on the body of each dead hyena. If the body of a hyena revealed evidence of snaring, spearing, or poisoning, or if resident pastoralists informed us they had killed the hyena, we attributed the cause of death to humans. Other sources of mortality included lions, disease, starvation, den flooding, infanticide and siblicide. Most deaths could not be reliably attributed to one particular source, so we restricted our dataset to 83 deaths of known causes. From this subset, we calculated the proportion of deaths that could be attributed to humans in each of the 18 years of the study. We recorded the same information for Mara River hyenas, which were monitored between January 1^{st}, 2001 and September 1^{st}, 2006. For this clan, eight deaths could be reliably attributed to known causes.

Naturalistic observations of vigilance:

Individual hyenas in both study clans were videotaped in the field between June 2005 and July 2006 to document variation in their naturally-occurring vigilance behavior. Daily observations of the study animals took place between 0600 - 1100 h (the AM period), and between 1500 - 1900 h (the PM period) from a field vehicle that served as a mobile blind. During observations, the field vehicle was parked no closer than 15 m from each focal hyena. Hyenas are well habituated to our vehicle as all natal animals were exposed to it since infancy. We documented vigilance in three different behavioral contexts: while resting, feeding at kills and nursing cubs. Hyenas were considered to be resting when they were lying down in the absence of food for at least 5 min, and not interacting with conspecifics; the eyes of resting hyenas were usually shut. Hyenas were considered to be feeding at kills when we found them consuming a fresh ungulate carcass; hyenas feeding on low quality scraps were not included in this study. Female hyenas were considered to be nursing when they suckled their litters while lying down. Upon finding a hyena engaged in one of these three activities, we set up a Sony DCR-H65video camera mounted on a window tripod and videotaped the focal animal for 2 - 7 min ($\overline{X} = 4.25 \pm 0.04$ s).

At the time of filming, we recorded various types of ecological and social variables, including the number of conspecifics present within 100 m of the focal individual (referred to hereafter as the "group size"). "Clan size" refers to the size of the entire social unit, although all members are seldom present concurrently. Spotted hyenas live in fission-fusion societies in which clan members are found in groups of varying size and composition (Smith et al. 2008). We also recorded the distance between the focal individual and the closest patch of bushes (using a Bushnell range finder), as hyenas may view bushes as refugia or bushes might conceal lions. Lions were considered to be present with the focal hyena if they were less than 200 m from it. During daily observations, we also recorded the presence, and estimated the size, of any livestock herds seen in the territory of the Talek West clan; no livestock were ever seen in the Mara River territory (Table 3.1). Only herds containing cows were recorded, although herds of sheep and goats are also seen occasionally in the Talek West territory.

Tourist visitation to the Reserve varied seasonally, peaking during western holiday periods. To evaluate the potential effect of tourist presence on vigilance in hyenas, we noted whether our filming was taking place during months of heavy tourism, which we determined using data available from Heath (2007). The number of tourists visiting the Reserve each month ranged from 5,336 to 23,847; heavy tourism months were considered those during which the number of tourists exceeded 10,000 ($N = 6$): June, July, August, September, October and December. As tour vehicles are abroad in the Reserve during only two specific periods each day (0630 - 0900 h and 1630 - 1900 h; Kolowski et al. 2007), we also noted whether each filming event occurred during tourism hours or non-tourism hours.

Playback experiment:

Hyenas were exposed to two types of sounds during playback experiments: treatment sounds were cow bells ringing and control sounds were church bells ringing. Masai pastoralists generally hand bells on collars around the necks of several cattle in each herd. These metal bells ring whenever the cattle move their heads, and this ringing can be heard from over one kilometer away. Like cow bells, church bells are also made of metal, but their frequencies are much lower than those produced by cow bells (mean dominant frequencies calculated using Adobe Audition 1.5: $\overline{X}_{church\ bells} = 738$ Hz; $\overline{X}_{cow\ bells} = 1{,}121$ Hz), resulting in very different sounds.

Cow bell sounds were recorded from moving herds of cattle in and around the Talek West clan territory, using a Marantz PMD-22 portable cassette recorder and a Sennheiser ME66 shotgun microphone. All recordings ($N = 11$) were made from herds that had approximately ten individuals fitted with bells. Church bell sounds were recorded with the same equipment from eight different churches located around the city of La Rochelle, France. The recordings were obtained when bells rang in a carillon-style 15 minutes prior to mass (this specific ringing is called "l'appel de messe"). We manipulated all recordings using Adobe Audition 1.5 to shorten each recording to 60 s in duration.

Experimental and control sounds were played from our research vehicle to solitary hyenas resting on open savannah. A hyena was considered solitary if it was separated by at least 400 m from the nearest conspecific. Upon finding a suitable subject, the car was positioned approximately 100 m (range: 80 to 115 m; $\overline{X}_{distance} = 91 \pm 2.84$ m) from the hyena, at an angle of approximately 45 degrees to the plane formed by a straight line between the subject and the observer videotaping the hyena's response. Recordings used in the field were picked randomly from the sound library, and no recording was used more than twice to minimize pseudo-replication (McGregor et al. 1992). The recordings were played from a Creative Nomad Jukebox 3 linked to two loud speakers (Fender Passport P-150) placed on window mounts facing away from the focal hyena and thus hidden by the car. The two speakers were separated only by about 20 cm. Sound amplitude was calibrated by ear to match natural sounds. The playbacks were carried out between 0700 and 1830 h when cow bells are typically heard in the Talek West territory.

Before playing back any sound, all equipment was set up and turned on, and a digital video camera was aimed at the focal hyena. The observer (WMP) started filming at least three minutes before sound onset; filming continued throughout the playback, and for at least four minutes after sound onset. Fourteen individual hyenas were included in the playback experiment. Seven hyenas were exposed to both cow and church bell sounds in random order, with playbacks to any given hyena separated by at least two weeks (and, on average, by 28 days) to avoid habituation (McGregor et al. 1992). Seven hyenas were exposed to only one or the other of the sounds due to lack of additional opportunities in the field.

Data extraction:

We watched videotapes made during naturalistic observations and experiments using a Sony DRC TRV900 digital camcorder that superimposed a time code on the screen with a precision of 0.033 s, with each video frame uniquely labeled. We identified vigilance behavior whenever a focal individual lifted its head. Onset of a vigilance bout was considered to be the point at which the individual lifted its head (halfway through the raising of the head), and the end was considered to be the point at which the individual lowered its head again (halfway through the lowering of the head). From the video footage, we extracted the duration of each vigilance bout, and summed all bout durations before dividing this by the number of bouts to obtain an average bout duration. The total number of bouts in the filmed sequence was also used to calculate the number of bouts per minute filmed. From the average duration and the rate of vigilance bouts, we calculated the total percent of its time that an animal spent vigilant during the filmed sequence. Percent time spent vigilant was calculated for both naturalistic observations and experiments, although hyenas that lifted their heads following sound onset in the experiments typically oriented toward the sound source. In experimental trials, we also extracted the following data from each video tape for both the pre- and the post-playback periods: 1) latency to first movement by the focal hyena after sound onset; 2) direction of movement –away or toward speakers; and 3) percent time spent moving after sound onset.

Data analyses:

We tested assumptions of normality and homogeneity of variance in our response variables using the Wilks-Shapiro Test and the Levene's Test, respectively. All response variables met both assumptions once they were log-10, square-root, or arcsine-square-root transformed.

We analyzed data from our long-term monitoring program to test whether the proportion of known-cause deaths attributable to humans changed between 1988 and 2006 in the Talek West clan, and between 2001 and 2006 in the Mara River clan. To do this, we used linear regression to evaluate the relationship between year of the study and the proportion of hyena deaths of known causes each year that could be attributed to humans.

We analyzed data from the naturalistic observations to determine whether vigilance differed between the two clans, and whether human-related activities could explain variation in vigilance. We first examined the effect of clan membership on vigilance using a general linear mixed-effect model (GLMM), in which hyena identity was entered as a random effect, nested within clan membership, to avoid potential pseudo-replication (Pinheiro and Bates 2000). Significance of the random identity effect in this model and subsequent models was tested using likelihood ratio tests, comparing models with and without random effects (Pinheiro and Bates 2000). In this GLMM, we also included the time at which each observations was made (AM vs. PM), lion presence or absence, group size, and the interaction between these factors and clan membership as fixed effects, because these factors are known to affect hyena vigilance (Chapter 1). We ran this analysis on the percent time spent vigilant in each of the three behavioral contexts (resting, feeding and nursing) separately. In addition, we also evaluated the effect of clan membership on distance between nursing females and the nearest bushes using a GLMM in which female identity was entered as a random effect. We also included group size in this model, but not lion presence, as we never observed nursing in the presence of lions.

Whenever differences between clans were revealed in our analyses, we then used GLMMs to inquire whether this effect could be attributed to anthropogenic activity associated with tourism or livestock grazing. This analysis included livestock presence (yes or no) and tourist presence (2 variables: tourism months or non-tourism months, tourism hours or non-tourism hours, and their interaction) as fixed effects, as well as time of day (AM vs. PM), group size, lion presence or absence, clan membership and hyena identity, which was nested within clan membership and entered as a random effect. For this analysis, we only included observations of resting hyenas ($N = 633$, on 34 Talek West hyenas and 24 Mara River hyenas), and evaluated effects on the percent time spent vigilant.

We analyzed the response variables recorded during playback experiments in two different ways. To test the effect of the playback sounds on the percent time spent vigilant, we used a 3-way analysis of variance with clan membership, playback type, and pre vs. post playback period as the three factors. We also used a chi-square analysis, applying Yates' correction for small sample sizes as necessary, to examine effect of clan membership and playback type on whether or not subjects moved in response to playback sounds.

All analyses were performed in the statistical software package R, v.2.1.0 (R Development Core Team 2005), using two-tailed tests with an alpha level of 0.05. The GLMMs were done using the R library 'nlme' (Pinheiro et al. 2005). Unless otherwise indicated, means ± 1 standard error are presented.

RESULTS

Lethal effects of humans on spotted hyenas:

Between 1988 and 2006, 20 of 83 hyena deaths of known causes in the Talek West clan could unambiguously be attributed to humans. The relative proportion of human-caused deaths increased significantly during the years of our study ($F_{1,17} = 11.28$, $p = 0.004$, $r^2 = 0.40$; Figure 3.1). We observed a similar increase when we examined the actual number of deaths attributable to humans during the years of our study ($F_{1,17} =$

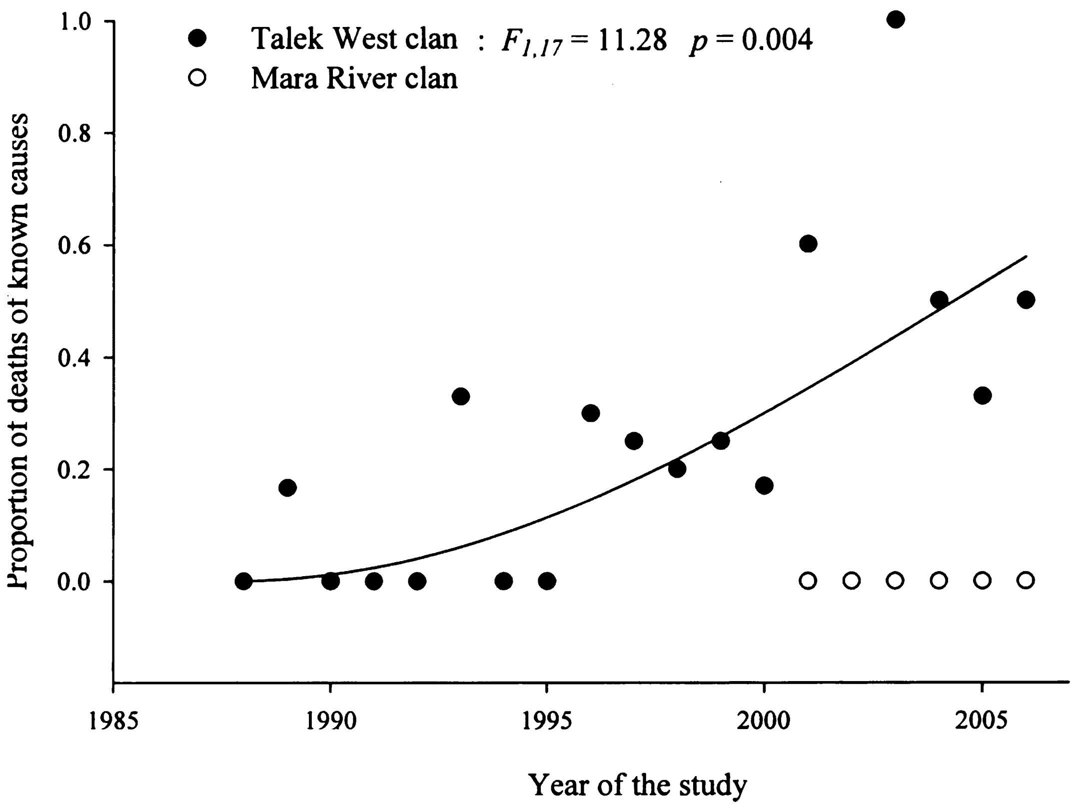

Figure 3.1. Proportion of hyena deaths of known causes that could be attributed to humans in each year of the study in two clans, the Talek West clan (filled circles) and the Mara River clan (empty circles). The Mara River clan was not monitored before 2001. The line represents a linear regression performed on transformed data but plotted on untransformed data; the regression analysis only includes data points for the Talek West clan.

6.76, $p = 0.02$, $r^2 = 0.28$). In the Mara River clan, only 8 hyena deaths of known causes were observed, and none could be attributed to humans (Figure 3.1).

Naturalistic observations of vigilance in hyenas from both clans:

The number of observations collected, and the number of individuals sampled in each behavioral context in each clan, are reported in Table 3.2. When resting, Talek West hyenas were more vigilant than Mara River hyenas ($F_{1,58} = 6.53$, $p = 0.01$; Figure 3.2a), with Talek West hyenas spending more than twice as much time vigilant as Mara River hyenas ($\overline{X}_{Talek} = 16.17 \pm 1.55$ %; $\overline{X}_{Mara\ River} = 7.21 \pm 0.88$ %; Figure 3.2a). Although both clans were significantly more vigilant in the morning than in the evening ($F_{1,576} = 29.47$, $p < 0.001$; Figure 3.2a), vigilance of resting Talek West hyenas was consistently greater than that of Mara River hyenas regardless of time of day (the clan x time interaction was not significant). The interaction between clan and group size was also not significant, despite the fact that vigilance was significantly less in both clans when hyenas rested in large than small groups ($F_{1,576} = 7.29$, $p = 0.007$). Interestingly, the difference in vigilance between clans was apparent in the absence of lions, but not in the presence of lions, resulting in a significant clan x lion interaction ($F_{1,577} = 3.63$, $p = 0.05$; Figure 3.3). Specifically, when lions were present, resting hyenas approximately doubled their percent time spent vigilant over that when lions were absent ($F_{1,576} = 57.70$, $p < 0.001$; Figure 3.3); the two clans did not differ significantly on this measure.

Table 3.2. Number of naturalistic vigilance observations collected (*N obs*) on adult hyenas (*N ind*) sampled in each behavioral context (resting, feeding and nursing) in the two study clans (Talek West and Mara River clans) in the presence or absence of lions. We never observed adult females nursing in the presence of lions.

	Talek West				Mara River			
Context	without lions		with lions		without lions		with lions	
	N obs	*N ind*	*N obs*	*N ind*	*N obs*	*N ind*	*N obs*	*N ind*
Resting	412	34	42	22	170	22	15	9
Feeding	75	29	15	11	26	21	5	4
Nursing	42	9	-	-	39	7	-	-

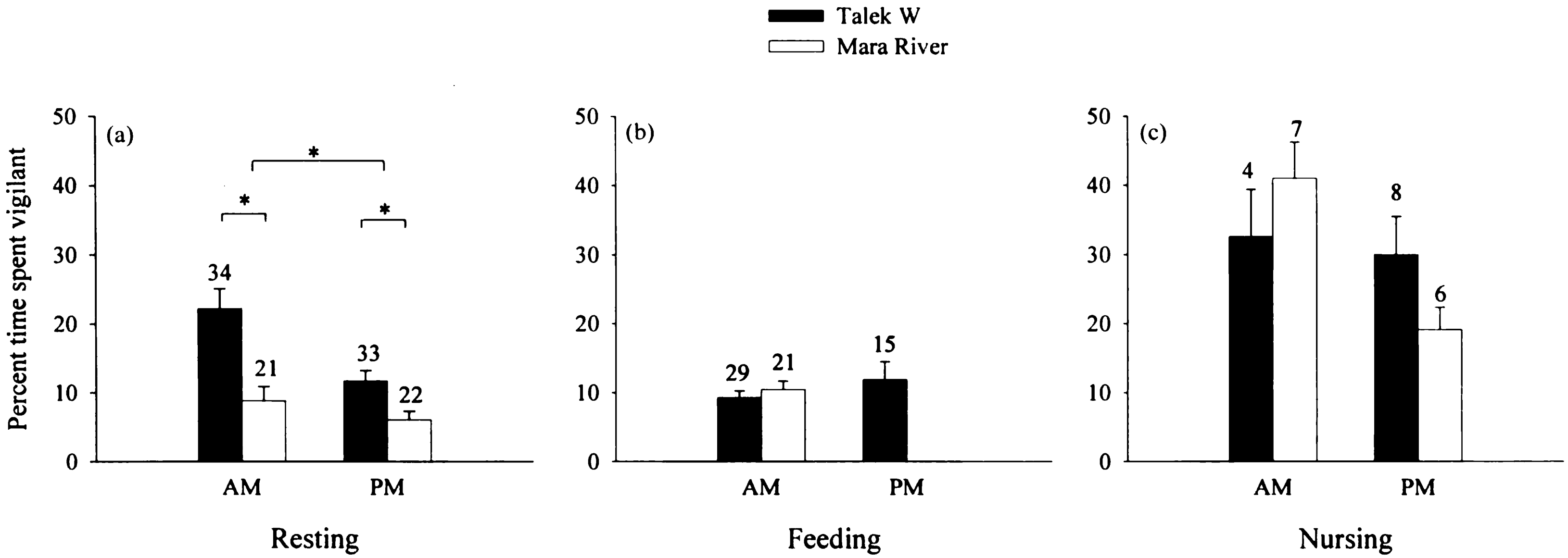

Figure 3.2. Percent time spent vigilant by hyenas from the Talek West clan (black bars) and the Mara River clan (white bars) during morning (AM) and evening (PM) observation hours while observed (a) resting, (b) feeding, and (c) nursing their cubs. Means (± SE) are represented, with the number of individuals sampled indicated above each mean. Asterisks (*) represent statistically significant differences ($p < 0.05$). We never observed Mara River hyenas feeding in the evening hours.

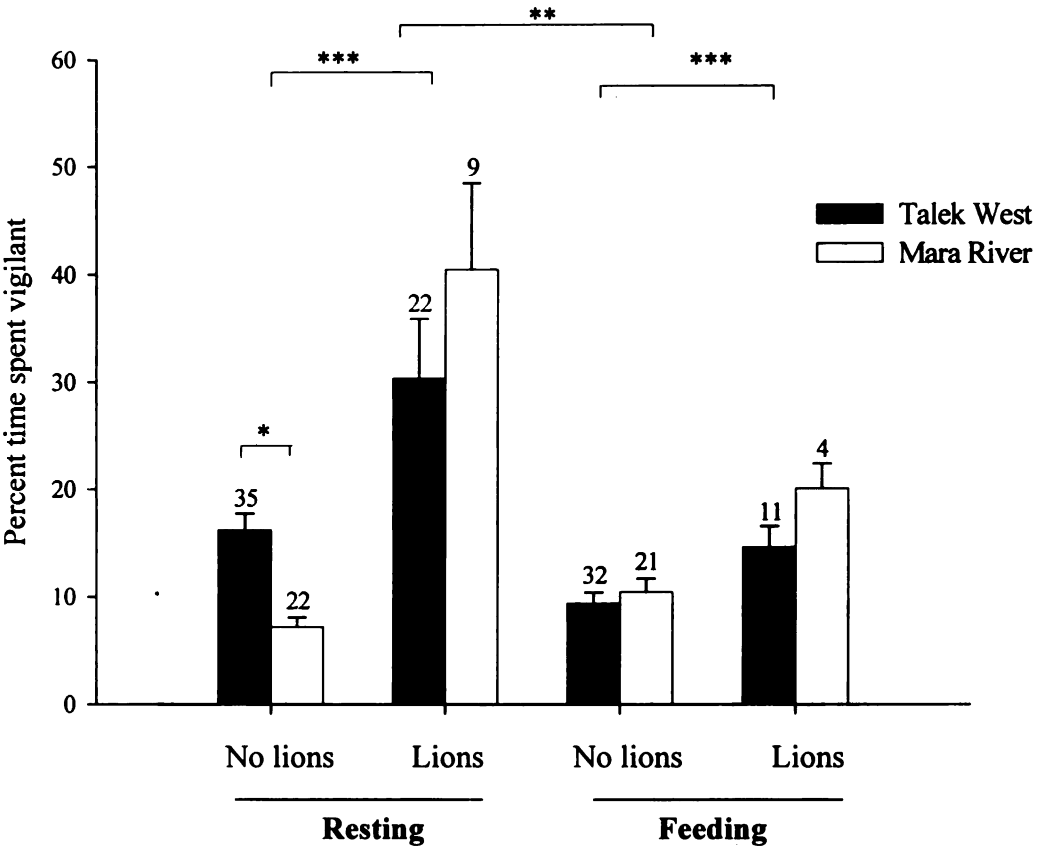

Figure 3.3. Percent time spent vigilant by spotted hyenas of the Talek West clan (black bars) and Mara River clan (white bars) while resting and feeding in the presence or absence of lions. Means (± SE) are represented, with the number of individuals sampled indicated above each mean. Asterisks represent statistically significant differences (*$p < 0.05$, **$p = 0.01$; ***$p < 0.001$).

We did not observe differences in vigilance between clans when hyenas were feeding or nursing (Figure 3.2b, c). Talek West and Mara River hyenas spent roughly the same percent time vigilant while feeding ($\overline{X}_{Talek} = 9.39 \pm 1.00$ %, $\overline{X}_{Mara\ River} = 10.43 \pm 1.22$ %; $F_{1,47} = 1.55, p = 0.22$; Figure 3.2b). Hyenas from both clans spent a larger percent time vigilant when feeding in the presence of lions than when lions were absent ($F_{1,69} = 9.83, p = 0.002$; Figure 3.3), and when feeding in large than small groups ($F_{1,69} = 5.18, p = 0.026$). Vigilance while feeding did not differ between AM and PM observation periods ($F_{1,69} = 1.73, p = 0.19$; Figure 3.2b). Hyenas from both clans spent similar percentages of their time vigilant while nursing their litters ($\overline{X}_{Talek} = 38.40 \pm 7.28$ %; $\overline{X}_{Mara\ River} = 28.94 \pm 4.57$ %; $F_{1,14} = 0.32, p = 0.32$; Figure 3.2c). Nursing mothers in both clans were more vigilant in the morning than in the evening ($F_{1,63} = 5.07, p = 0.03$). There was no effect of group size on vigilance while nursing ($F_{1,63} = 2.91, p = 0.09$).

Female hyenas choose where to suckle their litters, so we evaluated differences between clans in the distance that mothers nursed from bushes. Talek West females nursed significantly closer to bushes than did Mara River females ($\overline{X}_{Talek} = 77.47 \pm 23.65$ m; $\overline{X}_{Mara\ River} = 267.68 \pm 38.97$; $F_{1,14} = 6.18, p = 0.026$; Figure 3.4). Hyenas from both clans were observed further from bushes if they were nursing in large than small groups ($F_{1,60} = 4.54, p = 0.037$), but the difference between clans was apparent regardless of group size (i.e., non-significant clan x group size interaction). Distance to bushes did not vary between clans when hyenas were resting or feeding ($p > 0.1$).

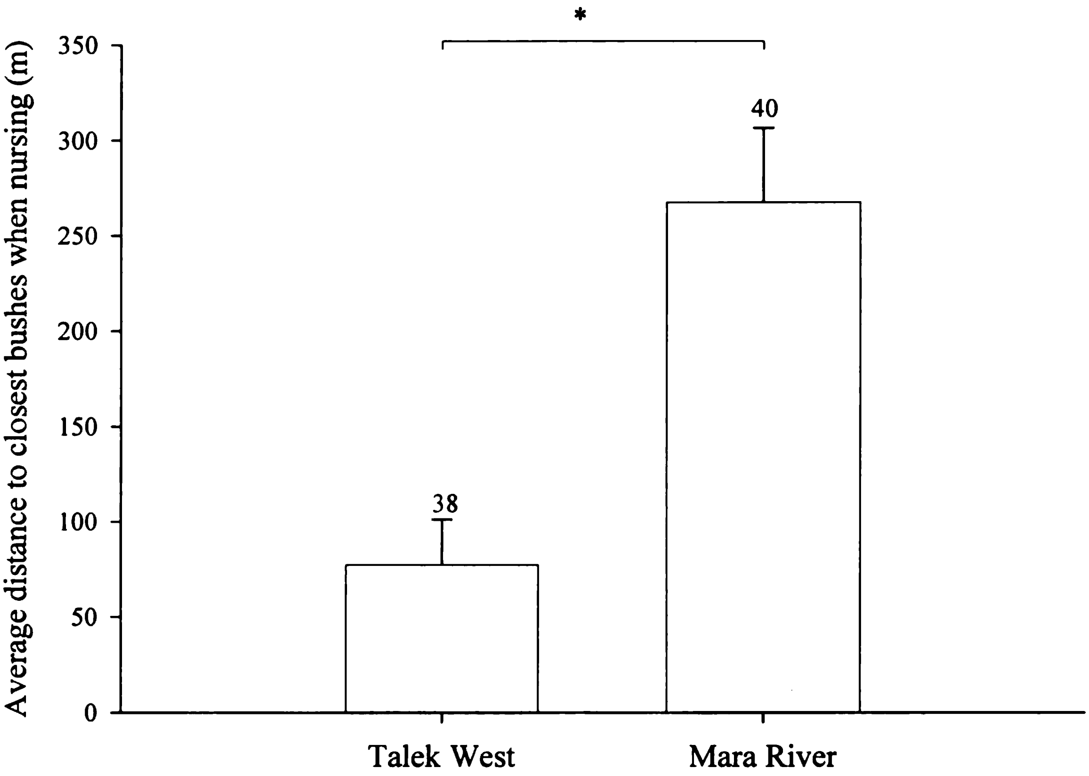

Figure 3.4. A comparison of the two study clans with respect to the average distance between focal hyena nursing and the closest patch of bushes. Means (± SE) are represented, with the number of individuals sampled indicated above each mean. Asterisks represent statistically significant differences (*$p < 0.05$).

We next focused on how different human activities affected vigilance among resting hyenas. Talek West hyenas were more vigilant on days when livestock were present in their territory than when livestock were absent ($F_{1,413} = 3.79, p = 0.02$; Figure 3.5). This effect was of the same magnitude regardless of whether there were 30 or 2200 livestock present in the territory (Figure 3.5). In contrast to pastoralist activity, there were no effects of tourist activity on vigilance by either Talek West or Mara River hyenas. Resting hyenas spent the same percent time vigilant in months when many tourists were visiting the Reserve as in months when few tourists were visiting the Reserve ($F_{1,565} = 0.05, p = 0.82$; Figure 3.6), and during hours when tour vehicles were present or absent from the Reserve ($F_{1,565} = 3.74, p = 0.06$; Figure 3.6).

Playback experiment:

We carried out a total of 13 playbacks on hyenas from the Talek West clan (7 cows bell playbacks and 6 church bell playbacks), and a total of 8 playbacks on hyenas from the Mara River clan (4 cow bell playbacks and 4 church bell playbacks). Hyenas from both clans spent more time vigilant after a sound stimulus was played than before, regardless of the stimulus type ($F_{1,38} = 10.16, p = 0.003$, Figure 3.7). However, unexpectedly, the increase in vigilance of hyenas after sound onset did not differ significantly between church and cow bells within each clan ($F_{1,34} = 0.65, p = 0.42$, Figure 3.7). Talek West hyenas were more vigilant than Mara River hyenas, regardless of the stimulus played ($F_{1,34} = 7.31, p = 0.01$, Figure 3.7). Specifically, Talek West hyenas

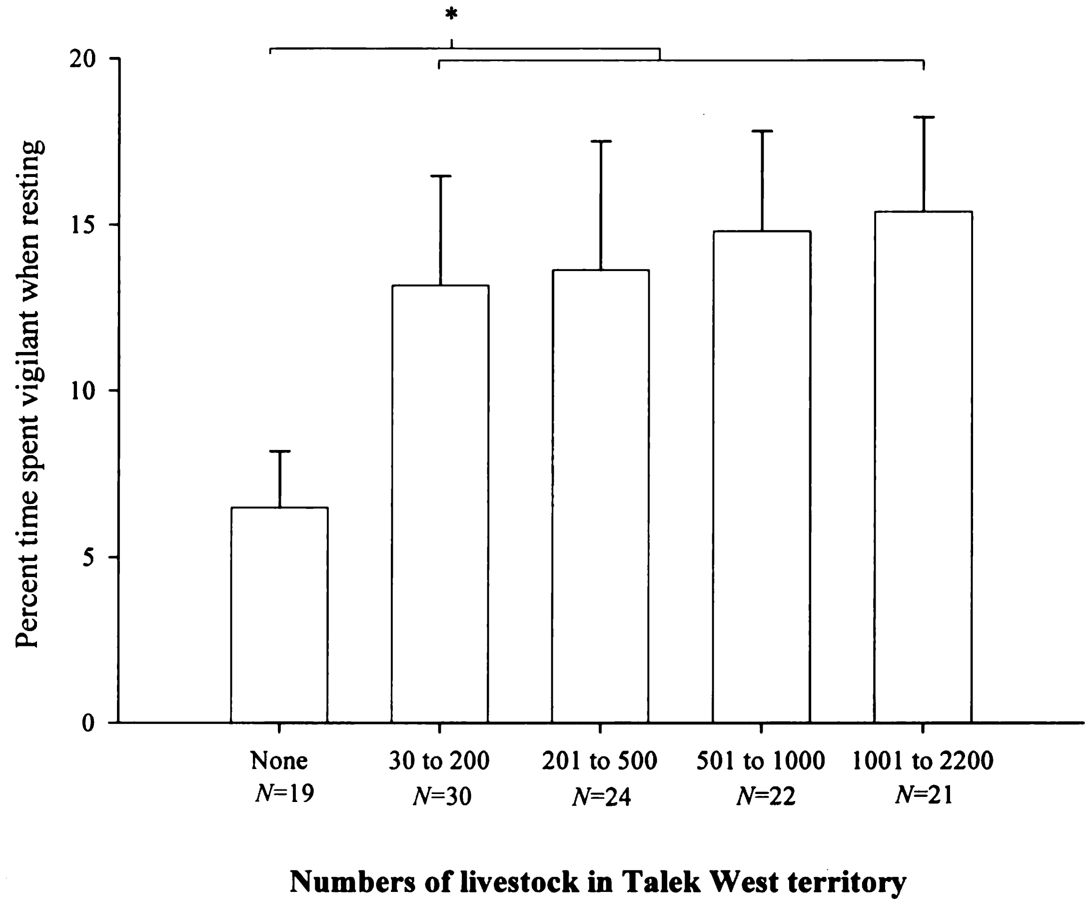

Figure 3.5. Effect of livestock presence on the percent time spent vigilance by Talek West hyenas while resting. Means (± SE) are represented, with the number of individuals sampled indicated below each mean. The percent time vigilant was obtained for hyenas resting on days during which livestock presence in the territory was known. The asterisk (*) represents a statistically significant difference (p = 0.02).

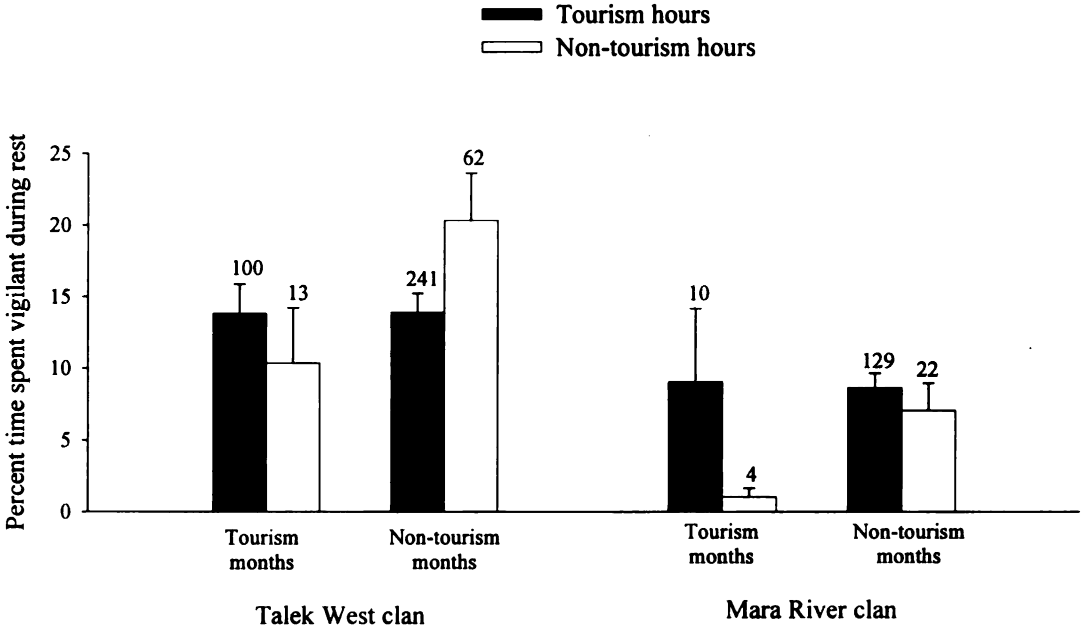

Figure 3.6. Effect of tourism on the percent time spent vigilant during rest by hyenas from the Talek West and the Mara River clans during months with many or few tourists, and during hours of the day when tour vehicles are abroad in the Reserve (black bars) or not (white bars). Means (± SE) are represented, with the number of observations indicated above each bar. There were no statistically significant effects of tourism on vigilance in either clan (mixed-effect models, in which hyena identity was included, $p > 0.05$; full model results are presented in the text).

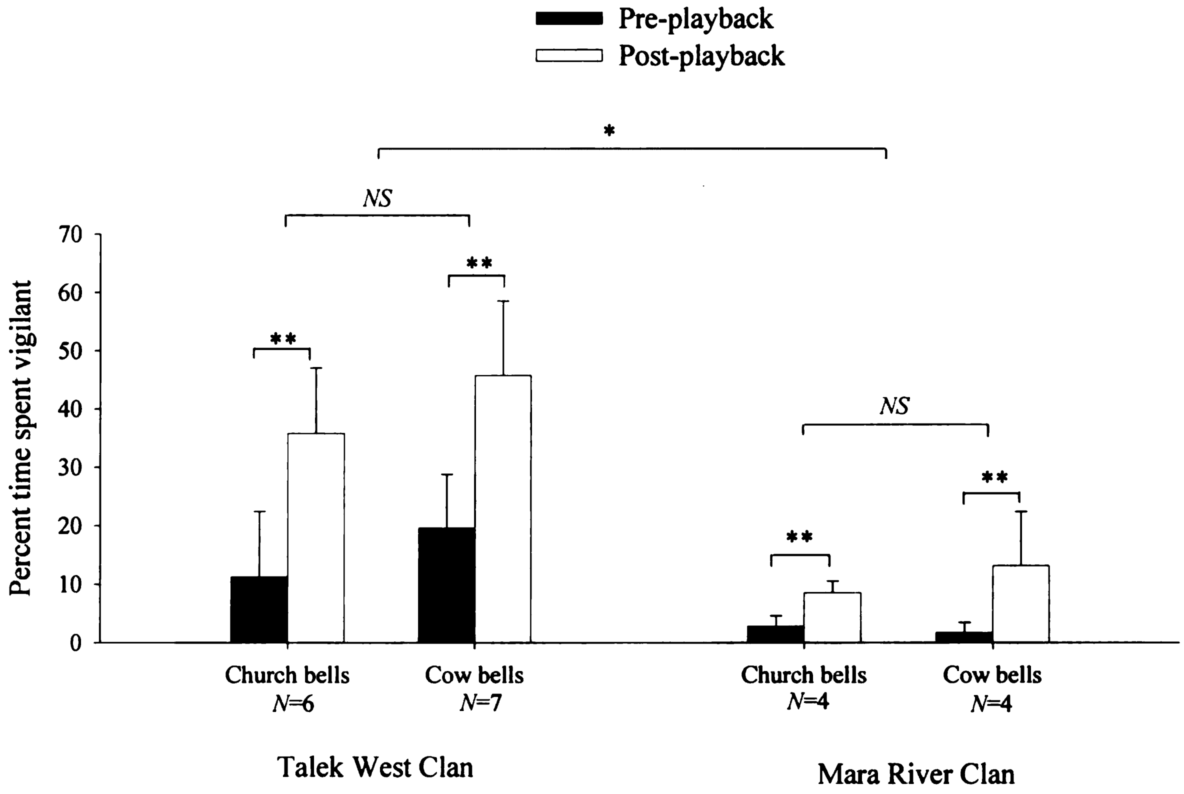

Figure 3.7. Percent time spent vigilant by Talek West and Mara River hyenas during a playback experiment involving use of either church bells (control sound) or cow bells (treatment sound). Behavior during the pre-playback period (black bars) is compared to that from the post-playback period (white bars). Means (± SE) are represented, with the number of individuals sampled indicated below each playback type. Asterisks represent statistically significant differences ($*p < 0.05$, $**p < 0.01$).

spent roughly 25 % more time vigilant than did Mara River hyenas (Figure 3.7) after sounds were played back from either type of bells.

The only hyenas that moved after being exposed to a playback sound were Talek West hyenas that had just heard cow bells. Two out of the 7 (28 %) Talek West hyenas that received the cow bell treatment moved, whereas no Mara River hyenas moved after either sound was played to them. However, this difference between the two clans was not statistically significant (Yates' $\chi^2 = 0.136, p = 0.71$). In the case of the two Talek West hyenas that moved after hearing cow bells, both hyenas started to move about 1 min after hearing the first cow bells, avoided the speakers, and spent about 22 % of their filmed time after sound onset moving away from the speaker; one of these hyenas moved only a few meters away, while the other moved about 200 m away.

DISCUSSION

Our results suggest that humans are having both lethal and non-lethal effects on spotted hyenas. The former was inferred from shifts in deaths of known causes, and the latter from behavioral data. We found that human-caused hyena mortality observed during long-term monitoring of the disturbed clan has comprised an increasingly greater proportion of known-caused hyena deaths since 1998. Hyenas alive today appear to be perceiving this increased risk, and modifying their behavior accordingly. Hyenas from the heavily disturbed Talek West clan spend about twice as much time vigilant during naturalistic observations at rest, and nursed closer to bushes, than do hyenas from the undisturbed Mara River clan. When we sought factors that might account for these differences, we found that hyenas from the disturbed clan spent more time vigilant when resting on days when livestock and herders were present in their territory than on the rare days when livestock and herders were absent. We experimentally tested for an effect of livestock presence on hyena vigilance, and we found that, although Talek West hyenas did not increase their vigilance after hearing cow bells (the treatment sounds) any more than after hearing church bells (the control sounds), their responses to both sounds were stronger than those of the Mara River hyenas. To put our experimental results in a broader perspective, Talek West hyenas spent a larger percentage of their time vigilant after cow bell playbacks than Mara River hyenas spent in the physical presence of lions. This suggests that Talek West hyenas showed greater responsiveness to unnatural sounds than did hyenas living in an undisturbed area.

In our behavioral observations, we detected an effect of livestock presence on hyena vigilance, but not an effect of tourist presence. The latter finding was encouraging because it suggests that the Reserve's regulations are sufficient to ensure that large carnivores such as hyenas do not perceive tour vehicles as threats. This was not the case in two recent studies that reported an increase in mammalian vigilance associated with tourist presence (e.g. polar bear: Dyck and Baydack 2004; marmots: Griffin et al. 2007). On the other hand, hyenas were more vigilant on days when livestock were present on their territory. Herdsmen always accompany their livestock when herds graze inside the Reserve, and pastoralists occasionally kill hyenas by spearing them. Therefore Talek West hyenas may associate livestock presence with potential danger, and be more vigilant in the presence of livestock than in their absence. Human-caused mortality is quite unpredictable, as pastoralists do not consume hyena meat; instead they corner and spear hyenas opportunistically or when hyenas attack their livestock. Behavioral changes have been observed in other animals in response to anthropogenic activity, but these were caused by more systematic poaching and hunting (Caro 1999; Brashares et al. 2001; Caro 2005b; Setsaas et al. 2007). Thus, our results suggest that sporadic killings are sufficient to induce detectable shifts in behavior.

Although factors other than human activities can certainly affect vigilance in hyenas, these factors appear unlikely to have caused the differences we observed between our two clans. Lion density may affect vigilance of spotted hyenas because lions are their main natural predators (Cooper 1991; Frank et al. 1995). However, the territories of both clans are used by similar numbers of lion prides, and lion subgroups observed on either territory are of similar sizes (Table 3.1; Dloniak 2006; Kolowski et al. 2007). The availability of refugia may also affect hyena vigilance, but there are no substantial differences in habitat structure or vegetation cover between the territories of the two clans (Kolowski 2007). Finally, the size of a clan may affect vigilance as well, as this in turn might affect the number of hyenas observed concurrently. The Mara River clan was smaller at the time of our study than the Talek West clan (Table 3.1). In our naturalistic observations, we found that hyenas in larger groups were less vigilant than in smaller groups, so Talek West hyenas should have been less vigilant if the observed differences were driven by clan size.

Since the late 1980s, we have accumulated evidence of the importance and magnitude of non-lethal anthropogenic effects on hyenas from the Talek West clan. In addition to the non-lethal effects observed in this study, Talek West hyenas have been shown to exhibit spatial avoidance of areas of their territory where the majority of the livestock grazing takes place (Boydston et al. 2003), and they have been found to exhibit temporal avoidance of interactions with pastoralists by becoming more strictly nocturnal (Kolowski et al. 2007). Talek West hyenas also excrete higher concentrations of glucocorticoid stress hormones than do Mara River hyenas, as with vigilance, and this is driven by pastoralist activity rather than tourism (VanMeter et al., in review). Little is known about how such non-lethal effects caused by humans ultimately affect fitness in spotted hyenas. However, recent studies of natural predator-prey interactions in other systems have shown that reductions in prey fitness caused by predator-induced non-lethal effects can be as large as, or larger than, reductions due to lethal predator effects (Nelson et al. 2004; Pangle et al. 2007; Creel and Christianson 2008). Animals may perceive human disturbance as a predation risk (Frid and Dill 1990), so non-lethal anthropogenic effects may comprise a substantial component of the net effect of humans on fitness of animals in disturbed populations. In addition, behavioral changes detected in earlier studies of Talek West hyenas predicted the proportional changes in mortality sources reported here, with a time lag of about three years (Watts 2007). Our study is the first to detect a significant increase over time in the lethal impact of humans on hyenas, most likely because of the statistical power available with 18 years of observations. Although we have no evidence that overall mortality rates among Talek West hyenas increased between 1988 and 2006, our data nevertheless strongly suggest that the proportion of total known-cause deaths attributable to humans has increased dramatically during this 18-year period.

Information on the effects of human disturbance on threat-sensitive behavior of mammalian carnivores is potentially useful as we attempt to conserve their populations. Relative to other carnivores, spotted hyenas are extraordinarily flexible in their behavior and ecology. Hyenas' reactions to human disturbance may therefore represent conservative indicators of how other mammalian carnivores exhibiting less behavioral plasticity might respond to such challenges, including species that are rare and endangered.

CHAPTER FOUR

A COMPARATIVE STUDY OF VIGILANCE IN EAST AFRICAN CARNIVORES

INTRODUCTION

Vigilance is a behavior that increases the likelihood that an animal will detect a given stimulus at a given time (Dimond and Lazarus 1974). The stimulus in question might be an approaching predator or an alarm signal emitted by a conspecific, but it might also be an approaching competitor or a potential mate (reviewed in Quenette 1990; e.g. Knight and Knight 1986; Roberts 1988; Coolen 2002; Trouilloud et al. 2004). Vigilance is most often studied in animals engaged in foraging, as this may produce a tradeoff between food intake and the ability to perceive danger (Lima and Dill 1990). More recently, there has been a call for studies of vigilance exhibited by resting individuals (Arenz 2003; Roberts 2003; Lima et al. 2005; Lima and Rattenborg 2007), as these are rarely examined. Tradeoffs animals might experience when resting are less clear than those experienced when foraging, because the function of rest is still poorly understood, but animals can nevertheless be at high risk during both activities. Vigilance is an easily quantifiable behavior, with important effects on survivorship (e.g. FitzGibbon 1989; Krause and Godin 1996; reviewed in Caro 2005a), so vigilance is often the focus of studies of antipredator behavior. In addition, vigilance in many mammals involves a common set of motor patterns; this facilitates interspecific comparisons, and allows us to gain insight into how vigilance behavior contributes to survival among species confronting different suites of challenges in the wild.

Several general patterns have emerged from the myriad past studies of vigilance in mammals and birds (reviewed by Quenette 1990 and Caro 2005a). First, as body size increases, vigilance generally decreases; body size appears to be a good proxy for the number of different predators that prey on a focal species (Quenette 1990), and thus the need for vigilance. Second, vigilance is found to decrease with increasing group size; this is often referred to as the "group-size effect" (reviewed in Elgar 1989). This can be due to a risk dilution effect such that, when larger numbers of individuals are present, the probability of one individual being attacked by a predator diminishes (Hamilton 1971). The group-size effect can also be due to an increase in overall vigilance at a particular moment in time as the number of conspecifics present increases; this is referred to as the "many eyes hypothesis" (Pulliam 1973; Elgar 1989; Fairbanks and Dobson 2007). Most studies documenting those general trends have focused on species that occupy low trophic positions in food webs, such as passerine birds, rodents or ungulates (e.g. Lima 1987; Blumstein et al. 2001; Hunter and Skinner 1998). Studies of species at higher trophic levels generally focus on their roles as predators (e.g. Mills and Shenk 1992; Murray et al. 1995; Cooper et al. 2007). Relatively little research has been done on vigilance behavior by predators, resulting in a lack of understanding of the mechanisms these animals possess for coping with danger. Mammalian carnivores confront many natural threats, including both intraguild predation and kleptoparasitism by members of their own and other species (Palomares and Caro 1999; Caro and Stoner 2003). The few past studies on antipredator behavior exhibited by carnivorous mammals suggest that vigilance might be important for predators as well as for prey (Caro 1987; Rasa 1989; Clutton-Brock et al. 1999; Switalski 2003; Di Blanco and Hirsch 2006; Hunter et al. 2007; Atwood and Gese 2008). Nevertheless, general trends in regards to vigilance behavior among mammalian predators remain largely unexplored.

Here we examined vigilance in adult mammalian carnivores in the wild while they were feeding or resting. We focused on eight sympatric species that occupy an East African savannah habitat in the northern part of the Serengeti ecosystem. These eight species represent four different families in the mammalian order Carnivora (see phylogeny in Figure 4.1): Herpestidae, including dwarf mongooses (*Helogale parvula*) and banded mongooses (*Mungos mungos*); Felidae, including cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), and lions (*Panthera leo*); Hyaenidae, including spotted hyenas (*Crocuta crocuta*); and Canidae, including black-backed jackals (*Canis mesomelas*) and wild dogs (*Lycaon pictus*). These species vary considerably in body size, in the intensity of the intra- and inter-specific feeding competition they experience, and in their social behavior (Table 4.1). This variation allowed us to inquire whether vigilance behavior by mammalian carnivores follows the same general patterns as those documented in other mammals and birds. A broad, comparative approach, involving multiple species concurrently, is rarely adopted in studies of vigilance, which usually focus on only one or two species (but see Blumstein 1996; Boinski et al. 2003; Beauchamp 2007). Our goals were to identify variables that predict patterns of vigilance in carnivores, and to compare patterns of vigilance between predators and prey.

METHODS

Study sites and study periods:

Our study was conducted in the Masai Mara National Reserve (MMNR – 1,500 km^2) in southwestern Kenya (1°40'S, 35°50'E), and in the northern portion of the Selous Game Reserve (SGR - 43,600 km^2) in Tanzania (7° 60' S, 38° 10' E). The MMNR

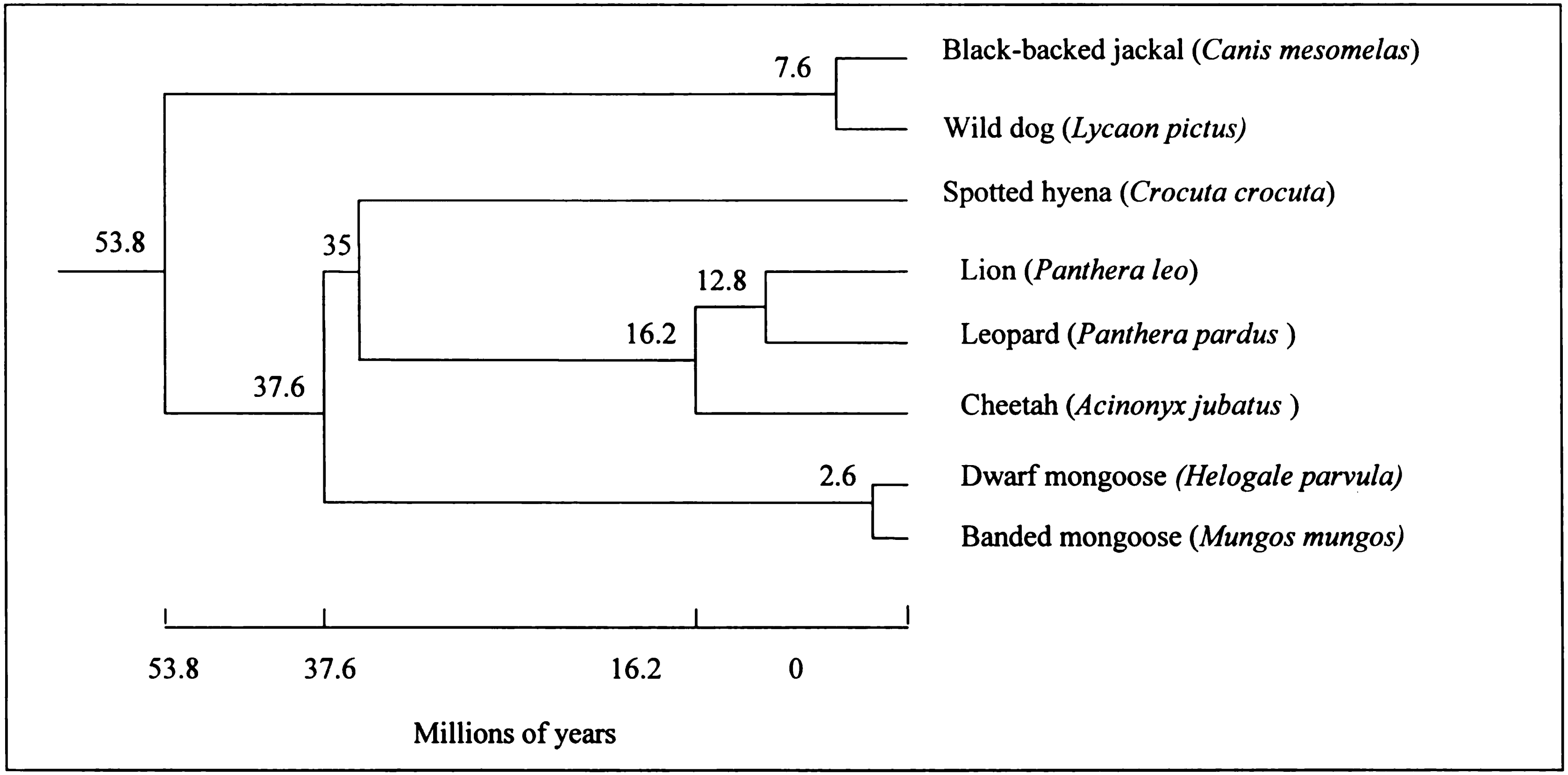

Figure 4.1. Hypothesized phylogenetic relationships and estimated times of divergence (numbers at the nodes, indicating millions of years) for the eight species included in the comparative analysis (adapted from Bininda-Emonds et al. 1999)

Table 4.1. Summary of the main characteristics of the eight carnivore species included in this study

Common Name	Latin Name	Body Mass (kg)	Annual Adult Mortality Rate*	Sociality **	Cohesiveness Index ***	Social Unit Size****	N Feeding	N Resting
Dwarf mongoose	*Helogale parvula*	0.3[a]	0.3[h]	Cohesive packs of up to 30[n,o]	5	10	20	-
Banded mongoose	*Mungos mungos*	1.5[a,b]	0.143[j]	Cohesive packs of up to 40[n, b]	5	17	21	-
Black-backed jackal	*Canis mesomelas*	10[a,c]	0.2[k]	Pairs or small family groups[n, c]	4	2	23	-
African wild dog	*Lycaon pictus*	24[a,d]	0.24[d]	Cohesive packs of up to 25[d]	5	8	22	-
Leopard	*Panthera pardus*	60[a,e]	0.18[e]	Solitary[e]	1	1	4	-
Cheetah	*Acinonyx jubatus*	50[f]	0.227[f]	Solitary or in small coalitions of males[f]	2	1	13	8
Spotted hyena	*Crocuta crocuta*	60[g]	0.17[g]	Fission-fusion groups of up to 80[g]	3	55	49	49
Lion	*Panthera leo*	Female: 125[m] Male: 190[m]	F: 0.04[m] M: 0.1[m]	Fission-fusion groups of up to 30[n,p]	3	9	F: 19 M: 12	F: 11 M: 14

* Only adult mortality rate is presented here, since this study included adults only.

** The number of animals given in the column includes young of the year and juveniles.

*** The cohesiveness index was determined to capture how likely an observer was to see all members of a given group when one individual of the group was detected. This dimension of sociality is not captured by the social unit size. We determined this index using information on sociality for each species; a species was categorized as 1 if members of a given group were solitary, and as 5 if all members of a group were found within close proximity of each other at any given time.

**** All from Gittleman 1989

a. Kingdon 1977; b. Rood 1975; c. MacDonald and Sillero-Zubiri 2004; d. Creel and Creel 2002; e. Bailey 1993; f. Caro 1994; g. Kruuk 1972; h. Rood 1990; j. Otali and Gilchrist 2004; k. estimation from mortality rates of other canids in this geographic area (MacDonald and Sillero-Zubiri 2004); m. Packer et al. 1988; n. Estes 1991; o. Gittleman 1989; p. Schaller 1972 consists primarily of rolling grassland and scattered bushland, with riparian forest along the major watercourses, whereas the SGR is dominated by miombo woodlands. African wild dogs were studied in the SGR between 1991 and 1996 by Scott Creel (Montana State University) who provided us with video tapes of wild dogs when they were feeding. All other carnivore species included here were monitored directly in the MMNR between 1988 and 2006, mainly in 2005-2006. Although a few wild dogs still occur sympatrically with the other MMNR carnivores, their population was decimated by a rabies epidemic in 1989 (Kat et al. 1995), and they are seldom seen today.

Study species:

Our eight study species occur sympatrically throughout much of Eastern Africa. Although other carnivores are present in this region, we restricted our observations to these eight species because all of them can be observed and filmed easily. The eight focal species have different diets, mating systems, and body masses, and they occur in social groups that vary in size and cohesiveness. Table 4.1 summarizes salient characteristics for each species. All subjects used here were adult individuals.

Data collection and data extraction from videotapes:

Individual members of each focal species were filmed while feeding or resting, and behavioral measures of vigilance were later extracted from the video footage. All data collection in the field was done between 0600 and 1900 h when there was sufficient daylight to film. All species sampled except leopards were regularly found feeding during daylight hours. Because we rarely witnessed leopards feeding in the MMNR during daylight, we increased our sample size by including two male leopards filmed while feeding in South Africa by Phil Perry, a wildlife photographer. We considered an individual to be feeding when it was consuming a fresh ungulate carcass (jackals, wild dogs, cheetahs, leopards, spotted hyenas and lions) or foraging on smaller food items (dwarf and banded mongooses, which feed on invertebrates and small vertebrates; Estes 1991) for more than five consecutive minutes. Thus, mongooses were sampled during both search for and handling of prey, while all other carnivores were sampled only during prey handling. We considered an individual to be resting when it was lying down for more than ten minutes in the absence of food, and not interacting with conspecifics. Each individual was filmed only once in all species except hyenas; we avoided re-sampling either by knowing the identities of all focal animals (wild dogs, cheetahs, leopards, spotted hyenas and lions), or by using footage acquired in areas that were distant from one another in space (at least three km apart) or time (at least two years apart) for jackals and both mongoose species. Individual adult spotted hyenas were sampled multiple times, but animals were known individually so an average was calculated for each individual across its different trials, and this mean was used in all analyses. Multiple conspecifics were sometimes filmed simultaneously while feeding on a single kill (jackals, wild dogs, cheetahs, hyenas and lions). Under these circumstances we extracted data for all animals fully visible throughout filming. Because data points derived from animals feeding on the same kill are not independent, we initially chose one individual at random at each kill and used its data in analyses. However, as no result generated by using a single individual per kill differed from that generated using all individuals feeding at each kill (t-tests, all $p > 0.2$), we present results here based on the full dataset to increase our sample sizes.

All filming in Kenya was done using a digital Sony camcorder (Sony DCR HC65). We used vehicles as mobile blinds for filming all species except mongooses, and most footage was obtained when our vehicle was parked no closer than 15 meters from the subject animal. All subject animals were routinely watched by tourists, so they were well habituated to cars. Mongooses were filmed from the car, as with other species, but also in camp grounds or grounds of tourist lodges, and were well habituated to the presence of humans on foot. Therefore, most footage of mongooses was obtained by following foraging individuals on foot. For each individual from each species, we extracted data from 1 to 8 min ($\overline{X} = 4.04$ min) of naturally occurring feeding at kills (all species except mongooses) or while foraging (both mongooses species). For individual cheetahs, lions and hyenas, we also extracted data from 4 to 10 min ($\overline{X} = 4.64$ min) of footage taken when the focal animal was resting undisturbed. Because we filmed some species for longer durations than others, we inquired whether vigilance behavior varied with the length of the filmed sequence.

Videotapes were watched in slow-motion with a Sony DCR TRV900 digital camcorder that superimposed a time-code on the screen with a precision of 0.033 s. We identified vigilance behavior whenever a focal individual lifted its head. The onset of a vigilance bout was considered the point at which the animal lifted its head (midway through the raising of the head), and the end was considered the point at which the animal lowered its head again (midway through the lowering of the head). From the video footage, we extracted the duration of each vigilance bout, as well as the total number of bouts in the filmed sequence. The latter number was used to calculate a rate of bouts per minute filmed. A mean bout length was also calculated for each filmed sequence. From the average duration and the rate of vigilance bouts, we calculated the total percent time each animal spent vigilant in the filmed sequence.

We recorded several factors at the time of filming that are known to affect vigilance in other species. In conjunction with each filmed sequence, we recorded the number of conspecifics present within 100 m of the focal individual (referred to hereafter as “group size”), the distance between the focal individual and the closest conspecific, the distance between the focal animal and the car or observer on foot, and the distance to the closest patch of bushes (using a Bushnell range finder). We also noted the time of day at which the film sequence began, as well as the strength of the wind at the time of filming and the height of the grass where the focal animal was filmed. Grass height was evaluated relative to the head of the focal animal, and ranked from 0, if there was no grass, to 6, if the grass was higher than the raised head of the focal individual.

In order to evaluate variation in vigilance behavior among species, we also obtained other variables from the literature; all relevant sources of information are indicated in Table 4.1. First, we obtained mean body mass of each carnivore species. In the case of lions, we determined mass separately for adults of each sex, as this was the only species included here that exhibited strong sexual dimorphism in body size. From the literature, we also gathered data on the mean adult mortality rate for each species. Third, for each species we obtained information on mean “social unit size”, defined as the average number of individuals sharing a common territory; note that this differs from the “group size”, as defined above as the number of conspecifics present with the focal animal at the time of filming. Finally, we calculated a "cohesion index" to reflect the degree of social cohesion characteristic of each focal species. Species with high cohesion, those in which all members of a group are always found together, were ranked as 5 (this included wild dogs and both species of mongooses), whereas species rarely seen with conspecifics except when mating (such as leopards) were ranked as 1 (see Table 4.1).

Data Analysis:

We conducted separate analyses for three measures of vigilance: duration of head raises, rate of head raises, and percent time spent vigilant. We tested assumptions of normality and homogeneity of variance in each measure using Wilks-Shapiro and Levene's Tests, respectively. Duration of head raises, rate of head raises, and mortality rate of all species met both assumptions once they were square-root transformed. Body mass of each species and social unit size variables also met both assumptions after being log10-transformed, and percent time spent vigilant for each focal animal was arcsine-square-root transformed to meet both assumptions. Prior to analysis, we tested and found no effect on any dependent measure of time of day, wind, or distance between subjects and observer (multiple linear regressions, all $p > 0.05$). We therefore pooled our data across these conditions to increase our statistical power. Sample sizes are shown in Table 4.1.

Interspecific comparisons:

Data from feeding individuals were analyzed for all eight species. Considering individuals as the statistical units of analysis would be inappropriate when comparing species, as this would inflate degrees of freedom (Harvey and Pagel 1991). Thus, each species in the following analyses is represented by a single data point. Because our analyses included comparisons among multiple species with shared evolutionary history, the data points could not be considered to be independent of each other (Harvey and Pagel 1991; Freckleton et al. 2002). To determine whether phylogenetic relationships influenced clustering in the vigilance data, we used Generalized Least Squares linear regressions through the origin of phylogenetically independent contrasts (Felsenstein 1985; Harvey and Pagel 1991; Garland and Ives 2000; Garland et al. 1992). To carry out those analyses, we used two Phenotypic Diversity Analysis Programs (PDAP), available upon request from T. Garland (Garland et al. 1993, 1999). Using the phylogenetic hypothesis for the order Carnivora produced by Bininda-Emonds et al. (1999; Figure 4.1), we first entered the phylogenetic tree into the program PDTREE. Using this tree, we then created an across-species variance-covariance matrix with program PDDIST (Garland et al. 1993; Garland et al. 1999; Garland and Ives 2000; Ashton 2004) and used this matrix in the MATLAB (vR2006a) Regressionv2.m (Spoor et al. 2007) to run Phylogenetic Generalized Least Square (PGLS) regressions. We evaluated the strength of the various variables by comparing Akaike Information Criteria (AIC), and considering the model with the lowest AIC value as the strongest model (Burham and Anderson 2002).

Data from resting individuals were compared to data from feeding individuals using 2-way ANOVAs that evaluated the effects of species, activity and the interaction between species and activity.

Intraspecific comparisons:

In addition to comparing vigilance among species, we examined variation within each species separately using a multivariate approach. All species except leopards provided a large enough sample to permit such analyses. We included group size, distance to nearest conspecific, distance to nearest patch of bushes, and grass height as independent variables in a multiple linear regression, and examined their relationship to the percent time spent vigilant by feeding individuals. From this full model, we eliminated distance to nearest conspecific, since it was a non-significant ($p > 0.05$) explanatory variable for all species. For purposes of brevity, we report results only for the percent time spent vigilant; however, results for duration and rate of head raises were similar to those for percent time spent vigilant.

All analyses other than the phylogenetic analyses were carried out using a significance level of alpha = 0.05 and two-tailed tests. Unless otherwise indicated, means ± 1 standard error are presented.

RESULTS

Interspecific comparisons: Vigilance during feeding and resting

Vigilance in the carnivores observed here varied among species and between activities. Percent time spent vigilant while feeding ranged from 3.6 % in wild dogs to 21 % in dwarf mongooses (Figure 4.2a), with a mean of 12 ± 2.16 %. The two mongoose species and wild dogs had the shortest head raises (1.9 s), whereas cheetahs had the

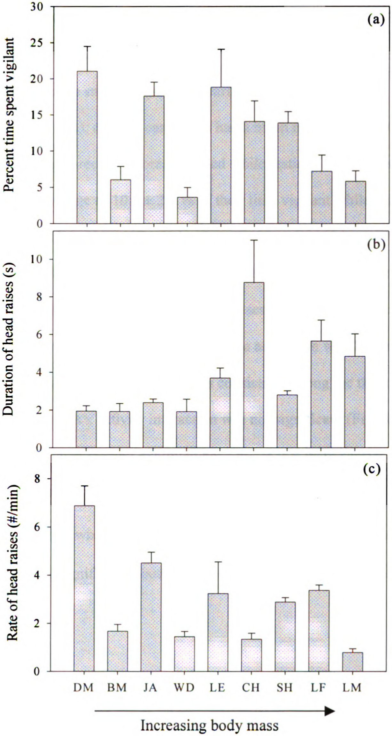

Figure 4.2. Vigilance while feeding in eight carnivore species: (a) mean ± SE percent time spent vigilant, (b) mean ± SE duration of head raises, and (c) mean ± SE rate of head raises. Species abbreviations on the X-axis are: DM = dwarf mongooses; BM = banded mongooses; JA = black-backed jackals; WD = wild dogs; CH = cheetahs; SH = spotted hyenas; LF = female lions; LM = male lions. Species are presented from left to right in order of increasing body mass.

longest (8.7 s), and overall, carnivores had a mean head raise duration of 3.8 ± 0.8 s (Figure 4.2b). The largest animals, male lions, raised their heads least often (0.8 head raises / min), whereas the smallest species, dwarf mongooses, raised their heads most often (7 head raises / min); overall, carnivores had a mean rate of 2.9 ± 0.6 head raises / min (Figure 4.2c). The three carnivores sampled while resting (cheetahs, spotted hyenas and lions) spent an average of 10.5 ± 2.2 % of their time vigilant while resting (range: 1.8 % to 14 % - Figure 4.3a). This vigilance level was achieved with a mean head raise duration of 23.5 ± 5.8 s (range: 11.6 to 35.1 s – Figure 4.3b) at an average rate of 1 ± 0.4 head raise every 3 min (range: 0.05 to 0.58 head raises / min – Figure 4.3c).

The components of vigilance varied with the activity in which animals were engaged when sampled, and this variation was consistent among the three species examined, but the species x activity interaction was not significant (Figure 4.3). Carnivores sampled when feeding exhibited head raises that were shorter in duration ($F_{1,142} = 30.56, p < 0.001$; Figure 4.3b) and greater in frequency ($F_{1,162} = 61.61, p <$ 0.001; Figure 4.3c) than when they were resting. However, the overall percent time spent vigilant did not differ significantly between feeding and resting ($F_{1,175} = 0.001, p = 0.97$, Figure 4.3a).

Interspecific comparisons: Predictors of vigilance during feeding

Body mass was a significant predictor of rate of head raises in the carnivores sampled ($r = -0.68, p = 0.03$, Table 4.2), with larger carnivores raising their heads less frequently than smaller carnivores. Body mass was also a significant predictor of the percent time carnivores spent vigilant ($r = -0.78, p = 0.02$, Table 4. 2), with larger

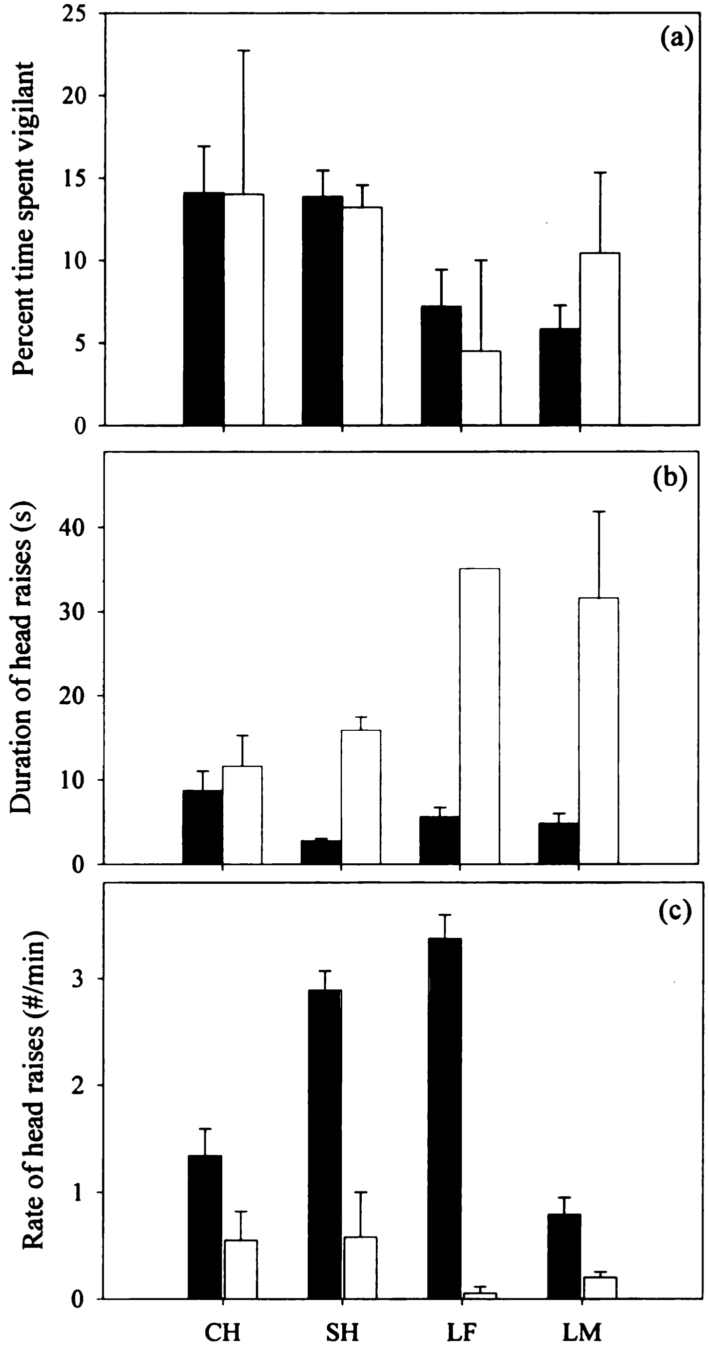

Figure 4.3. Comparison of vigilance while feeding and resting in three carnivore species: (a) mean ± SE percent time spent vigilant, (b) mean ± SE duration of head raises, and (c) mean ± SE rate of head raises. Black bars represent data from feeding animals and white bars represent data from resting animals. Species abbreviations on the X-axis are: CH = cheetahs; SH = spotted hyenas; LF = lion females; LM = lion males. Statistics were done on transformed data, but untransformed data are presented here. Feeding means were significantly different from resting means in panels b and c (all $p < 0.001$).

Table 4.2. Results from the phylogenetic analyses of eight carnivore species; NS indicates statistically non-significant variables, * indicates marginal relationships ($p < 0.1$), and ** indicates significant relationships ($p < 0.05$). All degrees of freedom are 6. The column "PGLS regressions" shows the results from Phylogenetic Generalized Least Squares regressions in which phylogeny is controlled for (see Methods for details).

		PGLS regressions		
		r	***AIC***	***p***
Percent time spent vigilant	Body Mass	-0.78	-9.70	**
	Mortality Rate	0.81	-10.86	**
	Social Unit Size	-0.56	-5.39	NS
	Cohesion Index	-0.28	-3.08	NS
Duration of head raises	Body Mass	0.10	11.14	NS
	Mortality Rate	0.10	11.14	NS
	Social Unit Size	-0.63	7.16	*
	Cohesion Index	-0.61	7.48	*
Rate of head raises	Body Mass	-0.81	21.76	**
	Mortality Rate	0.81	21.78	**
	Social Unit Size	-0.46	28.49	NS
	Cohesion Index	-0.17	30.14	NS

carnivores spending less time vigilant than smaller carnivores. However, body mass was not a strong predictor of duration of head raises (Table 4.2). Mortality rate was a significant predictor of rate of head raises ($r = 0.81$, $p = 0.015$, Table 4.2), with species experiencing higher mortality rates raising their heads more frequently during feeding. Mortality rate was also a significant predictor of the percent time the carnivores spent vigilant ($r = 0.81$, $p = 0.015$, Table 4.2). Mortality rate was not a good predictor of duration of head raises.

Mean social unit size tended to predict the duration of head raises, although this remained marginally non-significant ($r = -0.63$, $p = 0.09$, Table 4.2): species living in larger social units tend to have shorter head raises than those living in smaller units. Similarly, highly cohesive species tended to have shorter head raises than less cohesive species ($r = -0.61$, $p = 0.11$, Table 4.2). However, neither social unit size nor degree of cohesiveness among group members significantly predicted rates of head raises, or percent time spent vigilant.

Intraspecific analyses: Variation in vigilance within species

We did not find any factors that could explain within-species variations in the percent time spent vigilant while feeding in dwarf and banded mongooses, wild dogs, cheetahs, and female lions. Group size was a significant factor only in spotted hyenas ($F_{1,138} = 7.69$, $p = 0.006$, Table 4.3), which spent less time vigilant as group size increased. Distance to bushes was only a significant factor in explaining variation in vigilance for male lions ($F_{1,7} = 11.22$, $p = 0.01$, Table 4.3), with male lions spending more time vigilant when bushes were closer. This relationship explained a large part of

Table 4.3. Results from modeling within each species the percent time spent vigilant while feeding in relation to group size, distance to bushes, and grass height. Sample sizes, representing the number of individuals filmed, appear in parenthesis after each common species name. Bold values represent statistically significant ($p < 0.05$) values. Group size indicates the number of conspecifics present when the focal individual was feeding. Distance to bushes indicates the distance from the focal animal to the closest patch of bushes. Grass height was evaluated relative to the head of the focal animal, and was categorized as 0 if there was no grass and 6 if the grass was taller than the head of the focal individual. This analysis was not carried out on leopards because of insufficient sample sizes. We had no information on distance to bushes for wild dogs.

	Group size		**Distance to bushes (m)**		**Grass height***		**Model**	
Species (*N*)	$\overline{X}$ ± SE (range)	*p*	$\overline{X}$ ± SE (range)	*p*	$\overline{X}$ ± SE (range)	*p*	*r*	*p*
Dwarf mongooses (20)	20 ± 0 (20)	-	1.05 ± 0.05 (1-2)	0.46	2.2 ± 0.19 (1-4)	0.55	0.22	0.63
Banded mongooses (21)	19.05 ± 0.89 (10-25)	0.26	194 ± 44 (1-450)	0.21	2.05 ± 0.15 (1-3)	0.57	0.40	0.37
Jackals (23)	1.96 ± 0.16 (1-5)	0.84	82 ± 14 (1-250)	0.94	3.19 ± 0.23 (2-5)	**0.01**	0.58	0.08
Wild dogs (22)	5.18 ± 0.55 (1-9)	0.9	-	-	2.5 ± 0.11 (2-3)	0.52	0.03	0.99
Cheetahs (13)	1.85 ± 0.32 (1-4)	0.56	284 ± 80 (3-700)	0.72	3.17 ± 0.44 (2-6)	0.14	0.57	0.41
Spotted hyenas (49)	7.96 ± 0.58 (1-21)	**0.006**	142 ± 13 (1-700)	0.23	2.36 ± 0.08 (1-6)	0.32	**0.26**	**0.02**
Lion females (19)	4.11 ± 0.46 (1-8)	0.49	101 ± 30 (1-500)	0.12	2.84 ± 0.28 (2-6)	0.85	0.45	0.39
Lion males (12)	3.42 ± 0.92 (1-11)	0.32	266 ± 84 (1-700)	**0.01**	2.67 ± 0.40 (1-6)	0.76	**0.80**	**0.05**

the variation in this measure among male lions ($r = 0.80$). Lastly, jackals were found to be less vigilant as grass height increased ($F_{1,16} = 8.06, p = 0.01$, Table 4.3).

DISCUSSION

The carnivores sampled in this study spent an average of 12 % of their time vigilant while feeding, achieved by having brief head raises (3.8 s on average) at a high rate (3 head raises/min). Those levels of vigilance are surprisingly similar to the levels reported for species occupying lower trophic positions. For example, the average percent time spent vigilance among multiple species of ungulates sampled in the Serengeti ecosystem is 12 % (average compiled from Burger and Gochfeld 1994; Hunter and Skinner 1998). Other studies have found levels of vigilance in small carnivores such as meerkats (e.g. Moran 1984) to be similar in magnitude to those in prey species, but our observations suggest that the need for larger carnivores to monitor their environment is also high. The maintenance of these levels of vigilance in the carnivore species sampled here might be explained by the high levels of competition and intra-guild predation that occur among Serengeti carnivores (e.g. Caro and Stoner 2003). It therefore seems likely that the vigilance of larger carnivores might serve more directly to detect conspecifics or intraguild competitors than does vigilance of species occupying lower trophic positions. Similar patterns of vigilance have been found in several species of primates that direct more of their vigilance toward conspecifics than toward predators (reviewed in Treves 2000).

Although all species sampled in the current study exhibited vigilance while feeding, we found significant differences among species. For instance, the two canid species had very different levels of vigilance, with jackals spending far more time vigilant than wild dogs. Such differences within families might be partly explained by the ecology of each species. For example, wild dogs live in larger and more cohesive social units than jackals, and have also much larger body masses (Table 4.1; Creel and Creel 2002), both of which may lead to wild dogs being less vulnerable to predation. Substantial differences were also observed between the two mongoose species; however, in this case, both dwarf mongooses and banded mongooses are small bodied and highly gregarious. The variation here might be explained instead by differences in their mortality rates: dwarf mongooses experience much higher mortality rates than do banded mongooses (Table 4.1; Rood 1990; Otali and Gilchrist 2004). Lastly, cheetahs were the most vigilant felids in our study. Cheetahs experience high levels of kleptoparasitism, and also have a high mortality rate for their body mass (Caro 1994), which might explain their high levels of vigilance. It is interesting to note that, overall, phylogenetic relationships offered little help in explaining carnivore vigilance behavior.

The three carnivore species sampled while resting spent about 10 % of their time vigilant. Resting is a necessary activity that is potentially dangerous, because animals are reducing their attention to environmental stimuli and therefore to potential danger (Rattenborg et al. 1999; Lima et al. 2005; Lima and Rattenborg 2007). Whereas vigilance during rest has gained attention only recently (Lima et al. 2005), the existing studies, mainly conducted with birds, suggest that resting animals continue to maintain vigilance behavior similar to that reported for feeding animals (Lendrem 1983, 1984; Gauthier-Clerc and Tamisier 2000; Gauthier-Clerc et al. 1998, 2002; Dominguez 2003).

Although we found that all monitored carnivore species spent roughly the same overall percent time engaged in vigilance during feeding and resting (means of 12 % and 10 %, respectively), these similar percentages were achieved differently. That is, when feeding, carnivores raised their heads briefly but at a high rate; when resting, they used prolonged head raises that occurred infrequently. Some have compared vigilance within a single species across several different activities (Cords 1995; Cowlishaw 1998; Hirtch 2002; Treves et al. 2001; Kutsukake 2006), but results from all these studies differed from those reported here in that the primates were less vigilant while foraging than while resting. Because vigilance in these primate studies was not broken down into duration and rate of head raises, we cannot inquire whether the two different vigilance strategies we observed in carnivores were also used by other species.

There are several possible explanations for the different vigilance strategies we observed during feeding and resting. One is that targets of vigilance might vary according to the activity in which individuals are engaged. For example, resting animals might be searching the environment for approaching predators, and this might require long durations of head raises. On the other hand, feeding animals might be monitoring their environment to detect competitors approaching to steal food, thus demanding more frequent, shorter head raises. A second possible explanation is that, when resting, animals are looking for distant targets, which might require long, infrequent head raises that need not necessarily be repeated often, whereas feeding animals are looking for very close targets, which might require short, frequent head raises. Lastly, it may be that the two activities, resting and feeding, occur in environments of differential complexity: resting animals here were typically lying down on open savannah, with little to monitor on a short-term basis, whereas feeding animals were often monitoring a shifting social environment containing multiple conspecifics.

In contrast to recent studies showing that animals can be vigilant while handling food (e.g. Lima and Bednekoff 1999; Makowska and Kramer 2007), the carnivores we studied often had restricted visual inputs because they had their heads deep in a carcass while feeding or had their eyes closed while resting. Although this study considered only vigilance through visual orientation, our subjects were most likely using multiple modalities to detect potential danger (e.g. Radford and Ridley 2007). For instance, we noticed that resting carnivores exhibited multiple ear-twitching movements even in the absence of insects, suggesting that they are using auditory cues to monitor the environment when resting. Similarly, olfaction is most likely a particularly important sensory modality for danger detection among carnivores.

When considering variation in vigilance among species, the carnivores sampled here exhibited the same general trends as those observed in other mammals and birds. Body size is often an important determinant of vigilance in other mammals, with vigilance increasing with decreasing body size (Quenette 1990). Our study confirms that this relationship holds for mammalian carnivores as well, at least in regard to percent time spent vigilant and rates of head raises. We did not find that duration of vigilance bouts increased significantly with body mass. We found that species experiencing higher mortality rates engaged in more vigilance by increasing the rate of head raises rather than their duration. Even though carnivores occupy high trophic positions, they nevertheless experience high adult mortality rates (e.g. Caro 1994). Lastly, we found sociality measures (both social unit size and cohesiveness) to be important predictor of vigilance across multiple species of carnivores, but they only affected the duration of vigilance bouts, not the bout rate or the overall percent time spent vigilant. More gregarious species (i.e. species that lived in larger social units or were more cohesive) engaged in shorter vigilance bouts than did gregarious social species. This is similar to what has been found in other mammals and birds (as reviewed by Caro 2005a).

When examining vigilance within each species, we found a group size effect only among spotted hyenas. The presence of a group size effect has been found in the majority of vertebrate species examined (reviewed in Elgar 1989 and Caro 2005a), so it is surprising that only hyenas exhibited a decrease in vigilance as group size increased here. It may be that hyenas are the only species for which we had both large sample sizes and considerable variation in the size of the groups in which animals were feeding.

Other factors previously shown to influence vigilance in species occupying lower trophic positions also helped explain within-species variation in the carnivores we observed. Male lions decreased their vigilance when feeding further from bushes. Other species, particularly birds and rodents, have been shown either to increase or decrease their vigilance in relation to distance to cover (e.g. Lazarus and Symonds 1992; Hughes and Ward 1993; reviewed in Caro 2005a). In the case of male lions, which defend territories and kills against intruders (Schaller 1972), bushes might conceal immigrant male lions that could pose a potential threat. We also observed decreasing vigilance by jackals with increasing grass height. Other studies done on rodents have reported vigilance changes in relation to grass height, especially in rodents species that use grass as protective cover and decrease their vigilance when grass is high (e.g. Tchabovsky et al. 2001), similarly to what we observed among jackals.

Our study points to the need for more broad scale investigations of vigilance that allow comparisons within species among activities, as well as among species, to generate robust understanding of the ways in which animals cope with danger. There is currently little information on vigilance behavior in carnivores due in part to the underlying assumption that large carnivores are vigilant to locate prey rather than to detect threats (e.g., Leyhausen 1979). However, carnivores rarely die of old age (e.g. Kruuk 1972; Rood 1975; Bailey 1993; Caro 1994; Packer et al. 1998; Creel and Creel 2002; Otali and Gilchrist 2004), and they regularly face intraguild predation and competition (Caro and Stoner 2003). We found that the carnivores studied here devoted roughly the same proportion of their time to vigilance as do ungulates, rodents and birds. Whether vigilance in carnivores serves to locate predators or to prevent kleptoparasitism will be difficult to assess until specific experiments are conducted (e.g. Hunter et al. 2007). Future studies should attempt to tease apart the relative importance of antipredator vigilance and vigilance toward potential competitors, as in recent studies of primates (e.g. Treves 2000; Hirsch 2002; Kutsukake 2007).

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