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Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve

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We evaluated long-term patterns of human-caused mortality among free-living spotted hyenas (*Crocuta crocuta*) in a Kenyan game reserve and also assessed nonlethal anthropogenic effects on hyena behavior. We monitored naturally occurring vigilance in 2 clans of hyenas, 1 disturbed and the other undisturbed. The disturbed clan, living on the edge of the reserve, experienced much human disturbance from both tour vehicles and livestock grazing, whereas the undisturbed clan, living in the center of the reserve, also experienced tour vehicles but no livestock grazing. The proportion of all deaths with known causes that could be attributed to humans increased between 1988 and 2006 in the disturbed population; humans caused no mortality in the undisturbed population. Disturbed hyenas were more than twice as vigilant when resting, and they nursed their young closer to bushes, than undisturbed hyenas. Disturbed hyenas also were most vigilant on days when livestock were present in their territory, but we observed no effects of tourism on hyena vigilance. We next conducted playback experiments in which we used cowbells as treatment sounds and church bells as control sounds to determine whether hyenas from the 2 clans responded differently. After hearing cowbells, disturbed hyenas increased their vigilance more than did undisturbed hyenas. However, disturbed hyenas also increased their vigilance after hearing church bells, suggesting that disturbed hyenas may exhibit heightened responsiveness to a wide array of anthropogenic sound stimuli. Our findings suggest that human activities related to pastoralism are having measurable effects on hyena mortality, and that hyenas appear to be responding to this threat by modifying their behavior. DOI: 10.1644/08-MAMM-A-359R.1.

Key words: antipredator behavior, *Crocuta crocuta*, East Africa, human disturbance, livestock, tourism, vigilance

Persecution by humans often represents a leading source of mortality for mammalian carnivores, even inside protected areas (Woodroffe and Ginsberg 1998, 2000), and such persecution can reduce population size (Creel and Creel 2002; Woodroffe 2000, 2001). Human-induced mortality frequently is associated with human–carnivore conflicts in areas where carnivores persist but human populations are expanding (Johnson et al. 2006; Ogutu et al. 2005; Woodroffe 2000). In addition to such lethal effects, humans potentially can have nonlethal effects on carnivores by modifying their behavior and physiology (Creel et al. 2002; Lima 1998). Carnivores display both spatial and temporal avoidance in response to increasing human activity (e.g., Boydston et al. 2003; Kitchen et al. 2000; Kolowski et al. 2007; Olson et al. 1998; Theuerkauf et al. 2003). Anthropogenic activity also has been linked to elevated concentrations of excreted stress hormones, reduced time spent feeding, and more time spent alert in various carnivores (e.g., Creel et al. 2002; Dyck and Baydack 2004; Frid and Dill 2002; Nevin and Gilbert 2005; Van Meter et al. 2009). Such findings suggest that efforts to conserve carnivores might be enhanced by better understanding of both lethal and nonlethal effects of human activity on these animals (e.g., Berger 1998, 2000; Caro and Durant 1995; 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 (Caro 1999; Lima and Dill 1990), 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., Cooper et al. 2007; Mills and Shenk 1992; Murray et al. 1995), resulting in a lack of understanding of the mechanisms they possess for coping with danger. Only a few studies have examined threat-sensitive behaviors in mammalian carnivores (Atwood and Gese 2008; Caro 1987; Clutton-Brock et al. 1999; Di Blanco and Hirsch 2006; Durant 2000a, 2000b; Hunter et al. 2007; Rasa 1989; Switalski 2003). Because vigilance is ubiquitous and easily quantifiable, it may provide a noninvasive indicator of how much risk a given animal perceives, especially in populations disturbed by human activity. 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, are generally nocturnal, and 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 (Kolowski et al. 2007; Kruuk 1972). Furthermore, their social organization in large ''clans'' that contain up to 80 individuals (Kruuk 1972) allows for repeated observations of many known individuals. In parts of the Masai Mara National Reserve (henceforth the Reserve), Kenya, spotted hyenas currently must cope not only with lions (*Panthera leo*), which are their only natural predators (Cooper 1991; Frank et al. 1995), but also with intensive disturbance by humans, particularly along Reserve borders (Boydston et al. 2003; Kolowski 2007).

We evaluated effects of human activity on hyenas by comparing 2 clans of *Crocuta* that differed dramatically in their exposure to anthropogenic disturbance. 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 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 3 different approaches in this study. First, we assessed long-term trends in human-caused mortality among hyenas in the 2 clans. Second, we documented naturally occurring vigilance behavior exhibited by wild hyenas in different behavioral contexts, both when lions were present with hyenas and when lions were absent. Finally, we tested whether vigilance behavior in hyenas is influenced by the presence of either tourists or livestock and herders. To evaluate effects of tourism we took advantage of temporal variation in tourist numbers. To evaluate effects of pastoralist activity we performed a small playback experiment.

Because of frequent exposure of Talek West hyenas to human disturbance, we expected that they would spend more time vigilant than Mara River hyenas. In southern Kenya local pastoralists always accompany their livestock, and herders sometimes kill or harass indigenous wildlife while guarding their herds. This occurs even within protected areas. Masai pastoralists generally hang 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 at distances of >1 km. These facts suggest that hyenas might associate the sound of cowbells with danger. In playback experiments we compared responses of hyenas in both study clans to cowbells (treatment sounds) and church bells (control sounds). We predicted that hyenas from the clan experiencing little human disturbance would react similarly to sounds of cowbells and church bells because both should represent novel sounds, whereas we expected that hyenas from the clan experiencing cowbells daily would show greater vigilance in response to these sounds than to sounds of church bells.

Table 1.—Salient characteristics of Talek West and Mara River clans of spotted hyenas. Unless otherwise indicated, all information from this table was obtained from Kolowski (2007). Sampling errors represent *SE*s.

	Talek West clan	Mara River clan
Clan size (no. hyenas)	47–55	28–43
Territory size (km^2)	28.4	31.0
Mean lion pride size[a]	15.33 ± 2.73	18 ± 2.08
Mean lion group size (no. lions)	3.9 ± 0.26	3.4 ± 0.30
Prey density (no./km^2)	210.8	196.6
Mean no. livestock grazing daily on the territory	1,386 ± 181	0
Distance to nearest Reserve border (km)[b]	0	6.5
No. tour vehicles approaching hyenas per hour	0.87	0.18

[a] S. M. Dloniak, Mara Carnivore Conservation Project, Kenya, pers. comm.
[b] Reserve = Masai Mara National Reserve.

Materials and Methods

Study site and study animals.—The Reserve (1,500 km^2), located in southwestern Kenya (1°40′S, 35°50′E) in an area of open, rolling grasslands, 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). The 2 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 1; see also Kolowski et al. 2007; S. M. Dloniak, Mara Carnivore Conservation Project, Kenya, pers. comm.). Because their territory lies along the border of the Reserve, Talek West hyenas live in close proximity to Masai villages and experience daily human disturbances in 2 forms: livestock herds guarded by herdsmen, and vehicles carrying tourists engaged in wildlife viewing. In contrast, although Mara River hyenas experience some visitation by tourists (Table 1), they do not encounter livestock herds because their territory is located more than 6 km from the nearest Reserve border, which is too deep in the Reserve for livestock to travel for daily grazing. 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—

Glickman et al. 1992; Matthews 1939) were included in this study.

Determination of causes of death.—The Talek West clan was observed between 1 July 1988 and 1 September 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 determined reliably 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 attributed reliably to 1 particular source, so we restricted our data set 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 1 January 2001 and 1 September 2006. In this clan 8 deaths could be attributed reliably 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 and 1100 h (the AM period) and between 1500 and 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 were well habituated to our vehicle because all natal animals were exposed to it since infancy. We documented vigilance in 3 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 1 of these 3 activities, we mounted a Sony DCR-H65 video camera (Sony, New York, New York) on a window tripod and videotaped the focal animal for 2–7 min ($\bar{X}$ = 4.25 min ± 0.04 *SD*).

Spotted hyenas live in fission–fusion societies in which clan members are found in groups of various sizes and compositions (Smith et al. 2008). At the time of filming we recorded various types of ecological and social data, including the number of conspecifics present within 100 m of the focal individual; this is referred to hereafter as the ''group size.'' ''Clan size'' refers to the number of individuals in the entire social unit, although all clan members seldom occur together concurrently. We also recorded the distance between the focal individual and the closest patch of bushes (using a Bushnell Yardage Pro Sport 450 laser range finder, Bushnell, Overland Park, Kansas). Hyenas use bushes as refugia from threats, and bushes also might conceal lions. Lions were considered to be present with the focal hyena if they were <200 m from it. During daily observations we also recorded the presence, and estimated the sizes, of any livestock herds seen in the territory of the Talek West clan. No livestock ever were seen in the Mara River territory (Table 1). Only cattle herds were recorded, although herds of sheep and goats also were seen occasionally in the Talek West territory. Herd size was estimated to the nearest 50 head.

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 tourist numbers exceeded 10,000 (n = 6): June, July, August, September, October, and December. Because tour vehicles are abroad in the Reserve during only 2 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 nontourism hours.

Playback experiment.—Hyenas were exposed to 2 types of sounds during playback experiments: treatment sounds were cowbells ringing, and control sounds were church bells ringing. Like cowbells, church bells also are made of metal, but their frequencies are much lower than those produced by cowbells (mean dominant frequencies calculated using Adobe Audition version 1.5; Adobe Systems Inc, San Jose, California: $\bar{X}_{\text{church bells}}$ = 738 Hz; $\bar{X}_{\text{cowbells}}$ = 1,121 Hz). Cowbell sounds were recorded from moving herds of cattle in and around the Talek West clan territory, using a Marantz PMD-22 portable cassette recorder (Marantz, Mahwah, New Jersey) and a Sennheiser ME66 shotgun microphone (Sennheiser, Old Lyme, Connecticut). All recordings (n = 11) were made from herds that contained approximately 10 individuals fitted with bells. Church-bell sounds were recorded with the same equipment from 8 different churches located around the city of La Rochelle, France. We manipulated all recordings using Adobe Audition 1.5 to limit each 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 ≥200 m from the nearest conspecific. Upon finding a subject, the car was positioned approximately 100 m (range: 80–115 m; $\bar{X}_{\text{distance}}$ = 91 m ± 3 *SE*) from the hyena, at an angle of 45° to the plane formed by a straight line between the subject and the observer videotaping the response of the hyena. Recordings used in the field were picked randomly from the sound library, but no recording was used more than twice to minimize pseudoreplication (McGregor et al. 1992). Recordings were played from a Creative Nomad Jukebox 3 (Creative Labs, Milpitas, California) linked to 2 loudspeakers (Fender Passport P-150, Fender, Scottsdale, Arizona) placed on window mounts facing away from the focal hyena and thus hidden by the car. The speakers were separated only by approximately 20 cm. Sound amplitude was calibrated by ear to match natural sounds. The playbacks were carried out between 0700 and 1830 h, when cowbells 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 3 min before sound onset. Filming continued throughout the playback and for at least 4 min after sound onset. Fourteen individual hyenas were included in the playback experiment. Seven hyenas were exposed to both cowbell and church-bell sounds in random order, with playbacks to any given hyena separated by at least 2 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. All procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data extraction.—We watched videotapes recorded during naturalistic observations and experiments using a Sony DRC TRV900 digital camcorder (Sony) 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 also was 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 the experimental trials we also extracted the following data from each videotape for both pre- and postplayback periods: latency to 1st movement by the focal hyena after sound onset; direction of movement—away or toward speakers; and 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 (Levene 1960; Zar 1999), respectively. All response variables met both assumptions once they were $\log_{10}$-, square-root, or arcsine-square-root transformed.

The Talek region now supports a high density of pastoralist settlements along the northern border of the Reserve (Reid et al. 2003) and thus along the northern edge of the Talek West clan territory. Kenyan census data indicate that the human population in the Talek area has approximately doubled every 15 years since 1950 (Lamprey and Reid 2004). Since the 1980s the Reserve has been one of the top safari destinations in the world. Tourist visits to the Reserve peaked in the early 1990s and have remained high and stable over the past decade (Okello et al. 2005). To investigate effects on hyenas of the burgeoning pastoralist population along the border of the home range of the Talek West clan we analyzed data from the 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, which we used as a proxy for pastoralist population density along the edge of the Reserve, and the proportion of hyena deaths of known causes each year that could be attributed to humans.

We analyzed data from our naturalistic observations to determine whether vigilance differed between the 2 clans and whether human activities could explain variation in vigilance. We 1st examined the effect of clan membership on vigilance using a general linear mixed-effect model, in which hyena identity was entered as a random effect (nested within clan membership) to avoid potential pseudoreplication (Pinheiro and Bates 2000). Significance of the random identity effect in this and subsequent models was tested using likelihood-ratio tests, comparing models with and without random effects (Pinheiro and Bates 2000). In this general linear mixed-effect model we also included the time at which each observation was made (AM versus 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 (Pangle 2008). We ran this analysis on the percent time spent vigilant in each of the 3 behavioral contexts (resting, feeding, and nursing) separately. In addition to evaluating differences in vigilance levels between the 2 clans, we also used the distance between hyenas and the nearest bushes to compare the 2 clans in all 3 behavioral contexts using general linear mixed-effect models in which hyena identity was entered as a random effect. Group size was included for all models, but lion presence was included only for resting and feeding hyenas because we never observed nursing in the presence of lions.

Whenever differences between clans were revealed in our analyses, we then used general linear mixed-effect models 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 nontourism months, tourism hours or nontourism hours, and their interaction), time of day (AM versus PM), group size, lion presence or absence, and clan membership as fixed effects, and hyena identity, which was nested within clan membership and entered as a random effect. For this analysis we included only observations of resting hyenas (n = 633 videotaped observations of 34 Talek West hyenas and 24 Mara River hyenas) and evaluated effects on percent time spent vigilant.

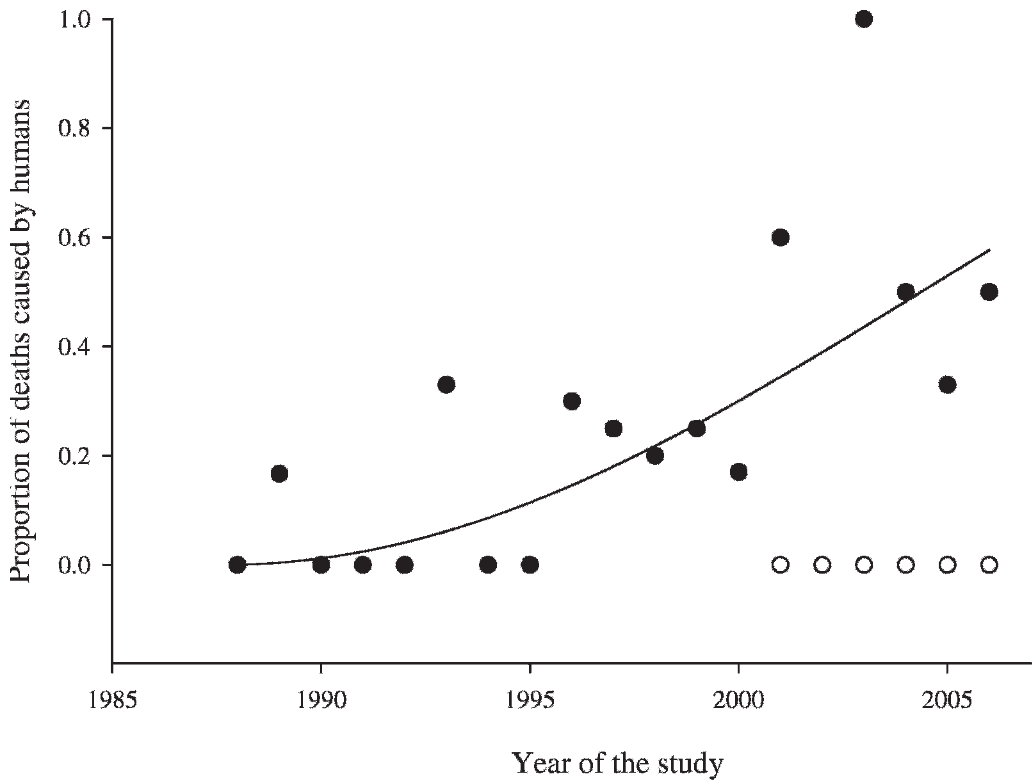

Fig. 1.—Proportion of hyena deaths of known causes attributed to humans in each year of the study in Talek West (●) and Mara River (○) clans. The Mara River clan was not monitored before 2001. The line represents a linear regression performed on arcsine square-root transformed data, but plotted on untransformed data, only for the Talek West clan.

We analyzed response variables recorded during playback experiments in 2 different ways. To test the effect of the played back sounds on the percent time spent vigilant we used a 3-way analysis of variance with clan membership, playback type, and pre- versus postplayback period as the 3 factors. We also used a chi-square analysis, applying Yates' correction when degrees of freedom equaled 1 (Zar 1999), to examine effects of clan membership and playback type on whether 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 2-tailed tests with $\alpha = 0.05$. The general linear mixed-effect models were done using the R library nlme (Pinheiro et al. 2005). Unless otherwise indicated, means $\pm$ 1 *SE* 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 be attributed unambiguously to humans, mainly by spearing, snaring, or poisoning. The relative proportion of human-caused deaths increased significantly during the years of our study ($F_{1,17} = 11.28$, $R^2 = 0.40$, $P = 0.004$; Fig. 1). We observed a similar increase when we examined absolute numbers of deaths attributable to humans during the years of our study ($F_{1,17} = 6.76$, $R^2 = 0.28$, $P = 0.02$). None of the 8 hyena deaths of known causes observed in the Mara River clan could be attributed to humans (Fig. 1).

Naturalistic observations of vigilance in hyenas from both clans.—The number of observations (video records) collected, and the number of individuals sampled in each behavioral context in each clan, are reported in Table 2. When resting, Talek West hyenas spent more than twice as much time vigilant as Mara River hyenas ($F_{1,58} = 6.53$, $P = 0.01$; $\bar{X}_{\text{Talek}} = 16.17\% \pm 1.55\%$; $\bar{X}_{\text{Mara River}} = 7.21\% \pm 0.88\%$; Fig. 2a). Although both clans were significantly more vigilant in the morning than in the evening ($F_{1,576} = 29.47$, $P < 0.001$; Fig. 2a), vigilance of resting Talek West hyenas was consistently greater than that of Mara River hyenas regardless of time of day (the clan $\times$ time interaction was not significant). The interaction between clan and group size also was not significant, despite a significant positive relationship between vigilance and group size ($F_{1,576} = 7.29$, $P = 0.007$).

We did not observe significant differences in vigilance between clans when hyenas were feeding or nursing (Figs. 2b and 2c). Talek West and Mara River hyenas spent roughly the same percent time vigilant while feeding ($\bar{X}_{\text{Talek}} = 9.39\% \pm 1.0\%$; $\bar{X}_{\text{Mara River}} = 10.43\% \pm 1.22\%$; $F_{1,47} = 1.55$, $P = 0.22$; Fig. 2b), and a significant positive relationship existed between vigilance and group size during feeding ($F_{1,69} = 5.18$, $P = 0.026$). Vigilance while feeding did not differ between AM and PM observation periods ($F_{1,69} = 1.73$, $P = 0.19$; Fig. 2b). Hyenas from both clans spent similar percentages of their time vigilant while nursing their litters ($\bar{X}_{\text{Talek}} = 38.40\% \pm 7.28\%$; $\bar{X}_{\text{Mara River}} = 28.94\% \pm 4.57\%$; $F_{1,14} = 0.32$, $P = 0.32$; Fig. 2c). Nursing mothers in both

Table 2.—Number of naturalistic vigilance observations collected by videography (n_{obs}) on adult hyenas (n_{ind}) sampled in each behavioral context (resting, feeding, and nursing) in Talek West and Mara River clans in the presence or absence of lions. Adult females were not observed nursing cubs in the presence of lions.

	Talek West				Mara River			
	Without lions		With lions		Without lions		With lions	
Context	n_{obs}	n_{ind}	n_{obs}	n_{ind}	n_{obs}	n_{ind}	n_{obs}	n_{ind}
Resting	412	35	42	22	170	22	15	9
Feeding	75	32	15	11	26	21	5	4
Nursing	42	9	—	—	39	7	—	—

clans were more vigilant in the morning than in the evening ($F_{1,63} = 5.07$, $P = 0.03$). We observed no significant effect of group size on vigilance while nursing ($F_{1,63} = 2.91$, $P = 0.09$).

Hyenas choose where to spend their time resting, feeding, or nursing, so we evaluated differences between clans in the proximity to the nearest bushes. Distance to bushes did not vary between clans when hyenas were resting or feeding ($P > 0.1$), but Talek West females nursed their young significantly closer to bushes than did Mara River females ($\bar{X}_{\text{Talek}} = 77.47 \pm 23.65$ m; $\bar{X}_{\text{Mara River}} = 267.68 \pm 38.97$ m; $F_{1,14} = 6.18$, $P = 0.026$; Fig. 3). Nursing females from both clans were observed further from bushes as group size increased ($F_{1,60} = 4.54$, $P = 0.037$), but the difference between clans was apparent regardless of group size (i.e., nonsignificant clan × group size interaction).

We then examined whether the presence of lions affected vigilance in hyenas. Although the difference in vigilance between clans for resting hyenas was apparent in the absence of lions, this difference was not apparent in the presence of lions, resulting in a significant clan × lion interaction ($F_{1,577} = 3.63$, $P = 0.05$; Fig. 4). Specifically, when lions were present, resting hyenas approximately doubled their percent time vigilant compared to when lions were absent ($F_{1,576} = 57.70$, $P < 0.001$; Fig. 4); vigilance in the 2 clans did not differ significantly when resting in the presence of lions. Hyenas from both clans spent a larger percent time vigilant when feeding in the presence of lions than when lions were absent ($F_{1,\ 69} = 9.83$, $P = 0.002$; Fig. 4). We never observed females nursing their litters in the presence of lions.

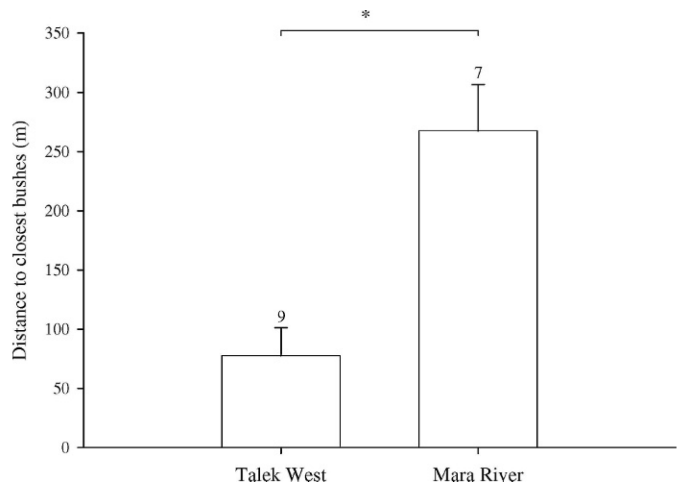

Fig. 3.—Mean (± *SE*) distance between focal female hyenas nursing their young and the closest patch of bushes. Sample sizes, representing the number of individuals filmed, are indicated above each mean. An asterisk (*) represents statistically significant difference ($P < 0.05$).

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 ($F_{1,413} = 3.79$, $P = 0.02$; Fig. 5). This effect was of the same magnitude regardless of whether there were 30 or 2,200 cattle present in the territory (Fig. 5). In contrast to pastoralist activity, no significant effects of tourist activity on vigilance among either Talek West or Mara River hyenas were found. Resting hyenas in both clans spent the same percent time vigilant in months when many tourists were visiting the Reserve as in months

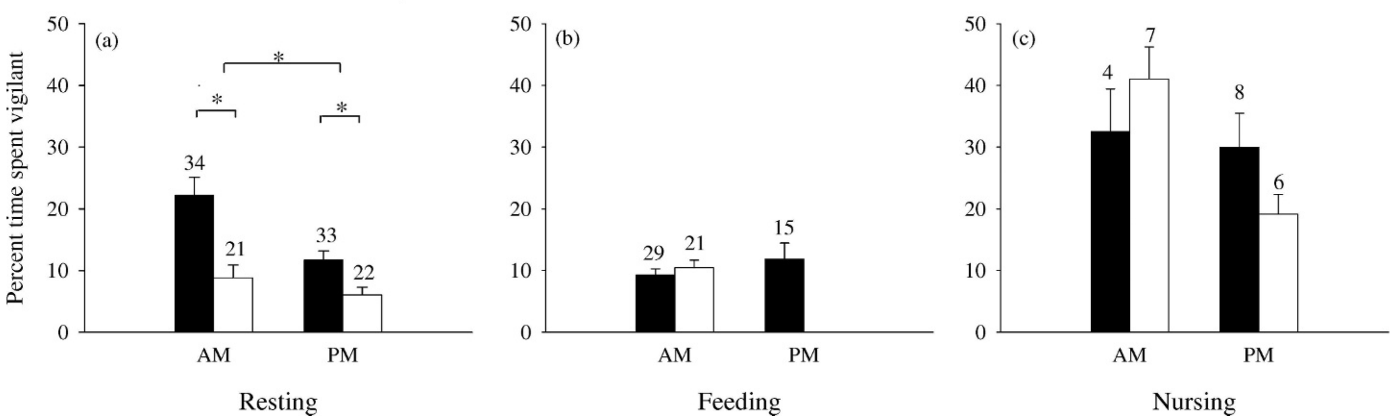

Fig. 2.—Mean (± *SE*) percent time spent vigilant by hyenas from Talek West (black bars) and Mara River clans (white bars) during morning (AM) and evening (PM) observation hours while a) resting, b) feeding, and c) nursing their cubs. Sample sizes, representing the number of individuals filmed, are indicated above each mean. An asterisk (*) represents statistically significant difference ($P < 0.05$). Mara River hyenas were not observed feeding during evening hours.

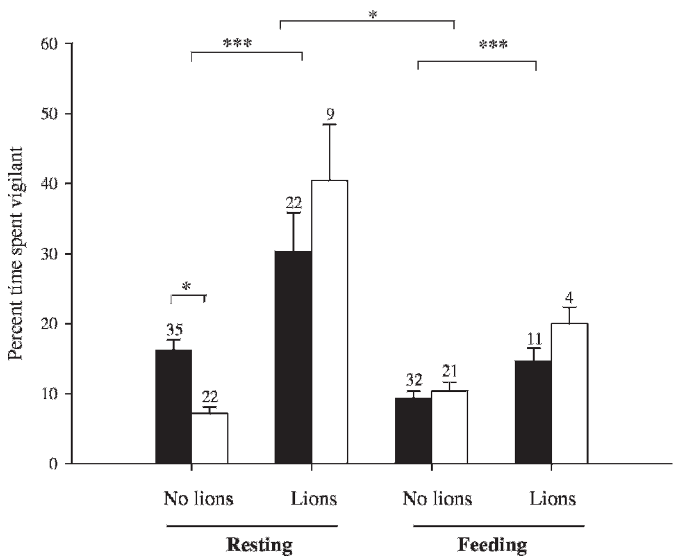

Fig. 4.—Mean (± *SE*) percent time spent vigilant by spotted hyenas of the Talek West clan (black bars) and Mara River clan (white bars) while resting and feeding in the presence or absence of lions. Sample sizes, representing the number of individuals filmed, are indicated above each mean. Asterisks represent statistically significant differences (* $P < 0.05$; *** $P < 0.001$).

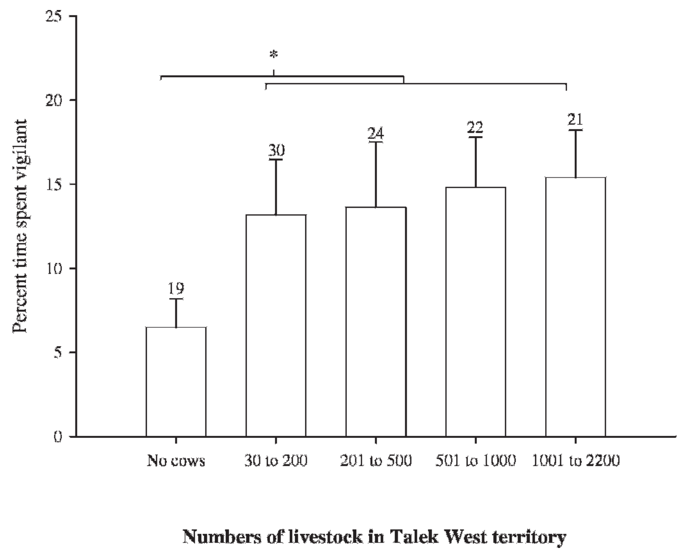

Fig. 5.—Mean (± *SE*) percent time spent vigilant by Talek West hyenas while resting in the presence of livestock. Sample sizes, representing the number of individuals filmed, are indicated above each mean; number of livestock indicated along x-axis. An asterisk (*) represents statistically significant difference ($P < 0.05$).

when few tourists were visiting ($F_{1,565} = 0.05$, $P = 0.82$; Fig. 6). Although a trend existed for Mara River hyenas to spend more time vigilant during hours when tour vehicles were present than absent from the Reserve, this difference was not statistically significant ($F_{1,565} = 3.74$, $P = 0.06$; Fig. 6), and we observed no such trend among Talek West hyenas.

Playback experiment.—We conducted a total of 13 playbacks (7 cowbell playbacks and 6 church-bell playbacks) on hyenas from the Talek West clan, and 8 playbacks (4 cowbell playbacks and 4 church-bell playbacks) on hyenas from the Mara River clan. Hyenas from both clans spent more time vigilant after than before a sound stimulus was played, regardless of the stimulus type ($F_{1,38} = 10.16$, $P = 0.003$; Fig. 7). However, the increase in vigilance of hyenas after sound onset did not differ significantly between church bells and cowbells within each clan ($F_{1,38} = 0.70$, $P = 0.41$; Fig. 7). Talek West hyenas were more vigilant than Mara River hyenas, regardless of the stimulus played ($F_{1,38} = 7.50$, $P = 0.01$; Fig. 7). Specifically, Talek West hyenas spent roughly 25% more time vigilant than did Mara River hyenas (Fig. 7) after sounds were played back of either bell type. Although Talek West hyenas appeared to be somewhat more vigilant than Mara River hyenas in these experiments, even before sound playback began this difference was not statistically significant ($F_{1,38} = 1.76$, $P = 0.12$; Fig. 7).

The only hyenas that moved after being exposed to a playback sound were Talek West hyenas that had just heard cowbells. Two (28%) of the 7 Talek West hyenas that received the cowbell treatment moved, whereas no Mara River hyenas moved after either sound was played to them. However, this difference between the 2 clans was not statistically significant ($\chi_1^2 = 0.136$, $P = 0.71$). In the case of the 2 Talek West hyenas that moved after hearing cowbells, both hyenas started to move about 1 min after hearing the 1st cowbells, 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, whereas the other moved about 200 m away.

Discussion

Our results suggest that humans are having both lethal and nonlethal 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 increasing proportion of known-caused hyena deaths since 1988. 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 they also nursed their cubs closer to bushes, than did hyenas from the undisturbed Mara River clan. That females tended to nurse cubs closer to bushes suggests that bushes might serve as effective refugia for hyenas from human-imposed threats. When we sought factors that might account for the observed differences between clans 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, but hyenas in both clans responded similarly to the 2 types of bell stimuli. Clearly, the differences between church bells and cowbells were not as obvious to hyenas as they were to human listeners. Vigilance among Talek West hyenas was greater

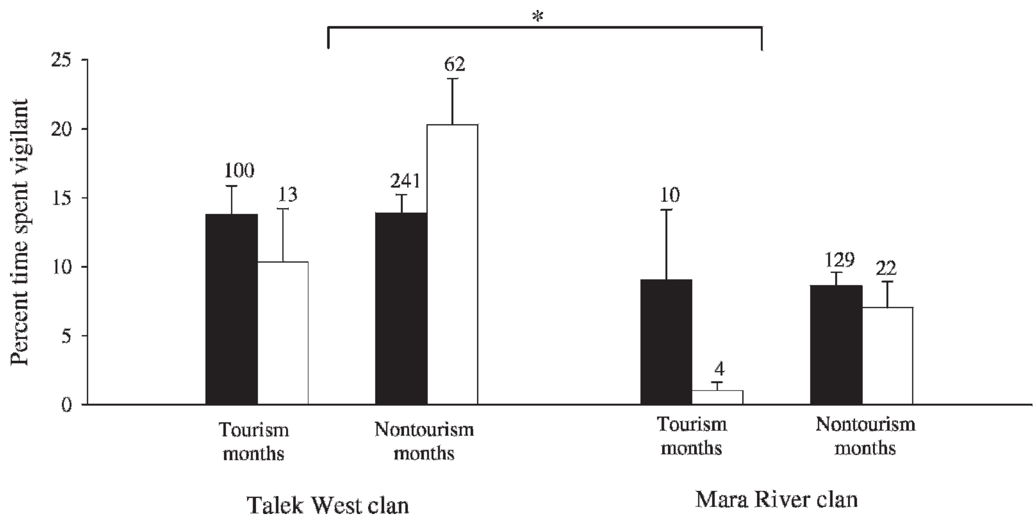

Fig. 6.—Mean (± *SE*) percent time spent vigilant during rest by hyenas from Talek West and Mara River clans during months with many or few tourists, and during hours of the day when tour vehicles were abroad in the Masai Mara National Reserve (black bars) or not (white bars). Sample sizes, representing the number of trials, are indicated above each mean. An asterisk (*) represents a statistically significant difference ($P < 0.05$). No effect of tourism was observed on vigilance in either clan.

than that among Mara River hyenas both before and after bell sounds were played. We found that Talek West hyenas spent a larger percentage of their time vigilant after these playbacks (Fig. 7) than Mara River hyenas spent in the physical presence of lions (Fig. 4).

Although factors other than human activity certainly can affect vigilance in hyenas, these factors appear unlikely to have caused the differences we observed between our 2 study clans. Lion density may affect vigilance of spotted hyenas because lions are their principal natural predators (Cooper 1991; Watts and Holekamp 2009). However, lion subgroups observed on both clan territories were of similar sizes (Table 1; Kolowski et al. 2007). The availability of refugia also can affect hyena vigilance, but no substantial differences in habitat structure or vegetation cover were observed between the territories of the 2 clans (Kolowski 2007). Finally, the size of a clan also can affect vigilance, as this in turn might affect the number of individuals observed concurrently in the fission–fusion societies of spotted hyenas. The Mara River clan was smaller at the time of our study than the Talek West clan (Table 1). However, if the observed differences in vigilance between the 2 clans were driven by clan size, we would expect Talek West hyenas to be less vigilant than Mara River hyenas, which is contrary to our results. In contrast to

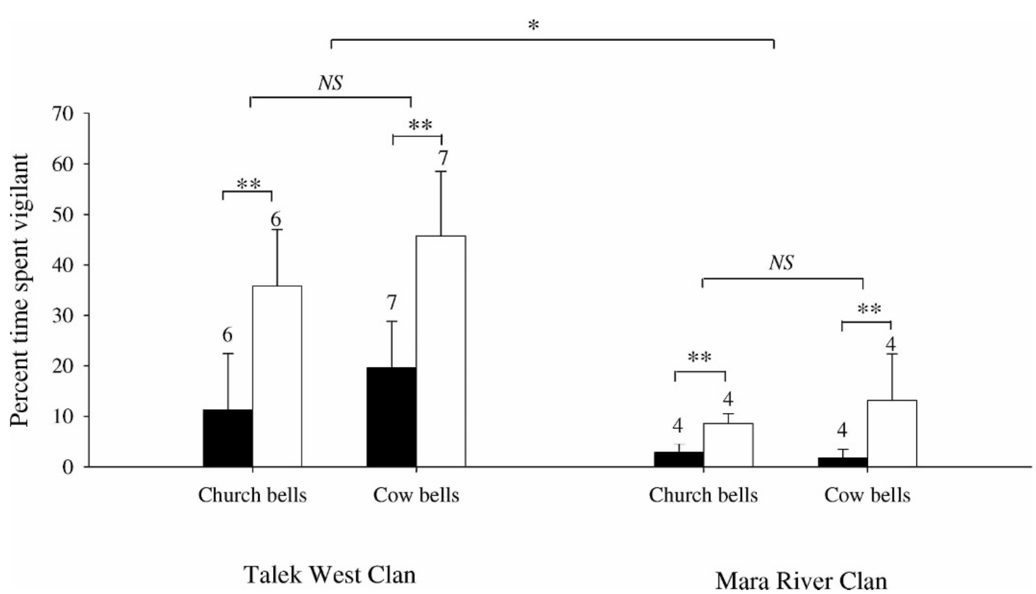

Fig. 7.—Mean (± *SE*) percent time spent vigilant by Talek West and Mara River hyenas during a playback experiment involving use of either church bells (control sound) or cowbells (treatment sound). The period before sound onset is indicated with black bars, and the period after sound onset with white bars. Sample sizes, representing the number of trials, are indicated above each mean. Asterisks represent statistically significant differences (* $P < 0.05$; ** $P < 0.01$).

the lack of effects for clan size, we found that hyena vigilance increased with group size when resting, and that distance from bushes at which females nursed their cubs increased with group size, suggesting that vigilance among hyenas might function to detect threats both from conspecifics as well as from other sources of danger.

In our behavioral observations, we detected a marked effect of livestock presence on hyena vigilance but no strong effect of tourist presence. Despite large sample sizes and a great deal of statistical power, we found only a marginal effect of tourism hours on the vigilance of Mara River hyenas, and no effect of months of the year on hyena vigilance in either clan. This finding is consistent with tourists not being allowed to exit their vehicles, and with the fact that they do not harm large carnivores. Our data were encouraging because they suggest that regulations of the Reserve are sufficient to ensure that large carnivores such as hyenas do not perceive tour vehicles as threats. This was not the case in 2 recent studies that reported an increase in mammalian vigilance associated with tourists (e.g., polar bears [Dyck and Baydack 2004] and marmots [Griffin et al. 2007]).

In contrast to their modest responses to tour vehicles, we found that hyenas were substantially more vigilant on days when livestock were present on their territory than on days when livestock were absent. Pastoralists always accompany livestock when their herds graze inside the Reserve, and herdsmen in the Reserve with their livestock chase and throw rocks at hyenas, and occasionally even spear them. Therefore, Talek West hyenas might 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, because 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 human activity, but these were caused by more systematic poaching and hunting (Brashares et al. 2001; Caro 1999, 2005; Setsaas et al. 2007). Thus, our results suggest that sporadic killings might be sufficient to induce detectable changes in behavior.

Since the late 1980s we have accumulated evidence of the importance and magnitude of nonlethal anthropogenic effects on hyenas from the Talek West clan. In addition to the nonlethal effects observed in this study, Talek West hyenas have been shown to exhibit spatial avoidance of the open areas in their territory where the most frequent 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 or hyenas in a different park where cattle are prohibited, and these differences are driven by pastoralist activity rather than tourism (Van Meter et al. 2009). Little is known about how such nonlethal 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 nonlethal effects can be as large as, or larger than, reductions due to lethal predator effects (Creel and Christianson 2008; Nelson et al. 2004; Pangle et al. 2007). Mammalian carnivores may perceive human disturbance as a predation risk (Frid and Dill 2002), so nonlethal anthropogenic effects may comprise a substantial component of the net effect of humans on fitness of carnivores 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 3 years (Watts 2007). Our study is the 1st 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, examination of our data nevertheless strongly suggests that the proportion of total known-cause deaths attributable to humans has increased dramatically during this 18-year period, coincident with rapid growth of the local pastoralist population.

Although spotted hyenas currently are considered a species of Lower Risk by the World Conservation Union (International Union for Conservation of Nature 2006), their remarkable plasticity suggests that these animals may be monitored usefully to gauge the impact of humans on carnivores inhabiting many African ecosystems. In contrast to most other carnivores, spotted hyenas breed year-round, they can be active day or night, they occur in a diverse array of habitat types, and they can survive on foods ranging from insects to elephants (Cooper et al. 1999; Kruuk 1972; Mills 1990; Sillero-Zubiri and Gottelli 1992). Thus, compared to many other carnivores, spotted hyenas are extraordinarily flexible in their behavior and ecology. Therefore, the reactions of these animals to human disturbance may represent conservative indicators of how other mammalian carnivores exhibiting less behavioral plasticity, including species that are rare and endangered, might respond to such challenges.

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