Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives

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Abstract. Carnivore communities face unprecedented threats from humans. Yet, management regimes have variable effects on carnivores, where species may persist or decline in response to direct or indirect changes to the ecosystem. Using a hierarchical multispecies modeling approach, we examined the effects of alternative management regimes (i.e., active vs. passive enforcement of regulations) on carnivore abundances and group sizes at both species and community levels in the Masai Mara National Reserve, Kenya. Alternative management regimes have created a dichotomy in ecosystem conditions within the Reserve, where active enforcement of regulations maintains low levels of human disturbance in the Mara Triangle and passive enforcement of regulations in the Talek region permits multiple forms of human disturbance. Our results demonstrate that these alternative management regimes have variable effects on 11 observed carnivore species. As predicted, some species, such as African lions and bat-eared foxes, have higher population densities in the Mara Triangle, where regulations are actively enforced. Yet, other species, including black-backed jackals and spotted hyenas, have higher population densities in the Talek region where enforcement is passive. Multiple underlying mechanisms, including behavioral plasticity and competitive release, are likely causing higher black-backed jackals and spotted hyena densities in the disturbed Talek region. Our multispecies modeling framework reveals that carnivores do not react to management regimes uniformly, shaping carnivore communities by differentially producing winning and losing species. Some carnivore species require active enforcement of regulations for effective conservation, while others more readily adapt (and in some instances thrive in response) to lax management enforcement and resulting anthropogenic disturbance. Yet, high levels of human disturbance appear to be negatively affecting the majority of carnivores, with potential consequences that may permeate throughout the rest of the ecosystem. Community approaches to monitoring carnivores should be adopted as single species monitoring may overlook important intra-community variability.

Key words: apex predator; Bayesian analysis; carnivore conservation; community modeling; distance sampling; enforcement of regulations; imperfect detection; protected area; Serengeti-Mara.

INTRODUCTION

Carnivores play important roles in ecosystem structure and function, and many are targeted for conservation because of their threatened status and charismatic nature (Ripple et al. 2014). As predators in their ecosystems, carnivores influence energy flow and control abundance of other species through interspecific interactions, such as predation and competition (Ritchie and Johnson 2009, Estes et al. 2011). Carnivores affect lower trophic levels both directly and indirectly, and in some instances,

the extirpation of apex carnivores can consequentially result in trophic cascades (Ritchie and Johnson 2009, Estes et al. 2011, Ripple et al. 2016). Loss of top carnivores has led to increases in mesopredators through release from competition and intra-guild predation, resulting in decreased abundances of herbivore species through consumption by mesopredators (Ripple et al. 2013). In other cases, reduced carnivore abundance has led to drastic increases in herbivore populations, inadvertently decimating local vegetation (Beschta and Ripple 2009). Whatever the specific outcome, reductions in carnivore abundance usually result in ecosystem degradation (Ritchie and Johnson 2009, Estes et al. 2011, Ripple et al. 2014).

Despite their importance, many populations of carnivores worldwide are declining, often existing only in

small fractions of their historical ranges (Ripple et al. 2014, Wolf and Ripple 2017). Of nearly 290 recognized carnivore species, 27% are listed as "threatened" on the International Union for Conservation of Nature's "Red List," with 10% listed as "near threatened" (IUCN 2017). Anthropogenic disturbances including development, agriculture, mining, resource exploitation, pollution, and climate change are responsible for the declines of most carnivore species (Ripple et al. 2014, IUCN 2017). Relative to other wildlife, carnivores have disproportionately high rates of conflict with humans because of frequent encounters due to their expansive home ranges and threats they pose to livestock or humans themselves (Woodroffe and Ginsberg 1998, Treves and Karanth 2003, Hampson et al. 2015). Increased conflict has often led humans to target carnivores for lethal removal (Treves and Karanth 2003), but carnivore populations are vulnerable to high mortality rates because of their low population densities, slow reproduction, and K-selected life history (Ripple et al. 2014); thus, carnivores are ill-equipped to adapt to human pressure.

Perhaps the most common strategy used in carnivore conservation is the designation of protected areas (Di Minin et al. 2016). Protected areas delineate habitats in which species can exist with presumably minimal human interference (Watson et al. 2014). Protected areas encompass over 18.4 million km^2 worldwide and generally contribute to conservation of ecosystem function and biodiversity (Geldmann et al. 2013, Watson et al. 2014). However, inadequate resources (e.g., lack of funding, monetary benefits to local communities, poor infrastructure, and inadequate law enforcement), along with limited monitoring of wildlife, reduce the efficacy of protected areas in many regions (Leverington et al. 2010, Geldmann et al. 2013, Watson et al. 2014) and can lead to species declines even within protected areas (Woodroffe and Ginsberg 1998, Burton et al. 2011, Durant et al. 2011, Riggio et al. 2013, Ripple et al. 2014). Active management within protected areas that includes law enforcement, wildlife monitoring, management planning, regulation of tourism, community engagement, and infrastructure maintenance is usually necessary to effectively prevent loss of carnivores (Leverington et al. 2010, Watson et al. 2014).

The Serengeti-Mara ecosystem in East Africa is one of the last refugia for multiple sympatric carnivore species and exemplifies the ongoing struggle facing carnivores inhabiting areas characterized by increasing anthropogenic disturbance (Hampson et al. 2015, Di Minin et al. 2016). This ecosystem contains one of the richest and most diverse carnivore communities in the world, with over 30 species (Craft et al. 2015). Human encroachment into the region has led to rapid development of areas that previously served as wildlife habitat (Lamprey and Reid 2004, Green 2015). Agriculture and pastoralism are reducing available habitats for wildlife, restricting geographic ranges, and creating additional human–wildlife conflicts (Ogutu et al. 2005, 2011, 2016,

Hampson et al. 2015). The tourism industry also places pressure on wildlife through development of tourist accommodations and increased rates of human–wildlife interactions (Walpole and Leader-Williams 2001, Green 2015). As a result, the ability of protected areas to buffer wildlife from human disturbance may be inadequate to prevent population declines (Craft et al. 2015, Hampson et al. 2015). Carnivores must either alter their behaviors to avoid humans or risk interacting with them (Kolowski et al. 2007, Oriol-Cotterill et al. 2015, Gaynor et al. 2018).

Impacts of anthropogenic disturbances and effectiveness of wildlife management regimes on carnivore populations and communities are largely unknown in the Serengeti-Mara ecosystem (Craft et al. 2015, Ogutu et al. 2016). Worldwide, few studies simultaneously monitor multiple carnivore species (Burton et al. 2011, Durant et al. 2011, Rich et al. 2016, Van der Weyde et al. 2018); most research and conservation efforts are limited to single species due to logistical constraints, low population densities, and cryptic or elusive behavior of carnivores (Craft et al. 2015). Even studies that observe multiple carnivore species often discard data on rare or elusive species.

In this paper, we develop a hierarchical multispecies distance sampling model to evaluate effects of wildlife management on a carnivore community within the Serengeti-Mara ecosystem (Goyert et al. 2016, Kéry and Royle 2016, Sollmann et al. 2016). Multispecies models integrate data from all observed species (i.e., no discarding of data-deficient species) in a unified analytical framework to characterize an entire community while also preserving the identities of individual species (Dorazio and Royle 2005, Dorazio et al. 2006, Warton et al. 2015, Thorson et al. 2016). Community modeling approaches allow for estimation of species-specific parameters (e.g., occurrence, abundance, and/or covariate effects) as well as community-level effects (Zipkin et al. 2010). Though communities likely contain species with variable responses to environmental conditions, including all species within a single modeling framework provides more precise estimates than analyzing multiple subgroups or individual species (Zipkin et al. 2009, Pacifici et al. 2014). Importantly, these approaches can account for detection biases incurred during the sampling process (Iknayan et al. 2014, Beissinger et al. 2016, Goyert et al. 2016, Sollmann et al. 2016). Failure to account for unequal detection among species can lead to misleading, or even erroneous, conclusions about community dynamics (Ruiz-Gutiérrez and Zipkin 2011, Guillera-Arroita 2017).

We estimated species-specific densities and the effect of two disparate wildlife management regimes on carnivore communities in the Masai Mara National Reserve (MMNR), Kenya, a protected area within the Serengeti-Mara ecosystem. The MMNR is divided by the Mara River into western and eastern regions that are managed by separate entities, which implement contrasting

regimes of active and passive enforcement of regulations (Green 2015, Mara Conservancy 2017, Green et al. 2018). The discrepancy between management enforcement creates a striking disparity in the amount of anthropogenic disturbance experienced by resident animals (Green 2015). This in turn provides a unique opportunity to use a classical experimental design to evaluate the effectiveness of two different wildlife management regimes in a complex ecological system.

Because human–wildlife conflicts are known to decrease survival and densities of African lions (*Panthera leo*; Riggio et al. 2013, Hazzah et al. 2014, Blackburn et al. 2016), we predicted that the eastern region, which has passive enforcement of regulations and higher levels of anthropogenic disturbance, would have lower abundances of lions than the relatively undisturbed western region. Declining numbers of lions, the apex predator in this ecosystem, could potentially lead to cascading effects on other members of the local carnivore community (Ogutu et al. 2005, Green et al. 2018). Long-term research on spotted hyenas (*Crocuta crocuta*) in the eastern MMNR indicates that this species is increasing in areas with high levels of human disturbance (Green et al. 2018), perhaps as a release from competition or intra-guild predation by lions. Organization of carnivore communities oftentimes depends on the degree of human interaction, species compositions at high trophic levels, and the distribution of prey or other important habitat features. As such, we hypothesized that densities of subordinate members of the carnivore community would be differentially affected by management alternatives.

MATERIALS AND METHODS

Study area

The MMNR is an administratively designated protected area in southwestern Kenya bounded by the Serengeti National Park, Tanzania, to the south (Fig. 1). The MMNR is an unfenced reserve of 1,510 km^2 consisting primarily of open, rolling grasslands interspersed with ephemeral wetlands and seasonal creeks. The Mara River divides the MMNR into two regions that are managed independently. The Mara Triangle, the region west of the Mara River, comprises approximately one-third of the MMNR, and is managed by the Mara Conservancy, a local not-for-profit organization. In response to widespread wildlife declines and increases in poaching and security problems, the Mara Conservancy was solicited by the Trans-Mara County Council of the Kenyan Government to manage the Mara Triangle starting in 2001 (Walpole and Leader-Williams 2001). The Mara Conservancy improved conditions in the Mara Triangle by limiting numbers of livestock grazing inside the Reserve, implementing frequent anti-poaching patrols, establishing a moratorium on the development of new tourist facilities, and transparently dispersing tourism revenues to the local community (Mara Conservancy 2017). Thus, wildlife in the Mara Triangle experienced virtually no anthropogenic disturbances other than controlled visitation by tourist vehicles.

In contrast to the Mara Triangle, the region east of the Mara River is managed by the Narok County Government. Sections of this region experience several anthropogenic disturbances due to minimal enforcement of management policies (Green 2015, Green et al. 2018). Due to an expanding population of Masai pastoralists along the northern boundary of the Reserve, and passive enforcement of reserve regulations by the Narok County Government, the Talek region is heavily disturbed. The Talek region is an 111-km^2 area within the eastern portion of the MMNR (Fig. 1), characterized by a booming tourist industry (Green 2015), frequent and massive livestock incursions into the protected area (Green et al. 2018), proximity to urban area (i.e., Talek Town), and killing of carnivores (e.g., lion, spotted hyena) through poisoning, snaring, or spearing by humans (Lamprey and Reid 2004, Ogutu et al. 2005, Holekamp and Dloniak 2010, Pangle and Holekamp 2010, Green et al. 2018).

Survey design

We surveyed for carnivores within the Mara Triangle and Talek regions of the MMNR from July 2012 to March 2014 (Fig. 1), using a distance sampling approach (Buckland et al. 1993). The survey was designed to sample the larger Mara Triangle and smaller Talek regions proportionately. We divided the surveys into transects that were approximately 10 km in length, for a total of 4 transects in the Talek region and 13 transects in the Mara Triangle. Straight line surveys were infeasible due to impassible terrain and off-road driving restrictions. A simulation study revealed that winding surveys did not create biases in estimates of abundance (Appendix S1). Transects were driven for three consecutive days every 4 to 6 weeks. We assumed closure of carnivore populations only during a single survey period (i.e., 3 consecutive days). A total of 13 and 16 surveys were completed within the Talek region and the Mara Triangle, respectively, resulting in 52 transect–survey combinations in Talek and 208 in the Mara Triangle.

Starting at sunrise, one or two observers recorded to species when either an individual or a group of carnivores was observed within 650 m of transects. Observers also recorded GPS location of the vehicle as well as the distance and bearing of each observation to the vehicle using a laser rangefinder (Nikon Laser 1200). Social behavior or adult carnivores with offspring caused grouping of individuals for some species. We considered all individuals of the same species within 200 m of one another to be a single group (in which a group consists of one or more individuals) to avoid violating the assumption of independent observations (Buckland et al. 1993). For each group, we recorded the number of
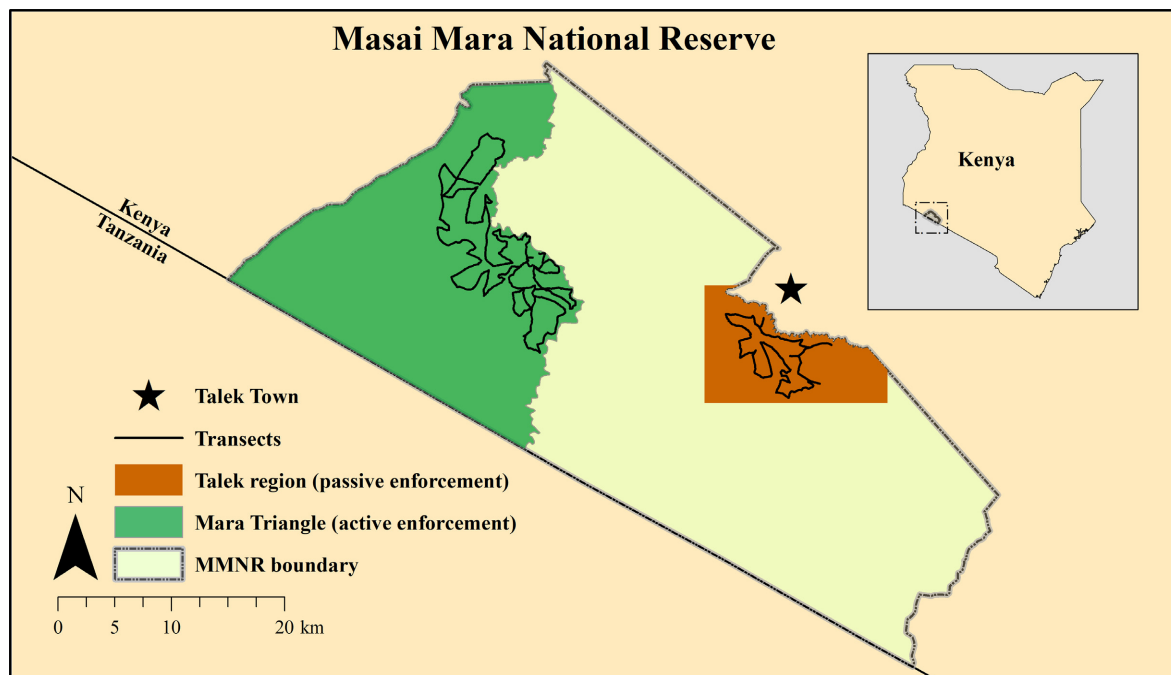
FIG. 1. Map of transects (solids lines) in the Talek region (passive enforcement; dark orange; ■) and Mara Triangle (active enforcement; dark green; ■) within the larger Masai Mara National Reserve, Kenya. Transects were conducted at 4–6 week intervals from July 2012 to March 2014.

individuals present and calculated the distance and bearing measurements to the center of the group. We observed African lions, banded mongoose (*Mungos mungo*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), cheetah (*Acinonyx jubatus*), slender mongoose (*Galerella sanguinea*), and spotted hyena in groups. We observed caracal (*Caracal caracal*), leopard (*Panthera pardus*), serval (*Leptailurus serval*), and side-striped jackal (*Canis adustus*) only as solitary individuals.

Data analysis

To estimate effects of management regime on the carnivore community and individual species within reserve areas, we developed a hierarchical multispecies distance sampling model (Goyert et al. 2016, Kéry and Royle 2016, Sollmann et al. 2016). Distance sampling models estimate density or abundance from count data of individuals or groups while accounting for imperfect detection using recorded distances between individuals or groups and a transect line (Buckland et al. 1993). Distance sampling models assume that observations are distributed uniformly in space, observations on the transect line are made without error, observations are detected at their initial locations, and distances are recorded accurately (Buckland et al. 1993). For species not in groups, we estimated expected abundance per 10 km transect directly in the two management regions. For species in groups, we estimated expected number of groups and group size to derive estimates of expected species

abundance per 10 km transect in each management region. We report density at the transect scale, defined as 10 km long by 1.3 km wide (double the width of the observable 650 m on each side of the transect) or 13 km^2.

We estimated species-specific detection probabilities as a function of distance from the transect line to individuals or groups, $g(x)$, using the half-normal distribution (Buckland et al. 1993):

$$g(x) = \exp\left(-\frac{x^2}{2\sigma_{js}^2}\right)$$

where x is the distance from the observation to the transect line, and σ_{js} is the scale parameter at each transect j for each species s. We modeled σ_{js} using a log-link function:

$$\log(\sigma_{js}) = \gamma 0_s + \gamma 1 \cdot \text{SIZE}_s + \gamma 2 \cdot \text{REGION}_j$$

where $\gamma 0_s$ is the species-specific intercept parameter, $\gamma 1$ is the effect of standardized average body size, SIZE_s (as reported by Gittleman 1989; pg. 189–191), and $\gamma 2$ is the effect of management regime. REGION_j indicates whether transect j was in the Talek region ($\text{REGION}_j = 1$) or in the Mara Triangle ($\text{REGION}_j = 0$). We included body size as a covariate because we hypothesized that larger species may be easier to detect than smaller species. We additionally added a region covariate because livestock grazing has caused shorter grass height in the

Talek region, which may influence detection probability. During preliminary analyses, we checked for effects of group size and vehicle type on species' detections but did not include those in the final model because they were not significant. We modeled species-specific intercepts, $\gamma 0_s$, by assuming they were random effects, drawn from a community-level distribution:

$$\gamma 0_s \sim \text{Normal}\big(\mu_\sigma,\ \tau_\sigma^2\big),$$

where the mean, μ_σ, is the average intercept parameter (log scale) across the carnivore community with variance, τ_σ^2.

To calculate detection probabilities for each observed individual or group, we classified distance of each observation into 50 m wide classes ($k = 1, 2, \dots 13$). We calculated detection probability for each distance class by species, π_{ktjs}, for survey t at transect j, as the integral of $g(x)$ across distance class k from the start of the distance class, b_k, to the beginning of the next class, b_{k+1}, divided by the width of distance class (50 m):

$$\pi_{ktjs} = \frac{\int_{b_k}^{b_{k+1}} g(x)dx}{50}.$$

The vector consisting of the number of observed individuals or groups within each distance class, $\boldsymbol{y_{tjs}}$, is the realization of a multinomial process:

$$\boldsymbol{y_{tjs}} \sim \text{Multinomial}\big(n_{tjs},\ \boldsymbol{\pi_{tjs}^c}\big),$$

where n_{tjs} is the observed number of individuals or groups summed across all distance classes, $\sum_k y_{ktjs}$, and the vector $\boldsymbol{\pi_{tjs}^c}$ contains each of the conditional cell probabilities, $\pi_{ktjs}/\sum_k \pi_{ktjs}$, or the probability of an observation falling into distance class k. These values sum to one because an observation must be in one of the 13 distance classes. Note that both $\boldsymbol{y_{tjs}}$ and n_{tjs} were observed quantities and our objective was to estimate $\boldsymbol{\pi_{tjs}^c}$. The observed number of individuals or groups, n_{tjs}, follows a binomial distribution based on true abundance (species not in groups) or number of groups (species in groups), N_{tjs}, that were present, which is an unknown latent quantity:

$$n_{tjs} \sim \text{Binomial}\big(N_{tjs},\ \pi_{tjs}\big).$$

The parameter π_{tjs} is the sum of cell probabilities from each distance class, $\sum_k \pi_{ktjs}$, or the realized detection probability for the number of individuals or groups of species s during survey t at transect j.

We modeled latent abundance (for solitary species) or number of groups, N_{tjs}, by assuming it is a value derived from a negative binomial distribution (specified as a Poisson-gamma mixture):

$$N_{tjs} \sim \text{Poisson}\big(\tilde{\lambda}_{tjs}\big),$$

with mean $\tilde{\lambda}_{tjs} = \lambda_{tjs} \cdot \rho_{tjs}$ in which ρ_{tjs} is a gamma distributed random variable to account for overdispersion.

To evaluate response of the carnivore community to management alternatives, we included a covariate for management regime (i.e., passive management in the Talek region or active management in the Mara Triangle) on λ_{tjs} using a log-link function:

$$\log\big(\lambda_{tjs}\big) = \alpha 0_s + \alpha 1_s \cdot \text{REGION}_j + \varphi_{js} + \log\big(\text{offset}_j\big).$$

Here, $\alpha 0_s$ is the species-specific intercept parameter, and $\alpha 1_s$ is the species-specific effect of management regime where REGION_j indicates whether transect j was in the Talek region ($\text{REGION}_j = 1$) or in the Mara Triangle ($\text{REGION}_j = 0$). We added a transect-level random effect, φ_{js}, which we let vary by species to account for any temporal variation in transects and the pseudo-replication in our study design (i.e., resampling the same transects). The offset parameter was added to account for slight variation (± 2 km) in transect length (i.e., where offset was the actual length for transect j divided by 10 km). We drew $\alpha 0_s$ and $\alpha 1_s$ from community-level distributions:

$$\alpha 0_s \sim \text{Normal}\big(\mu_{\alpha 0},\ \tau_{\alpha 0}^2\big)$$

$$\alpha 1_s \sim \text{Normal}\big(\mu_{\alpha 1},\ \tau_{\alpha 1}^2\big)$$

where the means, $\mu_{\alpha 0}$ and $\mu_{\alpha 1}$, are average intercept and effect parameters across the observed carnivore community and the variances, $\tau_{\alpha 0}^2$ and $\tau_{\alpha 1}^2$, represent variation among species. Thus we obtained estimates for effects of management at both species (e.g., $\alpha 1_s$) and community (e.g., $\mu_{\alpha 1}$) levels on the expected abundance or number of groups per transect.

For species that were observed in groups (i.e., more than one individual), we estimated species-specific expected group sizes using a zero-truncated negative binomial distribution (specified as a Poisson-gamma mixture), which accounted for overdispersion in group size. We used a truncated distribution because an observed group cannot contain zero individuals. Most groups contained one or two individuals although groups of over 20 individuals were occasionally observed for some species. We modeled group size G_i, for each observation i as follows:

$$G_i \sim \text{ztPoisson}\big(\tilde{\mu}_{tjs}\big)$$

where ztPoisson is a zero truncated Poisson distribution with mean $\tilde{\mu}_{tjs} = \mu_{tjs} \cdot \phi_{tjs}$, in which ϕ_{tjs} is a gamma distributed random variable to account for the overdispersion in group sizes, which varies by species, transect, and survey. Note that each observation i is associated with a unique species and survey event. We estimated μ_{tjs} using a log-link function and included an effect of management regime and the transect-length offset

$$\log\big(\mu_{tjs}\big) = \beta 0_s + \beta 1_s \cdot \text{REGION}_j + \log\big(\text{offset}_j\big).$$

The parameter $\beta 0_s$ is the species-specific intercept and $\beta 1_s$ is the species-specific effect of management regime

where REGION$_j$ indicates whether transect j was in the Talek region (REGION$_j$ = 1) or in the Mara Triangle (REGION$_j$ = 0). Due to variation in social behavior of carnivores and how they group with conspecifics (Gittleman 1989), we estimated intercepts, $\beta 0_s$, independently (i.e., not using a community-level distribution). However, we hypothesized that the effects of management regime would likely affect group size similarly (i.e., forming smaller or larger groups with conspecifics) across species. As such, we assumed that each $\beta 1_s$ was a random effect drawn from a community-level distribution:

$$\beta 1_s \sim \text{Normal}\left(\mu_{\beta 1}, \tau^2_{\beta 1}\right)$$

where mean $\mu_{\beta 1}$ is the average effect parameter across the observed carnivore community and variance $\tau^2_{\beta 1}$ is the variation in the effect parameter across species.

For species that were observed in groups, we derived species-specific abundance estimates by multiplying $\tilde{\lambda}_{tjs}$ (expected number of groups) and $\tilde{\mu}_{tjs}$ (expected group size) to compare abundance at the transect-level between management regions. We assumed independence between the number of groups and group size with zero covariance, which was consistent with what we observed in the data. We only report estimated transect-level abundances for species with at least 20 observations because abundance estimates for species with few observations can be biased (Sollmann et al. 2016). We converted these abundance estimates to density at 13 km^2 (i.e., area of a transect). We then compared region-specific densities of species.

We implemented our model using a Bayesian framework in JAGS (version 4.2.0; Plummer 2003) via program R (version 3.4.1; R Core Team 2017) with the JagsUI package (version 1.4.2; Kellner 2016; see Appendix S2 for JAGS code; all code/data are publicly available; see *Data Availability*). We ran three parallel chains for 150,000 iterations with a burn-in of 100,000 iterations and thin by 10 for a total of 15,000 draws to approximate posterior distributions for each parameter. We used uninformative priors for all parameters (Appendix S2). We visually inspected the model output and used the Gelman-Rubin statistic (<1.1) to determine convergence. Posterior distributions were used to calculate percent probabilities, which are calculated as the percent of posterior draws above zero.

RESULTS

We recorded 1,838 individuals of 11 carnivore species in 574 observations in the Mara Triangle and Talek regions (Table 1). The mean community-level effect of management regime on the expected number of groups (abundance for species not in groups; $\mu_{\alpha 1}$) was negative (mean [95% credible interval, CI]: −0.24 [−1.21, 0.58], on the log scale), indicating a lower expected number of groups per transect for the average carnivore species in the passively managed Talek region. However, the 95% CI was fairly wide and overlapped zero suggesting a wide range of carnivore responses. The mean community-level effect of management regime on expected group size ($\mu_{\beta 1}$) was also negative (−0.65 [−1.48, −0.03], on the log scale), indicating that group sizes of carnivores were smaller in the Talek region compared to the Mara Triangle.

Species-specific effects of management regime on the expected number of groups ($\alpha 1_s$) were highly variable (Fig. 2, Appendix S3: Table S1). The expected number of lion groups per transect had a 98.5% probability of being higher in the Mara Triangle than the Talek region (i.e., negative values; −1.20 [−2.38, −0.10]). For solitary species, leopards (−0.73 [−3.18, 0.93]) and servals (−0.68 [−2.45, 0.68]), respectively, had a 77.1% and 81.7% probability of higher abundance for transects in the Mara Triangle compared to the Talek region. The model estimated the reverse effect (i.e., positive values) for black-backed jackals (0.63 [−0.40, 1.71]) and spotted hyenas (0.65 [−0.13, 1.43]) with 88.9% and 94.9% probabilities of more groups in the Talek region compared to the Mara

TABLE 1. Number of observations (i.e., observed number of groups) and the total number of observed individuals for each carnivore species within the Talek region (52 transect–survey combinations) and Mara Triangle (208 transect–survey combinations) during distance sampling surveys from July 2012 to March 2014.

| Species	Talek region		Mara Triangle		Total	
	Groups	Individuals	Groups	Individuals	Groups	Individuals
African lion	4	7	46	172	50	179
Banded mongoose	23	217	53	604	76	821
Bat-eared fox	3	4	43	126	46	130
Black-backed jackal	45	63	45	82	90	145
Caracal	NA	0	NA	1	NA	1
Cheetah	3	5	4	4	7	9
Leopard	NA	0	NA	2	NA	2
Serval	NA	1	NA	7	NA	8
Side-striped jackal	NA	2	NA	1	NA	3
Slender mongoose	2	2	5	8	7	10
Spotted hyena	136	287	148	243	284	530
Total	216	588	344	1,250	560	1,838
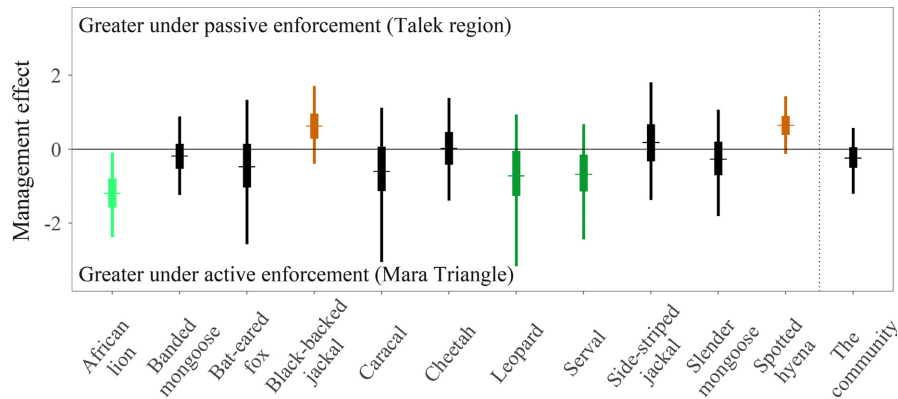
Fig. 2. Estimates of the effect of management regime on the expected number of individuals or groups by species ($\alpha 1_s$) and for the community as a whole ($\mu_{\alpha 1}$). Mean values are indicated with small horizontal bars; 50% and 95% credible intervals are shown with thick and thin vertical bars, respectively. Orange fill indicates a higher expected number of groups in the Talek region, in which the 95% CI (light orange ■) and the 50% CI (dark orange ■) do not overlap zero. Green fill indicates a higher expected number of groups in the Mara Triangle, in which the 95% CI (light green ■) and the 50% CI (dark green ■) do not overlap zero. Black fill indicates no difference in the expected number of groups between regions. Note, no species experienced higher expected number of individuals or groups in the Talek region with 95% CI (light orange ■).

Triangle, respectively. The effect of management regime on expected group size ($\beta 1_s$) also varied but most (six of seven species in groups) had larger estimated group sizes in the Mara Triangle than the Talek region (i.e., negative effects; Fig. 3, Appendix S3: Table S1). The one exception was spotted hyena (0.03 [−0.31, 0.36]), which had similar group sizes between the regions.

Only 5 of the 11 detected species had enough total observations (i.e., ≥20; Table 1) to estimate density, and there was considerable variation in density estimates between regions (Fig. 4). We estimated a 99.9% probability that lions had lower density for transects in the Talek region (0.35 [0.07, 0.95]) compared to the Mara Triangle (2.23 [1.41, 3.36]). We similarly estimated a 99.9% probability that bat-eared foxes had lower density

in the Talek region (0.66 [0.07, 2.15]) than in the Mara Triangle (7.73 [4.75, 11.63]). Banded mongooses had a 70.6% probability of lower density in the Talek region (24.37 [14.06, 39.10]) than in the Mara Triangle (28.21 [19.17, 39.65]). However, black-backed jackals had a 75.5% probability of higher density in the Talek region (2.40 [1.29, 3.95]) than in the Mara Triangle (1.86 [1.18, 2.81]). Spotted hyenas had a higher estimated density in the Talek region (10.63 [7.92, 13.86]) than in the Mara Triangle (3.49 [2.71, 4.46]) with nearly 100% probability. We report our density estimates at the transect level (13 km^2) to avoid any inaccuracies that might occur by extrapolating our results to a larger spatial scale. However, our results closely resemble density estimates from other studies within the Serengeti-Mara ecosystem when
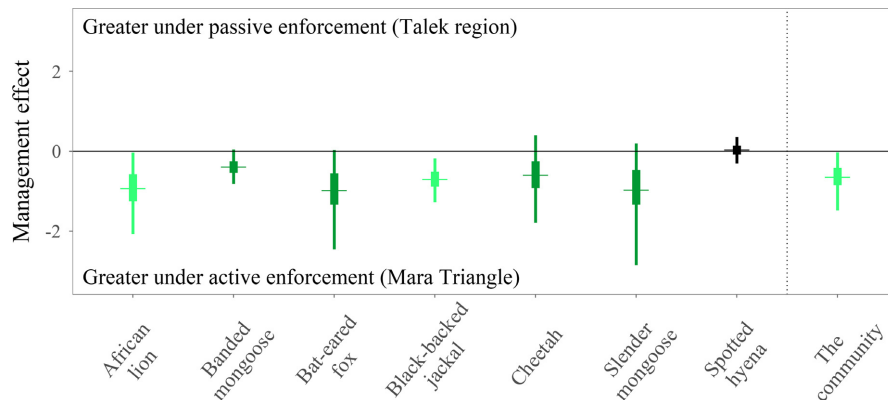

Fig. 3. Estimates of the effect of management regime on the expected group size for species in groups ($\beta 1_s$) and for the community as a whole ($\mu_{\beta 1}$). Mean values are indicated with small horizontal bars; 50% and 95% credible intervals are shown with thick and thin vertical bars, respectively. Orange fill indicates larger group sizes in the Talek region, in which the 95% CI (light orange ■) and the 50% CI (dark orange ■) do not overlap zero. Green fill indicates larger group sizes in the Mara Triangle, in which the 95% CI (light green ■) and the 50% CI (dark green ■) do not overlap zero. Black fill indicates no difference in the expected group size between regions. Note, no species experienced higher expected group sizes in the Mara Triangle with 95% (light orange ■) or 50% CI (dark orange ■).

rescaled (Durant et al. 2011, Craft et al. 2015, Elliot and Gopalaswamy 2017).

The mean community-level intercept parameter for detection (scale; μ_σ) was 61.97 (95% CI = 38.67, 93.00) on the inverse log scale, indicating that average species detection probability decays to 50% at 73 m from the transect and 10% at 133 m. Effect of average body size on detection, $\gamma 1$, was 0.43 (−0.01, 0.87) on the log scale, confirming that larger species were easier to detect. The effect of management regime on detection, $\gamma 2$, was also positive (0.52 [0.39, 0.65]), demonstrating that carnivores were easier to detect in the Talek region where grass height was generally shorter. Species-specific estimates ($\gamma 0_s + \gamma 1 \cdot SIZE_s$) varied greatly (Fig. 5). Slender mongooses had the smallest scale parameter at 24.63 (11.52, 49.83) with detection probability decaying to 50% at 29 m from the transect and to 10% at 53 m. Lions had the largest scale parameter at 214.20 (64.45, 715.70), with detection probability decaying to 50% at 252 m from the transect and 10% at 460 m.

DISCUSSION

Our hierarchical multispecies distance sampling model indicates that passive enforcement of wildlife regulations and policies in the Talek region of the MMNR is having adverse effects on some members of the carnivore community, including bat-eared foxes, leopards, lions, and servals, when compared to active enforcement of regulations within the Mara Triangle (Figs. 2 and 4). Our model also identified a subset of carnivore species, including black-backed jackal and spotted hyena, which are occurring at higher densities in the region with passive enforcement of wildlife regulations (Figs. 2 and 4). Multiple interacting mechanisms may be responsible for these differences such as human-caused mortality, competition (or lack thereof), habitat degradation, and prey depletion (Ogutu et al. 2005, Craft et al. 2015, Green 2015, Green et al. 2018). Additionally, some carnivore species seem to be altering their behavior by forming smaller groups in the passively enforced Talek region
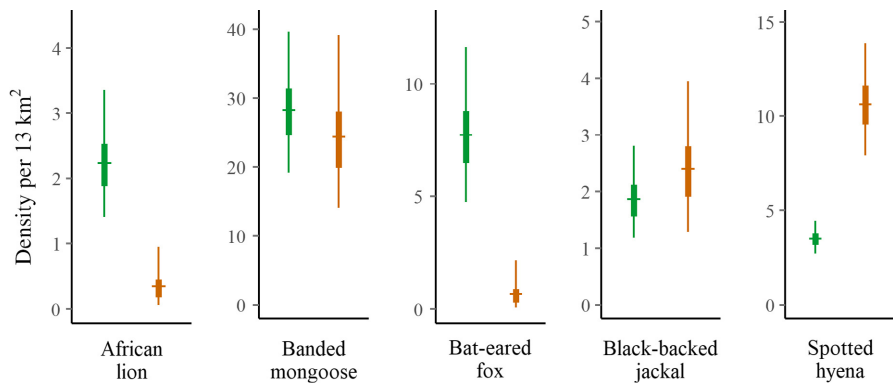

FIG. 4. Expected density at 13 km^2 within the Mara Triangle (dark green ■) and the Talek region (dark orange ■) for species with over 20 observations. Mean values are indicated with small horizontal bars; 50% and 95% credible intervals are shown with thick and thin vertical bars, respectively.
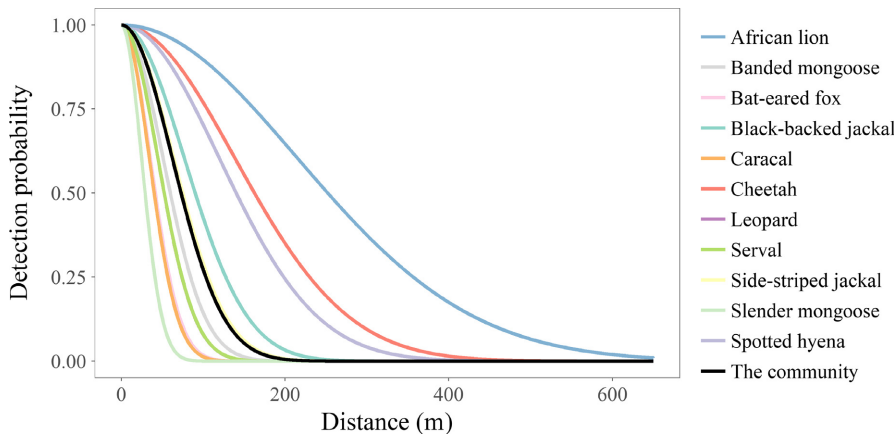

FIG. 5. Mean detection probabilities for each observed species and the entire monitored community relative to distance from the transect line.

(Fig. 3), which may be an adaptive approach to avoid human interaction. Our multispecies model reveals that members of carnivore communities have variable responses to anthropogenic disturbance.

Notably, lion density was lower in the Talek region compared to the Mara Triangle (Fig. 4), both supporting our prediction and corroborating multiple studies that have documented declines in lion populations due to anthropogenic disturbances (Riggio et al. 2013, Green et al. 2018). Spotted hyena density was higher in the Talek region compared to the Mara Triangle (Figs. 2–4), suggesting that spotted hyenas have benefitted from passive enforcement of wildlife regulations. Competition and intra-guild predation between lions and spotted hyenas have been well documented (Watts and Holekamp 2009, Périquet et al. 2015) and may be partly responsible for the negative abundance correlation we observed between these two species. Additionally, high behavioral plasticity allows spotted hyenas to quickly modify their behavior (e.g., space use, activity patterns, vigilance) in response to anthropogenic disturbances (Boydston et al. 2003, Pangle and Holekamp 2010) helping them more readily persist under changing ecological conditions (Holekamp and Dloniak 2010).

Other carnivore species are exhibiting variable responses to either management alternatives or additional unmeasured heterogeneity between regions (Figs. 2–4, Appendix S3: Table S1). For example, estimated densities of bat-eared foxes are significantly lower in the Talek region compared to the Mara Triangle (Fig. 4). Variation in prey (i.e., arthropods) distributions between regions could be contributing to this result (Kamler et al. 2013, Craft et al. 2015), as could sublethal and lethal effects from black-backed jackals (Blaum et al. 2009, Kamler et al. 2012, 2013, Bagniewska and Kamler 2014). Interference competition and intra-guild predation by black-backed jackals on bat-eared foxes have been documented (Kamler et al. 2012, 2013), and our results indicate higher jackal density in the Talek region compared to the Mara Triangle (Fig. 4). Behavioral plasticity by black-backed jackals could facilitate their increased density in the passively managed Talek region (Craft et al. 2015, Hayward et al. 2017, Van der Weyde et al. 2018). Underlying mechanisms causing trends estimated for banded mongoose, leopard, and serval are not readily apparent. The remaining carnivores (i.e., caracal, cheetah, side-striped jackal, slender mongoose) may not be responding to management regime or may be too data deficient to estimate an effect (Table 1). Empirical research testing for explicit mechanisms is needed to verify our assumption that observed differences within the carnivore community are directly or indirectly the consequence of management alternatives and resultant anthropogenic disturbance.

Our results show that group sizes for most carnivore species were smaller in the Talek region compared to the Mara Triangle (Fig. 3). Oriol-Cotterill et al. (2015) hypothesized that carnivores alter their behavior by becoming more solitary in the persistent presence of humans, and Kamler et al. (2013) suggested that decreased interspecific competition would result in smaller group sizes due to a lower threat of interference competition. Differences in group sizes between management regimes may be the result of shifting behaviors of carnivores in response to human disturbance and differences in carnivore distributions. Behavioral shifts in spotted hyena are well documented in this region (Boydston et al. 2003, Kolowski et al. 2007, Pangle and Holekamp 2010), but more research is needed to understand the connection between carnivore behavior and changes to their distributions as many potential mechanisms could be responsible for differences in grouping behaviors.

The Serengeti-Mara ecosystem is a global priority for carnivore conservation (Di Minin et al. 2016). Our analysis provides information on how variations in wildlife management enforcement in the MMNR can differentially affect carnivore species. Passive enforcement of wildlife regulations and corresponding anthropogenic disturbances in the Talek region may lead to local extinction and permanent shifts within the carnivore community, but may also change the basic structure and function of the ecosystem (Ritchie and Johnson 2009, Estes et al. 2011). Additionally, management alternatives may affect economic sectors, such as tourism. Lion declines are particularly concerning for tourism because of their charismatic status and high demand among tourists for lion sightings. Continued declines of lions, and other carnivores or herbivores, could jeopardize the local tourism industry and lead to monetary losses in Kenya.

Human populations continue to expand, creating further anthropogenic disturbances within the Serengeti-Mara ecosystem and around the world (Ogutu et al. 2011, 2016, Green 2015). Carnivore conservation depends on implementation of management regimes that are both effective and promote coexistence between carnivores and humans (Di Minin et al. 2016). Our results show that alternative management regimes (i.e., active and passive enforcement of regulations) and subsequent amounts of anthropogenic disturbance have differential effects on carnivore species. Wildlife research designed to evaluate the effectiveness of protected areas must consider multiple species within a community and their variable responses to management to develop lasting conservation solutions.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1845/full

Data Availability

Code and data are available on Zenodo: https://doi.org/10.5281/zenodo.1413562 or on GitHub https://github.com/zipkinlab/Farr_etal_2019_EcoApps.