African wild ungulates compete with or facilitate cattle depending on season

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Savanna ecosystems are vital for both economic and biodiversity values. In savannas worldwide, management decisions are based on the concept that wildlife and livestock compete for grassland resources[1-4], yet there are virtually no experimental data to support this assumption[1]. Specifically, the critical assessment of whether or not wild ungulates alter livestock performance (e.g., weight gain, reproduction or survival) has rarely been carried out, although diminished performance is an essential prerequisite for inferring competition[1]. Here we use a large-scale experiment in a semi-arid savanna in Kenya to show that wild ungulates do depress cattle performance (weight gain) during the dry season, indicating a competitive effect, but enhance cattle performance during the wet season, signifying facilitation. This is the first experimental demonstration of either competitive or facilitative effects of an assemblage of native ungulates on domestic livestock in a savanna ecosystem, and a unique demonstration of a rainfall-dependent shift in competition-facilitation balance within any herbivore guild. These results are critical for better understanding and management of wildlife-livestock coexistence

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in savanna ecosystems globally, and especially in the African savanna biome which crucially hosts the last remnants of an intact large herbivore fauna.

Savannas are critical ecosystems for both biodiversity conservation and livestock production worldwide. In most of these ecosystems, livestock and wild herbivores co-occur, and can potentially interact in several ways depending on the extent to which they share resources and availability of those resources. Interaction between herbivores is assumed to be competitive when a shared resource is limited and its use by two or more species results in reduced performance (e.g., survivorship, fecundity, or weight gain) of at least one species. Reduced performance is typically associated with reduced food intake and poor diet quality. Facilitation, the opposite of competition, is deduced to occur if one species enhances performance in another species, such as through improved food quality or intake via modification the habitat[1,5].

The food habits of domestic and wild ungulates, and dietary overlap between these herbivore guilds suggestive of competition have been documented in many savanna ecosystems[2,6-8]. Experimental studies have also shown that shared grazing with wild herbivores can alter cattle food habits and foraging patterns[9,10]. However, the question of whether cattle experience depressed performance (survival, growth rate, or reproduction) when they share foraging with an assemblage of wild ungulates has seldom been investigated scientifically, and never in a savanna biome. Such an appraisal is critical in determining any competition-related costs of wildlife to livestock production[1], an important step towards better understanding and management of wildlife-livestock coexistence in savanna rangelands. Here we use a controlled replicated experiment to assess whether or not wild herbivores (>15kg) compete for food resources with cattle on a natural ecosystem in northern Kenya. Specifically, we hypothesised that if native ungulates compete with cattle, then cattle should experience decreased weight gain associated with decreased forage availability and quality, reduced selection of major herbage species, depressed food intake and reduced diet quality, when they share foraging areas with wildlife. We predicted that these effects should be greater during the dry season when food is less abundant. Additionally, we predicted that these competitive effects would be greater in the additional presence of megaherbivores, especially elephant (*Loxodonta africana*), which also has dietary overlap with cattle.

We compared cattle weight gain, organic matter intake (OMI), diet selection, dietary digestible organic matter (DOM), crude protein (CP) and DOM/CP ratio, and herbage cover in treatment plots accessed exclusively by cattle and those they shared with medium-sized wild herbivores with or without megaherbivores. Consistent with our hypothesis, cattle experienced depressed weight gain when they foraged in areas accessible to wild herbivores during the dry season (Fig. 1a), evidence of competition. In contrast, this pattern was reversed in the wet season, with increased cattle weight gain in the treatments shared with wildlife (Fig. 1b), demonstrating a facilitative interaction.

Competition is associated with depressed food intake by cattle in the shared treatments (Table 1), which corresponds with reductions in cover and selection by cattle of *Pennisetum stramineum* (Figs 2a-c), suggesting that this grass is a major source of competition between wild ungulates and cattle. For all other major herbaceous species, cover was not significantly different among herbivore treatments. The proportion of bites on *Themeda triandra* increased in the treatment accessible to all the three guilds of herbivores during wet season, but no other major plant species showed treatment effects on selection by cattle (Supplementary Table S1). The importance of *P. stramineum* in cattle nutrition during dry season is further underscored by a strong positive correlation between the selection index of this grass and cattle weight gain ($r = 0.95$, $P = 0.0001$). The exact mechanism through which decreased selection of *P. stramineum* depresses the overall food intake in the dry season is unclear; there were no significant treatment differences in dietary DOM and CP during the dry season (Table 1).

Because several local wild ungulate species were excluded in this experiment, it is not possible to directly attribute these competitive effects to any specific herbivore species. However, we believe that these effects are largely driven by plains zebra (*Equus burchelli*), because zebras are by far the most abundant native ungulates in the study system[11], and because they have a high dietary overlap with cattle[7,8].

In contrast to the net competition between wildlife and cattle demonstrated in the dry season, net facilitation was demonstrated during the wet season, overcoming what appear to be ongoing competitive effects. This net facilitation was associated with differences in forage quality, including improved crude protein (CP) content and reduced DOM/CP ratio of cattle diet in plots shared with wild herbivores (Table 1). It appears enhanced dietary CP improves cattle performance even when forage quality is generally high (wet season)[12]. The ratio of DOM to CP is an index of the balance of nutrients available to rumen microbes and is related to performance[13]. In ruminants, a dietary DOM/CP ratio of 4:1 is considered optimal[13]. Above this threshold, increases in DOM/CP ratio have been associated with reductions in animal performance[13,14]. In our experiment, cattle select diets with DOM/CP ratios 11-17% closer to the optimal level when they share foraging areas with wildlife than when they forage exclusively (Table 1). Cattle performance appears to be very sensitive to relatively small changes in DOM/CP ratio as has been reported elsewhere[14].

We hypothesise that improved cattle nutrition in the presence of wildlife was related to decreased cover of standing dead grass stems in the shared treatments during wet season (Table 2). Although we did not separate cattle bites into different plant parts, we suspect that decreased cover of dead stems in the shared foraging areas lowers chances of their accidental consumption thereby improving the overall quality of cattle diet. The significance of reduced cover of dead stalks in driving facilitation during the wet season is further supported by a strong negative correlation (r = -0.90, P = 0.001) between weight gain of cattle and the cover of dead grass stems.

We suspect that reduced cover of dead grass stalks and the associated facilitation of cattle is due to plains zebra, by the virtue of their adaptation to cropping and processing fibrous stems[15,16]. Thus, we propose that the pathway to facilitation of cattle through reduced grass stemminess may be analogous to the postulated facilitative role of zebras in catalysing a grazing succession that culminates into enhanced access to high quality forage by native ruminants in the Serengeti ecosystem[15,17,18].

Megaherbivores tend to amplify the effects of medium-sized wild herbivores on cattle, as evidenced by slightly greater differences in most measured parameters between treatments MWC and C than between WC and C (Figs 1,2, Tables 1,2), although these were not statistically significant. If this megaherbivore impact is real, it is likely attributable to elephants, which utilize herbaceous vegetation extensively[19,20], but not to giraffes (*Giraffa camelopardalis*), which seldom feed on the herbaceous layer[21].

To our knowledge, the present study provides the first experimental evidence of both competitive and facilitative effects of a guild of native ungulates on cattle in the African savanna biome, and the only one directly measuring livestock performance. Hitherto, wildlife-livestock competition has to a limited extent only been shown in North America, where black-tailed prairie dog (*Cynomys ludovicianus*), a small mammalian herbivore, and Rocky Mountain elk (*Cervus elaphus canadensis*) have separately been reported to compete with cattle, resulting in reduced weight gains[22,23].

Notably, net facilitative effects of domestic stock by wild herbivores have not been shown previously in any ecosystem. Hobbs et al. [23,24] did document "weak enhancing effects" of Rocky Mountain elk on cattle diet quality in North America, but these were more than compensated for by large competitive effects. Our results show that facilitative increases in forage quality can seasonally overcome competitive reductions in forage quantity. We suggest the net effects of species interactions in all ecological systems are a result of both competitive and facilitative effects, with the net effect being the one that is quantitatively greater.

The seasonal shift between competition and facilitation in this large herbivore system is reminiscent with similar variation in plant systems. In plant systems, however, spatial or temporal increases in stress tend to be associated with greater facilitation[25], whereas here the net facilitation was during superficially less "stressful" conditions.

These results have the power to inform management strategies for fostering livestock-wildlife coexistence in human occupied savanna landscapes. It would be worth exploring whether the seasonal competition/facilitation shifts we demonstrate here are paralleled along spatial gradients in rainfall and primary productivity.

METHODS SUMMARY

Our study was conducted at Mpala Research Centre ($0^{o}17^{'}$N, $37^{o}52^{'}$E, 1800 m a.s.l.), using the Kenya Long-term Exclosure Experiment (KLEE). Treatments accessible to cattle only (C), medium-sized wild herbivores (> 15 kg) and cattle (WC) and megaherbivores, medium-sized wild herbivores and cattle (MWC) were used. Each treatment plot (4-ha) is replicated across three experimental blocks[26].

We conducted two 16-week trials spaced 14 months apart during 2007-2008. Each trial comprised a dry and a wet season. Nine separate herds of four randomly selected Boran heifers (*Bos indicus*) aged 2-3.5 years were herded in the nine treatment plots (one herd/plot) throughout each trial period. Live weight change was measured bi-weekly. Grab samples from the total collections in the dry periods and additional samples obtained twice or thrice during each wet period were analysed for dry organic matter (DOM) and crude protein (CP) using the near infrared reflectance spectroscopy[27]. Food intake (OMI) was estimated as faecal output/(1-DOM) once or twice during each dry period, with faecal output being measured by total faecal collection over 5-day period. Dung was generally too loose during wet periods to make total faecal collection reliable.

Individual heifers were observed in four 5-minute focal periods for diet selection bi-weekly. Herbage cover was measured as contacts/100 pins by placing a 1-m pin perpendicular to the ground at 1-m intervals along four 25-m transects randomly located on the grazing paths and recording all contacts with different species and parts (live/dead stems/leaves). We computed selectivity indices following Ivlev's formula[28].

Experimental units were treatment plots, with individual heifers and vegetation surveys used as plot sub samples. For each year, data were averaged across animals (or vegetation surveys) in each plot per season. Seasonal data were then averaged across year and each season analysed separately using ANOVA with block effects to test for differences among treatments. Tukey's HSD was performed to separate means. All data were normally distributed (one-sample Kolmogorov-Smirnov test Z = 0.387-0.81; P = 0.411-0.997).

TABLES

Table 1. Food intake and diet quality of cattle in different treatments.

	Herbivory treatments C	WC	MWC	*F*	*P*
Dry season					
OMI (kg OM/day)	**4.6[a] ± 0.03**	**4.3[b] ± 0.06**	**4.3[b] ± 0.04**	**11.1**	**0.02**
DOM (%)	57.1 ± 0.22	56.5 ± 0.27	56.9 ± 0.39	0.7	0.55
CP (%)	8.1 ± 0.33	7.9 ± 0.02	8.0 ± 0.11	0.2	0.61
DOM/CP ratio	7.1 ± 0.27	7.2 ± 0.02	7.1 ± 0.13	0.1	0.94
Wet season					
DOM (%)	59 ± 0.01	58.4 ± 0.28	58.6 ± 0.41	0.8	0.5
CP (%)	**10.6[a] ± 0.08**	**10.9 ± 0.16**	**11.1[b] ± 0.15**	**10.1**	**0.03**
DOM/CP ratio	**5.8[a] ± 0.05**	**5.6[b] ± 0.08**	**5.5[b] ± 0.08**	**33.8**	**0.003**

Data are means ± s.e.m. (n = 3). Rows listed in bold exhibited significant treatment effects. Means within a bold row sharing different superscripts are statistically different ($P < 0.05$).

Table 2. Treatment effects on cover (hits/100 pins) of different grass parts.

	Herbivory treatments				
	C	WC	MWC	*F*	*P*
Dry season					
Live leaves	88.7 ± 9.1	75.9 ± 3.3	80.7 ± 16.1	0.5	0.7
Dead leaves	147.6 ± 7.0	131.5 ± 6.1	139.4 ± 31.8	0.2	0.8
Live stems	15.4 ± 2.9	18.2 ± 2.2	10.9 ± 1.8	1.8	0.3
Dead stems	76.6 ± 8.7	76.1 ± 5.6	62.4 ± 12.2	1.4	0.3
Wet season					
Live leaves	181.1 ± 12.3	175.6 ± 4.6	160.8 ± 6.6	1.4	0.3
Dead leaves	64.8 ± 6.1	58.2 ± 1.3	61.8 ± 8.9	0.3	0.8
Live stems	33 ± 5.5	27.9 ± 4.6	21.5 ± 4.2	1.2	0.4
Dead stems	**42.1[a] ± 2.8**	**33.7[b] ± 2.7**	**31.6[b] ± 2.2**	**18.1**	**0.01**

Data are means ± s.e.m. (*n* = 3). Row listed in bold exhibited significant treatment effect. Means within a bold row sharing different superscripts are statistically different ($P < 0.05$).

FIGURE LEGENDS

Figure 1. Cattle weight gain within treatments. **a,** during dry season. **b,** during wet season. Error bars are s.e.m. (n = 3). The P-values are for comparisons of C to either WC or MWC (Tukey's HSD). Weight gain was lower in both WC both MWC than in C during dry season (F = 14.3, P = 0.01), but this pattern was reversed during wet season (F = 9.8, P = 0.03).

Figure 2. Cover of *Pennisetum stramineum* and its selection by cattle. **a,** cover during dry season. **b,** cover during wet season. **c,** relative bites during dry season. **d,** relative bites during wet season. **e,** selection index during dry season. **f,** selection index during wet season. Error bars are one s.e. (n = 3 blocks). The P-values represent difference between WC or MWC and C (Tukey's HSD). There were significant treatment effects for cover (F = 20.3, P = 0.008) relative bites (F = 18.3, P = 0.009) and selection index (F= 30.4, P = 0.004) during dry season.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank Margaret Kinnaird, Michael Littlewood and the Mpala Board of Trustees for accommodation, experimental site and test animals. In addition, we thank Kari Veblen, Corinna Riginos, Chris Odhiambo and George Aike for logistical support and Frederick Erii, Mathew Namoni, John Lochukuya, Jackson Ekadeli, Robert Kibet, Samuel Kaiyieuwa, Sangei Naiputari and Peter Ekai for field assistance. We appreciate comments and suggestions by Todd Palmer. The exclosure plots were built and maintained with grants from the James Smithson Fund of the Smithsonian Institution, The National Geographic Society, The National Science Foundation and the African Elephant Program of the U.S. Fish and Wildlife Service. Additionally, this work was supported by grants from the International Foundation for Science.

Author Contributions W.O.O. designed the study, collected and analysed data and wrote the paper. S.A.A., M.M.K. and T.P.Y. helped with study design and statistical analysis. T.P.Y. provided partial funding for the research, and established and maintained the KLEE exclosures. All authors discussed the results and edited the manuscript.

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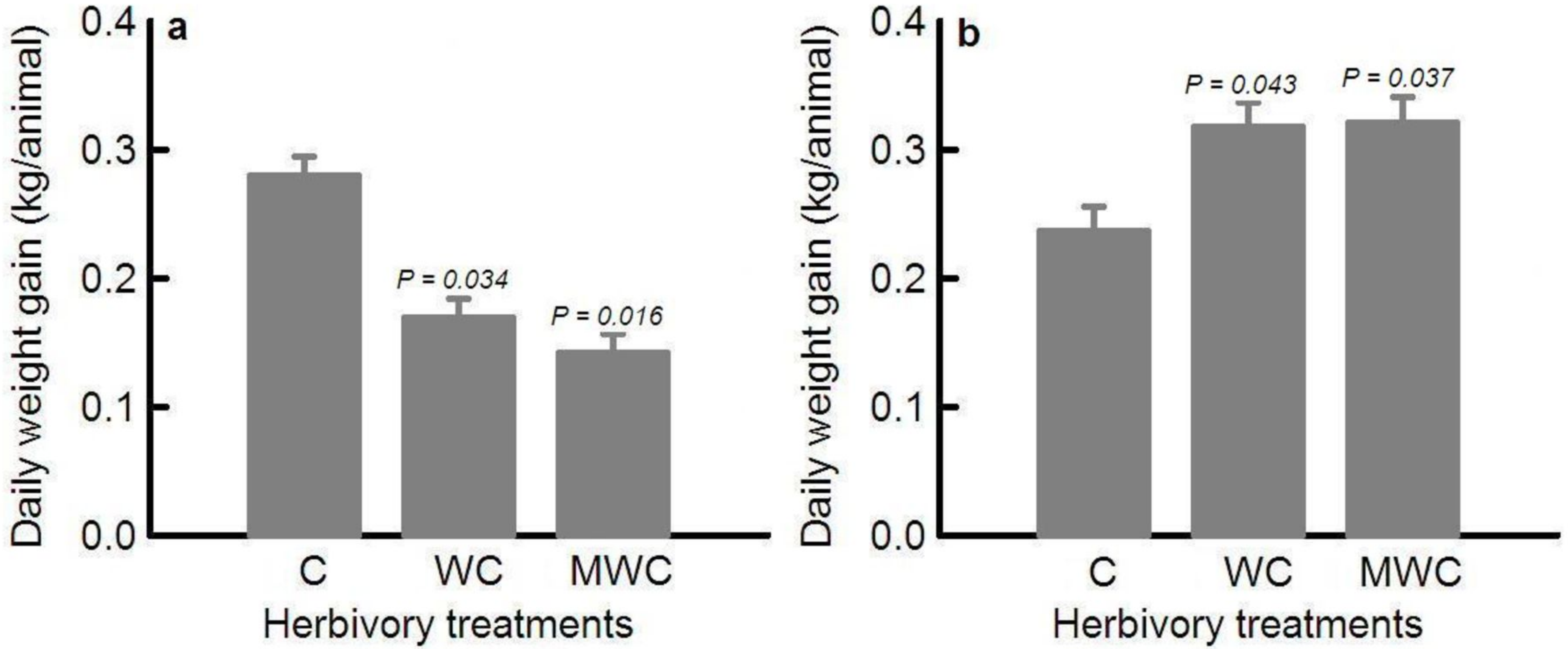

a
Daily weight gain (kg/animal)
0.0
0.1
0.2
0.3
0.4
P = 0.034
P = 0.016
C
WC
MWC
Herbivory treatments
b
Daily weight gain (kg/animal)
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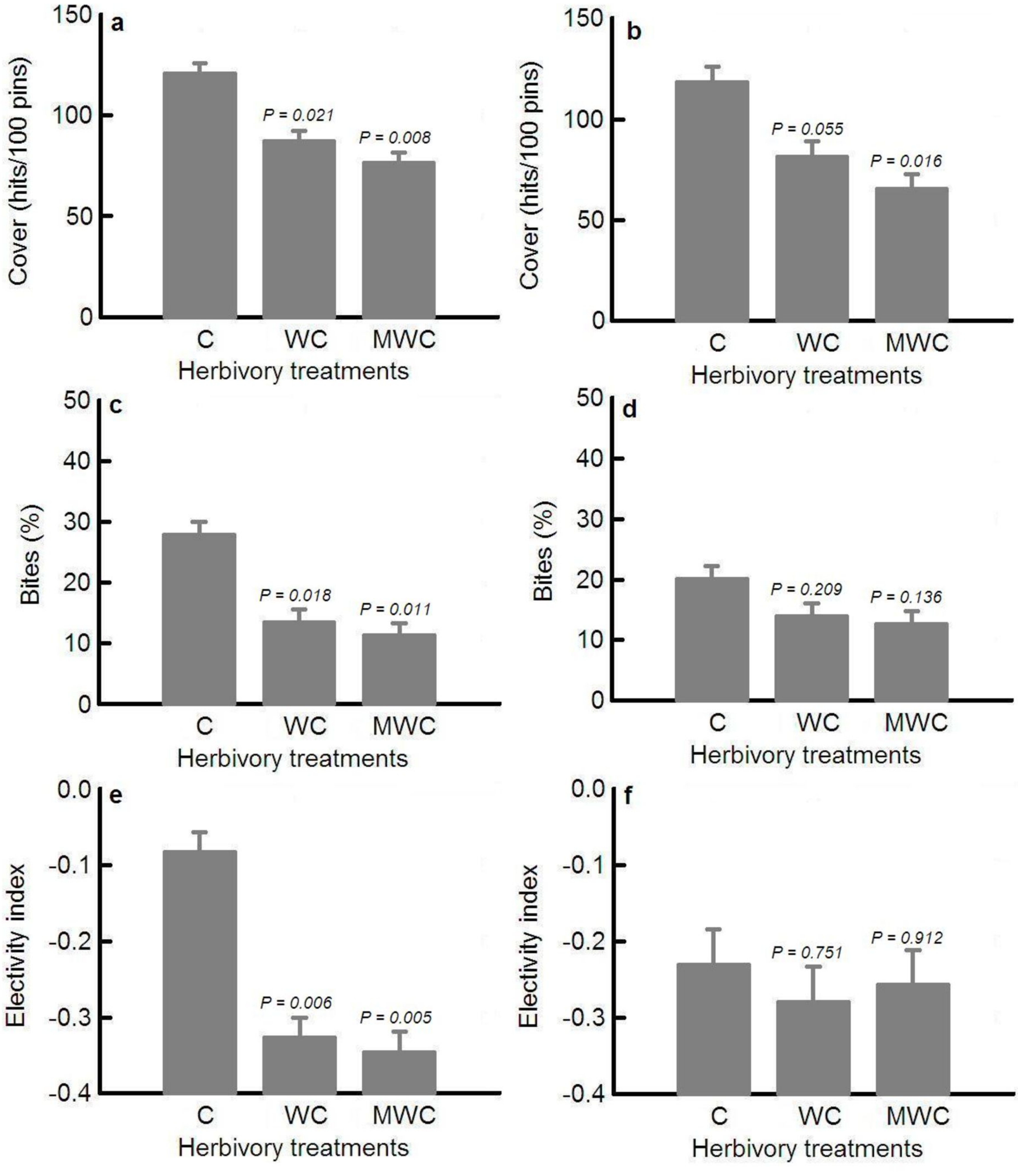
0.2
0.3
0.4
P = 0.043
P = 0.037
C
WC
MWC
Herbivory treatments


a
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0
P = 0.021
P = 0.008
C
WC
MWC
Herbivory treatments
b
Cover (hits/100 pins)
P = 0.055
P = 0.016
c
Bites (%)
50
40
30
20
10
P = 0.018
P = 0.011
d
Bites (%)
P = 0.209
P = 0.136
e
Electivity index
0.0
-0.1
-0.2
-0.3
-0.4
P = 0.006
P = 0.005
f
Electivity index
P = 0.751
P = 0.912