Long-term ecological changes influence herbivore diversity and abundance inside a protected area in the Mara-Serengeti ecosystem

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ABSTRACT

Protected areas in sub-Saharan Africa are fast becoming islands on which to conserve biodiversity as surrounding human populations grow exponentially, rangelands become urbanized, and natural habitats are fragmented. The Masai Mara National Reserve in the Mara-Serengeti ecosystem in Kenya is renowned for having one of the highest densities and diversities of large mammals in the world, but may be experiencing negative effects from anthropogenic disturbances (e.g., illegal livestock grazing) within Reserve boundaries. We monitored changes in the diversity and abundance of resident and migratory herbivores in response to temperature, rainfall, the size of the local pastoralist population, the burgeoning infrastructure for tourism, and the number of livestock grazing inside Reserve boundaries in the eastern portion of the Masai Mara over a 26 year period (1988–2013). Using hierarchical models fit in a Bayesian framework, we found that overall diversity and abundance of resident and migrant herbivores declined between 1988 and 2013 in the Talek region, which lies in the northeastern portion of the Reserve. The habitual grazing of livestock within the Reserve’s boundaries, as well as both human population growth and the development of tourism infrastructure beside the Reserve, had strong negative correlations with herbivore diversity and with the size of resident and migrant herbivore populations in the Talek region. We also found that rainfall was negatively correlated with the numbers and diversity of resident herbivores, and that temperature was positively correlated with numbers of resident herbivores. We expect herbivore diversity and abundance to continue to decline if current trends in livestock grazing and tourism development continue in the eastern Masai Mara.

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1. Introduction

Protected Areas (PAs) are an important tool for wildlife conservation because they can limit development and prevent conflicts between people and wildlife (Butchart et al., 2010). Even with this protection, nearly one-third of PAs globally are...
affected by people (Jones et al., 2018). In sub-Saharan Africa, fragmentation of available habitat in an expanding matrix of agriculture and urbanization has amplified the importance of PAs for conserving critical habitat for wildlife (Newmark, 2008). Intensive anthropogenic activity (e.g., human population growth, ecotourism) near PAs may exacerbate threats to biodiversity within PA boundaries (Craigie et al., 2010; Newmark, 2008; Veldhuis et al., 2019; Wittemyer et al., 2008; Woodroffe and Ginsberg, 1998). There is thus a critical need to understand how wildlife populations within PAs might be affected by anthropogenic activity around the edges of parks and reserves.

One of the most iconic PAs in East Africa is the unfenced Masai Mara National Reserve (henceforth, the Reserve) in southwestern Kenya because of its extraordinary biodiversity and the easy observability of its wildlife; the Reserve represents the northernmost portion of the Mara-Serengeti ecosystem. In addition to supporting high densities of resident herbivores and carnivores, it also serves as the northernmost destination for the annual migration of wildebeest (Connochaetes taurinus) and zebra (Equus quagga) from the Serengeti (Bell, 1971; Maddock, 1979; Sinclair and Arce, 1995). The Reserve is contiguous with the Serengeti National Park to the south, but is flanked by expanding populations of Masai pastoralists along all its other borders. Since the 1950s, rapid human population growth around the Reserve’s boundaries has led to loss of habitat suitable for wildlife, increased levels of mechanized agriculture, and heightened grazing pressure from livestock (Ogutu et al., 2005, 2009; Serneels et al., 2001; Thompson and Homewood, 2002; Veldhuis et al., 2019). These changes in habitat might be contributing to declining numbers of resident herbivores within and around the Reserve (Lamprey and Reid, 2004; Ogutu et al., 2009, 2005; 2011; Ottichilo et al., 2000; Serneels and Lambin, 2001). Since 1960, monitoring efforts have documented declines in observed resident herbivores at levels exceeding 50% for some species, both inside and outside Reserve boundaries (Homewood et al., 2001; Ogutu et al., 2011, 2016; Ottichilo et al., 2000, 2001; Serneels and Lambin, 2001; Veldhuis et al., 2019). Migrant herbivores visiting the Reserve have also declined by 35% since 1984 (Norton-Griffiths et al., 2008).

Coexistence between people and wildlife in and around the Reserve is a complex issue compounded by the changing lifestyles of local Masai pastoralists. Although previously nomadic, these pastoralists have become sedentary in recent decades (Ogutu et al., 2009), and are investing in agriculture and livestock production around Reserve boundaries (Homewood et al., 2001; Norton-Griffiths et al., 2008; Thompson and Homewood, 2002; Thompson et al., 2002). Overall numbers of livestock in the region are poorly documented, but are believed to be stable or to have increased since the 1970s (Norton-Griffiths et al., 2008; Ogutu et al., 2016, 2011). Furthermore, the subdivision of communally-owned lands around the Reserve, and lax enforcement of Reserve regulations, have encouraged pastoralists to rely on grazing their livestock illegally within the Reserve year-round (Boydston et al., 2003; Butt, 2014; Green et al., 2018; Kolowski and Holekamp, 2009; Ogutu et al., 2009). The long-term effects on herbivores of livestock grazing within the Reserve are unknown, but their grazing patterns do influence how some wild herbivore species aggregate within Reserve boundaries (Bhola et al., 2012). The presence of livestock has also already elicited changes in the behavior of the most abundant large carnivore, the spotted hyena (Crocuta crocuta; Boydston et al., 2003; Green et al., 2018; Kolowski and Holekamp, 2009; Kolowski et al., 2007).

In addition to livestock grazing, a poorly regulated tourism industry may also adversely affect wildlife. Hundreds of thousands of tourists visit the Reserve each year (Bhandari, 2014). Widespread disregard for a formal moratorium on the construction of new tourist facilities has resulted in the establishment of many new lodges and tented camps along the edges of the Reserve in recent years (Karanja, 2003; Reid et al., 2003; Veldhuis et al., 2019). It is unknown whether or how these tourist facilities affect local wildlife populations.

Here we investigate the effects of anthropogenic disturbance (e.g., livestock grazing, local human population growth, tourism infrastructure) and ecological change (e.g., rainfall, temperature) on wild mammalian herbivores in the Reserve using 26 years of monitoring data we collected from 1988 to 2013. These data document long-term changes in herbivore diversity and abundance, and provide an opportunity to examine how abiotic and anthropogenic variables influence population trends. We investigated whether annual herbivore abundance and diversity might be affected by temperature, rainfall, size of the local pastoralist population, the opportunity of a tourist facility near Reserve boundaries, and the abundance of livestock grazing within Reserve boundaries. We developed hierarchical models to examine these relationships and determine which, if any, of these factors might be associated with temporal change in herbivore diversity and abundance. Long-term declines in herbivore abundance could ultimately lead to declines in herbivore diversity, and this in turn means that certain species could become locally extirpated. Identifying trends in herbivore diversity should help us understand how exactly the herbivore community is changing over time, and which species appear to be most sensitive to ecological change. Furthermore, although Ogutu et al. (2009) identified livestock incursions and local human population growth as correlates of declining numbers of seven herbivore species in and around the Reserve, no previous study has explicitly tested potential interactions between abiotic and anthropogenic effects on herbivores.

2. Materials and methods

2.1. Study area

The Reserve is an unfenced PA composed primarily of open grassland interspersed with riparian areas. It has historically supported large herds of resident and seasonally migrant herbivores, and resident populations of both small and large carnivores (Bell, 1971; Craft et al., 2015; Sinclair and Norton-Griffiths, 1979; Stelfox et al., 1986). Rainfall patterns are bimodal, with most rain falling in November–December and March–May, but there is little seasonal variation in temperature. Our study took place in the northeastern portion of the Reserve (Fig. 1), immediately south of the Talek River, in conjunction with a
long-term study of spotted hyenas \textit{(Crocuta crocuta)} that began in 1979 \cite{Frank, Holekamp et al.}. Our study area is approximately 143 km$^2$ in size, bounded on the north by the Talek River; immediately across the Talek River from our study area, and within 2 km of the Reserve border, are many tourist facilities and a population of pastoralists tending herds of cattle, sheep, and goats \cite{Lamprey and Reid, Reid et al.}. Since 2005, several private conservancies managed by local Masai communities have been developed north of the Reserve, leaving an island of land sandwiched between their southern borders and the Reserve itself (Fig. 1); many thousands of livestock and humans now live on this land between PAs, and the town of Talek now exists at the western end of this island, where no town at all was present when our study began in the 1980s.

2.2. Herbivore data

To document trends in herbivore numbers and diversity over time, we drove two, 4-km line-transects biweekly in our study area from October 1988 to December 2013 \((n_{\text{transects}} = 1112)\). We recorded all herbivores by species within 100m on both sides of our transect lines, which allowed sampling of areas occupied by both grazers and browsers, while driving at 10 km/h between first light and 1000 h. The northernmost transect was located in short-grass habitat, whereas the southernmost transect was located in long-grass habitat (Fig. 1). Full details of the methods used for counting herbivores can be found in Boydston et al. (2003), Holekamp et al. (1999), and Van Meter et al. (2009). Monitored resident herbivores included impala \textit{(Aepyceros melampus)}, topi \textit{(Damaliscus lunatus)}, Coke’s hartebeest \textit{(Alcelaphus buselaphus cokii)}, warthog \textit{(Phacochoerus africanus)}, Grant’s gazelle \textit{(Nanger granti)}, African buffalo \textit{(Syncerus caffer)}, hippopotamus \textit{(Hippopotamus amphibius)}, giraffe \textit{(Giraffa camelopardalis)}, eland \textit{(Tragelaphus oryx)}, duiker \textit{(Sylvicapra grimmia)}, African elephant \textit{(Loxodonta africana)}, oribi \textit{(Ourebia ourebi)}, reedbuck \textit{(Redunca redunca)}, waterbuck \textit{(Kobus ellipsiprymnus)}, bushbuck \textit{(Tragelaphus scriptus)}, and Thomson’s gazelle \textit{(Eudorcas thomsonii)}. Thomson’s gazelle in the Talek region are non-migratory and present year-round, so we considered them to be residents in our analyses. The migrant herbivores we monitored were wildebeest and zebra.

2.3. Environmental and anthropogenic predictors and models

We collected data on the abiotic and anthropogenic factors hypothesized to affect the number and diversity of herbivores counted in the Talek region. We acquired mean monthly minimum and maximum temperatures from the Narok meteorological station (~72 km northeast of the Reserve) for the years 1988—2011. No temperature data were available for 2004, 2005, or after 2011. A weather station in our study area recorded total daily precipitation throughout the study. The effect of rainfall on herbivore numbers in this ecosystem varies by species and by age class \cite{Ogutu et al., Runyoro et al.}, but
periods of extreme rainfall or drought may negatively influence both herbivore numbers and the activities of pastoralists grazing their livestock (Ottichilo et al., 2000). We calculated the average daily mm of rain that fell during each biweekly interval.

The human communities around the Reserve are predominantly occupied by Masai pastoralists living in circular, fenced villages, called “bomas.” To investigate trends in the local human population, we counted the number of all bomas present within 2 km of Reserve boundaries in the Talek region at four time points during our study using extensive aerial photography in 1991, field surveys in 2000 and 2004, and satellite imagery in 2012 (Boydston et al., 2003; Kolowski and Holekamp, 2006). No bomas occur within Reserve boundaries. Although the number of people living in non-boma structures in the urban center of Talek has increased in recent years, we lacked accurate historical data to track the growth of this population over time. Thus, our boma counts represent only a minimalist index of the human population size in the Talek region. We also counted tourist lodges within 2 km of Reserve boundaries, and interviewed lodge managers, to document changes in numbers of lodges and beds available to tourists in the Talek region between 1988 and 2013.

No livestock were observed grazing on the open plains in the study area from 1988 to 1991, most likely due to low livestock numbers in the area, low human population density near the Reserve, absence of fencing outside the Reserve to limit livestock access there, and stronger enforcement of Reserve regulations. We started systematically counting livestock in 2000 by regularly driving through our study area and counting all sheep, goats, and cattle within Reserve boundaries (Kolowski and Holekamp, 2009). Henceforth, “livestock” refers to the total numbers of sheep, goats and cattle counted. Livestock counts took place as often as once per day from 2000 to 2008, but starting in May 2008, all counts were performed biweekly. All livestock counts used in our models were conducted between 1600 and 1900 h. In the early years of the study, livestock were herded into the Reserve each morning, and out each afternoon, so the timing of our counts in the late afternoon and early evening near the Reserve boundaries accurately captures numbers of livestock grazing daily in the Talek region. In later years, livestock were brought into the Reserve late in the day to graze after sundown, and these husbandry practices similarly permitted us to conduct accurate counts during the final hours before sundown.

We documented long-term variation in the abiotic and anthropogenic factors in the Talek region using generalized linear and generalized linear mixed-effects models to analyze temporal trends in each of the variables. The climatic variables were modeled using a normal distribution and the numbers of bomas, tourist lodges, and beds available to tourists were modeled using Poisson distributions. We modeled rainfall and temperature, numbers of tourist lodges and beds for tourists, as a function of year, and the number of bomas as a function of year and year$^2$. Counts of livestock were overdispersed, so we analyzed them using a negative binomial distribution. We modeled the number of livestock seen grazing inside the Reserve as a function of year, year$^2$, and year$^3$. In all analyses, we added the quadratic and cubic year terms to account for any non-linear trends. We fit month as a random effect on the intercept to account for seasonal variation in rainfall, temperature and livestock grazing.

### 2.4. Investigating herbivore trends over time

We developed hierarchical models to examine trends in herbivore abundance and diversity over time. In addition to modeling the total numbers of resident and migrant herbivores, we also analyzed two metrics to estimate trends in herbivore diversity. We calculated species richness to investigate total diversity, and Shannon’s diversity index of evenness (henceforth, “evenness”) to investigate the weighted abundance of each species in the herbivore community. We calculated species richness as the total number of herbivore species sighted on each transect ($n_{\text{transects}} = 902$), and we calculated evenness for all transects in which more than one species were seen ($n_{\text{transects}} = 773$); these sample sizes differed from the resident and migrant herbivore sample sizes ($n_{\text{transects}} = 1112$) because some observers referred to less common herbivore species as “others,” such that we were unable to use their herbivore counts to assess biodiversity. We modeled the total numbers of resident and migrant herbivores counted, species richness, and evenness from 1988 to 2013, as a function of year and transect identity as fixed effects, with the month of the survey included as a random effect on the intercept to account for seasonal movements of wildlife within the Reserve. We modeled evenness using a normal distribution, but the total numbers of resident and migrant herbivores and species richness on transects were overdispersed, so we modeled them with a negative binomial distribution. We coded transect identity as a fixed effect because of the difference in habitat type between the two transects (i.e., short versus tall grass). Counts of migrant and resident herbivores were also zero-inflated, most likely because of the daily movements and aggregations of animals within the Reserve, so we modeled them with a zero-inflation approach (Zipkin et al., 2010). The inclusion of a count was modeled as a Bernoulli-distributed random variable with a covariate for transect identity.

### 2.5. Investigating abiotic and anthropogenic factors influencing herbivores

Finally, using the same distributions and zero inflation parameterizations as in the previous analysis, we modeled total numbers of resident and migrant herbivores counted, species richness, and evenness in each biweekly interval, as a function of six ecological and anthropogenic variables: 1) transect identity, 2) rainfall, 3) average temperature, 4) number of livestock grazing, 5) number of pastoralist settlements and tourist facilities, and 6) an interaction between rainfall and livestock. We tested for collinearity among predictors using Pearson’s correlation coefficients. Numbers of bomas and tourist lodges were highly correlated with one another and with numbers of livestock (Pearson’s correlation coefficient $r > 0.85$), most likely
because all three of these variables were increasing simultaneously over time. To disentangle the effects of tourist lodges, human population growth, and the number of livestock grazing in the Talek region on wild herbivores, we averaged the number of tourist lodges and bomas together to create a new variable called "development." This is the variable included as the fifth predictor in the model described above. We then ran two separate models: one with development as an independent variable and one with the number of livestock as an independent variable, and used Deviance Information Criterion (DIC; Spiegelhalter et al., 2002) to determine which model best explained wild herbivore abundance or diversity. There were no significant correlations between any other covariates in our models (Pearson's correlation coefficient $r < 0.6$), so both models for each dependent variable included every other main effect (e.g., transect identity, rainfall, average temperature). The model with livestock also included an interaction between livestock and rainfall to determine if the effects of livestock on herbivores would be affected by the amount of rainfall. We did not consider any other interactions because we could not identify predicted relationships between other independent variables. We did not include transect identity in our analysis of evenness given the non-significant relationship found in our previous analysis.

We expected that the predictor variables would have had a lagged effect on herbivore abundance and diversity because of the extreme seasonality of this environment and the potential for interactions among covariates over time. Therefore, to assess relationships between our predictors and herbivore abundance and diversity, we evaluated the effects of our dependent variables of each independent variable during the previous two years. We did not evaluate other time lags because we expected a two-year lag would be the shortest time in which the effects of these variables can manifest in herbivore abundance and diversity, and longer time lags would reduce our sample sizes. We calculated 2-year averages for each independent variable based on data from biweekly intervals. We extrapolated predictions from our generalized linear models when biweekly data were unavailable for covariates. We then standardized these 2-year averages to have a mean of 0 and a standard deviation of 1 to examine the relative impact of each independent variable on our dependent variables.

2.6. Statistical analyses

We performed all statistical analyses using a Bayesian framework with Markov chain Monte Carlo in JAGS via R version 3.6.0 with the jagsUI package (Kellner, 2017; Plummer, 2003; R Core Team, 2015). We used uninformative prior distributions for all of our parameters. Posterior parameter estimates were calculated from 12,000 MCMC samples, taken from 3 chains run for 20,000 iterations, thinned by 5, following a burn-in of 20,000. We assessed model convergence by ensuring that $R$ values for all parameter estimates were $< 1.1$ and through visual inspection of the chains (Gelman et al., 2013, 1996). We present information regarding raw data as means and posterior parameter estimates are reported as medians with 95% Credible Intervals ["CIs"]. Posterior parameter estimates for which the CIs did not overlap zero were considered to be statistically significant. We present the mean intercept value for posterior parameter estimates of models in which the intercept was modeled as a random effect by month, although full model results are available in Tables S1–S4. Results are presented on the normal scale except where otherwise indicated.

3. Results

3.1. Meteorological data

Monthly mean minimum and maximum temperatures recorded increased significantly in Narok between 1989 and 2011 (Fig. 2a and 2b). Mean minimum temperatures increased by 1.6 °C (mean intercept = 10.22 °C [9.73, 10.7] and year effect = 0.07 °C [0.05, 0.09]), and mean maximum temperatures increased by 0.7 °C (mean intercept = 24.81 °C [24.37, 25.26] and year effect = 0.03 °C [0.01, 0.05]) during this study. The average daily mm of rain that fell during each biweekly interval did not change significantly over time (mean intercept = 3.05 mm/day [2.27, 3.82] and year effect = 0.02 mm/day [-0.01, 0.05]; Fig. 2c). The full results from the models investigating trends in rainfall and temperature appear in Table S1.

3.2. Numbers of pastoralist settlements and tourist facilities

The number of pastoralist settlements along the Reserve boundary in the Talek region increased by 406% from 1991 to 2012 (intercept = 62.24 bomas [51.62, 74.14] and year effect = 4.18 [2.54, 6.5]), and showed no signs of leveling off (year$^2$ effect = 0.06 [-0.1, 0.22]; Fig. 3a, b, & 3c). Between 1988 and 2013, numbers of tourist lodges and beds available for tourists increased by 500% and 366%, respectively (lodges intercept = 5.45 lodges [4.55, 6.43] and year effect = 0.39 [0.22, 0.63]; beds intercept = 454.41 beds [445.86, 463.13] and year effect = 25.69 [24.27, 27.66]; Fig. 3a, b, & 3d).

3.3. Livestock

The number of livestock grazing daily inside the Reserve increased from a mean of 0 in 1988, to 2,218.9 in 2013 (intercept = 496.21 livestock [402.68, 619.76], year effect = 41.33 [15.18, 82.52], year$^2$ effect = -22.31 [-21.17, -24.3], and year$^3$ effect = 1.99 [1.61, 3.11]; Fig. 4a). Furthermore, the number of sheep and goats seen grazing inside the Reserve also increased over time. Whereas cattle represented 85.0% of all livestock counted in 2000, they represented only 66.7% in 2013. The full results from the models investigating trends in livestock in Talek appear in Table S1.
Fig. 2. Temporal trends in (a) the mean ± standard error (SE) maximum and (b) minimum temperatures in Narok, Kenya, and (c) the amount of rain per day in the Talek region of the Masai Mara National Reserve. Solid lines are the median estimates fit to the data using generalized linear mixed-effects models, and the shaded regions indicate the 95% credible intervals around these estimates. The difference in scale is due to temperature being monitored at monthly intervals and rainfall being measured at daily intervals.
3.4. Herbivore abundance and diversity

Counts of herbivore abundance and diversity varied among months within years, and between short- and tall-grass transects (Fig. 5). We found evidence for significant declines in the total number of resident herbivores counted (year effect median [95% CI] = -0.01 [-0.02, 0] on the log scale), migrant herbivores counted (-0.05 [-0.07, -0.02] on the log scale), species richness (-0.02 [-0.02, -0.01]), and evenness over time (-0.01 [-0.01, 0]; Table 1, Fig. 6). Observed numbers of resident and migrant herbivores, as well as observed species richness, also varied with transect identity (transect effect median [95% CI] on the log scale for residents = 1.32 [-1.48, -1.15], migrants = 0.56 [0.22, 0.9], richness = -0.59 [-0.67, -0.51]; Table 1, Fig. 6); the transect located in long-grass habitat had fewer resident herbivores and lower species richness, but larger numbers of migrant herbivores, than did the transect in short-grass habitat (Table 1, Fig. 6). Evenness did not vary with transect identity (transect effect median [95% CI] = 0.05 [-0.01, 0.1]; Table 1, Fig. 6). Counts of herbivores were more likely to be greater than zero on the transect in short-than long-grass habitat (Table 1).

3.5. Modeling variables affecting herbivore abundance and diversity

Numbers of resident herbivores and species richness were best estimated by the models with livestock as an independent variable (Tables S3 and S4), but we found no differences in the model fit between the models that included livestock or development for migrant herbivores or evenness. We therefore present results from the models run with livestock as a predictor variable for resident herbivores and species richness, and we present the results from models with livestock and development as predictor variables for migrant herbivores and evenness.

Several of our ecological and anthropogenic factors were correlated with resident and migrant herbivore abundance, species richness, and species evenness. Numbers of livestock within the Reserve were negatively correlated with resident herbivore abundance (livestock effect median [95% CI] on the log scale = -0.3 [-0.48, -0.11]), migrant herbivore abundance (-0.52 [-0.95, -0.09]), and species richness (-0.12 [-0.24, -0.01]). Development was negatively correlated with migrant herbivore abundance (development effect median [95% CI] on the log scale = -0.54 [-0.85, -0.22]). Rainfall was negatively correlated with resident herbivore abundance (rainfall effect median [95% CI] on the log scale = -0.56, [-0.7, -0.42]) and
species richness ($-0.15, [-0.21, -0.09])$. Average temperature was positively correlated with resident herbivore abundance (temperature effect median [95% CI] on the log scale = $0.2 [0.05, 0.34]$), but negatively correlated with species evenness (livestock model temperature effect median [95% CI] = $-0.06 [-0.15, 0]$, development model temperature effect = $-0.06 [-0.12, 0]$). The interaction between rainfall and livestock grazing was negatively correlated with resident herbivore abundance (rainfall and livestock interaction effect median [95% CI] on the log scale = $-0.29 [-0.5, -0.08]$) and species richness ($-0.12 [-0.22, -0.01]$; Fig. 7). As in results from the previous model, transect location predicted resident and migrant herbivore abundance, species richness, and the zero-inflation inclusion parameter for resident and migrant herbivore abundance (Tables S3 & S4). None of our other variables were significantly correlated with herbivore abundance, richness, or evenness; full model results are presented in Tables S3 and S4.

4. Discussion

4.1. Herbivore abundance and diversity are declining

Our results revealed declines in resident and migrant herbivore abundance, species richness, and evenness between 1988 and 2013, and that both increasing numbers of livestock grazing within the Reserve and development near Reserve borders appear to play large roles in these declines. There is considerable debate about the extent to which PAs deliver positive conservation outcomes with respect to habitat and species protection (Geldmann et al., 2013). Our results indicate that the region of the Reserve we studied here may not currently be functioning effectively to protect herbivore abundance and diversity. The declines we observed in herbivore numbers and diversity may have future negative effects on key processes important to the productivity, stability and sustainability of the Reserve (Cardinale et al., 2012; Tilman et al., 2012). Our results are consistent with results from research on temporal changes in herbivore numbers in and around the Reserve collected with separate and independent data (Norton-Griffiths et al., 2008; Ogutu et al., 2011, 2009; 2005; Ottichilo et al., 2000).

4.2. Variables associated with declining herbivore abundance and diversity

Many of the abiotic and anthropogenic factors we assessed were important in predicting both abundances of resident and migrant herbivores as well as species richness. Herbivore numbers and species richness varied with transect location (i.e., short grass versus tall grass), indicating that herbivores within the Reserve appear to aggregate spatially in particular habitat types and may prefer short-grass habitat (Fig. 5), as has also been shown in previous research (Bhola et al., 2012). Increasing average temperatures were positively correlated with numbers of resident herbivores counted on transects, but negatively correlated with species evenness. Our study area is primarily covered with C4 grasses (McNaughton, 1983), and higher local temperatures are likely to increase their nutrient concentrations over time (Ritchie, 2008). Thus, in the short-term, higher
local temperatures may provide some benefit to some herbivores. The documented increase in temperature, however, also appears to elicit changes in the composition of the resident herbivore community, as it had a negative effect on species evenness.

Ogutu et al. (2008) report that rainfall has contrasting effects on newborn and adult ungulates; whereas heavy rainfall tends to increase the abundance of newborn ungulates, it tends to decrease the abundance of adult ungulates. Increased
rainfall may cause resident herbivores to disperse throughout the Reserve away from our transects, and future research should investigate this hypothesis. Our results showing that resident herbivore abundance and species richness were negatively correlated with rainfall support this possibility. However, the specific mechanisms mediating the correlations we observed remain unknown. We also observed a distinct decline in numbers of resident herbivores counted during months when migrant herbivores were present (Fig. 5), suggesting that residents may avoid areas in which migratory herds are present. It is unlikely that our results are confounded by changes in animal detections over time, as surveys were conducted using exactly the same protocols throughout the study. In fact, if anything, our ability to detect herbivores should have improved over time, as the extensive grazing of livestock in recent years has reduced grass height even in tall-grass areas.

Increasing numbers of bomas, tourist lodges, and their associated infrastructure in the Talek region were negatively correlated with migrant herbivore abundance. The Mara-Serengeti ecosystem is defined by the seasonal movements of wild herbivores, and habitat change and degradation are believed to be contributing to wildlife declines (Ogutu et al., 2011, 2009; Ogutu and Dublin, 2002; Ottichilo et al., 2000; Serneels et al., 2001; Serneels and Lambin, 2001; Veldhuis et al., 2019). Our finding that development was negatively correlated with numbers of migrant herbivores suggests that the rapid changes in habitat, stemming from increased tourism infrastructure and human population growth in and around Talek, might be restricting important wildlife corridors. For example, an increase in fencing associated with tourist facilities and land partitioning by pastoralists along and near the Talek River may keep migrant herbivores from the Loita plains to the northeast from entering the Reserve (Stelfox et al., 1986). There are also likely other indirect effects from the increase in pastoralist settlements and tourism infrastructure along the Talek River that may be negatively affecting the ecosystem. The Talek River is the northern boundary of the Reserve in the Talek region, and the only semi-permanent watercourse in this area (Fig. 1). Increasing numbers of pastoralist settlements and tourist lodges along its banks may be triggering broad ecological changes due, for example, to declining water quality. Future research should investigate the specific mechanisms by which bomas and
tourist lodges appear to be negatively influencing numbers of migrant herbivores (e.g., hot-air balloon flights, vehicular traffic, rubbish, water pollution, etc.).

Numbers of livestock grazing in the Reserve were negatively correlated with resident and migrant herbivore abundance and species richness. Livestock grazing has always been a part of this ecosystem even though it has been illegal in the Reserve since its establishment in 1961 (Reid, 2012; Talbot and Olindo, 1990). Small numbers of livestock were present inside the Talek region of the Reserve in our study area before 1992, but this was limited to tiny herds grazing surreptitiously in riparian habitat beside the Talek River. In 26 years, livestock grazing inside the Reserve changed from being low-intensity and highly restricted to the Reserve border in 1988–1991, to an average of more than 2,000 livestock counted daily in open plain regions many kilometers south of the Reserve border (Green et al., 2018; current study). Livestock grazing within Reserve borders may still be increasing, and sheep and goats are making up a larger proportion of all livestock, most likely because they are seen as more resilient and drought tolerant than cattle. Future research should investigate how sheep and goats may influence herbivore populations differently than do cattle. One livestock count in 2015 revealed 20,800 livestock grazing inside the Reserve in our study area in a single day. Our data indicate that the effects of livestock on indigenous herbivores may be more pronounced in years with higher rainfall (Fig. 7). One possible explanation for this is an increase in habitat degradation within the Reserve during years with higher than average rainfall when livestock move in and out of the Reserve (Fig. 4c).

4.3. Unanswered questions and management implications

Identifying the specific mechanisms mediating the apparent negative effect of livestock on wild herbivores in the Talek region is a pressing concern for wildlife conservation in the Reserve. Negative effects on wild herbivores might stem from competition for nutrients between livestock and wild herbivores (Prins, 1992; Riginos et al., 2012; Veblen, 2008), the compaction of soils in heavily grazed regions (Fig. 4b & 4c), increasing erosion, or changes in vegetation due to overgrazing (Homewood and Rodgers, 1988; Kiage, 2013). Regardless of the specific mechanism, livestock grazing most likely affects important food resources and other habitat features salient for wild ungulates (e.g., clumps of vegetation in which gazelle fawns can hide), and this negative effect appears to be widespread throughout the rangelands of Kenya (Ogutu et al., 2016).

It is important to note that the results from the current study are representative of what has been occurring in the Talek region until recently, but not throughout the Reserve as a whole. The Talek, Sekenani and Mara Rianta regions of the Reserve have rapidly expanding human populations along Reserve boundaries (Lamprey and Reid, 2004; Reid et al., 2003). Other parts of the greater Mara ecosystem, however, remain relatively pristine because they are much less strongly affected by people; this includes, for example, the entire area of the Reserve west of the Mara River managed by the Mara Conservancy (Walpole and Leader-Williams, 2001). Areas north of the Reserve made similar changes with the establishment of the private conservancies starting in 2005 (Fig. 1). The conversion of the northern rangelands to private conservancies has transformed
–956 km² of land once available for livestock grazing into heavily managed wildlife preserves. The long-term effects of these conservancies on wildlife within the Reserve have yet to be established. One possibility is that the development of these regions with restricted grazing might actually lead to more intensive livestock grazing within the Reserve itself. For example, many of the community conservancies limit or prohibit grazing by sheep and goats, and it is possible that these animals are now being shepherded into the Reserve. Data collected recently by Bedelian and Ogutu (2017) support this hypothesis.

Local wildlife management authorities have no control over abiotic factors such as rainfall or temperature; however, they can and should control the frequency and intensity of livestock grazing within Reserve boundaries and the development of tourist facilities. Prior to the creation of the Reserve, livestock were an integral part of the Mara ecosystem (Homewood and Rodgers, 1991; Reid, 2012), and they are unlikely to disappear from it any time soon. At lower levels of livestock grazing and with rotational grazing schemes, the possibility exists for mutual benefits from shared grazing by livestock and native ungulates (Arsenault and Owen-Smith, 2002; Prins, 2000; Riginos et al., 2012; Schuette et al., 2016), which can enrich savanna ecosystems (Adler et al., 2001; Augustine et al., 2011). Yet, without strict management, enforcement and compliance, habitual and intensive grazing of livestock has the potential to competitively suppress wild herbivore populations (Butt and Turner, 2012; Prins, 2000, 1992), and may lead to long-term declines in the abundance and diversity of native wildlife (Reid, 2012; Riginos et al., 2012). The massive increase in tourism infrastructure over the last 26 years may now be having negative effects on the number of wild herbivores in the Talek region. Federal and county government agencies should limit the development of new tourist facilities and find ways to alleviate the negative effects of those facilities already present in or beside the Reserve.

Research is urgently needed in the Mara ecosystem to understand how traditional Masai pastoralists and their livestock can best coexist with native wildlife, and how development around the Reserve is negatively affecting indigenous animals. We need a better understanding of how private conservancies are influencing the intensity of livestock grazing within Reserve boundaries, whether wildlife numbers and diversity can recover in the Reserve if livestock grazing is controlled there, and whether negative effects of tourism on wild herbivores in this region can be mitigated. We also need to investigate other potential anthropogenic and ecological sources of these herbivore declines, including bushmeat poaching and extreme weather events (i.e., drought). Without rapid collection of data to address these questions, enactment of management reforms that reduce grazing pressure on the Reserve and limitation of numbers of new tourist lodges being built, the abundance and diversity of wild ungulates in this once-spectacular Reserve are likely to continue to decline. Fortunately, in late 2017, the Narok County Government undertook massive management reforms that have reduced livestock grazing in the eastern portion of the Reserve. This represents a critical first step in allowing this magnificent landscape and its wildlife to recover.

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Appendix A. Supplementary data

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References


