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Fire-induced negative nutritional outcomes for cattle when sharing habitat with native ungulates in an African savanna

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Summary

1. Prescribed burning is used in tropical savannas to improve habitat conditions for domestic and wild herbivores, but its effects on the ecological interactions between these herbivore guilds have never been assessed experimentally. Understanding such effects will contribute towards more informed management of both guilds in landscapes where they share habitats.

2. We investigated the effects of burning on the nutritional outcomes for cattle sharing habitat with wildlife in a Kenyan savanna ecosystem. We compared forage availability and cattle forage and nutrient intake rates across burned and unburned areas cattle accessed exclusively, and those they shared with medium-sized wild ungulates, both with and without megaherbivores (elephants and giraffes). We performed these measurements in May 2013 (wet period, 2 months post-burning) and February 2014 (dry period, 11 months post-burning). Additionally, we monitored wildlife use of these areas.

3. Prescribed burning enhanced cattle nutrition, but only in areas cattle did not share with wildlife. Shared foraging with wildlife reduced cattle forage and nutrient intake rates by 37–97% in burned areas (burns), but not in unburned areas; these reductions corresponded with reduced herbage availability in the shared burns.

4. In May (the wet period), cattle met their nutrient intake requirements in burns, regardless of whether they were sharing these areas with wildlife. However, in February (the dry period), nutrient requirements were unmet or tended to be unmet in burns shared with wildlife; requirements were met or significantly exceeded in the unshared burns.

5. Experimental exclusion of megaherbivores did not moderate these effects, suggesting that they were primarily caused by medium-sized wild ungulates which were highly attracted to burns.

6. *Synthesis and applications*. Prescribed burning produces negative nutritional outcomes for cattle when sharing habitat with wild ungulates. Because these effects could negatively influence livestock–wildlife coexistence, burning should be applied prudently in such human-occupied savanna landscapes. Specifically, because unburned areas serve as refuge foraging areas during the dry season, interspersing burns with unburned areas could minimize fire-driven negative interactions between cattle and wild ungulates. Conversely, burning could be used to draw wildlife away from valuable cattle foraging areas, such as those near available water.

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Correction note: The author Ryan L. Sensenig was omitted from article in error by the corresponding author during first publication on 28 September and was added to the author list on 7 October.

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Introduction

Fire is a major agent of disturbance in many terrestrial ecosystems, and both its prevalence and ecological significance vary among biomes. In particular, fire is prevalent in many tropical savannas due to the existence of a continuous layer of highly flammable grass and distinct dry and wet seasons, which create ideal conditions for burning (Bailey 1988; Pyne *et al.* 2004; Russell-Smith *et al.* 2013). Because tropical savannas occur more extensively in Africa than in any other continent (Scholes & Archer 1997; White, Murray & Rohweder 2000), Africa is recognized as the most fire-prone landmass in the world (Pyne *et al.* 2004).

Prescribed burning is often used as a tool to meet management goals and maintain the functioning of ecological processes. From a management perspective, prescribed burning serves several purposes, including improving forage quality for domestic and wild herbivores through removal of moribund herbage material, controlling bush encroachment and reducing incidences of ticks and tickborne diseases in livestock (Augustine & Milchunas 2009; Klop 2009; Trollope 2011). Burned vegetation generally attracts higher densities of grazers (Sensenig, Demment & Laca 2010; Allred *et al.* 2011; Eby *et al.* 2014), which can increase grazing pressure in burned areas and potentially alter how herbivores interact with one another (Whisenant 2004).

While the responses of different ungulate species to burning have been widely documented across rangelands (Vermeire *et al.* 2004; Sensenig, Demment & Laca 2010; Allred *et al.* 2011; Eby *et al.* 2014), there has been no controlled experimental research on the effects of fire on interactions among different guilds or species of herbivores. Such information is particularly vital for landscapes where wild and domestic herbivores co-occur because fire-driven alteration of their interactions can have considerable conservation and socio-economic implications. Specifically, understanding the role of fire in shaping the interactions between wild and domestic herbivores is critical for management of both herbivore guilds. This need is great in African savannas where wild and domestic ungulates often share habitats, especially on private and communal lands, and livestock owners typically believe that native ungulates compete with their livestock for forage (Foufopoulos, Altizer & Dobson 2003; Odadi, Young & Okeyo-Owuor 2007). There has been growing research effort geared towards disentangling the complex and dynamic ecological interactions between wild and domestic ungulates in these savannas (Young, Palmer & Gadd 2005; Sitters *et al.* 2009; Odadi *et al.* 2011; Kartzinel *et al.* 2015). However, the effects of prescribed burning on these interactions have never been assessed experimentally. Fire-driven competition between domestic and wild herbivores can be manifested through altered nutritional outcomes for these herbivore guilds when sharing foraging areas.

We investigated the effects of replicated prescribed burns on the nutritional outcomes for cattle when they share habitat with wild ungulates in a savanna rangeland in central Kenya. Livestock in this region are typically actively herded, with access being concentrated on specific areas of the range for variable time periods depending upon forage availability. Wild ungulates roam the landscape freely and primarily interact with livestock indirectly by foraging in the same areas at different times.

We compared herbage characteristics (cover, grass height, percentage green leaves) and cattle nutrition attributes (diet quality, and forage and nutrient intake rates) across burned and unburned areas from which wildlife had been experimentally excluded, and those they shared with medium-sized wild ungulates, both with and without megaherbivores (elephants and giraffes). We hypothesized that cattle would benefit from burns in the absence of wildlife, but because burns would attract high concentrations of wild herbivores, herbage availability would be reduced in the shared burned areas, thereby adversely affecting cattle nutrition. Additionally, because elephants can consume considerable amounts of grass (Cerling *et al.* 2009), we hypothesized that their experimental exclusion would moderate the postulated fire-induced deleterious effects of wildlife on cattle.

Materials and methods

STUDY SITE

The study was conducted at Mpala Research Centre (0°17′ N, 36°52′ E; 1800 m above sea level) in Laikipia, Kenya. The research centre is established on Mpala Conservancy, a 20 000 ha property that combines livestock (mainly cattle) production with wildlife conservation. Rainfall at the study site averages 500–600 mm annually, and is weakly trimodal, with peaks in April, August and November, and a pronounced dry season in December–March. The study site is located in a black cotton (vertisol) soil ecosystem comprising a wooded savanna vegetation dominated by the whistling thorn tree (*Acacia drepanolobium*) and perennial grasses *Themeda triandra* Forssk. *Brachiaria lachnantha* (Hochst.) Stapf, and *Pennisetum stramineum* Peter. Several species of native ungulates occur in the study site, the most common of which include plains zebras (*Equus burchelli*), oryx (*Oryx beisa*), buffalo (*Syncerus caffer*) and elephants (*Loxodonta africana*) (see Table S1, Supporting Information for a complete list).

EXPERIMENTAL LAYOUT

We used the Kenya Long-term Exclosure Experiment (KLEE) comprising 4-ha plots that exclude or allow different combinations of cattle (‘C’), medium-sized wild ungulates (20–1000 kg, ‘W’) and megaherbivores (elephants and giraffes, ‘M’). The overall design comprises six herbivory treatments, each replicated across three experimental blocks (see Young, Palmer & Gadd 2005 for further details). In late February 2013, controlled burns were conducted in 30 m × 30 m subplots of each of these 18 KLEE plots (see Kimuyu *et al.* 2014 for further details). For the present study, we used the herbivory treatment plots that cattle accessed exclusively (C), and those they shared with medium-sized wild ungulates in the absence (WC) or presence (MWC) of megaherbivores. We established a 30 m × 30 m unburned (control) subplot adjacent to each burn (within each herbivory treatment plot), in areas which matched the burned area as closely as possible in terms of herb-layer species composition and tree density. Burned and unburned subplots were separated by 2-m buffer strips created as firebreaks at the time of burning.

CATTLE AND WILDLIFE USE OF PLOTS

Cattle herds (100–120 animals herd^{-1}) routinely access C, WC and MWC plots for 2 h on each of two to three consecutive days, typically three to four times yearly depending on forage availability. This grazing regime reflects typical livestock management strategies for the region where cattle are herded in one general area for several days until forage is depleted then moved to another area (Veblen *et al.* 2016). In the present study, 100 head of cattle accessed these plots three times: May 2013, August–September 2013 and January 2014 (Fig. 1). During each time, they grazed each plot for three consecutive days (2 h day^{-1}), with their use of burns being restricted to 2–3 min each day. This resulted in a stocking rate of 0·14–0·15 cattle ha^{-1} year^{-1} (assuming foraging time allowance of 8–9 h day^{-1}; Odadi & Rubenstein 2015), similar to Mpala Conservancy averages (0·1–0·2 cattle ha^{-1} year^{-1}; Odadi, Young & Okeyo-Owuor 2007). Wild herbivores primarily access the shared plots when cattle are absent, and therefore typically interact indirectly with cattle. We estimated wildlife use of these plots using camera traps (see Appendix S1 and Fig. 1 for details).

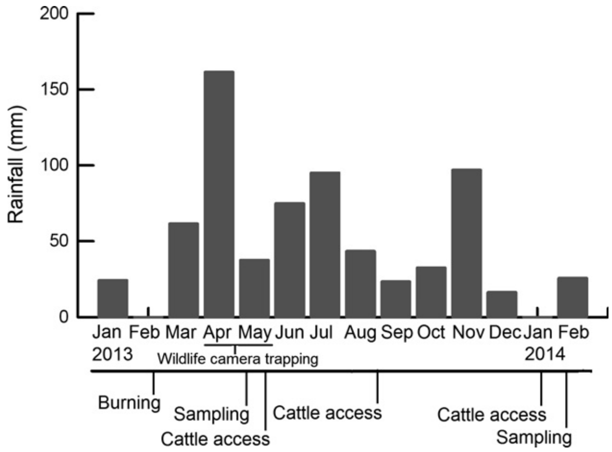

Fig. 1. Monthly rainfall and activity timeline during the study.

SAMPLING PERIODS, TEST ANIMALS AND ATTRIBUTES MEASURED

Sampling was conducted in two time periods: May 2013 and February 2014, 2 and 11 months post-burning, respectively (Fig. 1). Notably, May was wet while February was dry (Fig. 1). Sampling in May preceded the May 2013 access to experimental plots by the larger cattle herd, while sampling in February was conducted after the larger cattle herd had access to the plots in January 2014 (Fig. 1).

At the beginning of each sampling period, we randomly selected five *Boran* test steers, aged approximately 2 years and weighing 343 kg ± 14 (SD), from a larger herd located 1–2 km from the study plots. For the entire duration of each sampling period, test steers were herded separately but shared a *boma* (night enclosure) with the larger herd. The proximity of the *boma* to the experimental plots ensured that the test steers could be easily walked to study plots each morning.

We used the test steers to estimate diet quality and dry matter and nutrient intake rates in all subplots. Before each sampling period, we habituated the steers to observers and sampling procedures for approximately 1 week. We measured herbage cover (a proxy for biomass), grass leaf height and percentage green leaf in all subplots before introducing test steers for animal measurements.

VEGETATION MEASUREMENTS

We used the point intercept method to sample vegetation cover along four 25-m line transects evenly spaced (6 m between transects) across each subplot. Along each transect, we dropped a 1-m pin perpendicular to the ground every 1 m, and recorded all pin hits on vegetation by plant species and parts (live/dead leaves and stems), irrespective of whether the same plant was hit more than once at the same pin location. Pins not intercepted by any vegetation were recorded as hits on bare ground. Overall, 100 pin locations were sampled per subplot per sampling period. In addition, we measured the height of the topmost grass leaf that touched the pin. We summed all vegetation pin hits for each subplot and calculated herbage cover as the total number of hits per pin. Herbage leaf greenness was calculated as a percentage of vegetation pin hits with live leaves.

ANIMAL MEASUREMENTS

Plot sampling sequence

During each sampling period (May and February), we introduced steers to experimental blocks sequentially, while the order of steer introduction to herbivory treatment plots (C, WC and MWC) within each block was randomly predetermined. Steers were introduced to each herbivory treatment plot on a separate day, with its burned and unburned subplots being sampled on the same day sequentially in a randomly predetermined order. Within each subplot, steer observations were conducted in two sessions; the first session lasted approximately 30 min to accommodate bite mass simulation (described below), while the second lasted approximately 20 min. Each session included a 2-min pre-observation settling period. Once the first session was completed in the first subplot, the steers were immediately moved to the adjacent subplot for the first session there. The second session started immediately after the first, with the same sequence of sampling being maintained between subplots. All observation sessions were made between 0830 and 1200 h.

Forage intake estimation

We estimated instantaneous forage intake rate (IIR) as the product of bite rate (bites min^{-1}) and bite mass, and hourly intake rate (HIR) as the product of IIR and hourly grazing time (percentage grazing time × 60 min). We estimated bite rate using the focal-animal sampling technique (Altmann 1974). Bites, discerned as tearing sounds of prehension, were counted for each test steer during one bout lasting a maximum of 2 min in each subplot in each of the two observation sessions. Whenever a focal animal stopped grazing for more than 10 s, the bout was terminated and bites counted hitherto recorded. Test steers were observed in a sequence that was randomly predetermined each morning and maintained throughout the entire sampling duration that day, at an observer distance of 2–4 m. Bite counts were conducted by two experienced observers who routinely switched between observing and scribing after every sampling session. Bite rate was estimated by dividing the total bites counted in each bout by the total time (min) period of the bout.

Bite mass was estimated by mimicking and hand-plucking bites of the test steers (Bonnet *et al.* 2011). Bite mass sampling was executed by the same two observers who counted bites. In accordance with Bonnet *et al.* (2011), the observers were trained for 1 week prior to sampling to minimize observer bias. Because there were five test steers in a given subplot, one observer sampled three steers while the other sampled the remaining two within a given experimental block, and vice versa for the next block. Bite mass observations in each subplot were carried out during the first observation session, immediately after bite counts, and lasted for approximately 10 min. During this period, 25 bites taken by each steer were simulated (based on plant part, species and cropping height), hand-plucked and placed in a paper bag. Each forage sample was air-dried to a constant mass (measured to the nearest 1 g), which was then divided by 25 to obtain bite mass.

During each observation session, percentage grazing time was estimated in each subplot by scan-sampling test steers for grazing activity (searching for, gathering, prehending or chewing forage) every 2 min. Overall, we made 20–30 scans per steer per subplot during each sampling period (May and February). Percentage grazing time was calculated for each subplot as the total number of times the steers were observed grazing divided by the total number of scans.

Diet quality and nutrient intake measurements

Hand-plucked bite samples were analysed for nutritive quality at the University of Nairobi's Animal Nutrition Laboratory in Nairobi. The samples were ground to pass through a 1-mm screen and analysed for crude protein (CP) content and *in vitro* dry matter digestibility (IVDMD) using micro-Kjeldahl (AOAC 1990) and Tilley & Terry (1963) techniques, respectively. The rumen liquid used in IVDMD analysis was collected from a ruminally cannulated *Bos indicus* steer maintained primarily on natural pasture. We calculated crude protein intake (CPI) and digestible dry matter intake (DDMI) by multiplying the proportion of these nutrients in the diet by the hourly dry matter intake. In addition, we estimated the hourly net energy intake (NEI) using appropriate National Research Council (NRC 2000) equations (see Appendix S2).

DATA ANALYSIS

For each vegetation and cattle nutrition attribute, we averaged data per subplot per sampling period (May and February) and used a linear mixed-effects model to test for the effects of fire (burned vs. unburned), herbivory (C, WC and MWC) and sampling period, and their interactions. Random factors included block, herbivory treatment plot and fire treatment subplot, with subplot nested within plot and plot nested within block. We included an autoregressive AR(1) covariance structure to address the non-independence of repeated measures within the same subplot. To test whether cattle met nutrient intake requirements, we performed one-sample *t*-tests using appropriate nutrient requirement benchmarks (see Table S2).

We analysed camera trap data for the effects of herbivory (WC and MWC) and/or fire on wild herbivores, using linear mixed-effects models with subplots nested within plots nested within blocks. Additionally, we tested these effects for individual species excluding those that were relatively rare (<5% of total camera trap photographs) within each wild herbivore guild.

We used graphical tools (residual and Q–Q plots) to check homoskedasticity and normality of linear mixed-effects model residuals, and transformed data when necessary (see Appendix S3 for full models). However, we report all data as untransformed means ± SE. Tukey's *post hoc* tests were used to separate means for significant ($P < 0{\cdot}05$) or nearly significant ($P < 0{\cdot}1$) effects of herbivory and interactions. All statistical analyses were run in R 3.2.3 (R Core Team 2015).

Results

VEGETATION ATTRIBUTES

Both mean herbage cover and grass leaf height were significantly higher in May (wet period) than in February (dry period) (Fig. 2a–d and Appendix S3). Both were influenced by an interaction between fire and herbivory treatment (both $F > 7{\cdot}4$, $P < 0{\cdot}03$; Fig. 2a–d and Appendix S3). Specifically, across burns (but not non-burns) both measures were 41–60% lower in plots to which wildlife had access (WC and MWC) than in plots with cattle only (C). However, for both burns and non-burns, these measures did not differ significantly between WC and MWC. Additionally, grass was significantly shorter in burns than in non-burns in WC and MWC but not C (Fig. 2c,d). Herbage cover was significantly lower in burns than in non-burns in all herbivory treatments, but with greater relative reduction in WC (62–64%) and MWC (59–60%) than in C (38–39%) (Fig. 2a,b). These patterns were consistent across both May and February sampling periods.

Percentage green leaves tended to be influenced by the interaction among fire, herbivory and sampling period ($F = 3{\cdot}0$, $P = 0{\cdot}09$; Table 1 and Appendix S3). In May,

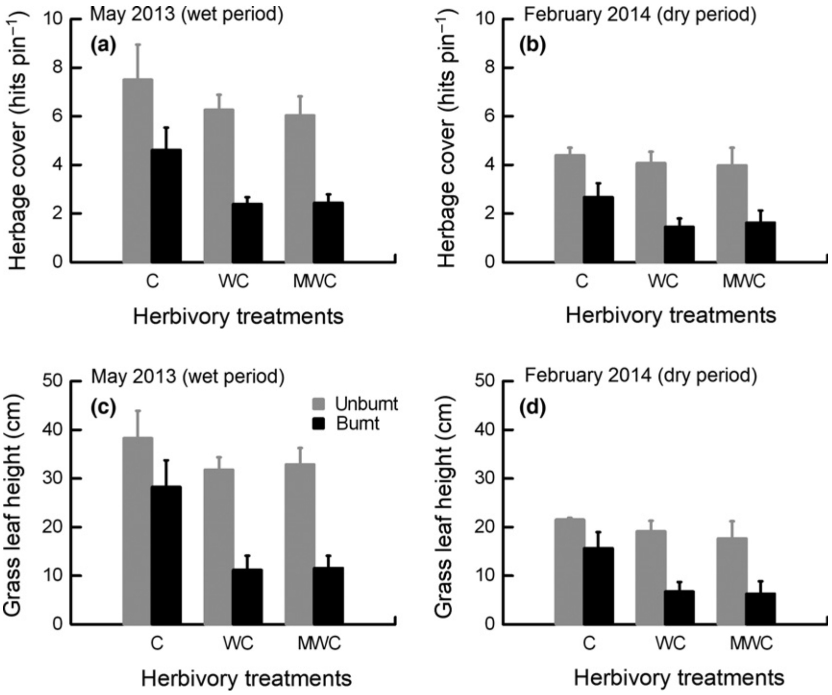

Fig. 2. Herbage quantity attributes (means ± SE) across wet (a & c) and dry (b & d) sampling periods and fire treatments cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores.

Table 1. Herbage green leaf content (mean ± SE %) across sampling periods and fire treatments in plots cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores

	Herbivory treatments		
	C	WC	MWC
May 2013 (wet period)			
Unburnt	57·7$^{A(a)}$ ± 1·0	56·5$^{A(a)}$ ± 1·7	60·7$^{A(a)}$ ± 3·0
Burnt	81·6$^{A(b)}$ ± 3·4	92·3$^{B(b)}$ ± 3·1	89·2$^{B(b)}$ ± 1·9
Feb 2014 (dry period)			
Unburnt	11·5$^{A(a)}$ ± 1·5	13·6$^{A(a)}$ ± 0·6	13·1$^{A(a)}$ ± 1·2
Burnt	11·8$^{A(a)}$ ± 0·6	15·2$^{A(a)}$ ± 1·7	14·9$^{A(a)}$ ± 0·2

Row means with different upper-case letter superscripts differ significantly between herbivory treatments. Within sampling periods, column means with different lower-case superscripts in parentheses differ significantly between fire treatments.

for burned areas, leaves were significantly greener in WC and MWC than in C. However, there were no significant differences among herbivory treatments in unburned areas during this period, and all significant differences disappeared by February.

CATTLE RESPONSES

Bite mass, bite rate and grazing time

Cattle bite mass was significantly lower in WC and MWC than in C for burns but not for non-burns (herbivory × fire interaction $F = 14·6$, $P = 0·01$; Fig. 3 and Appendix S3). Moreover, bite mass was significantly lower in burned than in unburned areas in WC and MWC but not in C. Bite mass was significantly lower in burned than in unburned areas in February (dry period) but not May (wet period) (fire × sampling period interaction $F = 27·3$, $P < 0·01$; Fig. 3 and Appendix S3). Also, bite mass was lower in February than in May for burned areas but not for unburned areas.

Cattle bite rate was influenced by the interaction among fire, herbivory and sampling period ($F = 19·8$, $P < 0·01$; Table 2 and Appendix S3). Specifically, in February (but not May), bite rate was lower in MWC ($P = 0·04$), but not significantly so in WC ($P = 0·11$), than in C for burns but not for non-burns. In addition, bite rate was significantly higher in May than in February for burns in WC and MWC, but not for burns in C.

The percentage of time cattle spent grazing (as opposed to non-grazing activities) was significantly higher in burns (95·4 ± 1·1%) than in non-burns (64·0 ± 4·7%) in May, but not February (77·9 ± 8·0% in burns vs. 90·3 ± 4·4% in non-burns) (fire × sampling period interaction $F = 22·1$, $P < 0·01$; Appendix S3). Percentage grazing time was also significantly lower in May (64·0 ± 4·7%) than in February (90·3 ± 4·4%) in non-burns, whereas this pattern was reversed in burns (95·4 ± 1·1% in May vs. 77·9 ± 8·0% in February).

Diet quality

Cattle diet crude protein (CP) content was higher ($F = 28·0$, $P < 0·01$) in May (wet period; 7·8 ± 0·3%) than in February (dry period; 6·1 ± 0·1%). This measure was also higher in MWC (7·2 ± 0·4%; $P = 0·01$) and tended to be higher in WC (7·3 ± 0·4%; $P = 0·07$) than in C (6·3 ± 0·3%) (herbivory effect $P = 0·07$, $F = 5·8$; Appendix S3). However, CP did not differ significantly between burns (6·9 ± 0·4%) and non-burns (7·0 ± 0·3%). Dietary dry matter digestibility was higher ($F = 14·9$,

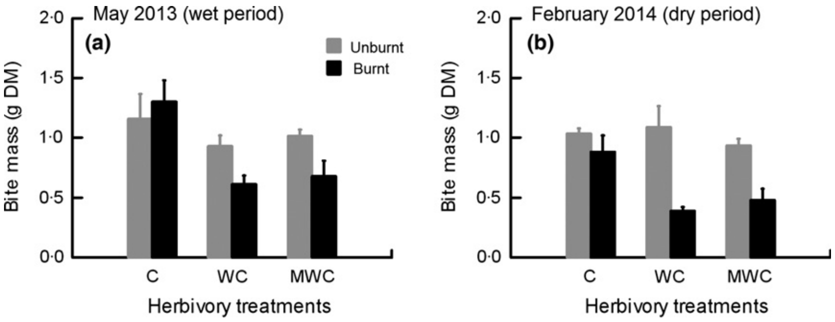

Fig. 3. Cattle bite mass (mean ± SE) across wet (a) and dry (b) sampling periods and fire treatments cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores.

Table 2. Cattle bite rate (mean ± SE bites min^{-1}) across sampling periods and fire treatments in plots cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores

	Herbivory treatments		
	C	WC	MWC
May 2013 (wet period)			
Unburnt	$25·0^{A(a)a} \pm 0·7$	$22·4^{A(a)a} \pm 2·2$	$25·2^{A(a)a} \pm 0·2$
Burnt	$37·4^{A(b)a} \pm 1·5$	$47·7^{A(b)a} \pm 2·9$	$37·4^{A(b)a} \pm 2·3$
Feb 2014 (dry period)			
Unburnt	$30·1^{A(a)b} \pm 0·9$	$31·8^{A(a)b} \pm 2·9$	$33·4^{A(a)b} \pm 1·1$
Burnt	$37·2^{A(a)a} \pm 2·2$	$29·1^{AB(a)b} \pm 2·4$	$28·2^{B(a)b} \pm 1·8$

Row means with different upper-case letter superscripts differ significantly between herbivory treatments. Within each herbivory treatment, column means with different superscripts in parentheses differ significantly between fire treatments, while those with different subscripts without parentheses differ significantly between sampling periods.

$P < 0·01$) in burns (51·7 ± 0·6%) than in non-burns (47·9 ± 0·7%). Digestibility was also significantly higher in May (50·1 ± 1·1%) than in February (46·5 ± 1·2%) in C but not in WC and MWC (herbivory × sampling period interaction $P = 0·06$, $F = 3·5$).

Dry matter and nutrient intake rates

Forage [instantaneous (IIR) and hourly (HIR)] and nutrient [crude protein (CPI), digestible dry matter (DDMI) and net energy (NEI)] intake rates were significantly lower in burns, but not in non-burns, in WC and MWC than in C (herbivory × fire interaction all $P < 0·06$, all $F > 4·5$; Figs 4a–d and 5a–f, Appendix S3). Notably, these reductions were greater in February (dry period; 60–97%) than in May (wet period; 37–47%). Forage and nutrient intake rates were also significantly higher in burns than in non-burns in C but not WC and MWC. Furthermore, these measures were influenced by an interaction between fire and sampling period (all $P < 0·01$, all $F > 33·0$; Figs 4a–d and 5a–f, Appendix S3). Specifically, in unburned areas, all the measures except NEI were significantly higher in February than in May. In burned areas, all the measures were significantly lower in February than in May. In May, all the measures except IIR were significantly higher in burns than in non-burns. In February, all measures except NEI were significantly lower in burns than in non-burns.

In both sampling periods, cattle met and in some cases significantly exceeded their nutrient (CPI and NEI) requirements for maintenance in all herbivory and fire treatments (all $t > -1·6$, all $P > 0·10$), except in burns in WC where CPI tended to be below maintenance ($t = -2·9$, $P = 0·05$) in February (Fig. 5 and Table S3). Cattle also met and sometimes significantly exceeded nutrient requirements for growth in all herbivory treatments for non-burns in both sampling periods and for burns in May (all $t > -1·5$, all $P > 0·08$). In February, CPI for burned areas was below growth requirement in WC ($t = -5·9$, $P = 0·01$) and MWC ($t = -4·2$, $P = 0·03$) but not in C where this requirement was met ($t = 1·1$, $P = 0·80$). Also during this dry period, NEI requirement for growth was exceeded across burns in C ($t = 5·2$, $P = 0·98$), but was barely met across burns in WC and MWC (both $t = -2·4$, $P = 0·07$).

WILDLIFE RESPONSE (CAMERA TRAPS)

Plains zebras were the most common medium-sized wild ungulates (64% of all medium-sized wild herbivore photographs), followed by oryx (15%) and buffalo (14%) (Fig. 6 and Table S1). All other medium-sized species were relatively rare (<5%; Table S1). Elephants were the more common megaherbivore species (99% of megaherbivore photographs; Table S1). Across both WC and MWC, all medium-sized wild ungulates combined, zebras and oryx occurred more frequently in burns than in non-burns (all $F > 20·0$, all $P < 0·01$; Fig. 6a–c). Buffalo exhibited a similar but non-significant pattern ($F = 4·3$, $P = 0·11$; Fig. 6d). Megaherbivores (principally elephants) tended to be more frequent in burns than in non-burns (477 ± 339 vs. 39 ± 33 photographs camera^{-1} month^{-1}; $F = 9·2$, $P = 0·09$).

Discussion

Consistent with our hypothesis, cattle forage and nutrient intake rates were reduced in burned plots they shared with wild herbivores. These reductions primarily resulted from reduced bite mass, driven by reductions in herbage quantity (cover and grass leaf height). Reductions in bite mass and forage intake rates of grazers due to reduced

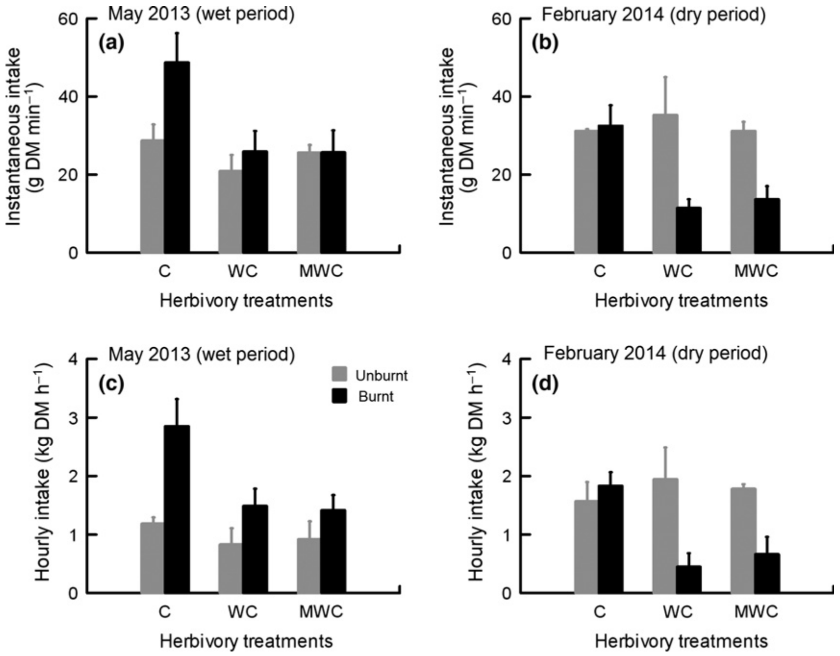

Fig. 4. Forage intake rates (means ± SE) of cattle across wet (a & c) and dry (b & d) sampling periods and fire treatments cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores.

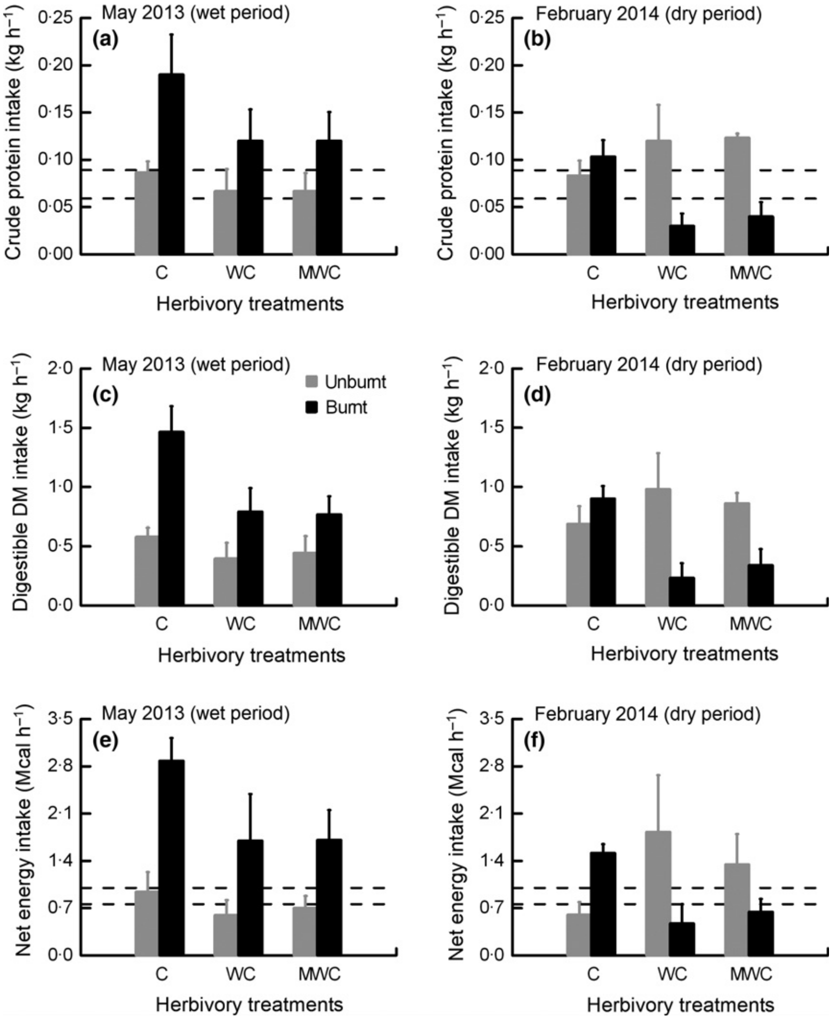

Fig. 5. Nutrient intake rates (means ± SE) of cattle across wet (a, c & e) and dry (b, d & f) sampling periods and fire treatments cattle accessed exclusively (C) or shared with wild herbivores excluding (WC) or including (MWC) megaherbivores. The lower and upper dashed lines represent minimum requirements for maintenance and growth (0·5 kg day^{-1}), respectively.

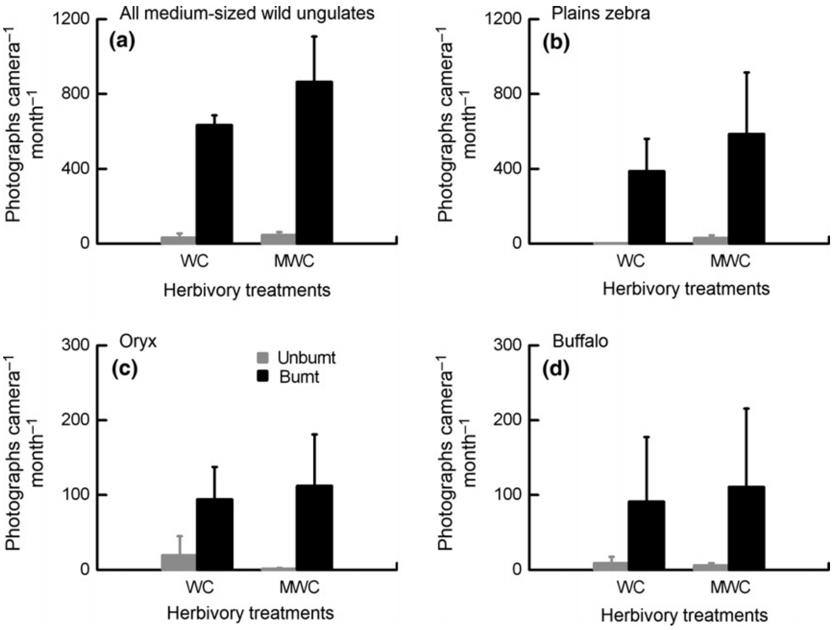

Fig. 6. Frequencies (camera trap photographs, means ± SE) of medium-sized wild herbivores combined (a) and the most common component species (c–d) across fire treatments in plots cattle shared with wildlife excluding (WC) or including (MWC) megaherbivores.

herbage quantity have been reported elsewhere (Hirata, Kunieda & Tobisa 2010; Heuermann *et al.* 2011; Carvalho *et al.* 2015; Raynor, Joern & Briggs 2015) and are generally associated with reduced bite depth or bulk density. However, we are the first to show that shared foraging with wild herbivores in burned areas can reduce herbage quantity, thereby reducing forage and nutrient intake by cattle.

Whereas cattle bite mass was lower in shared than in unshared burns, there were no concomitant increases in bite rate and time spent grazing; as a result, estimated intake rates were reduced in the shared burned areas. This was somewhat surprising because herbivores are expected to increase bite rate and grazing time to offset reduced bite mass (Erlinger, Tolleson & Brown 1990; Gregorini *et al.* 2006). However, our findings are consistent with other studies (Forbes 1988; Gordon 1994; Drescher *et al.* 2006; Amaral *et al.* 2012), which generally indicate that when herbage quantity falls below a certain threshold, grazers may be constrained by difficulty in grasping bites and are unable to increase their bite rate to compensate for low bite mass. It appears from our study that shared grazing with wildlife in burned areas reduced forage quantity below this threshold.

Cattle had greater intake rates on burns than on nonburns, but only when they were the only large herbivore present, consistent with our hypothesis that shared herbivory with wild herbivores subdues the positive effects of prescribed burning on cattle. Subdued positive responses of cattle to burning in shared plots were likely caused by the large reductions in herbage quantity by wildlife. The larger herbage quantity differences between fire treatments in shared than in unshared areas in May are attributable to wildlife grazing prior to cattle grazing post-burning. The fact that these differences persisted in February, after several cattle grazing episodes, confirms the persistent and important impacts of wildlife.

Wildlife-driven reductions in cattle nutrient intake in burned areas were likely primarily due to reduced forage intake rather than diet quality. Rather than reducing cattle diet quality, shared foraging with wild herbivores enhanced cattle diet crude protein, which is partly attributable to increased green leaf content in shared burns during the wet (May) sampling period. This corroborates findings from a previous study in this ecosystem that also found that shared herbivory with wildlife enhanced cattle diet quality through improved forage quality (Odadi *et al.* 2011).

That burning increased cattle diet digestibility was consistent with our expectation and findings elsewhere (Mbui 1985; Angell, Stuth & Drawe 1986; Svejcar 1989). However, the unaltered dietary crude protein following burning was unexpected because burning typically increases herbage crude protein content (Sensenig, Demment & Laca 2010). Lack of fire-driven enhancement of cattle diet crude protein content has been reported elsewhere and attributed to reduced forb consumption in burned areas (McGinty, Smeins & Merrill 1983; Svejcar 1989). However, our related study found no significant difference in forb consumption by cattle between burned and unburned sites (W.O. Odadi, unpublished data). Because fire-induced increases in herbage crude protein content in this ecosystem have been reported to be ephemeral (<5 months) and relatively mild (Sensenig, Demment & Laca 2010), we suspect that any such increases may have been insufficient or too short-lived to alter cattle diet crude protein content.

The indirect effects of wild ungulates on cattle, via herbage quantity, are typical for African savannas, where wildlife and livestock typically access the same foraging areas at different times. That cattle nutrition was not altered by shared foraging with wildlife in unburned areas in both sampling periods is, however, in contrast to findings of a previous study in this system, which demonstrated competitive and facilitative effects of wild herbivores on cattle during wet and dry seasons, respectively (Odadi *et al.* 2011). In the present study, wild herbivores concentrated their use on burned areas and used unburned areas less; this possibly muted their impacts on unburned areas.

The demonstrated fire-induced wild herbivore effects on cattle forage and nutrient intake rates appeared to be more detrimental to cattle during the dry period (February). During the wet period (May), the steers met and sometimes even exceeded their nutrient requirements both in shared and in unshared burned areas. However, this was not the case when they foraged in shared burned areas during the dry period. Notably, the steers met the nutrient requirements in shared unburned areas during this dry period, suggesting that unburned areas served as refuge forage source for cattle. These differential responses between sampling periods may have been reinforced by the longer time since burning in February (11 months) than in May (2 months). Specifically, by the February sampling, herbivores had had longer time and thus increased opportunity for repeated grazing in burned areas, leading to greater impacts on vegetation and cattle.

Because the shared foraging plots were accessible to several wildlife species, it is impossible to attribute the effects demonstrated here to a single wildlife species. However, because experimental exclusion of megaherbivores from plots that cattle shared with wildlife did not alter cattle response patterns, we attribute these effects to medium-sized ungulates, and especially zebras, oryx and buffalos, which frequented the shared burned areas. Although elephants frequented burned areas, their role in driving the observed patterns was minimal, possibly because the reduced grass height in the shared burns deterred their use of this forage class (Dublin 1995; Van De Koppel & Prins 1998), and muted their effects on herbage availability. It appears that elephants primarily frequented burns to utilize woody rather than herbaceous vegetation.

To our knowledge, this study provides the first experimental evidence of fire-induced adverse effects of wild herbivores on cattle nutrition in a tropical savanna ecosystem. These findings confirm the belief among some livestock managers that fire intensifies competitive interactions between wild and domestic ungulates. Although the scale of our experiment was small, our findings are relevant in the context of our study region where cattle grazing tends to be spatially restricted through active herding. Herded cattle may have limited ability to range more widely across unburned areas to compensate for reduced forage availability in burned areas. Furthermore, even when grazing access is less restricted, extensive movement may increase energetic expenditure of cattle, making them unable to fully offset these effects. Future studies should examine how the effects reported here vary across spatial scales.

Our study covered only the first year post-burning, and we do not know how long the effects seen here will persists. However, in this region, wildlife preference for burned areas persist for at least 6 years post-burning (D.M. Kimuyu, unpublished data). Additionally, we are initiating an investigation into how long the demonstrated fire-induced effects of wildlife on cattle persist. Meanwhile, we can conclude that because unburned shared areas were nutritionally more beneficial to cattle than burned shared areas during the dry period, interspersing burns with unburned areas could moderate fire-driven negative interactions between wild and domestic herbivores. Conversely, burning could be used to draw wildlife away from cattle forage in some areas, such as those near available water, creating spatial niche partitioning.

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Data accessibility

R scripts are uploaded as online supporting information (Appendix S3). Vegetation, cattle nutrition and wildlife data are archived in figshare, https://dx.doi.org/10.6084/m9.figshare.3509669.v1 (Odadi *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Frequency of wild ungulates in study plots based on camera traps.

Table S2. Estimated minimum nutrient requirements for steers.

Table S3. One-sample *t*-test results for whether experimental steers met nutrient requirements.

Appendix S1. Wildlife camera trapping protocol during the study.

Appendix S2. Equations used to calculate net energy intake rate of cattle.

Appendix S3. R scripts and statistical test results for all measured attributes.