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#### Supporting Online Material

www.sciencemag.org/cgi/content/full/333/6050/1750/DC1  
Materials and Methods

Figs. S1 to S3  
Tables S1 to S3  
References (32–34)

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# African Wild Ungulates Compete with or Facilitate Cattle Depending on Season

Wilfred O. Odadi,<sup>1\*</sup> Moses K. Karachi,<sup>2</sup> Shaukat A. Abdulrazak,<sup>3</sup> Truman P. Young<sup>1,4\*</sup>

Savannas worldwide are vital for both socioeconomic and biodiversity values. In these ecosystems, management decisions are based on the perception that wildlife and livestock compete for food, yet there are virtually no experimental data to support this assumption. We examined the effects of wild African ungulates on cattle performance, food intake, and diet quality. Wild ungulates depressed cattle food intake and performance during the dry season (competition) but enhanced cattle diet quality and performance during the wet season (facilitation). These results extend our understanding of the context-dependent–competition-facilitation balance, in general, and are critical for better understanding and managing wildlife-livestock coexistence in human-occupied savanna landscapes.

Savannas cover ~20% of the global land surface and occur more extensively in Africa than in any other continent (1). These ecosystems vitally support large proportions of the world's human, livestock, and wildlife populations (1). In savannas worldwide—and especially in the ungulate-rich African savannas (2)—domestic and wild herbivores commonly share food and other resources. Such sharing of habitat by guilds of herbivores can result in varied interactions ranging from negative (competition) to positive (facilitation) (3).

In savanna rangelands worldwide, management decisions are based on the supposition that wild fauna and domestic stock compete for forage resources, but there are little experimental data to support this assumption. For competition to occur, a shared resource must be in short supply, and its joint exploitation by two or more herbivore species must lead to reduced performance (such as survivorship, fecundity, or weight gain) of at least one species (3). Although changes in several factors—including food availability, quality, and intake—can alter herbivore performance, a change in one or more of these factors without an effect on performance of the species involved is not in itself evidence of competition (3).

The food habits of domestic and wild ungulates—and dietary overlap between these herbivore guilds—have been studied widely (4–7). In addition, the effects of wildlife on livestock food habits and foraging patterns have been documented (8, 9). However, the critical assessment of whether or not wild ungulates alter livestock

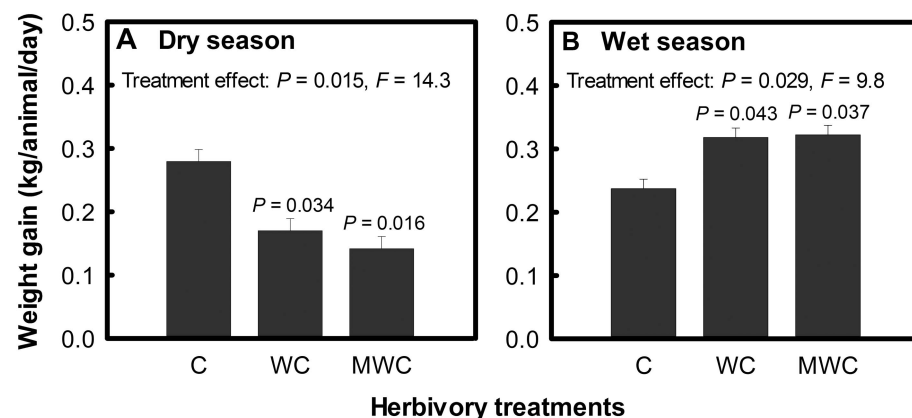
performance has rarely been carried out, and never in a tropical savanna biome. Yet, such an appraisal is urgently needed to guide management efforts toward enhancing wildlife-livestock coexistence in human-occupied landscapes, especially in the African savanna biome, which hosts the last remnants of an intact large herbivore fauna.

We used a controlled replicated experiment to assess whether or not medium-sized wild ungulates (>20 kg; plains zebra *Equus burchelli*, Grevy's zebra *E. grevyi*, African buffalo *Syncerus caffer*, eland *Tragelaphus oryx*, hartebeest *Acelaphus buselaphus*, oryx *Oryx gazella*, and Grant's gazelle *Gazella granti*) and megaherbivores (African elephant *Loxodonta africana* and giraffe *Giraffa camelopardalis*) compete with cattle in a savanna ecosystem in Kenya. Specifically, we hypothesized that if these ungulates compete with cattle, food availability and quality should decrease in the shared foraging areas, resulting in reductions in food intake, diet quality, and most importantly,

weight gain of cattle. Additionally, we hypothesized that these effects would reduce after experimental exclusion of megaherbivores, especially elephants, because of their documented seasonal resource overlap with cattle (10). Last, we expected greater competitive effects during the dry season, when food is less abundant.

We compared cattle weight gain, organic matter food intake (OMI), diet selection, dietary digestible organic matter (DOM), crude protein (CP), DOM/CP ratio, and herbage cover in treatment plots that cattle accessed exclusively and those they shared with wild ungulates, excluding or including megaherbivores, during wet and dry seasons (11). Consistent with our hypothesis, cattle experienced depressed weight gain when they shared foraging areas with wild herbivores during the dry season (Fig. 1A), providing evidence of competition. In contrast, this pattern was reversed in the wet season, with increased cattle performance in the shared treatments (Fig. 1B), demonstrating a surprising facilitative interaction that was nearly great enough to overcome the preceding season's competition.

Competition was associated with depressed food intake in the shared treatments (Table 1), which corresponded with reductions in cover and selection by cattle of *Pennisetum stramineum* (Fig. 2, A to C), suggesting that wildlife and cattle competed for this grass. For all other major herbaceous species, cover was not significantly different among herbivore treatments (table S1). Relative bites on *Themeda triandra* increased in the treatment accessible to all three guilds of herbivores during wet season, but no other major plant species showed treatment effects on either relative bites or selection by cattle (tables S2 and



**Fig. 1.** Weight gain of cattle within treatment plots they accessed exclusively (C) and those they shared with wild herbivores, with megaherbivores absent (WC) or present (MWC). (A) During dry season. (B) During wet season. Error bars are SEM ( $n = 3$  experimental blocks). The  $P$  values over the WC and MWC treatments are for comparisons with treatment C (Tukey's post hoc test).

<sup>1</sup>Mpala Research Centre, Post Office Box 555, Nanyuki 10400, Kenya. <sup>2</sup>Natural Resources Department, Egerton University, Post Office Box 536, Egerton 20115, Kenya. <sup>3</sup>National Council for Science and Technology, Post Office Box 30623, Nairobi 00100, Kenya. <sup>4</sup>Department of Plant Sciences, University of California, Davis, CA 95616, USA.

\*To whom correspondence should be addressed. E-mail: woodadie@yahoo.com (W.O.O.); tpyoung@ucdavis.edu (T.P.Y.)

S3). The importance of *P. stramineum* in cattle nutrition during dry season is further underscored by a strong positive correlation between its selection index and cattle weight gain (fig. S1). However, the exact mechanism through which decreased selection of *P. stramineum* depressed the overall food intake by cattle is unclear; there were no significant treatment differences in diet quality during the dry season (Table 1).

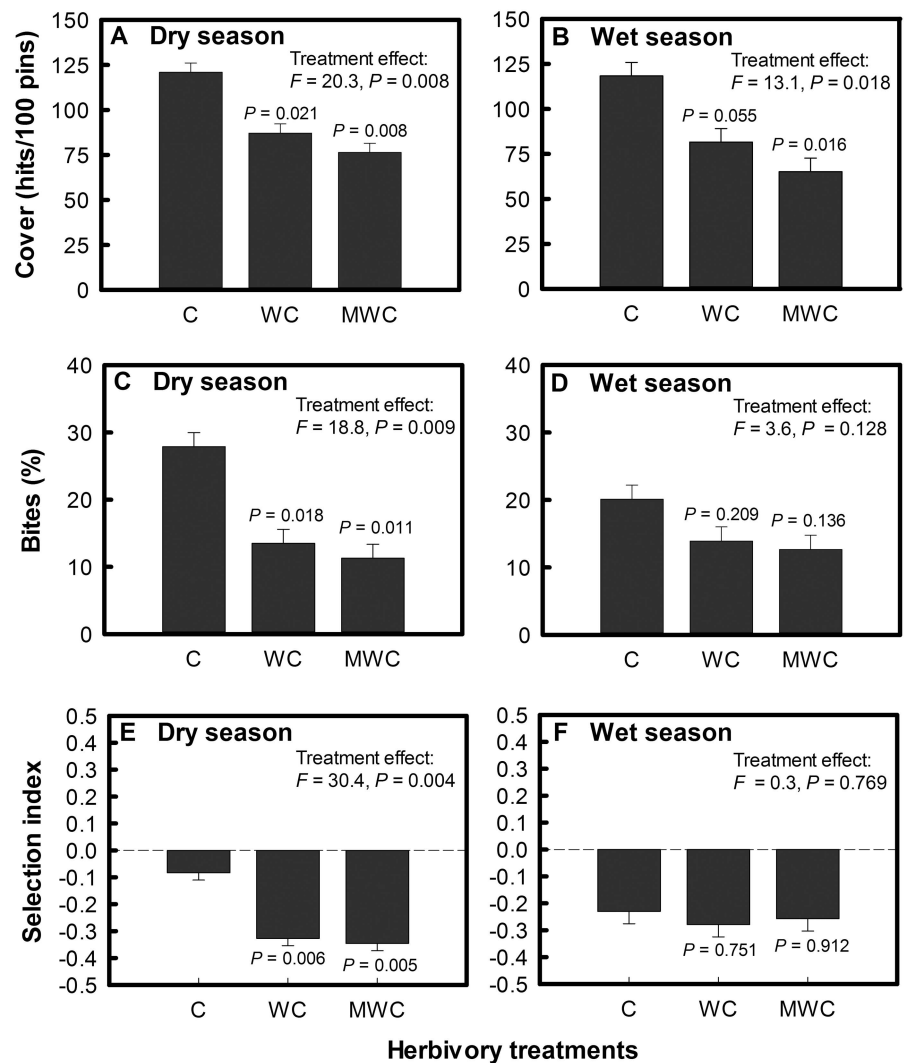
Because several wild ungulate species accessed the shared study plots, it is not possible to directly attribute the competitive effects demonstrated here to any specific herbivore species. However, because exclusion of megaherbivores did not alter the measured parameters (Figs. 1 and 2 and Tables 1 and 2), we attribute these effects largely to medium-sized herbivores. In particular, these competitive effects are largely attributable to plains zebras because they are by far the most abundant wild ungulates in the study system (12, 13) and have a high dietary overlap with cattle (6, 7). Megaherbivores did not significantly exacerbate competitive effects, probably because elephants consume minimal amounts of grass during dry periods (10).

Facilitation in the wet season was associated with enhanced dietary CP and DOM/CP balance in cattle after shared grazing with wild ungulates (Table 1). Enhanced dietary CP improves cattle performance even in the wet season, when forage quality is generally high (14). Dietary DOM/CP ratio indexes the balance of nutrients available to rumen microbes and correlates with performance (15). In ruminants, a DOM/CP ratio of 4:1 is considered optimal, and performance decreases with increasing deviation from this optimum (15, 16). In our experiment, cattle diet DOM/CP ratio was 11 to 17% closer to the optimum ratio in the presence of wild ungulates than in their absence (Table 1). Consistent with our findings, cattle have been shown to be responsive to relatively small changes in dietary DOM/CP ratio (16). We suspect that improved cattle nutrition in the presence of wildlife during the wet season relates to enhanced access to higher-quality food items, driven by the observed decrease in the cover of standing dead grass stems in the shared treatments (Table 2). This mechanism of facilitation is partly supported by a strong negative correlation between weight gain of cattle and the cover of dead grass stems (fig. S2).

We propose that the facilitative effects demonstrated in the wet season are driven both by increased ungulate density (in the shared plots), which stimulates herbage growth and enhances forage quality in such systems during rainy periods (17), and by a unique facilitative function of zebras. Specifically, we attribute the observed decreased cover of dead grass stems in the shared foraging areas (Table 2) to zebras because of the morphophysiological adaptations of their digestive system to cropping and processing fibrous grass stems (18, 19). We posit that this particular pathway to facilitation is analogous to the decades-old postulated facilitative role of zebras

**Table 1.** Cattle food intake and diet quality (means  $\pm$  SEM,  $n = 3$  experimental blocks) in plots cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores. Column means listed in bold fonts and bearing different superscripts are statistically different ( $P < 0.05$ , Tukey's post hoc test). Dashes indicate data not collected.

	OMI (kg/day)	DOM (%)	CP (%)	DOM/CP ratio
<i>Dry season</i>				
C	<b>4.6<sup>a</sup> <math>\pm</math> 0.03</b>	57.1 $\pm$ 0.22	8.1 $\pm$ 0.33	7.1 $\pm$ 0.27
WC	<b>4.3<sup>b</sup> <math>\pm</math> 0.06</b>	56.5 $\pm$ 0.27	7.9 $\pm$ 0.02	7.2 $\pm$ 0.02
MWC	<b>4.3<sup>b</sup> <math>\pm</math> 0.04</b>	56.9 $\pm$ 0.39	8.0 $\pm$ 0.11	7.1 $\pm$ 0.13
F	<b>11.1</b>	0.7	0.2	0.1
P	<b>0.02</b>	0.55	0.61	0.94
<i>Wet season</i>				
C	—	59 $\pm$ 0.01	<b>10.6<sup>a</sup> <math>\pm</math> 0.08</b>	<b>5.8<sup>a</sup> <math>\pm</math> 0.05</b>
WC	—	58.4 $\pm$ 0.28	<b>10.9<sup>ab</sup> <math>\pm</math> 0.16</b>	<b>5.6<sup>b</sup> <math>\pm</math> 0.08</b>
MWC	—	58.6 $\pm$ 0.41	<b>11.1<sup>b</sup> <math>\pm</math> 0.15</b>	<b>5.5<sup>b</sup> <math>\pm</math> 0.08</b>
F	—	0.8	<b>10.1</b>	<b>33.8</b>
P	—	0.5	<b>0.03</b>	<b>0.003</b>



**Fig. 2.** Availability and consumption of *Pennisetum stramineum* by cattle in treatment plots they accessed exclusively (C) and those they shared with wild herbivores, with megaherbivores absent (WC) or present (MWC) during dry and wet seasons. (A and B) Cover. (C and D) Relative bites. (E and F) Selection index. Error bars are one SEM ( $n = 3$  experimental blocks). The  $P$  values over the WC and MWC treatments are for comparisons with treatment C (Tukey's post hoc test).

**Table 2.** Cover of different grass parts (means  $\pm$  SEM,  $n = 3$  experimental blocks) in plots cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores. Column means listed in bold fonts and bearing different superscripts are statistically different ( $P < 0.05$ , Tukey's post hoc test).

	Live leaves (hits/100 pins)	Dead leaves (hits/100 pins)	Live stems (hits/100 pins)	Dead leaves (hits/100 pins)
<i>Dry season</i>				
C	88.7 $\pm$ 9.1	147.6 $\pm$ 7.0	15.4 $\pm$ 2.9	76.6 $\pm$ 8.7
WC	75.9 $\pm$ 3.3	131.5 $\pm$ 6.1	18.2 $\pm$ 2.2	76.1 $\pm$ 5.6
MWC	80.7 $\pm$ 16.1	139.4 $\pm$ 31.8	10.9 $\pm$ 1.8	62.4 $\pm$ 12.2
F	0.5	0.2	1.8	1.4
P	0.7	0.8	0.3	0.3
<i>Wet season</i>				
C	181.1 $\pm$ 12.3	64.8 $\pm$ 6.1	33 $\pm$ 5.5	<b>42.1<sup>a</sup> <math>\pm</math> 2.8</b>
WC	175.6 $\pm$ 4.6	58.2 $\pm$ 1.3	27.9 $\pm$ 4.6	<b>33.7<sup>b</sup> <math>\pm</math> 2.7</b>
MWC	160.8 $\pm$ 6.6	61.8 $\pm$ 8.9	21.5 $\pm$ 4.2	<b>31.6<sup>b</sup> <math>\pm</math> 2.2</b>
F	1.4	0.3	1.2	<b>18.1</b>
P	0.3	0.8	0.4	<b>0.01</b>

in catalyzing a “grazing succession” that culminates into enhanced access to high-quality forage by native ruminants in the Serengeti ecosystem (18, 20, 21).

We suggest that the net effects of species interactions in all ecological systems are a result of both competitive and facilitative effects, with the net effect being the one that is quantitatively greater. One paradigm of interspecific facilitation is that it tends to be greater in more stressful environments (22). This paradigm arose from plant facilitation research in which the main mechanism of facilitation was lessening of environmental stress (24). Our results suggest that other types of facilitation will produce different patterns, depending on the underlying mechanism. Here, the net facilitation was during superficially less “stressful” conditions. Similarly, in another examination of trophic interactions in this study system, it has been suggested that competition is greater in sites characterized by lower productivity (25). We extend this pattern to demonstrate that a decrease in competition occurs with temporal as well as spatial increases in productivity and that this trend can be so great that it results in not simply less competition but actual facilitation between two key herbivore guilds. The net effect of these competitive and facilitative forces will be driven by the relative proportions of “dry” and “wet” times throughout the year and probably by additional factors, such as herbivore densities and ecosystem productivity.

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#### Supporting Online Material

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Tables S1 to S6  
References (26–28)

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## Disentangling the Drivers of $\beta$ Diversity Along Latitudinal and Elevational Gradients

Nathan J. B. Kraft,<sup>1,2\*</sup> Liza S. Comita,<sup>3,4</sup> Jonathan M. Chase,<sup>5</sup> Nathan J. Sanders,<sup>6,7</sup> Nathan G. Swenson,<sup>8</sup> Thomas O. Crist,<sup>9</sup> James C. Stegen,<sup>10,11</sup> Mark Vellend,<sup>1,12</sup> Brad Boyle,<sup>13</sup> Marti J. Anderson,<sup>14</sup> Howard V. Cornell,<sup>15</sup> Kendi F. Davies,<sup>16</sup> Amy L. Freestone,<sup>17</sup> Brian D. Inouye,<sup>18</sup> Susan P. Harrison,<sup>15</sup> Jonathan A. Myers<sup>5</sup>

Understanding spatial variation in biodiversity along environmental gradients is a central theme in ecology. Differences in species compositional turnover among sites ( $\beta$  diversity) occurring along gradients are often used to infer variation in the processes structuring communities. Here, we show that sampling alone predicts changes in  $\beta$  diversity caused simply by changes in the sizes of species pools. For example, forest inventories sampled along latitudinal and elevational gradients show the well-documented pattern that  $\beta$  diversity is higher in the tropics and at low elevations. However, after correcting for variation in pooled species richness ( $\gamma$  diversity), these differences in  $\beta$  diversity disappear. Therefore, there is no need to invoke differences in the mechanisms of community assembly in temperate versus tropical systems to explain these global-scale patterns of  $\beta$  diversity.

Some of the most striking and frequently documented patterns in ecology are that species richness in local communities generally declines with increasing latitude and elevation, such that the diversity of many clades peaks in lowland, tropical areas (1, 2). The mech-

anisms underlying these gradients are often difficult to distinguish because multiple processes operating at multiple scales may govern geographic variation in diversity (3). For example, declines in diversity with elevation and latitude could result from deterministic community