

Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores

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Abstract. In many savanna ecosystems worldwide, livestock share the landscape and its resources with wildlife. The nature of interactions between livestock and wildlife is a subject of considerable interest and speculation, yet little controlled experimental research has been carried out. Since 1995, we have been manipulating the presence and absence of cattle and large mammalian herbivore wildlife in a Kenyan savanna in order to better understand how different herbivore guilds influence habitat use by specific wildlife species. Using dung counts as a relative assay of herbivore use of the different experimental plots, we found that cattle had a range of effects, mostly negative, on common mesoherbivore species, including both grazers and mixed feeders, but did not have significant effects on megaherbivores. The effect of cattle on most of the mesoherbivore species was contingent on both the presence of megaherbivores and rainfall. In the absence of megaherbivores, wild mesoherbivore dung density was 36% lower in plots that they shared with cattle than in plots they used exclusively, whereas in the presence of megaherbivores, wild mesoherbivore dung density was only 9% lower in plots shared with cattle than plots used exclusively. Cattle appeared to have a positive effect on habitat use by zebra (a grazer) and steinbuck (a browser) during wetter periods of the year but a negative effect during drier periods. Plots to which cattle had access had lower grass and forb cover than plots from which they were excluded, while plots to which megaherbivores had access had more grass cover but less forb cover. Grass cover was positively correlated with zebra and oryx dung density while forb cover was positively correlated with eland dung density. Overall these results suggest that interactions between livestock and wildlife are contingent on rainfall and herbivore assemblage and represent a more richly nuanced set of interactions than the longstanding assertion that cattle simply compete with (grazing) wildlife. Specifically, rainfall and megaherbivores seemed to moderate the negative effects of cattle on some mesoherbivore species. Even if cattle tend to reduce wildlife use of the landscape, managing simultaneously for livestock production (at moderate levels) and biodiversity conservation is possible.

Key words: competition; context-dependence; elephant; facilitation; indirect interactions; Laikipia; livestock-wildlife interaction; mesoherbivores; rainfall; savanna ecosystems; tree density; zebra.

INTRODUCTION

Savannas support higher densities of both domestic and wild large mammalian herbivores than any other biome (Du Toit and Cumming 1999, Reid 2012). In African savannas, interactions between livestock and wildlife are particularly important because (1) livestock husbandry is often the primary land use type (Odadi et al. 2011b), (2) most savanna and grassland wildlife share part or most of their range with livestock (Augustine et al. 2011, Mizutani et al. 2012), and (3) interactions between livestock and wildlife are generally thought to be

negative (Prins 1992, Odadi et al. 2011b, Reid 2012). Although interactions between livestock and wildlife have been a central theme in ecology and management of savannas (Odadi et al. 2011b), there is little consensus on the exact nature of these interactions (Butt and Turner 2012, Reid 2012). This lack of consensus limits our ability to accurately assess the conservation implications of different land management approaches. By exploring how additional ecosystem drivers (megaherbivores and rainfall) affect interactions between cattle and wild mesoherbivores (both grazers and browsers), this study provides greater dimensionality to our understanding of livestock–wildlife interactions.

Interactions between livestock and wildlife are driven, in part, by dietary overlap. Diet overlap is higher among members of the same trophic guild than across guilds.

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Hence, cattle, as predominantly grazers (Hibert et al. 2010), have a higher diet overlap with other grazers such as zebra than with browsers or mixed feeders such as eland and Grant's gazelle (Hofmann 1989, Arsenaault and Owen-Smith 2002, Beck and Peek 2005) and might therefore be expected to affect available forage and habitat use more for the former than for the latter.

Patterns of habitat use provide useful information in understanding species interactions. In a landscape where movement of animals is largely unrestricted, selection of a particular habitat is driven by availability of resources in that habitat relative to the surrounding matrix. Hence, depletion of resources in one area by one species could competitively displace another species. While several studies provide evidence for competitive displacement of wildlife by livestock (Loft et al. 1991, Ragotzkie and Bailey 1991, Coe et al. 2001, Stewart et al. 2002, Acevedo et al. 2008), most of these studies focus on pairwise relationships between specific livestock and wildlife species or on a functional group, such as grazer vs. mixed feeder or browser (Hobbs et al. 1996, Kauffman et al. 2004, Derner et al. 2006, Nelson et al. 2010). Such an approach, however, ignores the broader context of a complex and interconnected community of herbivores (Barton and Ives 2014). For example, by suppressing resource extraction by cattle, elephants may facilitate shared resource use and ameliorate direct resource competition between cattle and zebras (Young et al. 2005). Similarly, elephants' reduction of tree cover (Eckhardt et al. 2000, Holdo 2007, Sankaran et al. 2008, Holdo et al. 2009, Kohi et al. 2011) may affect the cattle and wildlife use of the landscape through diverse interactive pathways such as increases in grass productivity (Prins 2000, Ludwig et al. 2001, Riginos et al. 2009) or changes in perceived predation risk (Tchabovsky et al. 2001, Riginos and Grace 2008, Riginos 2015). Hence, the outcome of species interactions is due not only to direct relationships but to the aggregate of effects produced through both direct and indirect relationships involving multiple other abiotic and biotic factors within ecological communities (Miller 1994). For example, interactions between livestock and wildlife might vary depending on rainfall (abiotic factor) and the presence of a third herbivore guild, e.g., megaherbivores (biotic factor). However, the role of indirect interactions in the organization of ecological communities is often poorly understood, partly because of the complex experimental designs and the often long-term responses that are required to study the mechanisms through which they occur (Callaway and Walker 1997, Wilbur 1997).

In addition to biotic factors, temporal variation in rainfall may affect interactions between cattle and wildlife in terms of their habitat use. Temporal variation in rainfall creates pulsed quantity (Hatch and Tainton 1995, Aroeira et al. 1999), quality (Styles and Skinner 1997), and composition (Porensky et al. 2013) of plants (forage) that may influence habitat use by herbivores (Ogutu et al. 2014). For example, an earlier study in our system indicated that wild herbivores competitively suppress cattle during dry periods,

but facilitate them during wet periods (Odadi et al. 2011b). Such differences can be attributed to changes in forage quality and quantity (Odadi et al. 2011b). However, it remains unclear how cattle may, inversely, influence habitat use by wild herbivores during different rainfall periods.

We examined long-term responses of mesoherbivores (ranging in size from steinbuck [*Raphicerus campestris*; 13 kg] to eland [*Taurotragus oryx*; 700 kg]) to presence of cattle, megaherbivores (elephant [*Loxodonta africana*], 3000–5000 kg, and giraffe [*Giraffa camelopardalis*] 1000 kg), or both cattle and megaherbivores. Our design allowed us to test relative use of the different experimental plots by the different mesoherbivores and megaherbivores. Because the movement of wild mesoherbivores was largely unrestricted, their presence in any of our experimental plots that did not exclude them could be seen as a response to presence or absence of the other herbivore guilds. We hypothesized that (1) all mesoherbivore species reduce their use of plots grazed by cattle, and this is more pronounced among grazers than mixed feeders/browsers, (2) megaherbivores mitigate the negative effects of cattle on wild mesoherbivores, and (3) the negative effect of cattle on mesoherbivore habitat use is less during periods of high rainfall (when forage resources are more abundant) than during drier periods.

MATERIALS AND METHODS

Study area

We conducted this study at Mpala Research Centre (0°17' N, 36°52' E), located on the dry leeward side of Mt. Kenya at an altitude of 1800 m above sea level. The area receives a weakly trimodal mean annual rainfall of 550–600 mm, usually with a distinct dry season from December to March (Kimuyu et al. 2013). The soils in the study area are heavy clay (black cotton) vertisols, with impeded drainage. The overstory is dominated by *Acacia drepanolobium* trees, which make up 97% of the woody vegetation. Minor woody species include *Balanites aegyptica*, *Rhus natalensis*, and *Cabada farinosa*. The herbaceous layer is dominated by the perennial grass species *Pennisetum stramineum*, *P. mezianum*, *Themeda triandra*, *Brachiaria lachnantha*, and *Lintonia nutans* (Young et al. 1998). Common herbs include *Aspilia pleuriseta*, *Commelina* spp., *Solanum incanum*, and *Pseudognaphalium* sp. (Porensky et al. 2013: Supplement 1). Wild herbivore species classified as primarily grazers include plains zebra (*Equus burchelli*), Grevy's zebra (*Equus grevyi*), hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), and buffalo (*Syncerus caffer*). Those classified as primarily browsers include giraffe (*Giraffa camelopardalis*) and steinbuck (*Raphicerus campestris*). Those classified as mixed feeders include elephant (*Loxodonta africana*), eland (*Taurotragus oryx*), and Grant's gazelle (*Gazella granti*). Carbon isotope data from this ecosystem suggest that the diets of these mixed feeders contain more browse and forbs than grass (J. Sitters, unpublished data). Cattle are the primary

livestock in the study area. Other livestock species include camels, sheep, goats, and donkeys; however, only cattle are grazed within the experimental plots.

Exclosure plots

A series of 18 herbivore exclosure plots were established in 1995 (Appendix S1: Fig. S1); these manipulate the presence or absence of three groups of large mammalian herbivores. Each plot measures 200 × 200 m and is designed to differentially exclude or allow one of six different combinations of herbivores: (1) unfenced plots where megaherbivores, mesoherbivore wildlife and cattle can access (MWC); (2) unfenced plots accessible to megaherbivores and mesoherbivore wildlife but where cattle are not grazed (MW); (3) plots where the fence is designed to selectively exclude only megaherbivores but allow mesoherbivore wildlife, with cattle grazing (WC) and (4) without cattle grazing (mesoherbivore wildlife only; W); (5) completely fenced-off plots (excluding all wild herbivores >15 g) where only cattle are grazed (C); and (6) completely fenced-off plots where cattle are not grazed (O). Each treatment is situated in each of three replicate blocks (north, central, and south) for a total of 18 treatment plots (Appendix S1: Fig. S1). More details of the experimental design are provided in Young et al. (1998).

Cattle, accompanied by herders, are periodically grazed in C, WC, and MWC plots. Usually, a group of 100–120 head of cattle is grazed in the C, WC, and MWC plots for several hours on each of two to three consecutive days, three to four times per year. The amount of time that cattle access the plots is equal across all cattle-treatment plots. Although the precise number of grazing days and timing of grazing largely depends on average forage availability across all cattle plots, the return interval of cattle in the plots rarely exceeds 16 weeks. This grazing regime mimics the overall grazing patterns and intensity at Mpala Ranch (Young et al. 2005, Odadi et al. 2007) as well as other private and communal properties in the region, where livestock herds are individually tended by a herder who grazes them in one area for several days at a time until forage is depleted, then moves on to a different area until the forage recovers. This grazing pattern is also consistent with traditional herding practices used in East Africa for centuries, where cattle are housed in overnight bomas (corrals) for weeks to months at a time, foraging in their vicinity, before moving to new boma. The landscape is not fenced into paddocks, but rather herders guide livestock so that the entire range undergoes similar episodic grazing throughout the year. The effective stocking rate of the Kenya Long-term Exclosure Experiment (KLEE) plots is similar to the moderate overall Mpala Ranch stocking rate (0.10–0.14 cattle/ha; Odadi et al. 2007).

Caveats to the experimental design

Our experiment considers the effect of cattle at moderate stocking densities. We are aware that grazing

intensity in many African rangelands, especially in communal grazing lands, greatly exceeds the current stocking rates at Mpala and other pro-wildlife properties in the region. Our goal in this study is not to test the response of wildlife to multiple cattle grazing intensities, but rather to examine the functional response of wildlife to a cattle grazing regime that mimics practices in similarly managed East African rangeland (Adriansen and Nielsen 2002, Butt 2010, Butt et al. 2009, Melese and Mulinge 2013).

In addition, our experiment cannot distinguish the effects of interspecific (or interguild) interactions from the effects of intraspecific (or intraguild) interactions. For example, while we expect an increase in density of a given species following experimental removal of a potential competitor, it can also be argued that such an increase is subject to intraspecific competition among members of the target species.

Although the spatial scale at which this experiment was conducted (4 ha) is relatively large by experimental standards, there are several constraints on the ecological questions that the experiment can and cannot address (Young et al. 1998). With respect to cattle–wildlife interactions, we cannot examine numerical responses of herbivores (except very small ones, e.g., rodents) because the home range of most animals far exceeds the scale of our experiment. However, we can examine the functional responses of these animals, from which we may make inferences about numerical responses on a larger spatial scale.

Data collection

Between 2006 and 2014 (11–19 yr after the initiation of the experiment), we conducted biennial (March and October) dung surveys along six 4 × 100 m permanent transects within each of the 18 KLEE plots (see Appendix S1: Fig. S1). We used total dung per plot as a relative assay of individual herbivore species use of the different plots. Thus, our approach averts issues related to inferring population densities from dung counts (Fuller 1991), such as differential decomposition rates across seasons and habitats (Vernes 1999, Nchanji and Plumtre 2001, Rivero et al. 2004). There is ample evidence from our study system (Augustine 2003, Augustine et al. 2003, Young et al. 2005, Riginos 2015) and elsewhere (Altendorf et al. 2001, Marques et al. 2001, Blake 2002, Rasmussen et al. 2005, Daniels 2006, Lunt et al. 2007), that dung counts are robust for comparing relative habitat use by large mammals within a species, habitat type, and rainfall period.

To avoid recounting the same dung piles during subsequent surveys, we crushed all recorded dung piles during each session. For animals that defecate in middens (such as steinbuck and Grant's gazelle), we used the number of dung pellets and differences in shape and color to estimate the number of separate defecation events. Dung piles for all major herbivore species could be positively identified to species in the field, with two exceptions. The dung of

cattle and buffalo could not be distinguished, and we lumped them together. Combined density of cattle and buffalo dung decreased by 96% in plots that buffaloes (but not cattle) could access (W and MW) compared to plots that could be accessed by both (WC and MWC), suggesting that virtually all of the dung in this bovid category belonged to cattle. The dung of plains and Grevy's zebras also could not be distinguished from each other; hence we grouped them as "zebra." However, plains zebra far outnumber Grevy's (>20:1), so effectively we consider these to be plains zebra dung.

Over the nine-year study period, we conducted 18 surveys and counted 30778 dung piles. The enclosure fences were 96–100% effective in excluding targeted large mammals (Appendix S2: Table S1). Steinbuck (9–13 kg) were not excluded by our fences and had two times higher dung density in plots excluding larger wildlife (O and C). Among wildlife species, zebra contributed most to dung counts, constituting 28% of the total dung piles recorded. The remaining wildlife species (elephant, giraffe, eland, oryx, hartebeest, Grant's gazelle, and steinbuck) together constituted 39% of the total dung counted. Cattle (and buffalo) dung constituted 33% of the total dung counts.

We used averages of the total monthly rainfall, recorded daily in each block of the experiment, for the 3-month window preceding each dung survey, to examine the influence of rainfall on dung density. The mean rainfall for this window ranged between 0 and 190 mm (47 ± 26 mm [mean \pm SD]), with all the three blocks receiving very similar amounts of rain ($F(2,51) = 0.003$; $P = 0.996$).

To test for relationships between dung density and herbaceous vegetation cover, we conducted vegetation surveys twice each year, using the point intercept method. This method is based on the number of contacts ("hits") a lowered pin makes with vegetation (Radloff and Mucina 2007). A 10-point pin frame was used. In the middle of each experimental plot, a square grid of 100 sampling stations separated by 10 m was established. Every fifth grid point (20 stations per plot) was sampled. All pin hits were recorded and the number of pin hits per station used as an index of herbaceous aerial vegetation cover (Booth et al. 2006).

Data analysis

We excluded from analyses wild herbivore species whose dung was less than 1% of the total dung counted (impala, hare, and warthog). There remained six mesoherbivore species (zebra, eland, oryx, hartebeest, Grant's gazelle, and steinbuck) and two megaherbivore species (elephant and giraffe) for analyses. To examine the effects of cattle and megaherbivores on these wildlife species, we used dung surveys from the four (of six) herbivore treatments to which wildlife had access: MWC, MW, WC, and W.

To allow for appropriate comparison of dung density across different surveys, two transformations were carried out. First, for each species we converted raw dung density values to relative density values by applying the

following linear transformation: $y' = (y - a)/(b - a)$, where a and b are the smallest and highest (respectively) dung density values per species for each survey period (Smithson and Verkuilen 2006). Thus we converted dung density from the original scale to an open unit interval (0, 1) scale. Second, we compressed the relative dung density values from the open scale (0, 1) to a bounded scale [0, 1] by applying the following transformation: $y'' = [y'(N - 1) + s]/N$, where s is a constant between 0 and 1 (serving as a prior from Bayesian standpoint), and N is the sample size (Smithson and Verkuilen 2006).

We used GlmmADMB package version 0.7.4 (Skaug et al. 2013) in R (R Development Core Team 2009) to fit beta distributed (Ferrari and Cribari-Neto 2004) generalized linear mixed-effect models (GLMM) to test for differences in standardized dung density across treatments. We used the compressed standardized dung density [0, 1] per species for each survey period as the response variable in our models. To account for temporal autocorrelation as a result of repeated measures (several dung surveys per plot) we specified plot-within-block as a random effect in our models. We tested mesoherbivore response to cattle and megaherbivore treatments at three levels: (1) overall response of all mesoherbivores lumped together, (2) response of the six individual mesoherbivore functional groups (grazer and mixed feeder/browser), and (3) response of individual species. We first fit maximal full-factorial models with main effects of block (north, south and central), rainfall, cattle (presence/absence), and megaherbivore (presence/absence) treatments and their interactions. Where necessary (informed by changes in Akaike's information criterion [$\Delta AIC > 2$] values), we simplified the model by first removing the highest-order interactions, then main effects. We used linear models to test for differences in grass and forb cover across herbivore treatments and to test for any relationship between dung density and either grass or forb cover.

RESULTS

Overall mesoherbivore dung density (combined across all six mesoherbivore species and all time periods) was highest in mesoherbivore wildlife-only plots (W); mesoherbivore dung densities were at least 20% lower in plots shared with either cattle (WC), megaherbivores (MW), or both cattle and megaherbivores (MWC; Fig. 1A). The negative effect of cattle on overall mesoherbivore dung density depended on the presence of megaherbivores (cattle \times megaherbivore interaction, Wald $\chi^2 = 5.98$, $P = 0.014$): in the absence of megaherbivores, overall mesoherbivore dung density was 36% lower (Wald $\chi^2 = 29.77$, $P < 0.001$) in plots with cattle (WC) than plots without cattle (W), while in the presence of megaherbivores, mesoherbivore dung density was only 9% lower (Wald $\chi^2 = 1.89$, $P = 0.169$) in plots with cattle (MWC) than plots without cattle (MW, Fig. 1A). The negative effect of cattle on overall mesoherbivore dung density did not vary significantly with rainfall (cattle \times rain interaction, Wald $\chi^2 = 1.19$, $P = 0.27$).

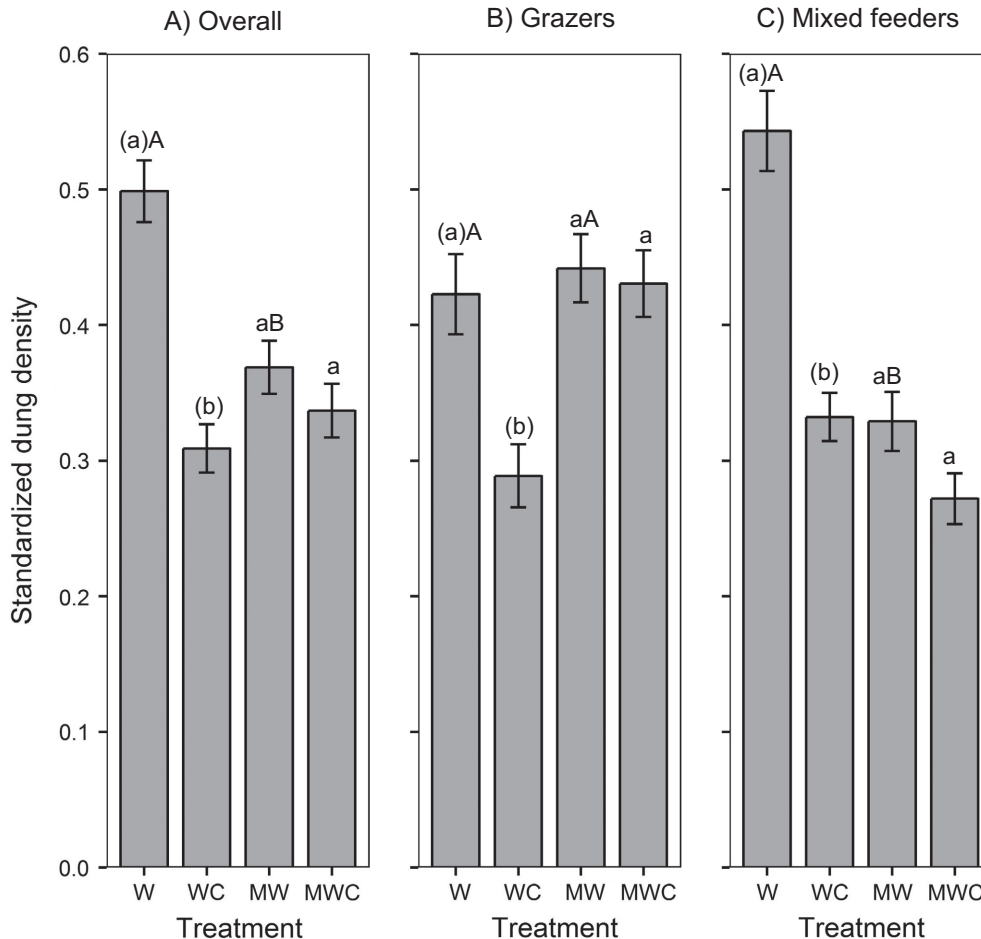


FIG. 1. Effect of cattle and megaherbivores on (A) overall dung density of mesoherbivore, (B) density of the dung of grazers (zebras, oryx, and hartebeest), and (C) density of dung of mixed feeders (eland, Grant's gazelle, and steinbuck). Error bars represent \pm SE. The x-axis labels denote the different herbivore combinations that are allowed in the plots: C, cattle; M, megaherbivores (elephants and giraffes); W, mesoherbivore (i.e., non-megaherbivore) wildlife >15 kg. The letter annotations above the bars indicate statistical significance of the effects tested as follows; (i) lower case letters in parenthesis denote the effect of cattle (W versus WC), (ii) upper case letters denote the effect of megaherbivores (W versus MW), and (iii) lower case letters without parenthesis denote the effect of cattle in presence of megaherbivores (MW versus MWC). For each kind of annotation, cases where the letters are different indicates that the means are significantly different ($P < 0.05$).

However, overall mesoherbivore dung density decreased with increasing rainfall (Wald $\chi^2 = 8.57$, $P = 0.003$). Cattle did not have a significant effect on megaherbivore dung densities (MW vs. MWC; elephant, Wald $\chi^2 = 0.05$, $P = 0.83$; giraffe, Wald $\chi^2 = 0.19$, $P = 0.66$).

Dung density for both grazers and mixed feeders was significantly lower in plots that they shared with cattle (WC) than in plots that they used exclusively (W) (Fig. 1B, C; grazer: Wald $\chi^2 = 12.16$, $P = 0.001$, mixed feeder: Wald $\chi^2 = 9.56$, $P = 0.002$). Grazer dung density did not differ significantly (Wald $\chi^2 = 0.53$, $P = 0.46$) between plots that mesoherbivores shared with megaherbivores (MW) and plots that mesoherbivores used exclusively (W), whereas mixed feeder dung was significantly lower (Wald $\chi^2 = 9.30$, $P = 0.002$) in plots that mesoherbivores shared with megaherbivores (MW). For both grazers and mixed feeders, the negative effect of cattle depended on whether

megaherbivores were allowed or not (cattle \times megaherbivore interaction; grazers, Wald $\chi^2 = 5.32$, $P = 0.020$; mixed feeders, Wald $\chi^2 = 4.01$, $P = 0.045$). Without megaherbivores, the density of grazer and mixed feeder dung was respectively 32% and 39% lower in plots shared with cattle (WC) than non-cattle plots (W), while in the presence of megaherbivores, grazer and mixed feeder dung was 3% and 17% lower in cattle plots (MWC) than in non-cattle plots (MW; Fig. 1B, C). The negative effect of cattle on grazer and mixed feeder dung density did not vary significantly with rainfall (cattle \times rain interaction; grazer, Wald $\chi^2 = 1.80$, $P = 0.18$; mixed feeder, Wald $\chi^2 = 1.79$, $P = 0.18$). The main effects of rainfall were significant for grazers but not mixed feeders: grazer dung density decreased with increasing rainfall (Wald $\chi^2 = 8.81$, $P = 0.003$) but the mixed feeder dung density did not vary significantly with rainfall (Wald $\chi^2 = 0.65$, $P = 0.42$).

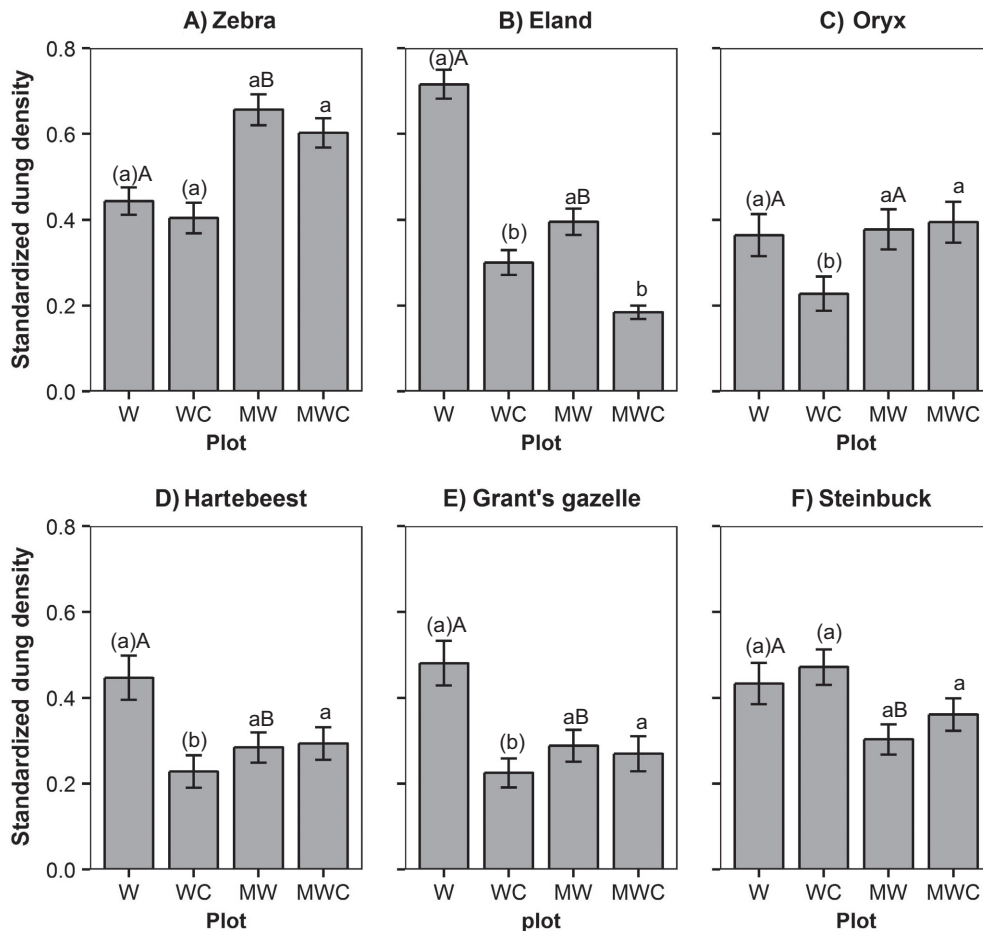


FIG. 2. Variations in individual species' dung density across different herbivore treatments. Error bars represent \pm SE. The x-axis labels denote the different herbivore combinations that are allowed in the plots: C, cattle; M, megaherbivores (elephants and giraffes); W, mesoherbivore (i.e., non-megaherbivore) wildlife >15 kg. See Fig. 1 caption for the meaning of letters above bars.

When we examined individual species' responses to cattle and megaherbivore treatments by fitting separate models for each species, we found that the effect of cattle on eland, oryx, hartebeest, and Grant's gazelle depended on whether megaherbivores were allowed or excluded (cattle \times megaherbivore interactions), but not on rainfall (cattle \times rainfall interactions; Appendix S3: Table S1). For each of these species, the negative effect of cattle was significant in the absence of megaherbivores (W vs. WC), but either less (for eland) or not significant (for oryx, hartebeest, and Grant's gazelle) in the presence of megaherbivores (MW vs. MWC; Fig. 2). For zebra and steinbuck, the effect of cattle did not vary significantly with megaherbivore presence (cattle \times megaherbivore interactions), but was significantly influenced by rainfall (cattle \times rain interaction; Appendix S3: Table S1). During drier periods, zebra and steinbuck dung densities were lower in plots grazed by cattle than non-cattle plots, but were higher during wetter periods (Fig. 3).

Grass cover was less than half ($F(1,4) = 27.58$, $P < 0.001$) in plots grazed by cattle (WC) than in plots excluding cattle (W; $26.6\% \pm 7.59\%$ vs. $66.5\% \pm 6.96\%$). Forb cover was similarly lower ($F(1,4) = 28.08$, $P < 0.001$) in plots grazed by

cattle than plots excluding cattle ($29.4\% \pm 12.09\%$ vs. $73.1\% \pm 2.23\%$). Grass cover tended to be higher ($F(1,4) = 3.04$, $P = 0.08$) in megaherbivore plots (MW) than plots excluding megaherbivores (W; $75.8\% \pm 7.84\%$ vs. $66.5\% \pm 6.96\%$), but forb cover was lower ($F(1,4) = 13.87$, $P < 0.001$) in megaherbivore plots than plots excluding megaherbivores ($38.3\% \pm 6.64\%$ vs. $73.1\% \pm 2.23\%$). There was no significant interaction between cattle and megaherbivore presence on grass and forb cover. Zebra and oryx dung density were both positively correlated with grass cover (Fig. 4; zebra, $r^2 = 0.42$, $P = 0.01$; oryx, $r^2 = 0.48$, $P = 0.04$). Eland, hartebeest, and Grant's gazelle dung density also had a positive (but nonsignificant) relationship with grass cover (Fig. 4). The density of eland dung was positively associated with forb cover ($r^2 = 0.68$, $P = 0.001$; Fig. 5). Grant's gazelle and hartebeest dung also had a positive (but nonsignificant) relationship with forb cover (Fig. 5).

DISCUSSION

The results of this long-term experiment indicate that cattle grazing, even at the relatively conservative

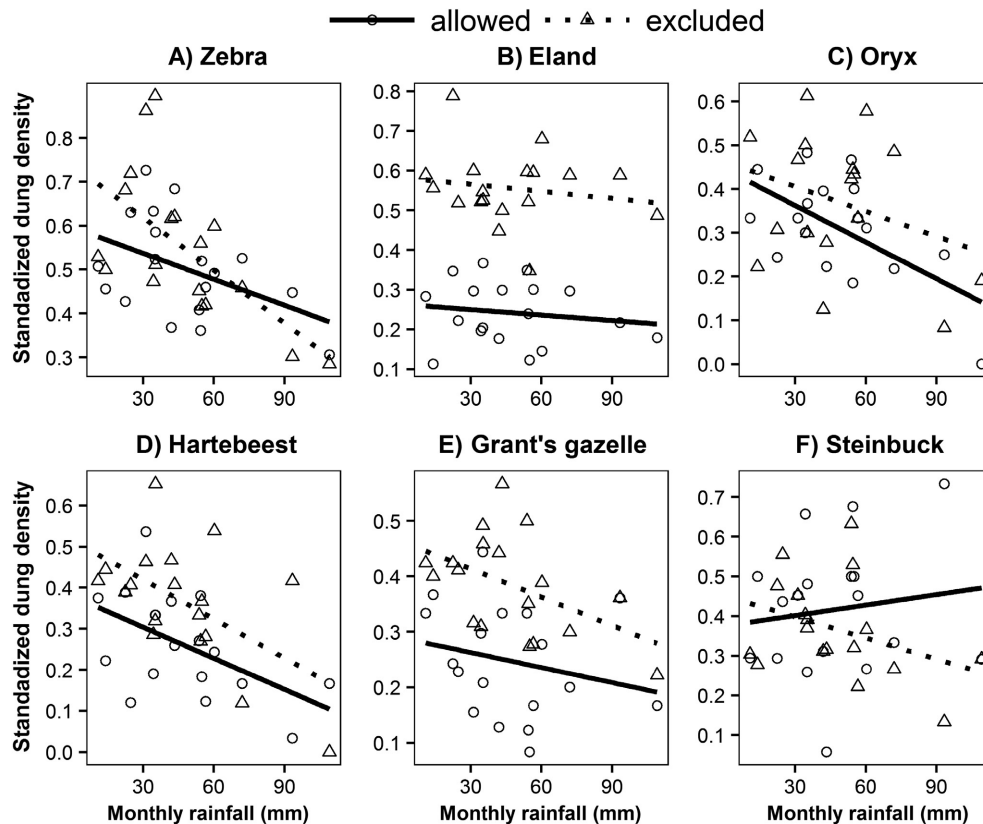


FIG. 3. Relationship between individual species dung density and mean monthly rainfall in presence (solid lines) and absence (dashed lines) of cattle.

livestock grazing intensities applied in the experiment, negatively affects habitat use by many wildlife species, suggesting competitive effects of cattle on these species. Experimental plots grazed by cattle had lower dung density for grazing mesoherbivore wildlife species and, surprisingly, browsers and mixed feeders as well, than plots without cattle (Fig. 1). Further, we found that the nature and strength of mesoherbivore response to presence of cattle was, for several species at least, contingent on the presence or absence of a keystone mega-herbivore (elephants) and on rainfall. These findings highlight the importance of considering the role of indirect interactions in explaining the nature of livestock-wildlife interactions, something that has rarely been done.

Effects of cattle on mesoherbivores

We observed lower mesoherbivore use (measured as dung densities) of plots exposed to cattle grazing than plots where cattle were not grazed. It is unlikely that these negative effects on mesoherbivore dung density are as a result of trampling of dung by cattle. If cattle trampling crushed dung, we would have encountered partially crushed dung groupings, which we did not. It is also unlikely that the negative effects are due to mesoherbivore

behavioral avoidance of cattle and their human herders (Sam et al. 2002, Young et al. 2005, Bates et al. 2007). The time spent by cattle in or near the plots is relatively small (<1% of the time); therefore, the direct presence of people and cattle is unlikely to cause wildlife to avoid the plots for more than a few days per year at most, whereas dung counts reflect months of wildlife plot use.

We do not consider the dung deposited in each plot to be a direct measure of (be composed of) the material eaten in that plot during the visit, regardless of passage times (e.g., Hanley 1997). Instead, we considered the amount of dung deposition to be simply a measure of herbivore presence.

The most plausible explanation for the lower wild mesoherbivore use of plots grazed by cattle is the reduction in preferred forage. Cattle have profound consequences on herbaceous vegetation cover and composition (Porensky et al. 2013, Veblen et al. 2016), and can therefore influence habitat use by other species. The observed effects may not be specific to cattle grazing, but could also result from an aggregate effect of greater grazing by cattle as well as interspecific interactions with other herbivores in the system. However, since cattle densities are higher than the densities of other herbivores in the system, it is reasonable to expect that they have a profound effect on forage availability and habitat use by other herbivores.

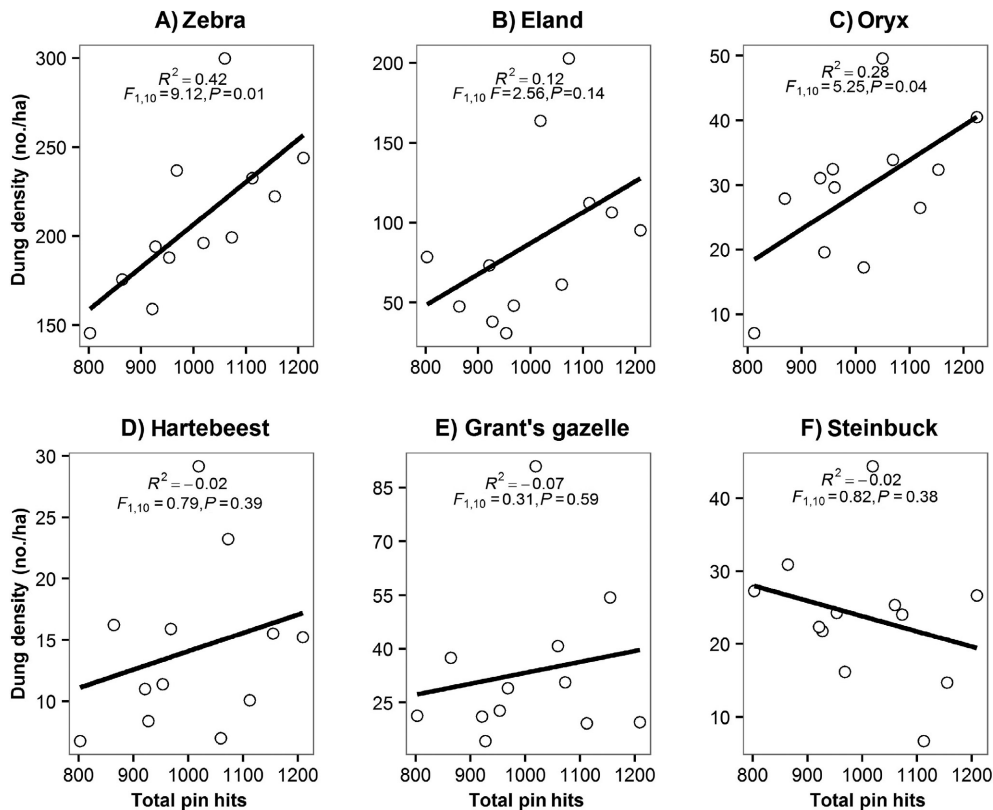


FIG. 4. Relationship between individual species dung density and cover by grasses (total number of pin hits; see *Materials and Methods: Data collection* for a description of cover estimation).

We predicted that cattle would reduce habitat use by all mesoherbivore wildlife, but the effect would be stronger for grazers than for mixed feeders because of the expected higher dietary overlap between cattle and grazing wildlife—since cattle forage almost exclusively on understory vegetation in this system, more than 90% of which is grass. Our results, however, provide a very different picture. While all species except steinbuck showed consistently lower use of plots grazed by cattle, the effect of cattle on mixed feeders was at least as great as on grazers and was significant even for species considered primarily browsers, such as eland. We suggest four possible explanations for this, which are not mutually exclusive.

First, since a considerable proportion of mixed feeders' diet consists of grasses (Cerling et al. 2003, Sponheimer et al. 2003, Shannon et al. 2013), it is possible that selective grazing by cattle (Katjiua and Ward 2006) depletes the grasses that are preferred by both grazers and mixed feeders. There was significant reduction in grass cover in plots grazed by cattle, and habitat use by some mixed feeders (eland and Grant's gazelle) in addition to grazers (zebra and oryx) was positively related with grass cover. This suggests that, even at moderate stocking densities, cattle might negatively affect the presence of herbivores (mixed feeders included) by reducing grass as a forage resource.

Second, it is also possible that cattle eat the same forbs that mixed feeders and browsers prefer. Although forbs

make up a small fraction of the understory, earlier studies in our system indicate that forbs constitute a significant proportion of cattle diet (up to 13%; Odadi et al. 2007) and are significantly related to cattle mass gain. Further, the presence of cattle reduces the availability of (palatable) forbs. Thus, we might expect wildlife to avoid areas where the preferred forbs (and grasses) have been depleted by cattle. Eland in particular showed a significant positive relationship with forb cover. Forbs constitute over 90% of eland's diet elsewhere (Wallington et al. 2007) and are much more limited than grass in terms of availability.

Third, because cattle greatly outnumber wildlife in our study system (Veblen et al. 2016), even eating a few favored forbs or grasses per cow could have a disproportionate effect on mixed feeders. Cattle biomass exceeds total wildlife biomass by more than 50% in most pro-wildlife cattle ranches in the Laikipia ecosystem, including Mpala Research Center (Georgiadis et al. 2007b). It is possible that the observed patterns are not specific to cattle grazing, but could also be obtained with other ecologically similar herbivores in the system such as buffaloes. Recent work in KLEE plots suggests that plant community composition shifts depending on overall herbivory pressure, rather than herbivore type or interactions among different herbivore types (Veblen et al. 2016).

A fourth possibility is that dung deposition rates do not match consumption rates within the experimental plots.

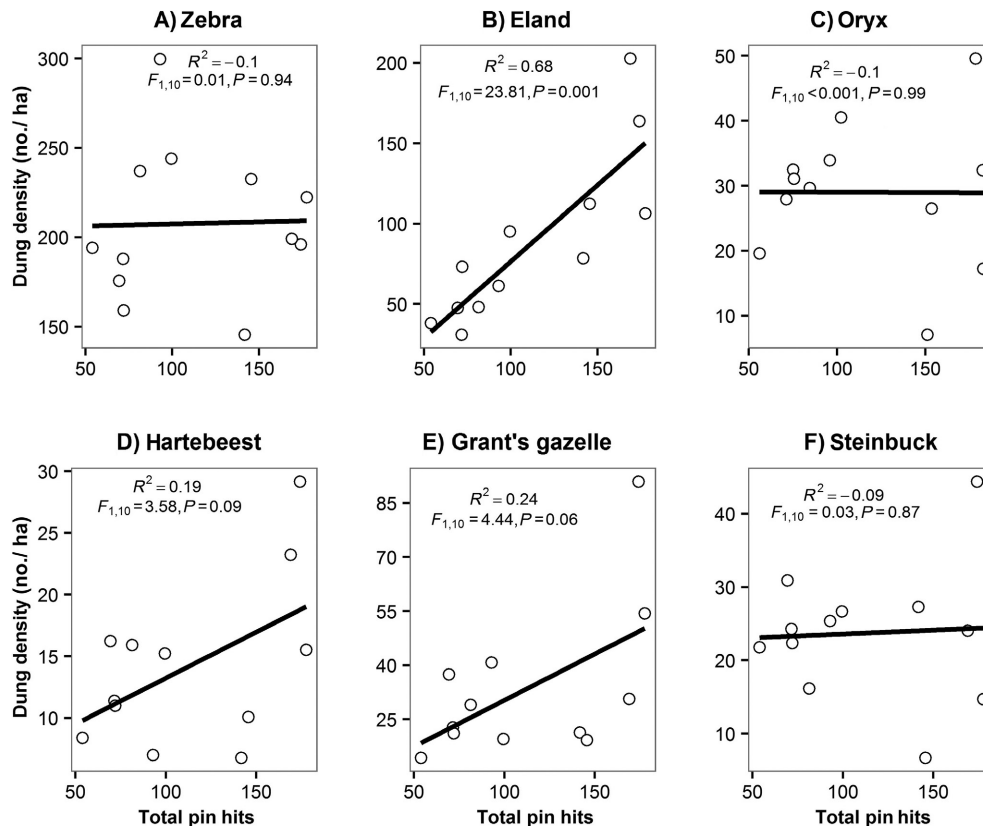


FIG. 5. Relationship between individual species dung density and cover by forbs (total number of pin hits).

Although large by experimental standards, the plots make up only a small part of a given herbivore's home range. It is conceivable that some herbivores defecate in the plots disproportionately to the amount of time spent the plots. For example, in treeless "glades" in this ecosystem, impala and Grant's gazelles defecate more than they consume because they use glades heavily at night to avoid risk of predation. However, there is no evidence or reason to suggest that herbivores use the KLEE experimental plots in this way. Indeed research indicates that wildlife dung density in open KLEE plots (MWC) is strongly related to the number of animals on the landscape (Veblen et al. 2016).

Regardless of the mechanism, our findings suggest that even partial overlap on minority components of the diet may be an important influence on wildlife habitat use; hence, relying primarily on broad dietary overlap (grass vs. non-grass) as a measure of species interactions may be inappropriate (Prins 2000, Riginos et al. 2012).

Effect of megaherbivore on mesoherbivores

Elephants in this ecosystem, as in many African savannas, play a unique and potentially keystone role. Elephants have a very high biomass density in this ecosystem and have been increasing in numbers over the last several decades (Georgiadis et al. 2007a). Their effects may be different

from most of the other megaherbivores in the system in several ways. First, they feed on a significant proportion of grasses (Codron et al. 2006) and forbs (Odadi et al. 2009) in addition to their woody browse diet, and therefore act as mixed feeders (Codron et al. 2006) in potential forage competition with mesoherbivores (in strong contrast to the other megaherbivores in this system, giraffes, which do not feed on the herbaceous layer). Second, elephants play a unique role in reducing tree cover in African savannas (Barnes et al. 1994, Birkett 2002, Jacobs and Biggs 2002, Skarpe et al. 2004, Boundja and Midgley 2010, Wahungu et al. 2011). In our study plots, the density of trees taller than 1 m is thus far lower in plots to which megaherbivores have access (D. M. Kimuyu, *unpublished data*). Elephant-mediated reduction in tree cover can have several cascading effects. For example, reduction in tree density may increase grass biomass and productivity (Prins 2000, Smit and Rethman 2000, Riginos et al. 2009, Riginos 2015), which in turn could favor mesoherbivores. Also, by reducing tree cover, elephants indirectly influence habitat use by mesoherbivores by modifying visibility and thus the perceived "landscape of fear." Many species of mesoherbivores in this system appear to favor more open habitat where their ability to see and avoid predators is greater (Riginos and Grace 2008, Riginos 2015). Habitat selection is often a trade-off between forage availability and perceived

predation risk (Abrams 1992, Hof et al. 2012, Riginos 2015), and elephants appear to shape both of these factors for mesoherbivores in this system.

We found higher use by eland and lower use by zebra and oryx in plots where megaherbivores had been excluded. These effects were most likely mediated by megaherbivores' effect on forage availability as well as their effects on visibility via modification in tree density. Megaherbivores, particularly elephants, reduced forb cover but not grass cover. The higher use by eland can thus be attributed to release from potential forage competition while the decrease in zebra and oryx use is likely a response to differences in tree cover. Even though eland are known to avoid areas with dense cover (Riginos and Grace 2008, Riginos 2015), and therefore would be expected to prefer relatively open megaherbivore plots, it appears that the effects of elephants via forage competition (especially for forbs and some trees and shrubs) outweigh their effects via habitat modification for at least some species of herbivores. In contrast, use by zebra was greater in megaherbivore plots, while oryx use remained essentially unaffected (Fig. 2). Among the six herbivores considered, zebra are the most tolerant of lower-quality diet (Odadi et al. 2011a) and respond strongly to reduction in tree density (Riginos 2015); hence, habitat selection by zebra could be governed more by anti-predator strategy rather than by direct forage competition with elephants.

Indirect facilitation

In addition to the individual effects of cattle and megaherbivores on mesoherbivores, megaherbivores appear to ameliorate the negative effect of cattle on mesoherbivores. The negative effect of cattle on eland, oryx, hartebeest, and Grant's gazelle was significantly less in plots with megaherbivores (MW vs. MWC) than in plots without megaherbivores (W vs. WC) (Fig. 2). A similar pattern was previously documented in this system with zebras (Young et al. 2005), but this study provides a broader scope, by considering more herbivore species and over a longer timescale. Although the mechanisms for this indirect facilitation remain unclear from this study (and therefore deserve further scrutiny), it is likely that facilitation occurs through elephants modifying cattle foraging behavior (Odadi et al. 2009) and diet (Odadi et al. 2007). For example, elephants, by limiting availability of forbs (Landman et al. 2013), may suppress resource extraction by cattle (particularly protein; Odadi et al. 2013), thus indirectly facilitating mesoherbivores (Young et al. 2005). The observed interaction between cattle and megaherbivore treatments reported here further affirms the important role of megaherbivores in promoting livestock-wildlife coexistence.

Influence of rainfall

We predicted that the negative effects of cattle on mesoherbivores would be more intense during periods of low

rainfall, when forage is most limited. We found evidence to support this prediction, but notably only for zebra and steinbuck, where we saw shifts from negative to positive effects of cattle with increasing rainfall (Fig. 3). In an earlier study in the same system, Odadi et al. (2011b) reported that mesoherbivores (particularly zebra) have a negative effect on cattle performance during the dry times when forage resources are limited, but facilitate cattle during wet periods. Taken together, these studies suggest that both cattle and mesoherbivores may negatively affect each other when forage resources are limited, i.e., reciprocal direct competition (Prins 2000, Codron et al. 2006). However, this competition may be strongest between cattle and zebra, which are more abundant than other species and, Zebras as caecal digesters ("bulk feeders"), consume a greater quantity of forage for their body size than most other wildlife species. During wet periods, when forage resources are more abundant, areas previously grazed by cattle may have higher-quality grass (Clark et al. 2000) and more diverse species composition (Porensky et al. 2013). This could facilitate zebras as well as other herbivores.

CONCLUSIONS

Our study illustrates the importance of considering both the direct and indirect interactions in livestock-wildlife competition (and facilitation) models. Models based only on dietary overlap are unlikely to sufficiently explain livestock-wildlife interactions. For example, because diet selection by herbivores greatly varies across rainfall periods, it is important that species interactions be evaluated in the context of rainfall. Although functional characterization of species as grazers, mixed feeders, or browsers has been a useful way of extrapolating community-wide interactions, it is important to note that there exist fundamental differences in the way individual species respond to different environmental contexts. Thus, generalizations based on functional groupings should be treated with caution.

This study also has important applied implications. Greater understanding of interactions between livestock and wildlife is critical for the management and persistence of wildlife in human-occupied landscapes. For example, our results suggest that megaherbivores may benefit some species of mesoherbivores that cattle negatively affect because they moderate negative effect of cattle. Further, the negative effect of cattle on wildlife during dry times may be at least partially mitigated by positive effects during wet times. While our results support the broadly-held assumption that cattle and wildlife generally compete via forage resources, our findings also indicate that management for a diverse set of wild meso- and megaherbivores, alongside cattle at moderate densities, is possible.

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LITERATURE CITED

- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *American Naturalist* 140:573-600.
- Acevedo, P., J. Cassinello, and C. Gortazar. 2008. The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by the presence of extensive goat livestock in central Spain. Pages 119-134 in D. Hawksworth and A. Bull, editors. *Biodiversity and conservation in Europe*. Springer, Dordrecht, The Netherlands.
- Adriansen, H. K., and T. T. Nielsen. 2002. Going where the grass is greener: on the study of pastoral mobility in ferlo, senegal. *Human Ecology* 30:215-226.
- Altendorf, K. B., J. W. Laundré, C. A. López González, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* 82:430-439.
- Aroeira, L. J. M., F. C. F. Lopes, F. Deresz, R. S. Verneque, M. S. Dayrell, L. L. de Matos, H. Maldonado-Vasquez, and A. Vittori. 1999. Pasture availability and dry matter intake of lactating crossbred cows grazing elephant grass (*Pennisetum purpureum*, Schum.). *Animal Feed Science and Technology* 78:313-324.
- Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313-318.
- Augustine, D. J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* 40:137-149.
- Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications* 13:1325-1337.
- Augustine, D. J., K. E. Veblen, J. R. Goheen, C. Riginos, and T. P. Young. 2011. Pathways for positive cattle-wildlife interactions in semiarid rangelands. *Smithsonian Contribution to Zoology* 632:55-71.
- Barnes, R. F. W., K. L. Barnes, and E. B. Kapela. 1994. The long-term impact of elephant browsing on baobab trees at Msembe, Ruaha National Park, Tanzania. *African Journal of Ecology* 32:177-184.
- Barton, B. T., and A. R. Ives. 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. *Ecology* 95:486-494.
- Bates, L. A., K. N. Sayialel, N. W. Njiraini, C. J. Moss, J. H. Poole, and R. W. Byrne. 2007. Elephants classify human ethnic groups by odor and garment color. *Current Biology* 17:1938-1942.
- Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. *Rangeland Ecology and Management* 58:135-147.
- Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology* 40:276-282.
- Blake, S. 2002. Forest buffalo prefer clearings to closed-canopy forest in the primary forest of northern Congo. *Oryx* 36:81-86.
- Booth, D. T., S. E. Cox, T. W. Meikle, and C. Fitzgerald. 2006. The accuracy of ground-cover measurements. *Rangeland Ecology and Management* 59:179-188.
- Boundja, R. P., and J. J. Midgley. 2010. Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa. *African Journal of Ecology* 48:206-214.
- Butt, B., A. Shortridge, and A. M. G. A. WinklerPrins. 2009. Pastoral herd management, drought coping strategies, and cattle mobility in Southern Kenya. *Annals of the Association of American Geographers* 99:309-334.
- Butt, B. 2010. Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. *Journal of Arid Environments* 74:403-413.
- Butt, B., and M. Turner. 2012. Clarifying competition: the case of wildlife and pastoral livestock in East Africa. *Pastoralism* 2:1-15.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958-1965.
- Cerling, T. E., J. M. Harris, and B. H. Passey. 2003. Diets of east African bovidae based on stable isotope analysis. *Journal of Mammalogy* 84:456-470.
- Clark, P. E., W. C. Krueger, L. D. Bryant, and D. R. Thomas. 2000. Livestock grazing effects on forage quality of elk winter range. *Journal of Range Management* 53:97-105.
- Codron, J., J. A. Lee-Thorp, M. Sponheimer, D. Codron, R. C. Grant, and D. J. De Ruiter. 2006. Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy* 87:27-34.
- Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. *Journal of Range Management* 54:51-76.
- Daniels, M. J. 2006. Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost-effectiveness of counting methods. *Mammal Review* 36:235-247.
- Derner, J. D., J. K. Detling, and M. F. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment* 4:459-464.
- Du Toit, J. T., and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8:1643-1661.
- Eckhardt, H. C., B. W. van Wilgen, and H. C. Biggs. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology* 38:108-115.
- Ferrari, S., and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. *Journal of Applied Statistics* 31:799-815.
- Fuller, T. K. 1991. Do pellet counts index white-tailed deer numbers and population change? *Journal of Wildlife Management* 55:393-396.
- Georgiadis, N. J., F. Ihwagi, J. G. N. Olwero, and S. S. Romañach. 2007a. Savanna herbivore dynamics in a livestock-dominated landscape. II: ecological, conservation, and management implications of predator restoration. *Biological Conservation* 137:473-483.
- Georgiadis, N. J., J. G. N. Olwero, G. Ojwang, and S. S. Romañach. 2007b. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biological Conservation* 137:461-472.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos* 79:209-218.

- Hatch, G. P., and N. M. Tainton. 1995. The influence of stocking rate, range condition and rainfall on residual herbage mass in the semiarid savanna of Kwazulu-Natal. *African Journal of Range and Forage Science* 12:76–80.
- Hibert, F., C. Calenge, H. Fritz, D. Maillard, P. Bouché, A. Ipavec, A. Convers, D. Ombredane, and M.-N. Visscher. 2010. Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodiversity and Conservation* 19:2003–2024.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecological Applications* 6:200–217.
- Hof, A. R., J. Snellenberg, and P. W. Bright. 2012. Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Animal Behaviour* 83:1099–1106.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457.
- Holdo, R. M. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* 17:558–568.
- Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications* 19:95–109.
- Jacobs, O. S., and R. Biggs. 2002. The impact of the African elephant on marula trees in the Kruger National Park. *South African Journal of Wildlife Research* 32:13–22.
- Katjiua, M. L. J., and D. Ward. 2006. Cattle diet selection during the hot-dry season in a semi-arid region of Namibia. *African Journal of Range and Forage Science* 23:59–67.
- Kauffman, J. B., A. S. Thorpe, and E. N. J. Brookshire. 2004. Livestock exclusion and belowground ecosystem responses in riparian meadows of eastern Oregon. *Ecological Applications* 14:1671–1679.
- Kimuyu, D. M., R. L. Sensenig, C. Riginos, K. E. Veblen, and T. P. Young. 2013. Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna. *Ecological Applications* 24:741–749.
- Kohi, E. M., W. F. de Boer, M. J. S. Peel, R. Slotow, C. van der Waal, I. M. A. Heitkönig, A. Skidmore, and H. H. T. Prins. 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. *Biotropica* 43:711–721.
- Landman, M., D. S. Schoeman, and G. I. H. Kerley. 2013. Shift in black rhinoceros diet in the presence of elephant: evidence for competition? *PLoS ONE* 8:e69771.
- Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55:16–26.
- Ludwig, F., H. de Kroon, H. H. T. Prins, and F. Berendse. 2001. Effects of nutrients and shade on tree-grass interactions in an East African savanna. *Journal of Vegetation Science* 12:579–588.
- Lunt, N., A. E. Bowkett, and A. B. Plowman. 2007. Implications of assumption violation in density estimates of antelope from dung-heap counts: a case study on grey duiker (*Sylvicapra grimmia*) in Zimbabwe. *African Journal of Ecology* 45:382–389.
- Marques, F. F. C., S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* 38:349–363.
- Miller, T. E. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* 143:1007–1025.
- Mizutani, F., M. Kadonira, and B. Phiri. 2012. Livestock-wildlife joint land use in dry lands of Kenya: a case study of the Loldiada Hills ranch. *Animal Science Journal* 83:510–516.
- Mulinge, M. M., and M. Getu. 2013. Impacts of Climate Change and Variability on Pastoralist Women in Sub-Saharan Africa. Fountain Publishers, Kampala. Pages 1–348.
- Nchanji, A. C., and A. J. Plumptre. 2001. Seasonality in elephant dung decay and implications for censusing and population monitoring in south-western Cameroon. *African Journal of Ecology* 39:24–32.
- Nelson, K. S., E. M. Gray, and J. R. Evans. 2010. Finding solutions for bird restoration and livestock management: comparing grazing exclusion levels. *Ecological Applications* 21:547–554.
- Odadi, W. O., T. P. Young, and J. B. Okeyo-Owuor. 2007. Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. *Rangeland Ecology and Management* 60:179–185.
- Odadi, W. O., J. Okeyoowuor, and T. P. Young. 2009. Behavioural responses of cattle to shared foraging with wild herbivores in an East African rangeland. *Applied Animal Behaviour Science* 116:120–125.
- Odadi, W. O., M. Jain, S. E. Van Wieren, H. H. T. Prins, and D. I. Rubenstein. 2011a. Facilitation between bovids and equids on an African savanna. *Evolutionary Ecology Research* 13:237–252.
- Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2011b. African wild ungulates compete with or facilitate cattle depending on season. *Science* 333:1753–1755.
- Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2013. Protein supplementation reduces non-grass foraging by a primary grazer. *Ecological Applications* 23:455–463.
- Ogutu, J. O., R. Reid, H.-P. Piepho, N. Hobbs, M. Rainy, R. Kruska, J. Worden, and M. Nyabenge. 2014. Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation* 23:573–596.
- Porensky, L., S. Wittman, C. Riginos, and T. P. Young. 2013. Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. *Oecologia* 173:591–602.
- Prins, H. H. T. 1992. The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19:117–123.
- Prins, H. H. T. 2000. Competition between wildlife and livestock in Africa. Pages 5–80 in H. H. T. Prins, J. G. Grootenhuis, and T. T. B. Dolan, editors. *Wildlife conservation by sustainable use*. Kluwer Academic Publishers, Berlin, Germany.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Radloff, F. G. T., and L. Mucina. 2007. A quick and robust method for biomass estimation in structurally diverse vegetation. *Journal of Vegetation Science* 18:719–724.
- Ragotzkie, K. E., and J. A. Bailey. 1991. Desert mule deer use of grazed and ungrazed habitats. *Journal of Range Management* 44:487–490.
- Rasmussen, H. B., O. Kahindi, F. Vollrath, and I. Douglas-Hamilton. 2005. Estimating elephant densities from wells and droppings in dried out riverbeds. *African Journal of Ecology* 43:312–319.
- Reid, R. S. 2012. *Savannas of our birth*. University of California Press, Berkeley, California, USA.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* 84:124–133.
- Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology* 89:2228–2238.

- Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. *Journal of Ecology* 97:1337–1345.
- Riginos, C., L. M. Porensky, K. E. Veblen, W. Odadi, R. L. Sensenig, D. M. Kimuyu, F. Keesing, M. L. Wilkerson, and T. P. Young. 2012. Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). *Pastoralism: Research, Policy and Practice* 2:10.
- Rivero, K., D. Rumiz, and A. Taber. 2004. Estimating brocket deer (*Mazama gouazoubira* and *M. americana*) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz, Bolivia. *European Journal of Wildlife Research* 50:161–167.
- Sam, M. K., C. A. K. Haizel, and R. F. W. Barnes. 2002. Do cattle determine elephant distribution in the Red Volta Valley of northern Ghana? *Pachyderm* 33:39–42.
- Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17:236–245.
- Shannon, G., R. L. Mackey, and R. Slotow. 2013. Diet selection and seasonal dietary switch of a large sexually dimorphic herbivore. *Acta Oecologica* 46:48–55.
- Skarpe, C., et al. 2004. The return of the giants: ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment* 33:276–282.
- Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2013. Generalized Linear Mixed Models using AD Model Builder. R package. <http://glmmadmb.r-forge.r-project.org/>
- Smit, G. N., and N. F. G. Rethman. 2000. The influence of tree thinning on the soil water in a semi-arid savanna of southern Africa. *Journal of Arid Environments* 44:41–59.
- Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11:54–71.
- Sponheimer, M., et al. 2003. Diets of Southern African bovidae: stable isotope evidence. *Journal of Mammalogy* 84:471–479.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229–244.
- Styles, C. V., and J. D. Skinner. 1997. Seasonal variations in the quality of mopane leaves as a source of browse for mammalian herbivores. *African Journal of Ecology* 35: 254–265.
- Tchabovsky, A. V., B. Krasnov, I. S. Khokhlova, and G. I. Shenbrot. 2001. The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. *Journal of Ethology* 19:105–113.
- Veblen, K. E., L. M. Porensky, C. Riginos, and T. P. Young. 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. *Ecological Applications* 26:1610–1623.
- Vernes, K. 1999. Pellet counts to estimate density of a rainforest kangaroo. *Wildlife Society Bulletin* 27:991–996.
- Wahungu, G. M., L. K. Mureu, D. M. Kimuyu, A. Birkett, P. G. Macharia, and J. Burton. 2011. Survival, recruitment and dynamics of *Acacia drepanolobium* *Sjostedt* seedlings at Olpejeta Conservancy, Kenya, between 1999 and 2009. *African Journal of Ecology* 49:227–233.
- Wallington, B. P., A. E. McKechnie, N. Owen-Smith, and S. Woodborne. 2007. Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *South African Journal of Wildlife Research* 37(2):127–131.
- Wilbur, H. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302.
- Young, T. P., B. D. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14:94–102.
- Young, T. P., T. M. Palmer, and M. E. Gadd. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation* 122:351–359.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1482/full>

DATA AVAILABILITY

Data associated with this paper have been deposited in Figshare <https://doi.org/10.6084/m9.figshare.4285832>