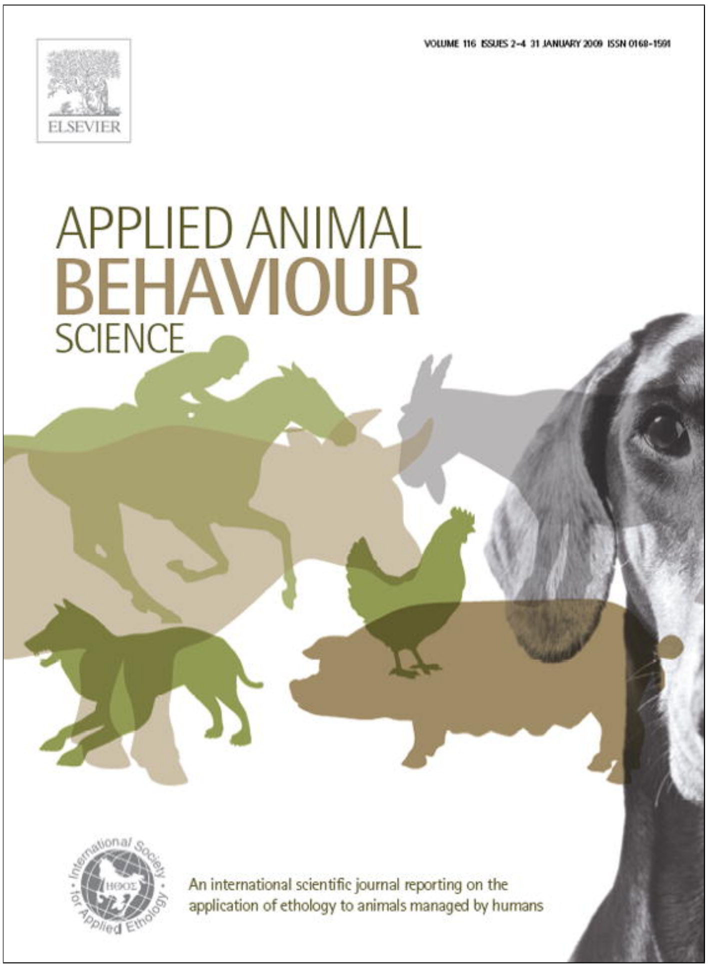
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Behavioural responses of cattle to shared foraging with wild herbivores in an East African rangeland

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ABSTRACT

We assessed whether prior foraging by wild herbivores affected foraging behaviour of cattle in Laikipia rangeland, Kenya, during February 2001, August 2001 and February 2002. The study compared cattle bite rate, step rate and bites per step in plots exclusively accessible to cattle and those accessible to cattle and large wild herbivores. During February 2001 when conditions were dry, cattle bite rate was 18–19% lower, step rate 25–26% higher, and bites per step 36% lower in plots shared by cattle and wildlife compared to those exclusively accessible to cattle. Differences in these measured foraging behaviour parameters were strongly correlated with reductions in herbage cover in plots accessible to wild herbivores. Plot differences in herbage cover and the measured foraging behaviour parameters were not significant in the subsequent trials when conditions were wet, suggesting that wild herbivore impacts reported here are short-term within season and dependent on weather conditions (and plant productivity). With reduced herbaceous plant cover in wildlife grazed realms in the dry season, cattle respond with increased travel and reductions in bite rate and bites per step, suggesting that wild herbivores can seasonally affect foraging behaviour of cattle. It remains to be demonstrated whether or not these altered behaviours of cattle affect weight gains or other measures of performance.

1. Introduction

In Africa, livestock and wildlife often share resources on both private and public rangelands (Western, 1989; Prins, 1992; Georgiadis et al., 2003), and perceived interspecific competition for forage can be a concern for stockmen. In East African rangelands, many graziers believe native fauna compete with their stock for forage (Mizutani, 1999; Georgiadis et al., 2003), and in some instances, have eliminated wild herbivores from their properties (Heath, 2000). Direct effects of wildlife herbivory on cattle foraging behaviour, however, have seldom been quantified (Prins, 2000; Prins and Grootenhuis, 2000, see Hobbs et al., 1996a,b for a rare North American example).

Overuse of forage resources can reduce their availability, especially during the critical growth stages, and alter foraging patterns, nutrition and weight gains of domestic and wild herbivores (Hepworth et al., 1991; Ungar and Noy-Meir, 1988). Whereas there is considerable amount of information on the impacts of livestock on wildlife (Prins, 2000; Bagchi et al., 2004; Young et al., 2005), there is very little knowledge on the effects of wild herbivores on domestic animals, especially in African rangelands. Our objective was to assess whether prior foraging by wild herbivores affected bite rate, step rate and

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bites per step of cattle. We hypothesised that cattle incur increased foraging costs when they share grazing areas with wild herbivores.

2. Materials and methods

2.1. Study area

The study was conducted at Mpala Research Centre (0°17′N, 36°52′E, 1800 m asl) in Laikipia District, Rift Valley Province, Kenya. The research centre is located within the 19,460-ha Mpala 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. This study was conducted in late February 2001, mid August 2001 and early February 2002. August 2001 was the wettest study period, with 55 mm and 214 mm of rainfall being recorded during this month and in the preceding three months respectively. February 2001 was the driest study period, with no rainfall being recorded during this month, and just 64 mm of rainfall being recorded in the preceding three months. Although there was no rainfall in February 2002, this study period was not as dry as February 2001 because it was preceded by relatively high rainfall totalling 251 mm in the preceding three months.

The study site is located in a black cotton soil ecosystem where the main vegetation type is bushed grassland dominated by *Acacia drepanolobium* Sjøstedt. The herbaceous vegetation is principally comprised of the perennial grasses *Pennisetum stramineum* Peter, *Brachiaria lachnantha* (Hochst.) Stapf, *Themeda triandria* Forsk. and *P. mezianum* Leeke. Other species in much lower proportions include the grasses *Lintonia nutans* Stapf, *Botriochloa insculpta* (Hochst. *ex* A. Rich.), *Dinebra retroflexa* (Vahl) Panzer and *Brachiaria semindulata* Hochst. *ex* A. Rich., and the forbs *Solanum* spp., *Aspilia pleuriseta* Schweinf., *Commelina* spp. and *Helichrysum glumaceum* DC. For further details of the study site vegetation, see Young et al. (1998).

Several species of mammalian wild herbivores occur in the study site, including plains zebra *Equus burchelli*, Grevy's zebra *E. grevyi*, hartebeest *Alcelaphus buselaphus*, eland *Tragelaphus oryx*, oryx *Oryx gazella beisa*, Grant's gazelle *Gazella granti*, buffalo *Syncerus caffer*, elephant *Loxodonta africana* and giraffe *Giraffa camelopardalis*. Cattle are the primary livestock in the study site, with an average density of 0.1–0.2 cattle ha^{-1}. Other livestock including sheep *Ovis aries*, goat *Capra hircus*, donkey *Equus africanus* and camel *Camelus dromedarius* occur in the study area, but in much smaller numbers.

2.2. Experimental plots

We used large herbivore exclosures established in 1995 by the Kenya Long-term Exclosure Experiment (KLEE; Young et al., 1998), consisting of a series of semi-permeable barriers designed to differentially exclude or allow cattle, moderate-sized wild herbivores (>15 kg; zebra, hartebeest, Grant's gazelle, oryx, eland, and buffalo) and megaherbivores (elephant and giraffe). The experimental plots used in this study comprised of three herbivory treatments: only cattle allowed ("C"), moderate-sized wild herbivores and cattle allowed ("WC") and megaherbivores, moderate-sized wild herbivores and cattle allowed ("MWC"). Three experimental blocks North, Central and South were used to replicate these treatments in a random stratified design. The size of each experimental plot was 4 ha. For details of the site and experimental set-up, see Young et al. (1998).

2.3. Cattle access and wildlife densities

KLEE allows controlled, timed 2-h access of 120 Boran cattle in each of the treatment plots used in this study 4–8 times per year, designed to reflect the ranch stocking rate of 0.1–0.2 cattle $ha^{-1}\,yr^{-1}$ (see Young et al., 2005). Prior to the first trial in February 2001, cattle accessed the experimental plots once in January. Two more grazing sessions were allowed with one in April–May and one in July, followed by three more with a single entry in each of September, November and January 2002 just prior to our February 2002 trial. Wild herbivores were able to access their respective plots throughout the year, and their presence in these plots was recorded through direct observations and dung surveys (see Young et al., 2005). While we did not measure wildlife density at the study site during our study, mean densities of megaherbivores and medium-sized wild herbivores in Laikipia District are 0.004 ± 0.002 and 0.05 ± 0.01 animals $ha^{-1}\,yr^{-1}$, respectively based on aerial surveys conducted between 1985 and 2005 (N.J. Georgiadis, unpublished).

2.4. Vegetation surveys

Herbaceous vegetation cover was sampled 2–3 weeks before each of the three trials (February 2001, August 2001 and February 2002). Herbaceous vegetation cover was measured in the central hectare of each plot along ten 100-m line transects using a ten-pin frame at 100 evenly spaced sampling points (100 frames, 1000 pins per plot). The sampling points were permanently staked and reused across trials. At each sampling point, pin hits were recorded for all plant species in contact with each pin (maximum 10 pin hits per species). Pins not in contact with vegetation were recorded as bare ground. For each 100-m transect, percentage aerial canopy cover of each plant species was calculated as total pin hits on that species.

2.5. Experimental animals

At the beginning of each trial, 10 Boran heifers aged 3 years were obtained by random selection from Mpala Ranch herds and used as test animals in all experimental plots. Different sets of heifers were used for different trials. Selected animals were herded together during the course of each trial. Prior to each trial, the animals were allowed a 7-day adjustment period during which tryout observations were made to prepare the animals for close-range observations.

2.6. Bite and step counts

Bite and step counts were carried out in each experimental plot once during each trial. For each experimental block, three to five focal heifers were randomly picked with replacement from the 10 test heifers for bite and step counts across treatment plots within the block. Treatment plots were sampled on different days, with the test animals being allowed a settling period of about 10 min in the designated plot at the start of each day prior to observations. On each sampling day, all 10 test animals were moved into a designated plot at 0800–0900 h and removed 1–2 h later. While in the plot, each focal heifer was observed for two non-consecutive 10-min (5-min for February 2001) focal periods, during which all bites taken and steps moved were recorded with the aid of two separate tally counters. A 'bite' represented the removal of whole or some part of a plant, while a 'step' was the forward displacement of either front limb. Bites and steps were recorded when the focal animals were actively foraging. A focal animal was considered to be actively foraging when searching for food or eating appeared to be of primary priority. If an animal being observed did not eat or move during the whole focal period, which was rare, bites and steps were recorded as zero. The interval of observation between one animal and the next was about 2 min, during which tally counter readings were recorded and the next focal animal located. All observations were made at a distance of less than 4 m from the focal animal. A single observer tallied all observations over the course of the study.

Bite or step rates were calculated for each focal sample by dividing the number of bites or steps counted in that sample by the length of time (minutes) of the focal observation. The number of bites per step was calculated by dividing the total number of bites recorded in a focal period by the total number of steps in that period. For each treatment plot, mean bite rate, step rate and bites per step data were calculated for individual focal animals within trials.

2.7. Statistical data analysis

Experimental units were treatment plots replicated across experimental blocks ($n = 3$), with vegetation transects and test animals being used as plot sub-samples. For each trial, herbaceous vegetation data were averaged among transects, and bite rate, step rate and bites per step data averaged among test heifers within each plot. Each trial was analysed separately with a randomized block design using the general linear model (GLM) of analysis of variance (ANOVA) procedure of Systat (SPSS, 1998) to test for treatment effects. Tukey's HSD was used for mean separations, with significant differences being accepted at $P < 0.05$.

Table 1
Percentage cover of grasses, forbs and total herbaceous vegetation during trial assessing cattle foraging behaviour responses to prior use of paddocks by medium and larger herbivores at the Kenya Long-term Exclosure Experiment (KLEE) in 2001 and 2002

Sampling periods	Vegetation class	*C*	WC	MWC	Effect (*P*)
February 2001	Grasses	**67.8** ± **4.1**^{a}	**45.9** ± **1.5**^{ab}	**41.8** ± **5.5**^{b}	**0.03**
	Forbs	**7.6** ± **1.0**^{a}	**7.4** ± **1.2**^{a}	**2.6** ± **0.3**^{b}	**0.02**
	Total	**75.4** ± **4.8**^{a}	**53.3** ± **2.0**^{a}	**44.4** ± **5.5**^{b}	**0.03**
August 2001	Grasses	51.5 ± 5.5	48.2 ± 3.7	52.2 ± 2.9	0.26
	Forbs	11.1 ± 0.9	13.5 ± 1.4	12.4 ± 2.2	0.57
	Total	62.6 ± 5.3	61.7 ± 2.7	64.6 ± 1.3	0.70
February 2002	Grasses	64.6 ± 1.7	66.4 ± 3.4	70.0 ± 2.30	0.29
	Forbs	**19.3** ± **0.7**^{a}	**16.0** ± **1.6**^{ab}	**12.9** ± **0.6**^{b}	**<0.05**
	Total	83.9 ± 2.1	82.4 ± 1.85	82.9 ± 1.70	0.67

C = plots exclusively accessible to cattle. WC = plots accessible to moderate-sized wild herbivores (>15 kg, zebra, hartebeest, Grant's gazelle, oryx, eland, and buffalo) and cattle. MWC = plots accessible to megaherbivores (elephants and giraffes), moderate-sized wild herbivores and cattle. Data are means ± S.E. ($n = 3$). Rows listed in bold fonts exhibited significant treatment effects. Means within a bold row sharing different superscripts are significantly different ($P < 0.05$, Tukey's HSD).

3. Results

3.1. Vegetation cover

For response variables total herbage cover and total grass cover, treatment effects were significant ($P < 0.05$) during February 2001, but not ($P > 0.20$) during August 2001 or February 2002 (Table 1). In addition, there was significant treatment effect on forb cover during February 2001 ($P = 0.02$) and February 2002 ($P < 0.05$) but not during August 2001 ($P > 0.50$) (Table 1).

During the February 2001 trial, total herbaceous cover was significantly ($P < 0.03$) lower in MWC than in *C*, and lower but not significantly so ($P = 0.10$) in WC than in *C* (Table 1). Likewise, total grass cover was significantly ($P < 0.03$) lower in MWC than in *C*, but not ($P = 0.06$) in WC than in *C* during this period (Table 1). Treatment differences in grass cover were stronger when *P. mezianum* (the least palatable of the dominant grass species) was excluded from the analysis (35.5 ± 2.0(S.E.)%, 26.9 ± 2.4% and 57.5 ± 5.0% in WC, MWC and *C* respectively; both $P < 0.04$).

3.2. Bite rate

We counted approximately 4000 bites in 54 (5-min) focal samples, 34,000 bites in 90 (10-min) focal samples and 14,000 bites in 61 (10-min) focal samples in February 2001, August 2001 and February 2002 respectively. Treatment effects on bite rate were significant ($P < 0.05$) during February 2001 but not ($P > 0.10$) during the subsequent trials (Table 2). During February 2001, bite rate was significantly lower in treatment WC ($P < 0.04$) and MWC ($P < 0.04$) than in *C*. In addition, bite rate was positively correlated with total grass cover ($r = 0.77$, $P < 0.01$; Fig. 1a), grass cover excluding cover of *P. mezianum* ($r = 0.77$, $P < 0.02$), or total herbaceous cover ($r = 0.75$, $P < 0.02$), and negatively correlated with step rate ($r = -0.73$, $P < 0.03$; Fig. 2) during this trial.

3.3. Step rate

We counted approximately 5000 steps in 54 (5-min) focal samples, 12,000 steps in 90 (10-min) focal samples and 5500 steps in 61 (10-min) focal samples in February 2001, August 2001 and February 2002 respectively. Step rate was significantly ($P < 0.03$) affected by treatment, being higher in WC and MWC than in *C* during in February 2001, but not (all $P > 0.1$) during either of the other trials (Table 2). In all trials, step rate was not significantly correlated with grass cover or total herbaceous cover (all $r > -0.65, P > 0.1$). However, excluding North block, where step rate was generally high, step rate correlated

Table 2
Cattle bite rate, step rate and bites per step during trial assessing cattle foraging behaviour responses to prior use of paddocks by medium and larger herbivores at the Kenya Long-term Exclosure Experiment (KLEE) in 2001 and 2002

Sampling periods	Variables	*C*	WC	MWC	Effect (*P*)
February 2001	Bites min^{-1}	**17.0** ± **0.45**^{a}	**13.7** ± **0.95**^{b}	**13.9** ± **0.28**^{b}	**0.03**
	Steps min^{-1}	**16.8** ± **2.49**^{a}	**21.0** ± **2.84**^{b}	**21.2** ± **1.80**^{b}	**0.03**
	Bites per step	**1.1** ± **0.15**^{a}	**0.7** ± **0.13**^{b}	**0.7** ± **0.05**^{b}	**0.01**
August 2001	Bites min^{-1}	37.4 ± 1.58	38.6 ± 2.16	34.9 ± 3.32	0.18
	Steps min^{-1}	15.5 ± 0.64	15.2 ± 0.31	14.5 ± 1.15	0.60
	Bites per step	2.4 ± 0.04	2.5 ± 0.19	2.4 ± 0.23	0.71
February 2002	Bites min^{-1}	21.8 ± 0.46	26.6 ± 2.86	21.8 ± 0.79	0.26
	Steps min^{-1}	7.9 ± 1.61	10.7 ± 1.24	9.9 ± 0.39	0.12
	Bites per step	3.0 ± 0.69	2.6 ± 0.43	2.2 ± 0.09	0.30

C = plots exclusively accessible to cattle. WC = plots accessible to moderate-sized wild herbivores (>15 kg, zebra, hartebeest, Grant's gazelle, oryx, eland, and buffalo) and cattle. MWC = plots accessible to megaherbivores (elephants and giraffes), moderate-sized wild herbivores and cattle. Data are means ± S.E. ($n = 3$). Rows listed in bold fonts exhibited significant treatment effects. Means within a bold row sharing different superscripts are significantly different ($P < 0.05$, Tukey's HSD).

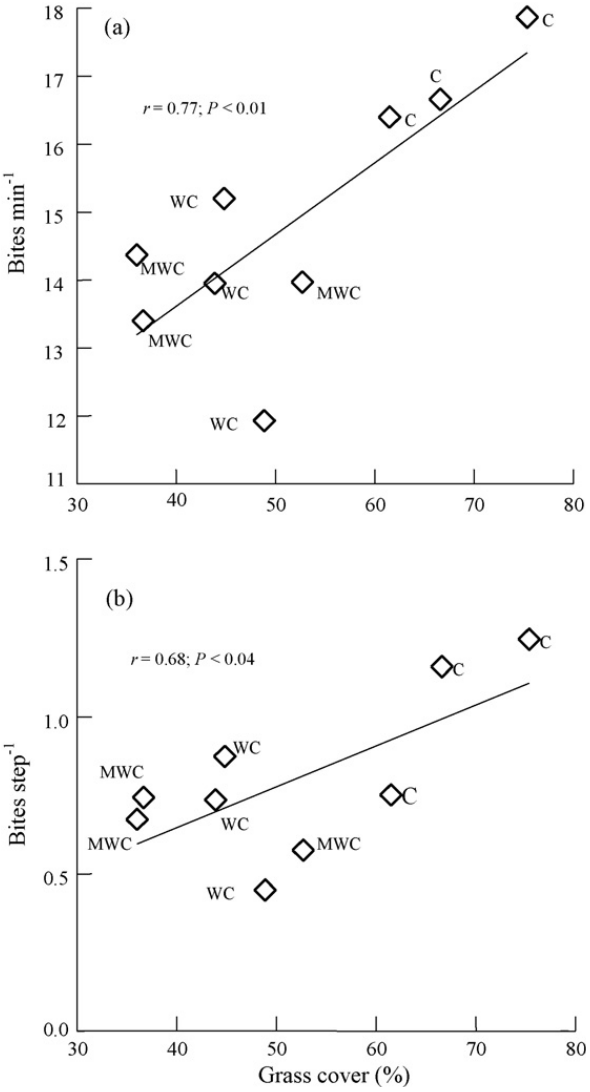

Fig. 1. Relationship between grass cover and: (a) bite rate and (b) bites per step during trial assessing cattle foraging behaviour responses to prior use of paddocks by medium and larger herbivores at the Kenya Long-term Exclosure Experiment (KLEE) in 2001 and 2002. Data presented are for February 2001. *C* = plots exclusively accessible to cattle. WC = plots accessible to moderate-sized wild herbivores (>15 kg, zebra, hartebeest, Grant's gazelle, oryx, eland, and buffalo) and cattle. MWC = plots accessible to megaherbivores (elephants and giraffes), moderate-sized wild herbivores and cattle.

negatively with total grass cover ($r = -0.90$, $P < 0.01$), grass cover excluding cover of *P. mezianum* ($r = -0.92$, $P < 0.01$), and total herbaceous cover ($r = -0.87$, $P < 0.02$) during February 2001.

3.4. Bites per step

The mean cattle bites per step across plots was 0.8 ± 0.1, 2.5 ± 0.1 and 2.6 ± 0.3 during February 2001, August 2001 and February 2002 respectively. For this response variable, treatment effect was significant in February 2001 ($P < 0.02$), but not in the subsequent trials (all $P > 0.30$). Mean bites per step was significantly lower in WC ($P = 0.02$) and MWC ($P = 0.02$) than in *C* during February 2001 (Table 2). During the same trial, mean bites per step was

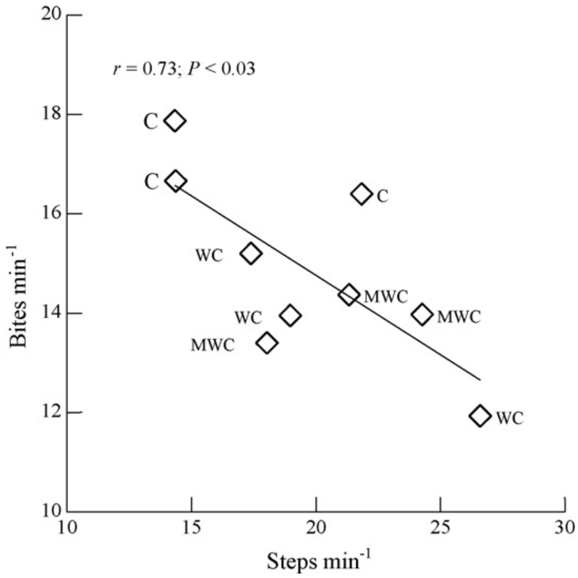

Fig. 2. Relationship between bite rate and step rate during trial assessing cattle foraging behaviour responses to prior use of paddocks by medium and larger herbivores at the Kenya Long-term Exclosure Experiment (KLEE) in 2001 and 2002. Data presented are for February 2001. *C* = plots exclusively accessible to cattle. WC = plots accessible to moderate-sized wild herbivores (>15 kg, zebra, hartebeest, Grant's gazelle, oryx, eland, and buffalo) and cattle. MWC = plots accessible to megaherbivores (elephants and giraffes), moderate-sized wild herbivores and cattle.

positively correlated with total grass cover ($r = 0.68$, $P < 0.04$; Fig. 1b), grass cover with *P. mezianum* excluded ($r = 0.76$, $P < 0.02$), and total herbaceous vegetation cover ($r = 0.71$, $P < 0.03$).

4. Discussion

Our results show that wild herbivores have significant effects on cattle foraging behaviour in dry, but not wet seasons (Table 2). It was only during the dry-low cover February 2001 trial that there were significant relationships between grass cover and foraging parameters (Fig. 1a). The positive correlation between bite rate and grass cover during this trial is consistent with predictions of several functional response models generally indicating that under conditions of low forage density, increasing forage availability leads to increased bite rate of herbivores (Ungar and Noy-Meir, 1988; Spalinger and Hobbs, 1992; Bradbury et al., 1996). Bite rate of herbivores can be limited either by search and rate of encounter of food items or by chewing and swallowing time (Bradbury et al., 1996; Spalinger and Hobbs, 1992). In our study, cattle bite rate during the dry-low herbage cover February 2001 was negatively correlated with step rate (Fig. 2), suggesting that bite rate during this trial was search- and encounter-limited.

Treatment differences in foraging behaviour attributes during February 2001 (Table 2) were associated with the reductions in grass cover in plots accessible to wild herbivores. Measured reductions in grass cover in wildlife-accessible plots were even stronger with the exclusion of *P. mezianum* because this grass is the least selected by cattle in the study site, especially during dry periods (Odadi et al., 2007). This grass has also been shown to be seldom selected by wild herbivores including zebra in such systems especially when mature (Owaga, 1975).

Distance between feeding stations can be several times greater in distinct patchy communities compared to communities with dense, continuous swards (Stuth, 1991). Because of the local patchiness of the herbaceous species in our study site, cattle foraging behaviour was largely driven by the distribution and availability of preferred food items within patches, which in turn influenced the amount of travel both within and between feeding patches. The observed treatment effects on herbaceous cover (Table 1) suggest that preferred food items within feeding patches were reduced in plots accessible to wildlife. This explains the observed reduction in bite rates and increased step rates in wildlife grazed plots (Table 2). In addition, the significant reduction in bites per step in plots accessible to wildlife (Table 2), suggests that cattle foraged less efficiently in these plots by taking fewer bites at each feeding station (see also Pfister et al., 1988).

Foraging herbivores move from feeding stations when preferred food items or the rate of forage acquisition within those stations fall below certain thresholds, and such thresholds are reached more quickly in poor patches than in rich ones (Senft et al., 1987; Bailey et al., 1996). Thus, the reduced bite rate and increased step rate in plots accessible to wildlife (Table 2) indicate that cattle took shorter residence times at feeding stations and moved more frequently between stations in these plots than in plots exclusively accessed by cattle because of reduced forage availability. Our results agree with the work of Smith et al. (2006) conducted in the southern-central highlands of Ethiopia, who found that cattle step rate increased and bites per step decreased with reduced forage availability.

Differences in herbaceous cover among experimental treatments and associated changes in cattle foraging behaviour are attributable to herbage utilization by wild herbivores prior to cattle entry. These treatment effects were evident during the dry February 2001 trial but not during the subsequent trials when conditions were relatively wet (Tables 1 and 2), suggesting that wild herbivore impacts reported here are short-term within season and dependent on weather conditions. Because herbage growth had likely ceased during the dry period, first access to, and use of commonly shared herbage by wildlife subsequently altered foraging behaviour of cattle. During the wet periods, however, herbage growth likely exceeded utilization by both wild and domestic herbivores, resulting in no significant treatment effects on foraging patterns of cattle (Table 2). This may be an example of a more general trend for trophic cascades to be less pronounced at higher productivities (Pringle et al., 2007; Veblen, 2008).

More than one species of wildlife foraged in the wildlife-accessible plots (see Young et al., 1998), so it is not possible to directly attribute treatment effects to any specific wildlife species. However, we suspect that most of these effects were related to plains zebra, which was the most frequent wild herbivore species in the study plots (see Young et al., 2005). Zebras are known to feed almost entirely on grasses (Casebeer and Koss, 1970; Owaga, 1975; Voeten and Prins, 1999), and are likely to be primarily responsible for the observed reductions in grass cover. Eland, the second most frequent in the study site (Young et al., 2005), is largely a browser (Field, 1975; Buys, 1990; Codron et al., 2005) and was likely to contribute less to changes in grass cover. The contribution of the other moderate-sized herbivores, hartebeest, oryx and Grant's gazelle, to the observed treatment differences was likely to be smaller (compared to zebra) as they were far less abundant in the study site (Young et al., 2005).

The observed reduction in forb cover in treatment MWC compared to WC and *C* (Table 1) can be largely attributed to elephant because giraffe, the other megaherbivore species, rarely feeds on vegetation below 50 cm (Young and Isbell, 1991). The effects of megaherbivores on cattle foraging behaviour via reduction in forb cover appears to be more pronounced during dry-low forage cover periods such as February 2001. This is because during February 2002 when herbage cover was high (82–84%), the significant reduction of forb cover in the MWC plots compared to the *C* plots (Table 1) did not affect cattle foraging behaviour (Table 2).

5. Conclusions

This study provides evidence that shared grazing with wild herbivores can seasonally alter foraging behaviour of cattle. With reduced plant cover in wildlife grazed realms in the dry season, cattle respond with reductions in bite rate and bites per step, and increased travel. We are currently testing whether or not these altered behaviours affect weight gains or other measures of performance of cattle.

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