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ORIGINAL PAPER

Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions

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Abstract Large carnivore populations are declining worldwide due to direct and indirect conflicts with humans. Protected areas are critical for conserving large carnivores, but increasing human-wildlife conflict, tourism, and human population growth near these sanctuaries may have negative effects on the carnivores within sanctuary borders. Our goals were to investigate how anthropogenic disturbance along the edge of the Masai Mara National Reserve, Kenya, influences the demography and space-use of two large carnivore species that engage in intense interspecific competition. Here we document, in one disturbed region of the Reserve, a rapid increase in the population size of one large predator, the spotted hyena (*Crocuta crocuta*), but a striking concurrent decline in numbers of another, the African lion (*Panthera leo*). Anthropogenic disturbances negatively affected lion populations, and decreasing lion numbers appear to have a positive effect on hyena populations, indicated here by an increase in juvenile survivorship. We also saw an increase in the number of livestock consumed by hyenas. Our results suggest human population growth and indirect effects of human activity along Reserve boundaries may be effecting a trophic cascade inside the Reserve itself. These results indicate both top-down and bottom-up processes are causing a shift in the carnivore community, and a major disruption of guild structure, inside the boundaries of one of the most spectacular protected areas in Africa.

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Introduction

Populations of large carnivores have been declining in most ecosystems as a result of habitat change, direct conflicts over livestock, utilization of their body parts for subsistence and trade, and depletion of their prey (Ripple et al. 2014). The reduction or complete extirpation of large carnivores can have ecosystem-wide consequences (Estes et al. 2011; Ripple et al. 2014). One common example of the restructuring of natural ecosystems that occurs when apex predators decline is a specific type of trophic cascade called a meso-predator release (Crooks and Soulé 1999; Prugh et al. 2009); this involves an increase in numbers of smaller carnivores that are ordinarily limited by the apex predators. A decline in numbers of large carnivores can also trigger predator-mediated trophic cascades in other sympatric wildlife populations (e.g., Hebblewhite et al. 2005; Johnson et al. 2007; Berger et al. 2008). The effects of these trophic cascades have been well documented, and may include declines in bird populations, altered vegetation structure, and potentially even climate change (e.g., Estes and Palmisano 1974; Beschta and Ripple 2009; Wilmers et al. 2012).

Protected Areas (PAs) play a crucial role in the conservation of large carnivores in myriad countries, including many developing nations (Woodroffe and Ginsberg 1998; Packer et al. 2013). Rapid human population growth around PAs, however, has the capacity to intensify anthropogenic threats to wildlife within reserve boundaries (Wittemyer et al. 2008; Newmark 2008; Craigie et al. 2010). Large carnivore populations are highly vulnerable to these types of threats due to their large home ranges and slow life histories (Woodroffe and Ginsberg 1998; Ripple et al. 2014). Thus, it is critical to understand how anthropogenic disturbances within and around existing PAs affect carnivore populations within PA borders.

The Mara-Serengeti ecosystem is considered to be a stronghold for the conservation of large carnivores in East Africa (Ogutu and Dublin 2002; Riggio et al. 2013). The Masai Mara National Reserve (henceforth, the Reserve), which comprises the northernmost portion of the Mara-Serengeti ecosystem, has historically contained high densities of large carnivores due to abundant prey throughout the year (Ogutu and Dublin 2002; Craft et al. 2015). Since the 1950s, however, an expanding population of pastoralists around the Reserve has induced many ecological changes, with negative consequences for native wildlife. For example, a massive increase in numbers of livestock grazing inside and near Reserve boundaries has been implicated as having a more profound negative effect on numbers of resident herbivores than any other anthropogenically-induced ecological change (Ottichilo et al. 2000; Serneels and Lambin 2001; Lamprey and Reid 2004; Ogutu et al. 2005, 2009, 2011; Green 2015).

Evidence suggests that livestock grazing and other pastoralist activity may also be affecting large carnivores living within Reserve boundaries. Herders guarding livestock both inside and outside the Reserve have been observed to spear and poison spotted hyenas (*Crocuta crocuta*), the most abundant large predators in this ecosystem, both in retaliation for depredation events and in attempts to thwart them in the first place (Pangle and Holekamp 2010). Humans now represent the largest source of mortality for spotted hyenas in areas of the Reserve exposed to livestock incursions (Pangle and Holekamp 2010; Holekamp and Dloniak 2010). Livestock grazing inside the Reserve has also been closely associated with behavioral (Boydston et al. 2003; Kolowski et al. 2007; Kolowski and Holekamp 2009; Pangle and Holekamp 2010; Greenberg and Holekamp 2017) and physiological (Van Meter et al. 2009) changes in spotted hyenas. Limited data suggest that anthropogenic disturbances associated with livestock grazing may also be having negative effects on lions (*Panthera leo*) in the Reserve (Ogutu et al. 2005), so this is an important area for research. Concurrently studying how lions and hyenas respond to livestock grazing and related anthropogenic disturbance can highlight how demographic change in one species affects the other because of their overlapping ecological niches (Périquet et al. 2015).

Here our goals were to document long-term trends in the population sizes and space-use patterns of spotted hyenas and lions in the Reserve, and to determine how these trends differed between areas characterized by high and low levels of anthropogenic disturbance. Using data collected since 1988, we exploited naturally-occurring variation in the exposure of large carnivores to anthropogenic disturbance within Reserve boundaries associated with variation in the carnivores' distance to the Reserve's edge and in numbers of livestock grazing near them. We predicted that spotted hyenas would be able to adapt to increasing disturbance because of their extraordinary behavioral flexibility (Holekamp and Dloniak 2010) and capacity to coexist with people (Yirga et al. 2017), and that human activity would thus have little effect on their numbers. We also predicted that numbers of lions would decline in disturbed areas because they exhibit less flexible behavior, larger body size, slower life histories, and less fear of humans than do spotted hyenas; these traits make them more vulnerable than hyenas to being speared by herders (Woodroffe 2001; Kissui 2008; González-Suárez and Revilla 2013). Finally we predicted that, in areas characterized by more intensive anthropogenic activity along Reserve borders, both species would be found deeper in the Reserve over time, and thus farther away from people and potential conflicts.

Because, in fact, we found that hyena numbers had increased dramatically between 1988 and 2013 in an area where they were exposed to high levels of anthropogenic disturbance, our final goal was to test three hypotheses suggesting explanations for this increase. Our first hypothesis suggested that increasing numbers of hyenas in the disturbed area were due to widespread ecological change throughout the Reserve. To test this, we compared demographic trends among hyena populations inhabiting areas of the Reserve that varied considerably in their exposure to anthropogenic disturbance. If this hypothesis was correct we expected to observe similar trends in all areas studied within the Reserve. Our second hypothesis suggested that bottom-up forces have effected changes in hyena numbers in disturbed areas. Here we focused on food availability, specifically testing the notion that hyenas in heavily disturbed areas might be supplementing or replacing their natural diet with livestock. Spotted hyenas are opportunistic foragers with a generalist diet (Cooper et al. 1999; Hayward 2006; Périquet et al. 2015), and they can take rapid advantage of novel food sources (Kruuk 1972; Yirga et al. 2012).

Finally, we tested a third hypothesis suggesting that top-down forces, which previously limited numbers of hyenas, had weakened over time in heavily disturbed areas. Specifically, we inquired whether declining lion numbers in disturbed areas might have allowed for hyena population expansion. Lions and spotted hyenas exhibit intensive interference and exploitation competition as well as intraguild predation, and lions have historically represented the greatest natural source of mortality for spotted hyenas (Kruuk 1972; Watts and Holekamp 2008, 2009; Périquet et al. 2015). In areas where lion numbers have declined, spotted hyenas can more easily maintain possession of their kills, and also kleptoparasitize food more easily from the remaining lions (Watts and Holekamp 2008).

This in turn enhances reproductive success among spotted hyenas by permitting younger weaning ages of cubs and shorter inter-birth intervals (Watts and Holekamp 2008). Thus, in addition to modeling change in the lion population over time in a heavily disturbed area, we tested an important prediction of the third hypothesis, which was that fewer lions should also be associated with improved hyena survivorship there.

Materials and methods

Study area

The Reserve is primarily comprised of open, rolling grassland. It has historically supported large herds of resident and migrant herbivores, together with populations of myriad carnivores that are present year-round (Bell 1971; Sinclair and Norton-Griffiths 1979; Stelfox et al. 1986; Craft et al. 2015). Rainfall in the Reserve is bimodal, with most rain falling in November–December and March–May (Ogutu et al. 2008).

There is considerable variation in the exposure of carnivores to anthropogenic disturbance within Reserve boundaries due to the presence of multiple management regimes and variation in carnivores' proximity to Reserve boundaries. The eastern portion of the Reserve, managed by the Narok County Government, has undergone change in recent decades involving massive increases in the number of human settlements and tourist facilities immediately outside the Reserve, and exponential growth in numbers of livestock grazed daily within Reserve boundaries (Boydston et al. 2003; Lamprey and Reid 2004; Kolowski and Holekamp 2009; Green 2015). The Talek region in particular, which is situated on the eastern side, just inside the Reserve's northern boundary (Fig. 1), is heavily affected by these forms of human activity; the number of livestock herded into the Talek region to graze has increased substantially over time (Fig. 2). In contrast to the Talek region, however, other portions of the Reserve remain relatively pristine and largely unaffected by anthropogenic activity. Since 2001 the western portion of the Reserve, called the "Mara Triangle," has been managed by the Mara Conservancy (Walpole and Leader-Williams 2001). Although poaching and livestock incursions were common in the Mara Triangle before 2001 (Ogutu et al. 2009, 2011; Bhola et al. 2012), the Mara Conservancy has curtailed these anthropogenic disturbances to wildlife in the Mara Triangle. Except along its westernmost border, since 2001, animals inhabiting the Mara Trangle have encountered no livestock whatsoever, and they experience no anthropogenic activity other than occasional visitation by tour vehicles. Here we exploited differences in exposure to anthropogenic disturbance between the unaffected region of the Mara Triangle and the Talek region to understand how large carnivores within the Reserve are being affected by human activity along Reserve boundaries.

Data collection

Demography and behavior of spotted hyenas

Spotted hyenas live in social groups, called clans, comprised of adult females and their juvenile offspring, and one to several immigrant males. Clan members defend a group territory (Kruuk 1972). Here, as part of a longitudinal study that began in 1979 (Frank 1986), six clans were monitored between 1988 and 2013. We studied five clans exposed to

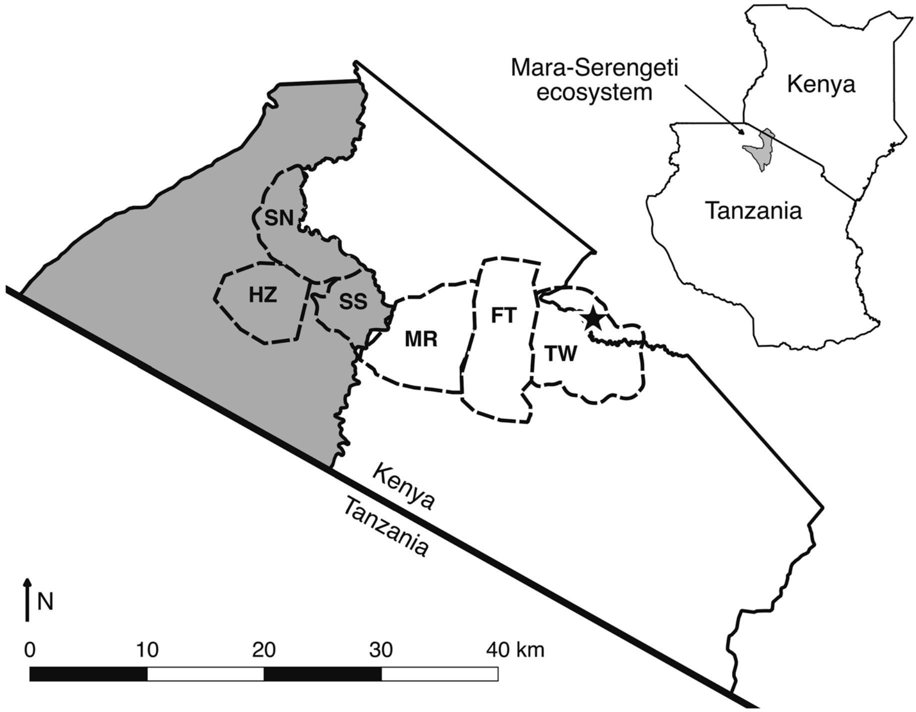


Fig. 1 Sites of carnivore monitoring in the Masai Mara National Reserve, Kenya. The approximate boundaries of the six territories defended by members of our hyena study clans are indicated with dashed lines. Territory boundaries for study clans were estimated using not only direct observations of hyena movements, latrines and clan wars at territorial boundaries, but also by tracking hyenas fitted with VHS and GPS radio collars. The Mara River divides the Reserve into two sections, each with a different management regime. Study clans in the Mara Triangle (shaded region), which is managed by the Mara Conservancy, are Serena North (SN), Serena South (SS), and Happy Zebra (HZ). Clans in regions managed by the Narok County Government (no shading) are Talek West (TW), Fig Tree (FT), and Mara River (MR). The TW clan is located in the Talek region of the Reserve, so called because of its proximity to the burgeoning town of Talek, indicated by the filled star

low levels of anthropogenic disturbance (Serena North, Serena South, Happy Zebra, Mara River, Fig Tree clans), and one clan exposed to a high level of disturbance in the Talek region (the Talek West clan; Fig. 1). All members of each study clan were known individually by their unique spots. We located, identified and observed hyenas daily by systematically driving 1–2 vehicles throughout the territories of one or more study clans during morning (0500–1000 h) and evening (1600–2100 h) observation periods in both disturbed and undisturbed areas. Monthly clan size was calculated as the total number of individuals in all age classes present during each month in which a particular clan was observed. Any time a hyena was observed feeding, we also recorded the species of the prey item being consumed. Starting in 1991, hyenas were also fitted with VHF (Telonics Inc., Mesa, AZ, USA) or GPS radio collars with VHF functionality (Vectronic Aerospace, Berlin, Germany). We used radio telemetry to help find hyenas, and recorded their location and identities each time they were found. Locations were triangulated and localized to within 50 m if collared hyenas could not be seen due to vegetation or darkness.

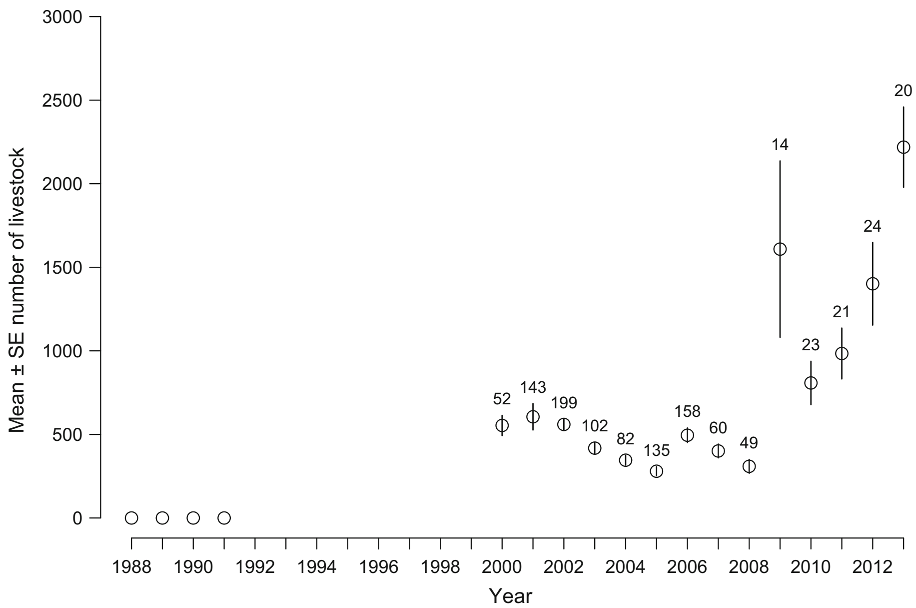


Fig. 2 The mean (± SE) number of livestock counted each year in the Talek region of the Masai Mara National Reserve, Kenya. No herds of livestock were observed in the Talek region from 1988 to 1991. We started systematically counting all sheep, goats, and cattle within the Talek region in 2000 (Kolowski and Holekamp 2009). Counts took place up to once per day from 2000 to 2008, but were performed biweekly starting in May, 2008. All counts used here were performed between 1600 and 1900 h. The numbers atop each point indicate the number of livestock counts that were performed in that year

Estimation of lion abundance and documentation of their space-use

Because we did not systematically track individual lions, as we did with spotted hyenas, we used two different metrics to investigate trends in lion abundance. First, between 1988 and 2013, we monitored the number of times lions were found within 200 m of spotted hyenas in the Talek West clan. Each time $\geq$ 1 lion was found with hyenas, this was referred to as a "lion-hyena interaction," and its GPS coordinates were recorded. Second, regardless of whether spotted hyenas were present with the lions, we also recorded the GPS coordinates of all "lion sightings" during the morning and evening observation periods described above within the territories of four of our hyena study clans (Talek West, Serena North, Serena South, and Happy Zebra). A lion sighting included the total number of lions separated from others by $\leq$ 200 m. All lion sightings were recorded between 2004 and 2013 in the territory of the Talek West hyena clan, and between 2009 and 2013 in the territories of the Serena North, Serena South, and Happy Zebra clans.

Monitoring of ecological and anthropogenic variables

To distinguish between natural ecological and anthropogenic influences on the distances from the Reserve boundary at which hyenas and lions were sighted, we calculated the mean numbers of herbivore prey, numbers of livestock grazing, and millimeters of rainfall in the territory of the Talek West clan from 2004 to 2013 during each biweekly interval. Prey were counted biweekly along three 4-km line-transects in the Talek West territory as described previously (Holekamp et al. 1999; Boydston et al. 2003; Van Meter et al. 2009). We similarly counted prey biweekly along three 4-km transects in the territories of our study clans in the Mara Triangle. During each biweekly interval we separately averaged the numbers of herbivores counted in disturbed and undisturbed areas on the three transects run in each area. Starting in 2000, we performed systematic livestock counts to estimate the total number of livestock grazing in the Talek West territory; no livestock were ever observed in the territory of any other study clan. Counts were performed up to twice daily from 2000 to 2008 between 0500 and 1000 h and 1600 and 2000 h. Starting in May 2008, all counts occurred between 1600 and 2000 h and were only performed biweekly. Finally, we used a rain gauge to measure rainfall during each biweekly interval in the Talek region.

Statistical analyses

Trends in numbers of lion-hyena interactions and lion sightings

To assess variation in lion numbers over time in the Talek West territory, we modeled temporal trends in the monthly frequency of lion-hyena interactions and inquired whether this changed significantly between 1988 and 2013. We modeled the number of lion-hyena interactions per month as a function of year coded as a time-series variable, using a generalized linear mixed-effects model. Here we fit the model using a negative binomial distribution and a zero-inflation adjustment following Zipkin et al. (2010); the probability of inclusion of a month when no lion-hyena interactions occurred was modeled as a random variable. We included as an offset the total number of locations at which hyenas were observed each month, regardless of whether or not lions were present with them.

To assess variation in lion numbers among clan territories with varying exposure to human activity, from 2004 to 2013 we tallied the numbers of lions sighted each month during systematic searches in each of four clan territories We used a generalized linear model to compare numbers of lions sighted in Talek West during two five-year periods, 2004–2008 and 2009–2013, to those in the territories defended by the Serena North, Serena South, and Happy Zebra clans during the five-year period from 2009 to 2013. Here we used a negative binomial distribution and included the number of hours each month observers spent searching for carnivores as an offset to account for variation in search effort expended.

Analysis of hyena and lion locations

We used a generalized linear model to investigate mean distances at which hyenas and lions in the Talek region were found from the Reserve boundary during each biweekly interval as a function of hour coded as a time series variable, prey abundance, rainfall, and the mean numbers of livestock grazing there during each interval. To investigate change over time, we grouped observations in a categorical variable representing two time-periods aligning with our lion sighting data: 2004–2008 and 2009–2013. Time-period and hour were included to investigate long-term trends and short-term daily patterns in these distances, respectively. We also included the quadratic term hour^2 to investigate the possibility of nonlinear relationships due to circadian rhythms. We set 1700 h as hour $= 1$. Hyena locations at dens, and locations of hyenas and lions less than 200 m from the Reserve boundary (3.1% of all locations), were excluded due to concerns regarding spatial autocorrelation and unexplained sources of variation on the Reserve borders themselves. We rounded each distance to the nearest meter and performed this analysis using a negative binominal distribution. We tested for collinearity among covariates, but found no significant correlations (Spearman's correlation coefficient $r < 0.5$).

Testing hypotheses suggesting explanations for changing numbers of hyenas in the Talek region

We first tested the hypothesis that changing numbers of hyenas in this clan were associated with Reserve-wide ecological change by comparing demographic trends among our six study clans. We next investigated the hypothesis that bottom-up forces, indicated by prey availability, have induced changes in the number of hyenas in the Talek West clan. We inquired whether hyenas in the Talek region might be using livestock as a new food source. We determined the number of times hyenas were observed each month feeding on wild resident herbivores, wild migrant herbivores, and livestock at kills and carcasses. We categorized wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) as wild migrant herbivores, and we categorized all other species as wild resident herbivores. Although Thomson's gazelles (*Eudorcas thomsonii*) migrate in other parts of the Mara-Serengeti ecosystem, they are non-migratory and present year-round in the Talek region, so we classified them as resident herbivores. Sparse resident herds of wildebeest are present elsewhere in the Reserve (Ottichilo et al. 2001), but wildebeest in the Talek region are rarely seen other than during their migration from Serengeti National Park; we therefore classified wildebeest as migrant herbivores in our analysis. We modeled the total numbers of monthly instances when hyenas were seen feeding on each of these classes of prey using a generalized linear model with a negative binomial distribution, and year coded as a time-series variable. We included as an offset the total number of observation sessions each month in which hyenas were seen feeding on any kill or carcass in which we could accurately identity the prey species being consumed.

Our final hypothesis suggested that top-down forces, which previously limited the number of hyenas in the Talek West clan, may have weakened over time. This hypothesis predicts that we should observe decreasing numbers of lion-hyena interactions over time, and that lion sightings in the Talek West territory in recent years should be rarer than in clan territories in undisturbed areas elsewhere in the Reserve but with habitat similar to that of the Talek West territory. Because lions represent the primary mortality source for young hyenas in this and in other hyena populations (Watts and Holekamp 2008), we also compared the survivorship of juvenile hyenas to sexual maturity (2 years of age) between the Talek West and Serena North clans. We used the Serena North clan here because its ecological conditions with respect to prey density and abundance of short-grass habitat are most similar to those in the Talek West territory. We compared survivorship of juveniles in Talek West during the two time periods for which lion sighting data were available (2004–2008 and 2009–2013) to concurrent data from Serena North from 2009 to 2013. If reduced numbers of lions in the Talek region enhance numbers of spotted hyenas there, we predicted better juvenile survivorship in 2009–2013 than in 2004–2008 in the Talek West clan, and better survivorship in Talek than in Serena North from 2009 to 2013. We modeled cub survivorship to sexual maturity using a Cox proportional-hazard model, with clan and time-period coded as fixed-effects. We censored animals still alive at the end of our study (31 December 2013).

Modeling and assessment of model convergence and fit

All analyses were conducted in a Bayesian framework using MCMC analyses in R v. 3.3.2 with JAGS accessed with the "JagsUI" package (Plummer 2003; Kellner 2016; R Core Team 2016). We used uninformative priors, ran our models with three chains for 45,000 iterations following a 100,000 burn-in, and thinned by 9. All offsets, and covariates in our analysis of hyena and lion locations, were standardized to have a mean of 0 and a standard deviation of 1. We assessed model convergence and fit with the Gelman–Rubin statistic ($\hat{R}$) and by calculating Bayesian p values as the discrepancy between our data and data simulated under our estimated model parameters (Gelman et al. 1996, 2013). All $\hat{R}$ values were < 1.1 and p values for all analyses also failed to indicate any lack of fit ($0.05 < p$ value < 0.95). We present median posterior parameter estimates and 95% credible intervals (CIs) based on 15,000 MCMC samples for all analyses. Parameter estimates for which the 95% CI did not overlap zero were considered to be statistically significant.

Results

Temporal trends in clan sizes of spotted hyenas

Between 1988 and 2013, monthly clan sizes in the Reserve ranged from 22 to 126 individuals (mean ± SE: 55.26 ± 0.87; Fig. 3). The Talek West clan was consistently the largest study clan, and its size increased dramatically over time; it also underwent two clan fission events when it split from one parent clan into two discrete daughter clans in 1989 and again in 2000 (Fig. 3; Holekamp et al. 1993; Watts and Holekamp 2009; Holekamp

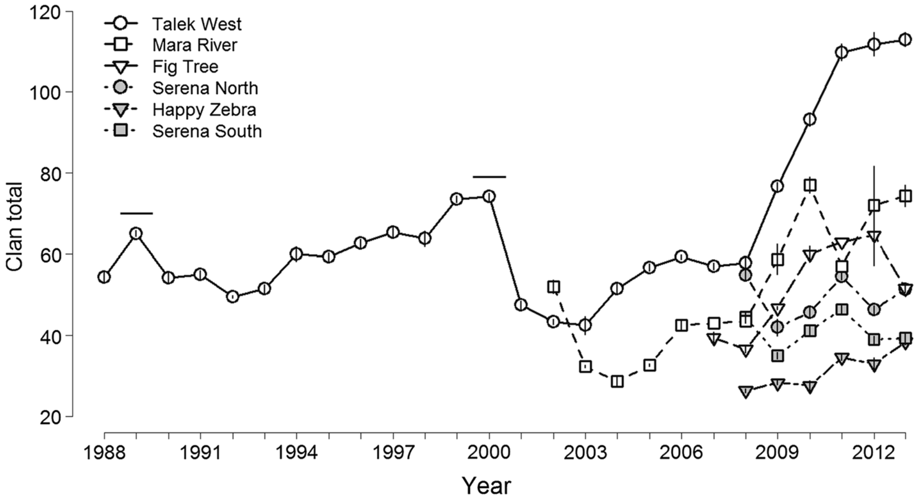


Fig. 3 Trends in the sizes of six study clans in the Reserve. Yearly mean clan sizes ± standard error (SE) are presented for the Talek West (1988–2013), Fig Tree (2007–2013), Mara River (2002–2013), Serena North (2008–2013), Serena South (2008–2013), and Happy Zebra clans (2008–2013). Years without SE bars did not have multiple censuses. The two clan fission events in Talek West occurred in 1989 and 2000, indicated with horizontal lines. Symbols for clans located in the Mara Triangle are filled with grey

et al. 2012). The Talek West clan underwent rapid growth starting in 2008, without any further clan fission events, whereas sizes of the other clans studied in the Reserve changed considerably less during the same period. The Talek West clan increased in size by 95% from 2008 to 2013, whereas Fig Tree increased by 41%, Mara River increased by 71%, Serena North declined by 6%, Serena South declined by 12%, and Happy Zebra increased by 46% during the same time period. The striking difference between 95% in the Talek West clan and the mean 23% change in other clans suggest that the increase in Talek West can size was not due to some Reserve-wide phenomenon.

Trends in numbers of lion-hyena interactions and lion sightings

Between 1988 and 2013, we recorded a total of 87,734 locations at which spotted hyenas were found in the Talek region, and lions were also present at 1188 of them. The number of lion-hyena interactions seen per month ranged from 0 to 18 (mean $\pm$ SE: 3.92 $\pm$ 0.23). The frequency of these interactions declined significantly during this 26-year period (intercept and [95% CI] median posterior estimate on the normal scale with mean effort: 5.81 [4.34, 7.66]; change per year median posterior estimate and [CI] $-$ 0.15 [$-$ 0.32, $-$ 0.03]).

We performed 315 monthly counts of lion sightings within the territories of 4 study clans between 2004 and 2013. Numbers of lions sighted ranged from 0 to 233 per territory per month (mean $\pm$ SE: 29.21 $\pm$ 2.08). There were significant differences among clans and between time periods with respect to numbers of lions sighted (Fig. 4). The number of lions sighted in Talek West declined significantly from 2004 to 2008 (median posterior estimate on the normal scale with mean effort [95% CI] = 36.68 [27.34, 47.54]) to 2009–2013 (16.2 [12.35, 21.61]), decreasing to a level lower than in Serena North (44.27

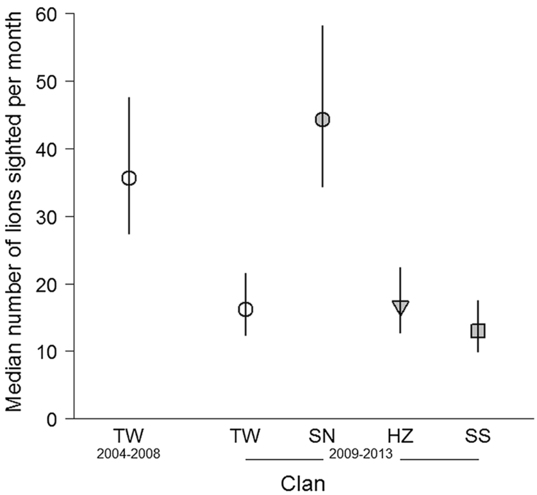


Fig. 4 The median number of lions sighted per month per clan territory between 2004–2008 and 2009–2013. These medians $\pm$ 95% credible intervals were based on the total number of lions sighted each month in each territory, regardless of whether or not hyenas were present with them. Counts are adjusted for the mean amount of effort expended searching for carnivores. Clan IDs and locations are as in Fig. 1. The expected median count in TW declined significantly between 2004–2008 and 2009–2013 (posterior parameter estimates 95% CIs did not overlap with one another). The expected median monthly count of lions in TW in 2009–2013 was significantly lower than in SN, but not different from those in SS or HZ, during the same time period

[34.23, 58.06]), but not different from those in Serena South or Happy Zebra during the same 2009–2013 time period (13.06 [9.95, 17.41] and 16.74 [12.78, 22.44], respectively). Serena North had the most lions sighted during the 2009–2013 period (Fig. 4). Numbers of lions sighted in Talek West from 2004 to 2008 did not differ significantly from those in Serena North in 2009–2013, but were significantly higher than those in Serena South and Happy Zebra during this same time period.

Analysis of hyena and lion locations

Between 2004 and 2013 and in the Talek West territory, we recorded the locations at which we found individual or groups of hyenas a total of 15,209 times (mean ± SE locations per year: 1689.89 ± 276.66); we also recorded 856 locations for lions (mean ± SE locations per year: 95.11 ± 16.31). The distances at which both hyenas and lions were found from the Reserve boundary increased over time, but more strongly for lions than hyenas (Fig. 5a; Table 1). Lions were also found deeper inside the Reserve than hyenas during both time periods (Fig. 5a). Hyenas and lions tended to be farther away from the edge of the Reserve during daylight observation hours than during dark hours of observation before sunrise or after sunset (Fig. 5b). Distances at which hyenas were found from the Reserve boundary were significantly predicted by the linear effects of rainfall, prey availability, and the number of livestock grazing inside the Reserve; hyenas were more likely to be found closer to the boundary during times of higher than average rainfall and livestock grazing, and farther away from the boundary when wild prey were more abundant inside the Reserve (Table 1). Lions were more likely to be closer to the Reserve boundary when relatively large numbers of livestock were seen grazing inside the Reserve (Table 1), but no other ecological effects were significant.

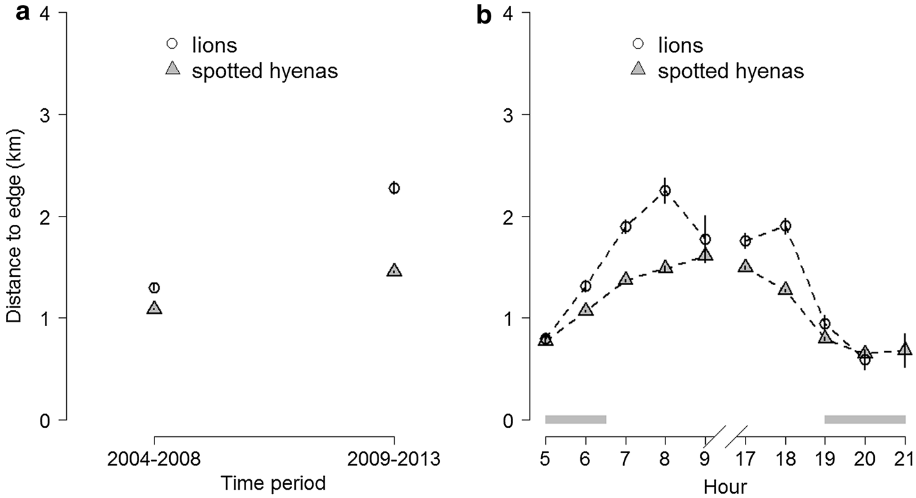


Fig. 5 Mean ± standard error distances at which spotted hyenas and lions were found from the Reserve boundary **a** over years of the study, comparing 2004–2008 with 2009–2013, and **b** over hours of the day from 2004 to 2013. Hours of darkness in **b** are indicated with grey shaded bars. These figures are based on 15,209 and 856 hyena and lion locations, respectively

Table 1 Posterior summaries for variables explaining the distances at which spotted hyenas and lions were found from the Reserve boundary over time in the Talek region of the Masai Mara National Reserve, Kenya

Parameter[a]	Mean	SD	Credible intervals		
			2.5%	50%	97.5%
Hyenas					
Intercept	6.62	0.02	6.59	6.62	6.65
Time period	**0.31**	**0.01**	**0.29**	**0.31**	**0.33**
Hour	**0.10**	**0.00**	**0.09**	**0.10**	**0.11**
Hour^2	**0.01**	**0.00**	**0.01**	**0.01**	**0.02**
Rain	**− 0.02**	**0.01**	**− 0.03**	**− 0.02**	**− 0.01**
Prey	**0.02**	**0.01**	**0.01**	**0.02**	**0.03**
Livestock	**− 0.02**	**0.01**	**− 0.03**	**− 0.02**	**− 0.01**
Lions					
Intercept	6.81	0.06	6.69	6.80	6.93
Time period	**0.58**	**0.05**	**0.49**	**0.58**	**0.68**
Hour	**0.11**	**0.02**	**0.08**	**0.11**	**0.13**
Hour^2	**0.01**	**0.00**	**0.01**	**0.01**	**0.02**
Rain	0.02	0.03	− 0.03	0.02	0.07
Prey	0.03	0.02	− 0.01	0.03	0.08
Livestock	**− 0.05**	**0.02**	**− 0.10**	**− 0.05**	**− 0.01**

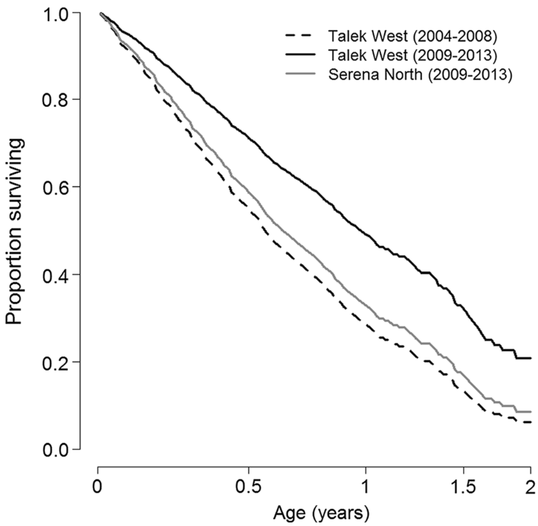
[a]Locations of hyenas and lions considered here were recorded from 2004 to 2013 (n = 15,209 and 856, respectively). Statistically significant posterior parameter estimates, not including the intercept, are indicated in bold font and presented on the log scale (95% CIs did not overlap with zero)

Testing hypotheses explaining the increase in Talek hyena population size

We rejected the hypothesis suggesting that increasing numbers of hyenas in the Talek region were due to widespread ecological change throughout the Reserve because the Talek West clan size uniquely increased over the course of this study by 108%, from a monthly average of 54 in 1988 to 113 in 2013 (Fig. 3). Furthermore, no other clans increased at a rate comparable to Talek West during the time period for which we monitored all six clans from 2008 to 2013. The frequency with which hyenas in Talek West fed on livestock increased significantly over time (livestock intercept and [95% CI] median posterior estimate on the normal scale: 0.05 [0.02, 0.13]; livestock year effect: 0.006 [0.003, 0.009]), but we observed no significant change over time in frequency of feeding on migrant (migrant intercept: 4.21 [3.4, 5.16]; migrant year effect = 0 [− 0.06, 0.07]) or resident herbivores (resident intercept: 4.53 [3.42, 5.94]; resident year effect = 0.06 [− 0.02, 0.18]). This suggests that bottom-up processes contributed to Talek West population growth.

The survivorship of juvenile hyenas to sexual maturity improved over time in Talek West (Fig. 6); survivorship there was significantly higher in 2009–2013 than in 2004–2008 (survivorship intercept: − 0.16 [− 2.09, 1.83]; 2009–2013 parameter effect: − 0.57 [− 0.97, − 0.15]). There was no significant difference between the survivorship of cubs born in Talek West between 2004 and 2008 to those born in Serena North between 2009 and 2013 (Serena North 2009–2013 parameter effect − 0.12 [− 0.55, 0.31]). Survivorship of cubs born between 2009 and 2013 was higher in Talek West than concurrently in Serena North (Fig. 6). These results are consistent with the hypothesis that lion declines facilitated growth of the Talek West clan.

Fig. 6 Differences in juvenile survivorship to sexual maturity between the Talek West clan in 2004–2008 and 2009–2013, and between Talek West and Serena North in the Mara Triangle from 2009 to 2013. Survivorship curves were estimated from 204 individuals born between 2004 and 2013. Juvenile survivorship in Talek West was higher in 2009–2013 than in 2004–2008, and higher in Talek West than Serena North in 2009–2013



Discussion

Our data strongly suggest that the large carnivores inside one of the most heavily touristed game reserves in the world may not be adequately buffered from the anthropogenic activity occurring along its boundaries. Multiple studies have documented declining carnivore populations, even within protected areas (e.g., Woodroffe and Ginsberg 1998; Burton et al. 2011; Ripple et al. 2014). Earlier workers have also documented changes in the space-use patterns of large carnivores in response to anthropogenic disturbance (e.g., Cozzi et al. 2013; van der Meer et al. 2015). To our knowledge, however, ours is the first study showing how anthropogenic disturbance near the edge of a PA can concurrently influence populations of multiple large carnivore species, and how the differential sensitivities of hyenas and lions to anthropogenic disturbance manifest in their space-use.

We predicted that spotted hyenas would be able to adapt to increasing disturbance, but we never anticipated the doubling of Talek West clan size. By 2013, the Talek West clan had become the largest hyena clan ever documented in Africa (Holekamp and Dloniak 2010), containing an average of 113 individuals each month. Clans of spotted hyenas average 29 members in sub-Saharan Africa (Holekamp and Dloniak 2010), and clans elsewhere in the Reserve ranged from 38 to 74 members in 2013 (Fig. 3).

While the Talek West hyena population burgeoned, we documented declines in both the frequency of lion-hyena interactions and numbers of lions sighted. We have no information on absolute numbers of lions in the Talek region. However, Dloniak's (2006) work, which was based on monitoring of known individual lions, indicated that the lion population in the Reserve had declined by 40% since Ogutu and Dublin (2002) estimated the lion population size there 13 years earlier. Our data suggest these downward population trends are continuing among lions in the Reserve, at least in the Talek region, and add to the growing evidence of lion declines throughout Africa (Packer et al. 2011; Riggio et al. 2013; Ripple et al. 2014; Bauer et al. 2015).

Like spotted hyenas (Kolowski et al. 2007), lions may have become more nocturnal over time to avoid encountering people, so the decline in lion sightings we documented here may simply have been due to reduced detectability. However, we searched for lions and hyenas during hours of both daylight and darkness, and our coverage of the territory of the Talek West clan was constant over time. Lions and hyenas show a high degree of spatial overlap where both species still occur in Africa (Creel and Creel 1996; Périquet et al. 2015), and they also commonly occupy the same regions of the Reserve (Ogutu et al. 2005; Watts and Holekamp 2008, 2009). Furthermore, because tourists are far more keen to see lions than hyenas, lions are often much easier to find than uncollared hyenas because we can home in on tour vehicles to find lions. Considering these facts, it seems unlikely that reduced detectability can account for the decline we observed over time in numbers of lions sighted in the Talek region.

Similarly, it seems highly unlikely that tourists in the Reserve affected numbers of either hyenas or lions. Although tour vehicles are abundant on both sides of the Reserve, neither lions nor hyenas avoid them, even at close distances, due to frequent exposure and extensive habituation. Tour vehicles rarely pose a direct threat to hyenas and have been present in this ecosystem for more than 4 decades. Maasai herdsmen, however, are armed with clubs and spears and represent a direct threat to both species of large carnivores (Fig. 7; Watts and Holekamp 2009; Hazzah et al. 2009; Pangle and Holekamp 2010; Hazzah et al. 2014). In contrast to tour vehicles, approaching pastoralists tending their herds on foot elicit flight responses from spotted hyenas. Thus, hyenas appear to perceive herdsmen as a threat because they often flee from guarded cattle herds, whereas cattle left unattended by herders are not avoided, and in fact may be attacked (Kolowski et al. 2007; Kissui 2008). Lions, on the other hand, are more likely than hyenas to prey on cattle during daylight hours and also to be targeted in retaliatory killings (Kissui 2008). Taken together, these observations along with our results suggest that livestock grazing affected both space-use and numbers of large carnivores in the Talek region.

Although the distances at which both hyenas and lions were found from Reserve borders increased over time in the Talek region, the change in lion space-use between 2004–2008 and 2009–2013 was more pronounced than was that of spotted hyenas. The increase in distances at which hyenas and lions were found from the Reserve boundary is consistent with the notion that the population changes we documented stem from anthropogenic disturbance, one major component of which is an increase in the number of livestock grazing inside the Reserve near Talek (Boydston et al. 2003; Kolowski and Holekamp

Fig. 7 A young adult male lion speared and killed by herders in late 2016, within the Masai Mara National Reserve, Kenya

2009; Pangle and Holekamp 2010; Green 2015). The livestock grazing within Reserve boundaries, and specifically, the herders accompanying them, now appear to be negatively affecting the number of lions in the Talek region. Although lions may simply be moving away from the Talek region to avoid conflicts with people altogether, the lions that do remain within this part of the Reserve are now subject to poisoning and spearing by Masai herders (Fig. 7). Furthermore, our observation that both lions and hyenas approached Reserve boundaries during hours of darkness suggests that both species might be leaving the Reserve at night and moving into the surrounding community lands to forage. This is a novel finding for spotted hyenas, and supplements earlier evidence that lions tend to approach areas containing dense human populations only at times of day when the least human activity is expected there (Schuette et al. 2013; Oriol-Cotterill et al. 2015). We also found that hyenas and lions were more likely to be closer to the Reserve edge when livestock were present in high numbers (Table 1). We believe this surprising finding might either be because carnivores are using livestock as a food source in the short-term, or because carnivores are unable to get out of harm's way solely by going deeper into the Reserve (e.g. other large carnivores have territories south of them). Conflict stemming from large carnivores leaving PAs to prey on livestock in community lands is a serious source of declining large carnivore populations worldwide, as it often results in retaliatory spearing, poisonings, and poaching (Woodroffe 2001; Woodroffe and Frank 2005; Ripple et al. 2014; Ogada 2014). In the current study, these human-induced mortality sources both inside and outside of Reserve boundaries may have contributed to the apparent decline in the Talek lion population.

The three hypotheses we put forth to explain the growth of the Talek West clan are not mutually exclusive. However, because the Talek West clan was unique in its massive growth relative to other clans in the Reserve, we were able to rule out an hypothesis suggesting that ecosystem-wide ecological changes were responsible for the increase in Talek West clan size. Our results suggest instead that anthropogenic disturbance along the edge of the Reserve may be causing a release of spotted hyenas through both the top-down effect of decreased lion-caused mortality among juvenile hyenas and the bottom-up effect of increased food availability in the form of livestock. This dual-process hypothesis is supported by declining numbers of lion-hyena interactions and lion sightings, as well as by concurrent increases in juvenile survivorship and numbers of hyenas. Furthermore, the lack of change in the frequency with which hyenas were seen feeding on indigenous prey, concurrent with an increase in the frequency of livestock consumption, suggests an overall human-caused increase in the food available to them.

In many respects, our observations here resemble other documented cases of mesopredator release (Johnson et al. 2007; Prugh et al. 2009; Ripple et al. 2014), but certain features distinguish this from other mesopredator release events. In contrast to most pairs of apex and mesopredators, lions and hyenas both prey primarily on medium- and large-bodied herbivores, and historically these species have exhibited a high degree of geographic and dietary overlap (Hayward and Kerley 2005; Hayward 2006; Périquet et al. 2015). Thus, it could be argued that they offer similar ecosystem services through the top-down controls they impose. On the other hand, Hayward (2006) suggested that, despite the extensive dietary overlap between lions and hyenas, lions significantly prefer buffalo, giraffe and plains zebra, all large-bodied species killed less often by hyenas. Thus the loss of lions might conceivably result in the release of large-bodied herbivores, which could then in turn have cascading effects in the Mara ecosystem. We currently know nothing about what the potential long-term effects might be of a carnivore community in the Reserve containing more spotted hyenas and fewer lions than found historically or the extent to which other species in this ecosystem might be affected by an increase in hyenas and a decrease in lions.

Above all, our data indicate that hyena and lion populations within the Reserve are changing in opposite directions, and suggest that carnivore guild structure inside the Reserve is being severely disrupted (Macdonald 2016). In other parts of Africa, lion populations are declining due to widespread habitat loss (Riggio et al. 2013), poaching (Williams 2015), preemptive or retaliatory killing (Hazzah et al. 2014), declining numbers of prey (Craigie et al. 2010), and poorly regulated sport hunting (Packer et al. 2009, 2011). If we wish to maintain the Masai Mara National Reserve as an iconic sanctuary for large carnivores, we need to perform a rapid and accurate assessment of the lion population, investigate in more detail the changes that are occurring within the carnivore community and their underlying causal factors, and assess the effects of this altered carnivore guild on ecosystem services. Fortunately, such efforts have recently begun in and around the Reserve (Elliot and Gopalaswamy 2017). Protected areas in sub-Saharan Africa are quickly becoming islands surrounded by degraded rangelands and growing human populations (Newmark 2008). The future conservation of large carnivores relies on the efficacy of these sanctuaries to protect species, like lions, that may be particularly sensitive to habitat degradation and at high risk for conflicts with people (Packer et al. 2013). Successful community conservation work can help to mitigate conflicts outside of PAs (Hazzah et al. 2014; Lichtenfeld et al. 2015; Blackburn et al. 2016), and is integral to long-term conservation of large carnivores. However, if sensitive species continue to decline within PAs, even the best conservation efforts in community lands may not be able to sustain large carnivore populations into the future.

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