

Facilitation between bovids and equids on an African savanna

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ABSTRACT

Background: Equids, especially zebras and donkeys, and cattle (bovids) share habitats in many savanna ecosystems in Africa. The issue of competition for food between these ungulate guilds remains largely unresolved. Resolving it will provide insights into how wild zebra are likely to interact with cattle on shared landscapes and suggest best practices for cattle owners who must decide whether to tolerate wild ungulates, some of which are severely threatened (e.g. Grevy's zebra, *Equus grevyi*).

Aim: Determine whether an equid and a bovid compete in a semi-arid savanna in Kenya.

Organisms: Boran cattle (*Bos indicus*) and donkeys (*Equus africanus asinus*) – the latter as surrogates for zebras.

Methodology: Experiments to measure performance (weight gains), bite rates, diet quality (digestible organic matter and crude protein), and gastrointestinal worm burdens (parasite egg count per unit weight of faeces) of the two ungulate species when herded separately (single species) or together (mixed species). We used two stocking levels: low-density (one animal per 7 ha), a level typical of commercial ranchers; and high-density (one animal per 2 ha), a level typical of pastoral herders.

Principal findings: When herded together, both species gained more weight, had higher bite rates (especially at low stocking density), and selected diets with a more favourable balance between digestible organic matter and crude protein, than when herded separately. In addition, parasite egg output in faeces of donkeys was reduced by 14–35% following shared foraging with cattle.

Conclusion: Cattle (a ruminant) and donkeys (hindgut fermenters, closely related to zebras) showed no evidence of competition with each other. Rather, our results show a facilitative, rather than a competitive, interaction between them.

Keywords: bite rate, bovids, cattle, competition, crude protein, digestible organic matter, donkeys, equids, facilitation, gastrointestinal parasites, grazing strategies, grazing succession, mutualism, weight gain, zebras.

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INTRODUCTION

African savannas host diverse assemblages of large mammalian herbivores. Conspicuous among these are bovids and equids, the most dominant medium-sized grazing herbivores since the Paleocene (Duncan *et al.*, 1990). When herbivore guilds or species share habitats, they can compete with, facilitate or have no effect on each other, depending on the availability of forage resource and the extent to which they share those resources. Herbivores are assumed to compete when a resource is in short supply and its joint use by two or more species (or guilds) results in reduced performance (measured as fecundity, survivorship or growth) of at least one of the interacting species (Begon *et al.*, 1990; Prins, 2000). Yet bovids and equids have co-existed for millions of years (Kurten and Anderson, 1980; Prothero and Schoch, 1980; MacFaden, 1992). Facilitation, the opposite of competition, may occur when one species modifies its habitat to the benefit of another species, such as through improved food intake or forage quality (Prins, 2000; Arsenault and Owen-Smith, 2002), resulting in enhanced performance. In the special case of mutualism, each species' actions benefit the other. What makes the African savanna ecosystem so intriguing for evaluating the degree to which competition, facilitation or even mutualism structures the grazing community is that it is inhabited by ungulates that have evolved two very different mechanisms for extracting energy and nutrients from vegetation. Both mechanisms rely on fermentation by microbes to break down fibrous material, but in the artiodactyls (even-toed ungulates) fermentation takes place in the rumen, which is located before the stomach, whereas in the perissodactyls (odd-toed ungulates) it takes place in the caecum, which is located after the stomach (Duncan *et al.*, 1990). The implications of this evolutionary divergence on herbivore co-existence as well as the economic value resulting from changes in performance of ungulates on African landscapes with and without humans and their livestock are likely to be profound.

Altered performance of herbivores is often associated with variations in food intake, diet selection/quality, and gastrointestinal parasite burden. The amount of nutrients a grazer harvests relative to its requirements determines the ability of the animal to convert critical nutrients, particularly crude protein and energy, for performance. Thus, maximization of net intake of energy and other nutrients is often a primary goal of foraging individuals. Dietary digestible organic matter, crude protein contents, and the digestible organic matter to crude protein ratio are the major nutritional determinants of animal performance, as they influence voluntary food intake (Zimmermann, 1980; Kidane, 2005). Gastrointestinal parasites affect the rates of growth, fecundity, and even cause mortality in mammalian herbivores through increased loss of nitrogen, damage to gastrointestinal tissue, and loss of appetite (Coop and Kyriazakis, 1999; Fleurance *et al.*, 2005). In addition, the level of nutrition can influence the susceptibility of a host to parasite infection (Van Houtert and Sykes, 1996). Thus, parasites can mediate functional interactions between ungulates.

Bovids and equids possess contrasting digestive systems, with bovids (ruminants) having systems of fermentation chambers in the foregut, and equids having hindgut fermentation systems (Duncan *et al.*, 1990). As a result, non-ruminants such as zebra can tolerate foods of lower quality than can ruminants because the former have high throughput rate and are thus able to process a large quantity of food. In addition, equids possess powerful sets of lower and upper incisors and are more adapted to cutting fibrous stems, as opposed to ruminants, which do not have upper incisors. It has been suggested that these contrasting dentition and digestive systems may promote resource partitioning and co-existence between these herbivore guilds (Duncan *et al.*, 1990), but the question remains whether, in the

long term, equids would outcompete ruminants because in savannas in particular recurrent droughts often cause prolonged periods of poor forage quality.

In the 1960s, it was hypothesized that in the Serengeti zebras, with their high tolerance of stems, lead a grazing succession in which they modify the herb layer of the area to which they move by trampling and increasing relative frequency of leaf by disproportionately selecting stems, thereby improving the vegetation structure for the ruminant wildebeest that follow (Gwynne and Bell, 1968). Thus, the relationship between a hindgut fermenter and a ruminant in such a grazing succession is thought to be facilitative rather than competitive (Gwynne and Bell, 1968). Yet, in many African savanna rangelands, there is a widespread belief among landholders, even those that maintain low stocking levels of cattle, that zebras and cattle compete intensely for forage resources (Mizutani, 1999; Georgiadis *et al.*, 2003). Despite half a century of opposing views, scientific assessments of whether equids (e.g. zebras, asses, and donkeys) and large ruminants (such as cattle or wildebeests) compete for food or facilitate one another have been limited. And these assessments have been observational and not experimental in nature.

To determine whether cattle and equids compete, we studied weight gains, bite rates, diet quality, and gastrointestinal worm burdens of cattle and donkeys (as surrogates for zebras) grazed separately (single species) or together (mixed species) on a natural rangeland in northern Kenya. To assess the effect of grazing intensity, we ran the experiment at high and low stocking densities, with animal density at each stocking level being kept constant between single and mixed species combinations by varying plot size. The low stocking level was chosen to mimic average/normal total stocking levels where East African commercial ranchers believe resources start to become limiting (M. Littlewood, personal communication). We would have preferred to use zebras rather than donkeys as the representative equids, but this was not practicable because zebras are much more difficult to manipulate for live weight measurements, are harder to observe without disturbing them and because, under Kenyan law, zebras, like other wild animals, cannot be owned except by the State. We used experienced local herdsmen to keep the groups of animals separated and at the required stocking densities.

We hypothesized that if cattle and donkeys compete, weight gain of either or both species will be lower when they forage together than when each forages alone in single species herds. In addition, either or both species will have decreased bite rates, a poorer quality diet (reduced digestible organic matter and crude protein, and increased digestible organic matter to crude protein ratio), and increased gastrointestinal worm burden following shared foraging. Furthermore, we expected these competitive effects to be more pronounced at high stocking density, where food availability per individual is less abundant than at low stocking levels.

METHODS AND MATERIALS

The experiment was carried out in accordance with Kenyan laws and was approved by the Ministry of Education, Science, and Technology. All animal use conformed to the provisions of the Prevention of Cruelty to Animals Act Cap 360 of the laws of Kenya, and the regulations established by the Kenya Veterinary Board.

Study area

The study was conducted at Mpala Research Centre (0°17'N, 36°52'E, 1800 m above sea level) situated in Laikipia North District in Rift Valley Province, Kenya. The research centre is located within the 20,000-ha Mpala Research Centre and Conservancy, which also encompasses Mpala Ranch. The area experiences a mean annual rainfall of 500–600 mm. Rainfall generally peaks in March–May, July–August, and October–November, with marked inter-annual variation.

The study site is located within a fairly homogeneous black cotton soil ecosystem. The dominant vegetation is bushed grassland. The overstory vegetation is comprised principally of *Acacia drepanolobium* Sjøstedt, while perennial grasses dominate the herb-layer vegetation. Several medium-sized wild herbivores frequent the study site, including plains zebra, Grevy's zebra, hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), oryx (*Oryx gazella*), Grant's gazelle (*Gazella granti*), and buffalo (*Syncerus caffer*), but all occur in low to very low densities and the herders prevented interaction with our experiment. Cattle are the primary livestock species in the study site. On average, approximately 2000–3000 head of cattle are maintained on Mpala Ranch. Sheep (*Ovis aries*) and donkey are also present, but in much smaller numbers. The management of the farm ensured that these animals did not interfere with the experiment.

Study period, experimental plots, and animals

The trial was conducted over a period of 12 weeks during July to October 2006. Total rainfall during the trial period was approximately 107 mm. Based on the De Wit (De Wit, 1960) approach for evaluating competition, we created treatments accessed by cattle and donkeys as single or mixed species herds at low (one animal per 7 ha) and high (one animal per 2 ha) stocking densities. Each stocking level was kept constant between combination treatments by varying plot size while keeping animal numbers of each species constant (Table 1). This was a landscape-scale experiment comprising six large plots (20–175 ha) and covering a total area of 450 ha (Table 1). At such a scale, replication was not feasible (Werner, 2005), and thus our experimental design might at first appear to constitute pseudo-replication. But this

Table 1. Experimental design showing numbers of animals, combinations of species, plot sizes, and stocking densities

	Number of cattle	Number of donkeys	Plot size (ha)
<i>Low stocking density</i> (1 animal per 7 ha)			
Single species (cattle)	15	0	105
Single species (donkeys)	0	10	70
Mixed	15	10	175
<i>High stocking density</i> (1 animal per 2 ha)			
Single species (cattle)	15	0	30
Single species (donkeys)	0	10	20
Mixed	15	10	50
Totals	60	40	450

concern was taken into account in selection of the experimental site, as well as in the data collection and analysis. In particular, we made our study plots as similar as possible by establishing them as close to one another as possible, and on a homogeneous site with similar precipitation, soil, and vegetation characteristics. This homogeneity was confirmed by a vegetation survey conducted a week before the trial, which did not show any significant ($P > 0.08$) vegetation differences among plots (Table 4). Therefore, a vegetation difference at the onset of the experiment was of no significance in understanding treatment effects on measured parameters.

Experimental animals were 60 Boran heifers aged 3–5 years and weighing 319 ± 33 kg (mean \pm S.D.), and 40 adult female donkeys (> 2 years) weighing 156 ± 32 kg, at the beginning of the experiment. At the start of the trial, the animals were randomly grouped by species into four equal-sized herds: two single species herds for each ungulate species (15 animals per herd and 10 animals per herd for cattle and donkeys, respectively), and two mixed species herds (each comprising 15 cattle and 10 donkeys). The animals were ear-tagged for identification and allocated to the six study plots (Table 1). The mean live weights of our test animals translate to mean metabolic weights (i.e. body mass^{0.75}) of ~ 75 kg and ~ 44 kg for cattle and donkeys, respectively. Therefore, in terms of metabolic weight, our donkeys were about 41% lighter than cattle. However, it is well known that food intake is 40–50% higher in equids than in bovids (Duncan *et al.*, 1990). Specifically, it has been shown that donkeys, which are 100% lighter than cattle, in terms of live body weight, remove nearly 100% more vegetation than cattle (Bagchi *et al.*, 2004). We therefore believe that based on the well-documented differential food intake between cattle (bovids) and donkeys (equids), our design ensured that grazing pressure was equal between single and mixed species treatments for both species. The ratio of 15 cattle (4785 kg) to 10 donkeys (1560 kg) maintained in each mixed species plot was based on the biomass density estimates for cattle ($2459 \text{ kg} \cdot \text{km}^{-2}$) and zebras ($792 \text{ kg} \cdot \text{km}^{-2}$) on most livestock properties in the Laikipia region (Georgiadis *et al.*, 2007).

Treatment herds accessed study plots for 7 h each day starting at 08.00–09.00 h, in keeping with the local grazing time allowance for livestock. They were kept in separate bomas (corrals) proximate to the study plots during the night. Herds were walked to and from the bomas along dirt roads lacking vegetation to avoid feeding outside their plots. Throughout the trial, experienced local Laikipia Maasai and Turkana traditional pastoral herders herded the experimental animals. Their unique rapport with livestock, indigenous knowledge, good herding practices, and trustworthiness essentially ensured that experimental herds foraged only within their respective plot boundaries. Drinking water was provided at the bomas. Cattle were sprayed for tick control once every week. No experimental animals were dewormed during the course of the study.

Baseline vegetation survey

We assessed the pre-trial vegetation cover in each plot at four random locations about 1 week before the trial began. Each location consisted of four 25-m transects radiating from a fixed stake, with an equal angle ($\sim 90^\circ$) between transects. On each transect, we placed a 1-m long pin perpendicular to the ground 25 times at one-pace (~ 1 -m) intervals, mimicking a grazing track. At each sampling point, all pin hits on herbage were recorded. We calculated the absolute herb-layer vegetation canopy cover at each location as the total number of pin–herbage contacts per 100 pins.

Focal observations

We randomly selected five individuals (by species) from the experimental animals in each single species plot and four individuals in each mixed species plot and used them as focal animals for feeding observations, diet quality estimation, and parasite egg counts over the course of the study. Focal observations were carried out once every 1–2 weeks during the trial. Study plots were sampled on different days in a sequence randomly predetermined at the start of the experiment. All observations were conducted between 09.00 and 11.00 h when most animals were actively foraging. During each survey, individual focal animals in the sampled plot were successively observed in three (in mixed species plots) or four (in single species plots) non-consecutive 5-min sessions for the number of bites taken after allowing a settling period of 10–20 min following entry of the animals into the plot. The time interval between observations was approximately 2 min. All observations were made as close as possible (< 4 m) to the focal animals. Bite rate (bites per minute) was calculated for each focal animal per survey, then averaged over the trial period.

Diet quality characterization

Grab samples of fresh dung voided by individual focal animals were collected weekly. The samples were sun-dried and pooled for each focal animal every 3 weeks. The samples were taken to the Kenya Agricultural Research Institute (KARI), Naivasha, for estimation of dietary crude protein and digestible organic matter contents using the near infrared reflectance spectroscopy (NIRS) technique (Stuth *et al.*, 2003a). Dietary crude protein and digestible organic matter contents were predicted using calibration equations developed for each of the two ungulates in sub-Saharan African rangelands (Stuth *et al.*, 2003b; Kidane *et al.*, 2008). Data were averaged per individual test animal for the entire sampling period.

Parasite egg counts

Gastrointestinal parasite eggs were counted from faecal grabs of the focal animals in each plot (four animals per species in mixed herds, and five animals per species in single herds). Grab samples were collected once at the start of the experiment (baseline) and once every 2–3 weeks thereafter. In total, five samples were collected from each focal animal during the course of the experiment. On collection, samples were first preserved in a cool box (field) and later in a refrigerator (laboratory) and analysed within 3 days. Each sample was examined for parasite egg output (eggs per gram of faeces) in 2–3 replicates using the McMaster technique (Ministry of Agriculture, Fisheries and Food, 1986). Because treatment groups did not share foraging areas and bomas, there was no cross-infection between groups.

Live weight measurements

All the experimental animals (60 heifers and 40 donkeys) were weighed once every 2–3 weeks at 07.00–08.00 h after overnight starvation without feed or water. Initial live weights of the animals were measured using a fixed platform weighing scale located >5 km from the experimental site. Subsequent measurements were carried out using a hanging scale weighing system located at the boma site. All measurements were made to the nearest 1 kg. Average daily weight gain was calculated for each test animal for the entire trial period.

Data analysis

Individual animals ($n = 15$ cattle and/or 10 donkeys per plot for live weight change; $n = 4$ cattle and/or 4 donkeys per plot for all other animal measurements) were used as experimental units. For all animal data, we used a hierarchical mixed effects analysis of variance, with individual animals nested within treatment plots, to test for the effects of combination (single vs. mixed species), species (cattle vs. donkeys), and stocking density (low vs. high), and all interaction terms. Because this was a landscape-level pseudo-replicated experiment, the use of the mixed effects ANOVA model was preferable as it eliminated any plot-influenced variations and enabled detection of treatment-induced differences in the measured parameters.

Because the combination \times species interaction was significant for parasite egg count, this variable was analysed separately for each species. Pre-treatment faecal parasite egg output tended to differ between herds and was included as a covariate in the analysis of parasite data. For baseline vegetation, individual sampling locations ($n = 4$ per plot) were nested within plots. All percentage data were arcsine-transformed prior to analysis. All analyses were performed using SYSTAT v.9 statistical software (SPSS Inc., 1998).

RESULTS

Weight change

The weight gains of cattle and donkeys across treatment plots are presented in Fig. 1. Average daily weight gain was greater in cattle (0.24 kg; 95% confidence limits [CL] 0.21–0.28 kg) than in donkeys (0.16 kg; 95% CL 0.12–0.20 kg). Weight gain was significantly affected by mixed grazing, with cattle and donkeys gaining on average 60% and 51% more weight, respectively, under mixed species grazing than under single species grazing at both levels of stocking density. In addition, there was a significant species \times stocking rate interaction with cattle ($P = 0.005$), but not donkeys ($P > 0.90$), performing

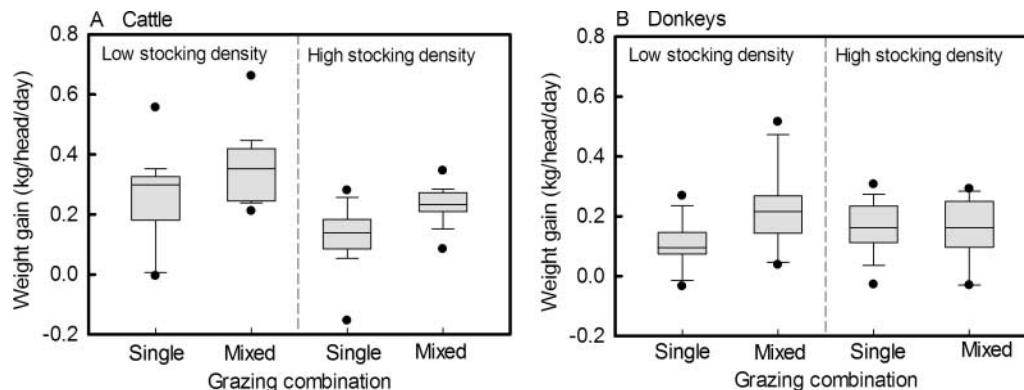


Fig. 1. Box-and-whisker plots of live weight gains of (a) cattle and (b) donkeys herded as single or mixed species ($n = 15$ cattle and/or 10 donkeys). The figures show median weight gains (lines), 25% to 75% quartiles (boxes), and ranges (whiskers). Significant effects were observed for combination ($F_{1,62} = 8.0$, $P < 0.006$), species ($F_{1,62} = 7.6$, $P = 0.008$), stocking density ($F_{1,62} = 9.9$, $P = 0.009$), and species \times stocking density ($F_{1,62} = 4.2$, $P = 0.045$).

better at low than at high stocking density. All other interaction terms were not significant ($F < 3.0$, $P > 0.10$).

Bite rates

Average bite rate was higher in cattle (36.0 bites per minute; 95% CL 35.2–36.5) than in donkeys (31.1 bites per minute; 95% CL 29.7–32.5). Both ungulates increased bite frequency by up to 17% when they shared land at low ($P = 0.008$), but not at high ($P > 0.90$), stocking density (Fig. 2).

Diet quality

Digestible organic matter contents of the diets selected by cattle and donkeys averaged 51.8% (95% CL 51.2–52.3%) and 53.0% (95% CL 52.1–54.0%), respectively. Combination \times species \times stocking density interaction was significant for dietary digestible organic matter content, with donkeys selecting a less digestible diet when herded with cattle than when grazed as a single species at low stocking density (Table 2). In addition, donkey diet was more digestible than cattle diet only when the two ungulates foraged separately at low stocking density.

Cattle and donkeys selected diets with an average crude protein content of 7.7% (95% CL 7.4–8.0%) and 9.2% (95% CL 8.7–9.6%), respectively. Dietary crude protein was not affected by grazing combination, but was significantly higher in donkeys than in cattle, and higher at low than at high stocking density (Table 2). The digestible organic matter to crude protein ratio of the diets selected by cattle and donkeys averaged 6.9 (95% CL 6.6–7.2) and 5.9 (95% CL 5.6–6.2), respectively. For both species, this ratio was reduced significantly following combined grazing (Table 2). In addition, the digestible organic matter to crude

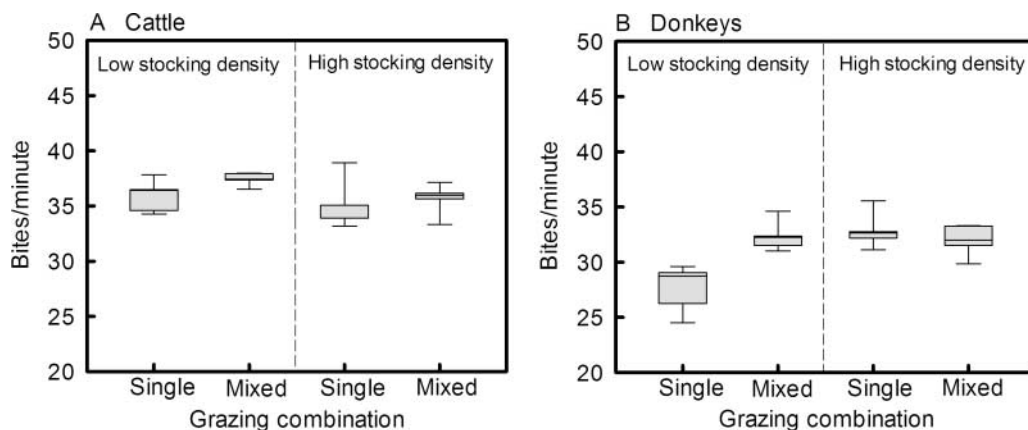


Fig. 2. Box-and-whisker plots of bite rates of (a) cattle and (b) donkeys herded as single or mixed species ($n = 5$ cattle and/or 5 donkeys for single species plots, and $n = 4$ cattle and/or 4 donkeys for mixed species plots). The figures show median bite rates (lines), 25% to 75% quartiles (boxes), and ranges (whiskers). Significant effects were observed for combination ($F_{1,21} = 5.7$, $P = 0.027$), species ($F_{1,21} = 63.8$, $P < 0.001$), combination \times stocking density ($F_{1,21} = 7.6$, $P = 0.012$), and species \times stocking density ($F_{1,21} = 9.1$, $P = 0.007$).

Table 2. Quality of diets selected by cattle and donkeys grazed as mixed or single species at different stocking densities (mean values with 95% confidence limits in parentheses)

	Low stocking density		High stocking density	
	Single species	Mixed species	Single species	Mixed species
<i>DOM (%)</i>				
Cattle	51.1 (50.2, 52.0)	50.9 (49.4, 52.4)	53.0 (52.3, 53.7)	52.0 (50.6, 53.5)
Donkeys	55.2 (53.4, 56.9)	50.2 (48.4, 52.1)	53.1 (51.6, 54.5)	52.9 (50.9, 54.9)
Significant effects	C ($F_{1,21} = 11.1, P = 0.003$), S ($F_{1,21} = 4.4, P = 0.049$), C × S × D ($F_{1,21} = 6.7, P = 0.017$)			
<i>CP (%)</i>				
Cattle	8.4 (7.8, 9.1)	8.0 (7.2, 8.8)	6.7 (6.4, 7.0)	7.4 (7.1, 7.8)
Donkeys	9.5 (8.5, 10.5)	10.0 (9.1, 11.0)	8.3 (7.7, 8.9)	8.9 (8.0, 9.9)
Significant effects	S ($F_{1,21} = 44.7, P < 0.001$), D ($F_{1,21} = 25.1, P < 0.001$)			
<i>DOM:CP ratio</i>				
Cattle	6.2 (5.7, 6.6)	6.5 (5.9, 7.1)	8.0 (7.5, 8.4)	7.0 (6.6, 7.5)
Donkeys	6.0 (5.3, 6.7)	5.1 (4.7, 5.6)	6.5 (6.0, 7.0)	6.0 (5.5, 6.6)
Significant effects	C ($F_{1,21} = 6.7, P = 0.017$), S ($F_{1,21} = 31.6, P < 0.001$), D ($F_{1,21} = 31.0, P < 0.001$)			

Note: DOM = digestible organic matter content, CP = crude protein content. Effects are C = combination, S = species, D = stocking density. For each species, $n = 5$ and 4 for single and mixed species plots respectively.

protein ratio was lower at low than at high stocking density, and lower in the donkey diet than the cattle diet.

Parasite egg output

Worms recovered in the faeces of both ungulates comprised mainly strongyle nematodes (98–100% in donkeys and 71–95% in cattle). Parasite egg count in cattle faeces was not affected by mixed species grazing ($F < 0.1, P = 0.961$; Table 3). However, parasite egg output of donkeys was reduced by 14–35% ($F = 14.2, P < 0.001$) when they foraged together with cattle (Table 3).

Baseline herbage cover

The canopy cover of herb-layer vegetation averaged 77.8% (95% CL 72.9–82.4%). Herbage canopy cover did not differ significantly between treatment plots or stocking densities ($F < 3.6, P > 0.08$; Table 4).

DISCUSSION

Ecological implications

The greater weight gain by both cattle and donkeys when they grazed together than when they grazed separately (Figs. 1A and B) suggests facilitation. This was not consistent with our prediction that either or both species would experience reduced weight gain following

Table 3. Gastrointestinal parasite egg output (eggs per gram of faeces) in cattle and donkeys in herds of single or mixed species at different stocking densities (least squares means \pm S.E.)

	Low stocking density		High stocking density	
	Single species	Mixed species	Single species	Mixed species
Cattle	57 \pm 10.3	78 \pm 14.6	74 \pm 10.4	56 \pm 12.8
Donkeys	1852 \pm 114.8	1585 \pm 140.1	1985 \pm 123.1	1282 \pm 128.8
Significant effects	Cattle: none ($F_{1,5} < 3.0$, $P > 0.15$); Donkeys: C ($F_{1,6} = 11.8$, $P = 0.014$)			

Note: Effect is C = combination. For each species, $n = 5$ and 4 for single and mixed species plots respectively.

Table 4. Baseline herbaceous vegetation canopy cover (pin–herbage contacts/100 pins) in plots accessible to cattle and donkeys as single or mixed species (means with 95% confidence limits in parentheses)

Combination	Low stocking density	High stocking density
Cattle	70.5 (46.1, 89.9)	80.9 (57.5, 96.3)
Mixed	78.2 (68.3, 86.7)	77.9 (47.3, 97.3)
Donkeys	86.2 (73.2, 95.4)	74.2 (64, 83.1)
Significant effects	None ($F < 3.6$, $P > 0.08$)	

Note: $n = 4$ for each plot.

shared foraging. Facilitation of the two animal species could have been partly driven by the observed reduced digestible organic matter to crude protein ratio of their diets when they grazed together (Table 2). Cattle are believed to have an unfavourable balance of protein and energy when the digestible organic matter to crude protein ratio of their diet exceeds 7 (Zalesky, 1997; Newman *et al.*, 2002). In the present study, the digestible organic matter to crude protein ratio of the diet selected by cattle in the mixed species treatment was below this value (Table 2), indicating a favourable protein–energy balance. The relatively high digestible organic matter to crude protein ratio of the cattle diet when they grazed as single species signifies crude protein deficiency relative to energy, and may partly explain the observed reduced weight gain in those plots (Fig. 1A). Although the optimum dietary digestible organic matter to crude protein ratio for donkeys is unclear, the observed high dietary digestible organic matter to crude protein ratio and reduced weight gain of donkeys under single species grazing (Fig. 1B and Table 2) suggest that the donkey optimum might be close to that of cattle.

Negative correlations between the dietary digestible organic matter to crude protein ratio and food intake have been reported for both ruminants (Moore and Kunkle, 1995) and equids (Kidane, 2005). Thus, one way through which this dietary parameter may affect weight gains is by altering food intake. Although we did not measure food intake in the present study, the observed increases in the bite rates of both herbivore species when they foraged together, particularly at low stocking density (Figs. 2A and B), imply possible increases in food intake. The effect of the digestible organic matter to crude protein ratio on food intake by ruminants is mediated via its associated effects on microbial growth, digestibility, and pH of the rumen (Stuth *et al.*, 1999). However, the mechanism through which variation

in the digestible organic matter to crude protein ratio alters food intake in non-ruminants is unclear.

A number of mechanisms could be responsible for the enhancement of diet quality and increases in bite rates for the mixed species treatment. We hypothesize that donkeys, by virtue of their adaptation to cropping and processing of fibrous stems, initiated these changes by reducing sward stemminess, thereby enhancing forage access and utilization by cattle. This in turn stimulated grass regrowth facilitated by the light to moderate showers of rainfall over the trial period, leading to enhanced forage quality and/or increased bite rates for both species. We also hypothesize that in addition to this long-term effect, there was a shorter-term effect, whereby the immediate removal of stems by the equids could have made it easier for bovids to feed continuously, which in turn would increase intake rate. We believe that the mechanism driving facilitation between cattle and donkeys may be analogous to the postulated role of zebras in catalysing a grazing succession that culminates in enhanced access to high-quality forage by native ruminants in the Serengeti ecosystem (Gwynne and Bell, 1968; Bell, 1970, 1971) and other catena (hillslope) ecosystems (Rubenstein, 2010).

The observed 14–35% reduction in worm egg output in the faeces of donkeys when they shared foraging areas with cattle (Table 3) suggests that another possible pathway by which donkeys benefited from combined grazing with cattle was through attenuation of their worm burden. Notably, because the reduction in parasite egg output in faeces of donkeys in the shared plots (Table 3) was not counterbalanced by an increase in worm egg output in cattle faeces (Table 3), it can be concluded that these two ungulate species did not share many of the gastrointestinal nematodes, and that cross-infection of parasites between them was minimal.

High levels of worm infestation can increase disease incidence and reduce animal performance (Yoseph *et al.*, 2005; Odoi *et al.*, 2008). Nematode infestation in equids becomes severe when faecal parasite egg count exceeds 1500 eggs per gram of faeces (Segwagwe *et al.*, 2000). In the current study, parasite egg output in donkey faeces was equal to or below this level in the mixed treatment, but exceeded the threshold in the donkeys-only treatment (Table 3), indicating that shared grazing with cattle attenuated severity of worm infestation among donkeys.

There are a variety of ways that donkeys sharing rangeland with cattle could incur reduced worm burden. We propose that, as cattle foraged, they removed the equid-specific infective parasite larvae from the vegetation without themselves being infected, thereby reducing the chance of infestation among donkeys. Alternatively, we suggest that the enhanced bite rate, diet quality (digestible organic matter to crude protein ratio), and weight gain of donkeys following mixed grazing with cattle could have reduced the susceptibility of donkeys to parasitic infestation. Equids are known to share parasites, and susceptibility of donkeys to diseases associated with parasitism has been suggested to be close to that of zebras (Segwagwe *et al.*, 2000; Matthee *et al.*, 2004). Therefore, our findings provide an insight into how susceptibility of zebras to diseases associated with gastrointestinal worm infestation may be altered when they share land with cattle.

Evolutionary implications

Our study uniquely demonstrates facilitation between donkeys and cattle. Facilitation between bovid and equid species has rarely been shown previously in the wild, with the only evidence to date being a reported decrease in abundance of plains zebra following removal

of cattle from the Ngorongoro Crater (Prins and Olf, 1996). Because of the close phylogenetic, physiological, and ecological relationships between donkeys and zebras (Bauer *et al.*, 1994; Rubenstein, 1994, 2001, 2011; Chopineau *et al.*, 1999; Segwagwe *et al.*, 2000; Matthee *et al.*, 2004), our findings suggest a mechanism behind the observations of 50 years ago (Gwynne and Bell, 1968; Bell, 1970, 1971), highlighting how zebras could structure the community of grazers inhabiting regional migratory systems like the Serengeti, or at a more local scale, the movement of grazers up and down catena, or hill slope, ecosystems (Rubenstein, 2010). The two major guilds of herbivores – perissodactyls typified by equids and artiodactyls exemplified by bovids – evolved different digestive systems in the Paleocene, since when they have co-existed side by side. In Africa, species turnover is common. Hyracooids were replaced by perissodactyls, and within this group equids replaced rhinocerotoids (see, for example, Prothero and Schoch, 1980), yet over this very long evolutionary period ruminants and hindgut fermenters have continued to co-exist, suggesting that competition among these groups has been reduced in part by resource partitioning.

Our results demonstrate that such an evolutionary divergence not only leads to resource partitioning and avoidance of competition, but also fosters facilitation among certain members of both herbivore guilds both at the level of direct food intake and with respect to parasite dynamics. This has important implications for the understanding of the evolution (and apparent stasis) of herbivore assemblages and ecosystem functioning over very long periods (see also Sues, 2000).

Economic implications

In addition to assessing the potential ecological impact of zebras on landscapes inhabited by wild species, our results also shed light on the ecological as well as the likely economic impacts of zebras on landscapes shared with livestock via the actions of their close evolutionary kin, donkeys. The fact that cattle performed better in the presence of equids argues for cattle owners to show increased tolerance to wildlife, especially the endangered Grevy's zebra (Low *et al.*, 2009; Rubenstein, 2010).

Our results also suggest that tolerance can be translated into financial gain under a variety of livestock management practices. Although our results show that average weight gain by *individual* cows is greater in the presence of equids than when grazing solely with other cows, computing the economic gain to the livestock owners depends on the owner's strategic goals. When averaged, the percentage weight gain of cows in mixed treatments at high and low stocking levels is 60% greater than when reared alone. Since Kenyan law prohibits the utilization of wildlife for profit, ranchers might still do better if equids were excluded either by culling or fencing and cattle herds were increased to fill the void. If a livestock owner were to replace 10 donkeys with 10 cows, for example, and each gained weight at the low rate that our cows did when raised without equids, then the total daily weight gain of a herd of 25 cows would be $4.875 \text{ kg} \cdot \text{day}^{-1}$. For a smaller herd of 15 cows grazing with 10 donkeys, the total daily weight gain would be $4.425 \text{ kg} \cdot \text{day}^{-1}$. Having more scrawny cows on a pasture would yield on average 10% more aggregate meat than having fewer cows in better condition sharing the pasture with equids. If the goal of livestock owners were to maximize beef production, then excluding wildlife would provide a small financial gain. To a large extent this is the strategy followed by traditional pastoralists (Prins, 1989, 1992). Yet it is interesting to note that at our high stocking level – one typically employed by pastoral herders – the aggregate daily weight gain of our smaller herd (15 cows) in the

mixed treatment is actually higher ($3.6 \text{ kg} \cdot \text{day}^{-1}$) than what we predict would be the case for a larger herd (25 cows) grazing alone ($3.25 \text{ kg} \cdot \text{day}^{-1}$). On heavily grazed lands, where the goal is to maximize meat production, our findings suggest that herding cattle with equids would be beneficial.

But it is not clear that the aim of all livestock owners is to maximize total meat production at the end of a long growing season. The longer livestock owners let cattle graze, the more risks they incur with respect to cattle being preyed upon or becoming lame or diseased. Thus the more costs livestock owners are likely to accrue with financial outlays on veterinary bills or dietary supplements. Therefore, for more market-oriented livestock owners, an alternative goal might be to minimize the time it takes cows under different grazing regimes to reach a desired weight before sale. For example, if ranchers wanted to sell cows at 400 kg and each cow on average weighed 300 kg at the start of a grazing regime, then for a herd of 25 cows grazing without donkeys it would take 513 days to reach the target weight if the daily weight gain was $0.195 \text{ kg} \cdot \text{day}^{-1}$, the same as that of a cow in our single species herd. If instead the herd consisted of 15 cows and 10 donkeys, the time for each cow to grow from 300 to 400 kg would only be 339 days, given that the daily per capita growth rate in our mixed herds averaged $0.295 \text{ kg} \cdot \text{day}^{-1}$. Thus if the goal of livestock owners is to minimize risk and maintenance costs by getting beef to market at a target weight quickly, then grazing cattle with equids would be the most profitable strategy.

Moreover, many herders raise livestock for purposes other than meat sales. Many ranchers prefer to raise individually healthy animals even if this means raising fewer total individuals. Pastoral herders typically raise cattle to maximize milk yield to improve their family's diets; commercial livestock ranchers often raise prize cattle to improve their own breeding herds or for sale to improve the herds of other ranchers. Thus improvements in cattle performance facilitated by grazing in mixed species herds can produce financial gain under a variety of economic objectives.

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