

# Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya

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## Abstract

Competition and compatibility between livestock and wildlife in Africa has been a point of considerable speculation, with implications for conservation. However, controlled replicated experiments are lacking. Here we report on the results of a long-term enclosure experiment in Laikipia, Kenya, in which different guilds of large mammalian herbivores have been independently manipulated since 1995. In plots from which cattle were excluded, the density of zebra dung in 2000 was on average 46% greater than in control plots. This was due to differential zebra use, and not to differential rates of dung removal (by dung beetles or other factors). Vegetation data indicate that cattle fully compensate for the absence of wildlife; all plots accessible to cattle had similarly low grass cover. However, wildlife do not fully compensate for the absence of cattle; plots with only wildlife had more grass cover than plots accessible to cattle. Zebra dung density was strongly correlated with total grass cover, suggesting that zebras are effectively tracking resource abundance. There is also evidence of pair-wise competition between cattle and elephants, and between elephants and zebras. The strong competition between cattle and zebras appears to be mitigated by the presence of elephants. A significant cattle x elephant interaction on the abundance of zebra dung indicates that elephants reduce the negative effects of cattle on zebras. In the presence of cattle, elephants facilitate the abundance of zebra, apparently by suppressing resource extraction (bite rates) by cattle. The precise mechanism for this indirect facilitation is not clear, but it may be related to the demonstrated reduction in forb cover associated with elephant presence.

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## 1. Introduction

In semi-arid and arid biomes worldwide, livestock and large native herbivores share land, water, forage, and diseases. There has been considerable discussion about the compatibility of livestock production in the context of the conservation and restoration of large mammalian biodiversity in Africa (MacMillan, 1986; Mearns, 1997; Kinyua et al., 2000; Heath, 2000; Prins et al., 2000). It has been suggested that the fate of biodi-

versity outside of protected areas will often depend on the strength of interactions between wildlife and livestock (Grootenhuys and Prins, 2000).

In East Africa, the majority of the populations of most large mammal species occur outside protected areas, although this proportion is declining (Mbugua, 1986; Western, 1989; Ottichilo et al., 2000). These populations mostly occur on land that is also being used for the production of livestock, either by traditional pastoralists or by large-scale ranching enterprises. There is a widespread belief that grazing wildlife, particularly zebras (*Equus* spp.) and wildebeests (*Connochaetes taurinus*), compete with cattle for grass in Africa (Pratt and Gwynne, 1977; reviewed in MacMillan, 1986; Prins,

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1992, 2000; Voeten and Prins, 1999). Conversely, some conservationists suggest that resource partitioning minimizes competition, and that livestock production and the conservation of large mammal biodiversity are compatible goals (Hopcraft, 1990, 2000). Prins (2000) suggests that although there is considerable niche overlap between wildlife and cattle, competition is largely asymmetrical and diffuse, with cattle having a competitive effect on a number of wildlife species but wildlife having little or no competitive effect on cattle.

Elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*) have been demonstrated to modify ecosystems, mostly through the suppression and reduction of woody plants (Pellew, 1983; Van Wijngaarden, 1985; Owen-Smith, 1988; Buss, 1990; Dublin et al., 1990; Dublin, 1995). This reduction in woody cover can have indirect effects on the grass layer, potentially affecting both wildlife and livestock production (Prins, 2000). In contrast, the effects of elephants on the herb layer have been little studied. In addition, elephants are charismatic megaherbivores subject to special protection. We need to know more about their ecological interactions with livestock on the land they share.

Although there have been several studies of the potential niche overlap of cattle and wildlife in Africa (Ego et al., 2003; Voeten, 1999), there have been no controlled, replicated experiments that examine the effects of these species on each other and on the land they share (Prins, 2000). Globally, experimental studies are exceedingly rare, and usually measure the effects of wildlife on livestock (Hobbs et al., 1996a,b), or the indirect effects of cattle on wildlife (Loft et al., 1987; Fritz et al., 1996), but not yet both in the same system (Prins, 2000).

Cattle diets are more similar to zebra diets than to the diets of many other wildlife species (Casebeer and Koss, 1970; Voeten, 1999), and cattle and zebra have considerable overlap in habitat use (Voeten and Prins, 1999). Competition has been inferred from this dietary and habitat overlap, but as Voeten (1999) and Prins (2000) point out, such overlap will only result in competition if food is limiting. Competition is better revealed through direct manipulations of one or both competitors. Pratt and Gwynne (1977, p. 233) report that “(zebras) compete with cattle for grass and water and often concentrate on areas that are nominally being rested from grazing”. However, controlled experiments demonstrating any such response are thus far lacking in the literature.

Long-term multi-way experiments have the potential to reveal complex interactions among species, including the ability of species to compensate for others' absence (Brown et al., 2001). We define compensation here as an increase in a species when its competitor is excluded, or the lack of a decrease in a shared resource (grass) when one competitor, but not the other, is excluded. Indirect effects occur when the impacts of one species

on another are mediated through changes in a third species (Strauss, 1991). Exploitative competition is the most straightforward indirect effect, but more complex indirect effects are beginning to be revealed, such as indirect facilitation occurring in trophic cascades (cf., Adams et al., 2003). Within trophic levels, when different pairs of species compete for different combinations of resources, facilitation can occur between two species (in the presence of a third) that would otherwise compete (Levine, 1976, 1999). Elephants eat both grass and forbs, and may compete differentially with cattle (which eat both) and zebras (which eat only grass).

Since 1995, we have been conducting a large-scale enclosure experiment in Kenya in which we independently manipulate the presence of wildlife, megaherbivores, and cattle (Young et al., 1998). Here we report on the effects of these selective exclusions on vegetation and herbivore presence. These results suggest that pairwise combinations of cattle, elephants, and zebras are competitive, but that there is indirect facilitation of zebras by elephants in the presence of cattle.

## 2. Study site and methods

### 2.1. Study site

This research was carried out from 1995 to 2002 at the Mpala Research Centre in Laikipia, Kenya (1800 m asl; 0°17'N, 37°52'E). Rainfall at this site averages 500–600 mm/year. The study period included one of the wettest (1997–1998) and one of the driest (1999–2000) years on record. Deep clay ‘black cotton’ vertisols soils of impeded drainage and moderate fertility underlay the study area (Ahn and Geiger, 1987). Similar soils with similar vegetation occur throughout Laikipia, and at other sites in East Africa including Nairobi National Park, and parts of Serengeti National Park.

In September 1995, we erected a set of large mammal enclosures on an area of flat black cotton soil with homogeneous vegetation. We used a series of semi-permeable barriers to differentially exclude cattle, megaherbivores (elephants and giraffes), and all “wildlife” (here referring to large mammalian herbivores >15 kg) from a series of study plots. Each plot is 200 m × 200 m (4 ha). In each of three blocks, we have the following six treatment plots, in a random stratified design:

1. All large mammals excluded (“O”).
2. Only cattle allowed (“C”).
3. Only wildlife allowed (“W”).
4. Wildlife and cattle allowed (“WC”).
5. Wildlife and megaherbivores allowed (“MW”).
6. All large herbivores allowed (“MWC”).

For full details of this experiment and the study ecosystem, see Young et al. (1998).

In plots where cattle are allowed (C, WC, MWC), *Bos indicus* cattle are herded into each plot on a regular basis, calculated to approximate the stocking rate of the ranch. Mean cattle density on the ranch is 11–15/km<sup>2</sup> (see Section 3). Before 1999, we used mixed herds of cows, calves and heifers, but since 1999 the herds have been heifers only.

Mean zebra density in Laikipia's *Acacia drepanolobium* bushland is 5–6/km<sup>2</sup> (Khaemba et al., 2001). Most zebras using the plots are Burchell's zebras (*Equus burchelli*); less than 5% of the zebras in the study system are Grevy's zebras (*E. grevyi*). Other large mammalian herbivores include buffaloes (*Syncerus caffer*), elands (*Tragelaphus oryx*), Grant's gazelles (*Gazella granti*), hartebeests (*Alcelaphus buselaphus*), oryx (*Oryx gazella beisa*), steinbucks (*Raphicerus campestris*) and the mega-herbivores elephants and giraffes. Impalas are abundant in the adjacent red soil ecosystem (Young et al., 1995; Augustine, 2003), but do not occur at this study site on black cotton soils.

## 2.2. Estimates of effective cattle densities

We control cattle by limiting their access to timed "runs" several times per year with the help of ranch herders. During each cattle run, 120 cows are put into each 4ha enclosure for two hours. In order to estimate how this translated into an equivalent year-round density and to determine the number of cattle runs per year to conduct, we studied bite rates in January of 1999. During each cattle run, three cattle were chosen randomly from the herd. Each was observed for a series of five-minute focal samples throughout the day, from leaving the holding pens in the morning until returning in the evening, including their time in the enclosures. Cattle feed only during this daylight time. Between each focal sample the observer had ten minutes to find the next animal and begin another five-minute focal period. During each focal sample, the total number of bites taken by the animal was counted by the observer from a distance of less than 4m. This procedure was repeated during nine cattle runs. These data were used to calculate the number of runs that approximate the stocking rate of the ranch.

## 2.3. Dung surveys

In August–September 2000, we surveyed all large mammal dung in the plots. In each plot, we surveyed three 100 m transects, each 4m wide. Each pile of dung was attributed to species, with the help of local guides, guidebooks (Stuart and Stuart, 1994), and personal experience (see also Young et al., 1995). One of the three

blocks was surveyed by a different crew, and this data set produced a suspicious outlier, so this block was resurveyed by one of the original crew members in June of 2001. Zebra dung was divided into three classes: "Fresh dung" was black and relatively smooth. "Old dung" was straw-colored and had more surface texture. "Very old dung" was grey.

Because the dung of elephants occurred at lower densities than that of zebras, an elephant dung survey was carried out in May 2002 in the MW and MWC plots, using longer and wider transects (as part of a more detailed elephant use study). In each of the six plots to which elephants were allowed access, we counted elephant dung piles in two 200 m × 10 m transects.

Although there have been concerns about the use of dung counts as measures of mammal densities (Fuller, 1991), and documented effects of seasonality and habitat differences on decomposition rates (Plumptre and Harris, 1995; Vernes, 1999; Nchanji and Plumptre, 2001), there is ample evidence that when used to estimate relative habitat use within habitats and time periods, dung counts are not only reliable, but more reliable than aerial or ground counts (e.g., Marques et al., 2001; Altemendorf et al., 2001; Blake, 2002; see review by Barnes, 2001). We use dung counts here as relative assays of animal use, averaged across seasons within a homogeneous habitat type. For these purposes, it appears that dung counts are reliable measures in this ecosystem (Young et al., 1995; Augustine, 2003; Augustine et al., 2004).

## 2.4. Vegetation surveys

Surveys of herbaceous cover in the study plots are carried out every six months. In the central hectare of each plot, 100 sample points are laid out in a grid with points every 10 m. Each of these 100 points is surveyed for cover and presence/absence of herbaceous species. Cover is measured by setting down a 10-pin frame at each sampling point and counting each species hit by each pin (a maximum of one hit per species on each pin). There are 1000 pins per plot. The data used here were from the May 2001 survey.

## 2.5. Analysis

For each variable (dung density and plant cover by species), a mean value was calculated for each of the 18 plots. ANOVAs were carried out with three replicates per treatment and block effects. To measure the effectiveness of the enclosures, for each herbivore species we compared plots from which we attempted to exclude the species to the plots to which we allowed access, across all six treatments. For testing the effects of treatments on zebras we used only those treatments to which zebras had access (W, WC, MW, MWC). This allowed for a full factorial 2 × 2 ANOVA for the effects of cattle

and megaherbivores on zebra use, with an interaction term. Because there were significant differences in the density of zebra dung across the blocks, we also calculated residual dung values, subtracting the mean dung density for each plot from the mean dung density for the respective block. These residual values were used in a regression against total grass cover for all 12 plots to which the zebras had access.

### 3. Results

#### 3.1. Estimates of effective cattle densities

We counted ~40,000 cattle bites in 512 focal samples during the nine all-day samples. These focal samples indicate that cattle take  $24.2 \pm 1.8\%$  of their daily bites during the two hours of a cattle run in a given plot, independent of block ( $p = 0.66$ ) and treatment ( $p = 0.87$ ) effects. Therefore a two-hour cattle run with 120 cattle in each 4ha plot would be equivalent to an all-day presence of 29 cattle. For each cattle run, this equals an annual stocking rate of 0.02 cattle/ha (29 cattle per plot/4 ha per plot/365 days per year). Overall ranch density of cattle over the study period ranged from 2000 to 2800 in 18,000 ha, or 0.111 to 0.156 cattle/ha, a low to moderate stocking level in this ecosystem. Therefore, we estimated that six to eight cattle runs per year would give us an effective stocking rate similar to the rest of the property. Prior to this calculation, we conducted 4–6 cattle runs per year from 1995 to 1998. We have carried out 6–8 cattle runs per year since 1999.

#### 3.2. Dung surveys

We identified and counted the dung of eight wildlife species. The experimental barriers were effective in excluding the targeted species (Table 1). Dung densities of elephants and giraffes were 90% and 89% lower in plots from which we intended to exclude them. The bar-

riers intended to exclude other wildlife were 98–100% effective in reducing the presence of all non-megaherbivore ungulates except steinbucks (see also Young et al., 1998). Steinbucks are small enough to pass through our wildlife fences. Zebras accounted for 62% of all wildlife dung in the transects. This was more than 3.5 times as many dung piles as the second most common wildlife species, eland (a browser). Steinbuck dung piles were three times more abundant inside the wildlife fences than outside them (Table 1;  $p = 0.055$ ). This was especially pronounced in the plots from which cattle had also been excluded (more than four times more abundant,  $p = 0.025$ ). Among non-megaherbivore wildlife, only zebra dung was sufficiently abundant (see Table 1) for the analysis of the effects of cattle and megaherbivores.

Zebra dung showed a number of significant patterns (Table 2; Fig. 1). There was a significant block effect, with zebra dung twice as abundant in the north block as in the south block (the central block was intermediate). This gradient is associated with slightly increasing distance from water (from 2.5 to 2.8 km), and with strongly increasing proximity to a property where zebras were under greater risk of culling (from 2.5 to 0.5 km).

The exclusion of cattle was associated with a 44% increase in the presence of zebra dung (550 dung piles/ha in MWC and WC vs. 805 in MW and W). Although the zebra dung density was essentially the same in plots with and without megaherbivores (680 in MW and

Table 2  
ANOVA for the effects of the presence of cattle and megaherbivores on the density of zebra dung

Source	df	SS	MS	F ratio	p
Block	2	660	330	32.50	0.0006
Cattle	1	241	241	23.85	0.0028
Megaherbivores	1	0.13	0.13	0.013	0.91
Cattle × megaherbivores	1	116	116	11.39	0.015
Error	6	61	10.2		

The interaction terms involving Block were not significant.

Table 1

Densities of dung piles (per ha) for different wildlife species in plots from which they were not excluded, and in plots from which we intended to exclude them

Species	Accessible plots	Exclusion plots	% reduction	F	p
Elephants	17.4	1.8	90	10.26	0.0055
Giraffes	19.2	2.1	89	8.98	0.0085
Zebras	676	6.9	99	42.47	<0.0001
Elands	190	4.2	98	34.13	<0.0001
Hartebeests	102	1.4	99	13.22	0.0022
Grant's gazelles	85	1.4	99	21.43	0.0003
Oryx	2.8	0.0	100	1.52	0.23
Steinbucks	13.2	39.0	200%	4.28	0.055
			Increase		

For elephants and giraffes, the exclusion plots were those enclosed either by the wildlife fence or the megaherbivore fence. For all other species, the exclusion plots were those enclosed by the wildlife fence. We include steinbucks here, even though they are not effectively excluded by the wildlife fence.

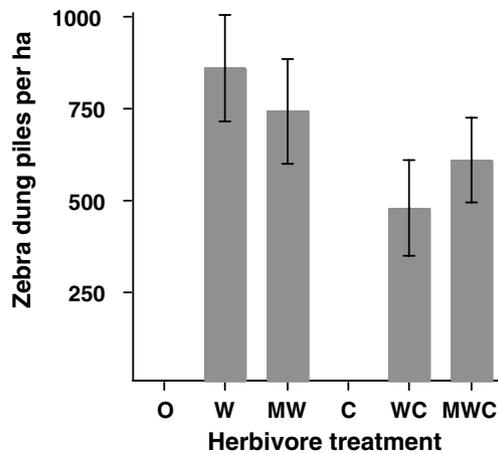


Fig. 1. The density of zebra dung in 2000/2001 in plots from which cattle and megaherbivores had been excluded since September 1995. Error bars ( $\pm 1$  SE) are large because of consistent block effects. Sample size was three blocks. There were significant block effects, but the patterns within blocks were consistent, resulting in significant effects of cattle, and a significant cattle  $\times$  megaherbivore effect (see Table 2).

MWC vs. 670 in W and WC), there was a significant cattle  $\times$  megaherbivore interaction (Table 2). In plots without megaherbivores, there was 79% more zebra dung in plots where cattle were excluded than in plots where cattle were allowed (485 in WC vs. 865 in W). In contrast, in plots with megaherbivores, zebra dung was only 22% more abundant where cattle had been excluded than where cattle were allowed (610 in MWC vs. 745 in MW). Megaherbivores appear to mitigate competition between cattle and zebras. All of these patterns are consistent within each block, and across years. The ratio of old to very old dung was independent of treatment ( $F = 0.66$ ,  $p = 0.60$ ) (less than 1% of the zebra dung found was classified as fresh), suggesting similar rates of dung disappearance.

Although there were numerical reductions in the dung of other wildlife species in the presence of cattle in 2000 and 2001, there were fewer dung piles counted for these species because they occurred at low densities, and none of these comparisons was statistically significant. In the 2002 survey, however, elephant dung was 40% less abundant in plots where cattle had been allowed to graze ( $F = 206.3$ ,  $p < 0.005$ ).

### 3.3. Vegetation surveys

The zebra dung patterns are strikingly consistent with the vegetation survey in 2000. The rank order of increasing grass cover and zebra dung was WC < MWC < MW < W. Cattle reduce total grass cover ( $p = 0.02$ ). In addition, grass cover showed a cattle  $\times$  megaherbivore interaction similar to the zebra dung data ( $p = 0.07$ ; Fig. 2(a)). In plots with wildlife, cattle alone reduced

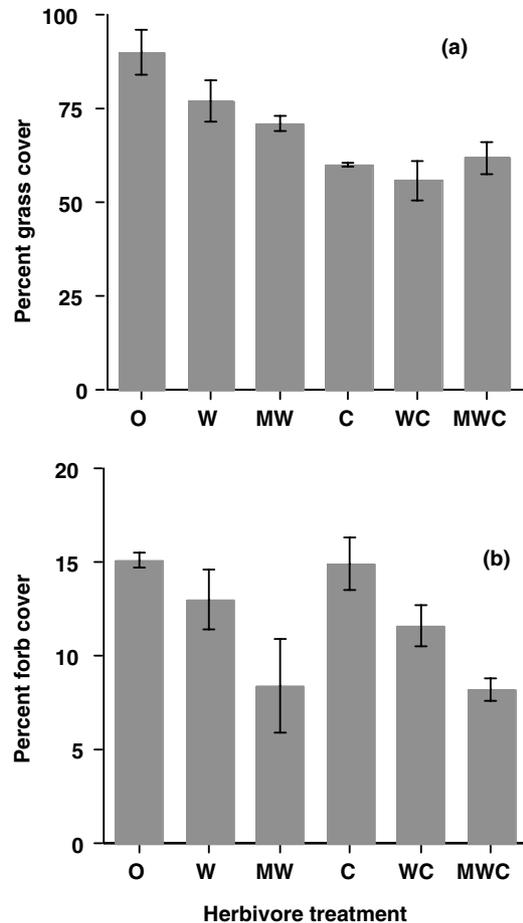


Fig. 2. Total grass cover (a) and total forb cover (b) in the different herbivore treatment plots. The letters represent the class of herbivores allowed access to the plots: O, none; C, cattle; W, wildlife (>15 kg); M, megaherbivores (elephants and giraffes). Bars are one standard error. Sample size was three blocks.

grass cover by 28%, and elephants alone also reduced grass cover, but by only 8%. Cattle in the presence of elephants reduced grass cover less (20%) than in the absence of elephants. Cattle had no effects on total forb cover ( $F = 0.256$ ,  $p = 0.63$ ), but megaherbivores reduced total forb cover by 33% compared to plots with wildlife but no megaherbivores ( $F = 5.77$ ,  $p = 0.05$ ; Fig. 2(b)). There was no significant relationship between forb cover and grass cover across the 18 plots ( $r^2 = 0.07$ ,  $p = 0.75$ ).

It is likely that the megaherbivore effects described here are due to elephants, not giraffes. Giraffes are strict browsers, and rarely feed on vegetation less than 50 cm above the ground (Young and Isbell, 1991; Ginnett and Demment, 1999). All of the forbs measured in the vegetation survey were herbaceous and less than 50 cm tall. Therefore the reductions in grass and forb cover reported from the megaherbivore plots can be mostly attributed to elephants.

Grass cover was tightly correlated with the abundance of zebra dung, averaged across all three blocks

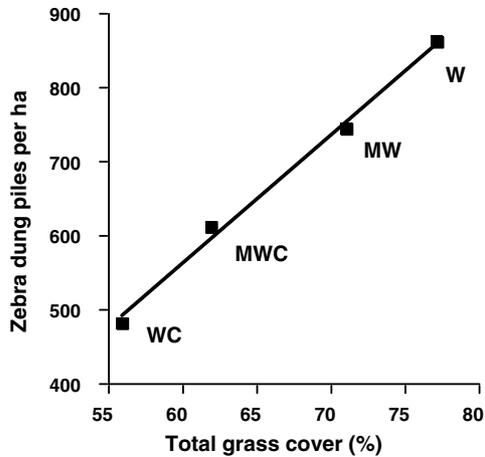


Fig. 3. The relationship between total grass cover and the density of zebra dung for the four wildlife treatments, averaged across all three blocks.

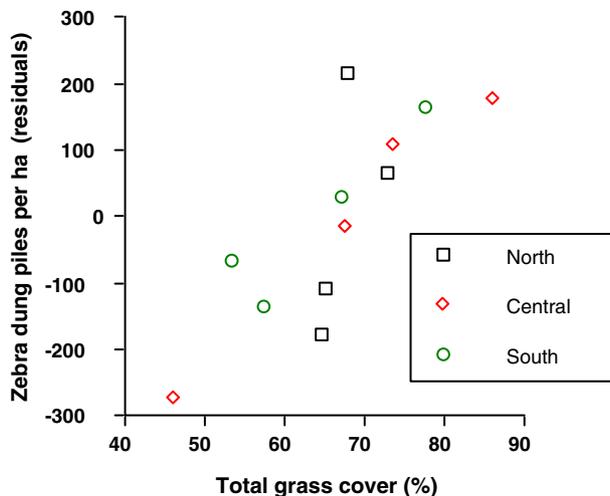


Fig. 4. The relationship between total grass cover and the density of zebra dung, for all 12 plots accessible to zebras. Because there were large Block differences, we used the residuals of dung densities, corrected for Block.

for these four treatments ( $r^2 = 0.9986$ ,  $df = 2$ ,  $p = 0.0007$ ; Fig. 3). Again, this pattern was consistent within replicate each block as well (Fig. 4).

#### 4. Discussion

We achieved mean annual stocking rates of 8–12 cattle/km<sup>2</sup> over the course of this experiment. At these stocking rates, the removal of cattle appears to increase the presence of zebras by an average of 46%. It is unlikely that the physical presence of cattle and herders deterred zebras; there were at most six two-hour cattle runs per year per plot, or cattle/herder presence less than 0.02% of the time. It is also unlikely that these differences in dung densities were due to differential removal

rates of zebra dung in the plots. The ratio of old to very old dung was independent of treatment ( $F = 0.66$ ,  $p = 0.60$ ) (less than 1% of the zebra dung found was classified as fresh), suggesting similar disappearance rates. Grazing by cattle also reduced habitat use by elephants.

Zebra dung was half as dense in the southern block as in the northern block, although the two plots are only 1200 m apart. The southern block was further from permanent water, but only ~10% further. Our research presence in the plots was equally divided among the three blocks. Cattle use (at least inside the experimental area) was kept constant across all blocks. However, the southern block was 300–500 m from properties with higher zebra culling, whereas the northern block was 1400–1800 m from this boundary. The southern block also had greater woody cover. We suspect that the observed decline in zebra dung along this gradient was due to increased mortality risk.

#### 4.1. Competition and compensation

Our data demonstrate a strong suppression of zebra by cattle, in the form of reduced presence of zebra in plots grazed by cattle. Its worth considering that such suppression is to factors other than competition (Morris, 2003) such as apparent competition via shared predators or wildlife avoidance of areas where cattle have fed due to avoidance of humans. These cattle are individually herded by protective herders, and do not attract predators. Although the significant block effect may be due to avoidance of area of higher risk of human culling, there is no evidence that wildlife associate cattle with this risk. Wildlife do keep their distance from individual herds, but they do not abandon areas where cattle are feeding (personal observations).

But the strongest evidence that this suppression is due to competition is that after controlling for block effects, zebra dung density was strongly correlated with grass cover (Figs. 3 and 4), which was negatively associated with cattle presence (Fig. 2(a)). Taken together with published reports of strong dietary overlap (Casebeer and Koss, 1970; Hoppe et al., 1977; Voeten, 1999; Voeten and Prins, 1999), these data suggest that zebras compete with cattle for food. Data from detailed vegetation surveys of the enclosure plots (Young, unpublished data) show that cattle substantially reduce cover by each of the five dominant grasses (*Pennisetum stramineum*, *P. mezianum*, *Lintonia nutans*, *Brachiaria lachnantha*, and *Themeda triandra*) as well as total grass cover. Wildlife (mostly zebras) significantly reduced *P. stramineum* and total grass cover. Cattle foraging data (Odadi, 2004) show a significant preference for *P. stramineum*, *B. lachnantha*, and *T. triandra*.

Compared to the total enclosure plots, cattle alone reduced grass cover by 33% at the time of the vegetation survey, and there were no further reductions in grass

cover with the addition of wildlife (see Fig. 2(a)). In contrast, wildlife alone (mostly zebras) reduced grass cover only 14% and wildlife plus megaherbivores reduced grass cover 21%. It appears that cattle can fully compensate for the absence of zebras and other wildlife. However, while zebras do compensate for the absence of cattle, they and other wildlife do not fully compensate, in terms of grass cover.

The demonstrated suppression of zebra presence by cattle occurred during a relatively dry period; Laikipia was just coming out of one of the worst droughts on record (Georgiadis et al., 2003). We do not yet know whether this response would occur in relatively wet years when grass resources are more abundant (see Hobbs et al., 1996b). However, zebra responses were still evident in 2002, after more than a year of normal rainfall. Dung counts carried out in 1997 did not show any significant responses of wildlife to these experimental treatments (see Fig. 6 in Young et al., 1998). Although this may have been due to the fact that the experiment was less than two years old, two years was more than enough time for rodents to respond to herbivore exclusion (Keasing, 1998). Drought accentuated negative effects of cattle on competing wildlife in Zimbabwe, and these effects persisted long after the drought had ended (Dunham et al., 2003).

The zebra response we are reporting here is a behavioural response, not a population growth response. Cattle were excluded from a total area of 36 ha out of an area of several thousand ha. The effect on wildlife of the exclusion of cattle may have been either accentuated or muted by the fact that each exclusion area was surrounded by areas grazed by cattle. Precise calculations of the effects on zebra or other wildlife populations of large-scale removals of livestock based on this experiment would be premature. Nonetheless, we suspect that this functional response would be paralleled by a numerical response if cattle were removed from a large area with no other limitations on zebra population growth. In any case, the data reported here represent some of the only experimental evidence that cattle compete with wildlife in Africa (Prins, 2000).

#### 4.2. Indirect facilitation

The significant interaction term between cattle and megaherbivores (Table 2, Fig. 1) means that zebras respond significantly less to the absence of cattle when megaherbivores are present. This appears to be because the herbivore treatments affect grass cover in complex ways, and zebras are closely tracking grass cover. The interaction term appears to be a combination of two effects. First, in the absence of cattle, megaherbivores reduce both grass cover and zebra presence. Elephants are known to eat grass, which sometimes makes up a significant part of their diet (Lindsay, 1982; McKnight, 1995;

Koch et al., 1995; Gadd, 1997; but see Cerling et al., 1999). Second, in the presence of cattle, elephant presence appears to increase grass cover and increase zebra presence. In other words, elephants indirectly facilitate zebras in plots where cattle are grazed. This may be because elephants change the composition and density of the ground layer, which decreases the amount that cattle reduce grass cover. One possibility is that the elephant suppress the forbs enough (they suppress forbs by 33%; Fig. 2(b)) that the cattle feed less in plots accessible to megaherbivores. We controlled cattle density in these plots, so this must be a trait-mediated effect (Werner and Peacor, 2003). We are discovering that cattle feed significantly less (bites/minute) in plots with elephants than in plots without them (Odadi, 2004). Our monitoring of the woody vegetation previous to 2002 had shown no significant decreases in stem densities in plots accessible to elephants (Okello, unpublished data), so it is unlikely that they had opened up the habitat enough (by reducing woody cover) that zebras are attracted to increased grass cover or increased predator visibility.

This experimental demonstration of indirect facilitation among mutual competitors is part of a growing literature of such effects (Levine, 1999; Werner and Peacor, 2003, and references therein). Previous studies have focussed on plants or granivores. This appears to be the first demonstration of indirect facilitation within an herbivore guild. The complex dietary overlaps within the rich assemblage of large mammalian herbivores in African savannas suggest that other examples may exist there, if we find the tools to reveal them.

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