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Protein supplementation reduces non-grass foraging by a primary grazer

Wilfred O. Odadi,[1,5] Moses K. Karachi,[2] Shaukat A. Abdulrazak,[3] and Truman P. Young[1,4]

[1]*Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya*
[2]*Natural Resources Department, Egerton University, P.O. Box 536, Egerton, Kenya*
[3]*National Council for Science and Technology, P.O. Box 30623, Nairobi, Kenya*
[4]*Department of Plant Sciences, University of California, Davis, California 95616 USA*

Abstract. It is believed that wildlife and livestock can coexist in semiarid savanna rangelands. However, this coexistence is threatened by intense competition for scarce, but nutritionally vital, forage resources. Specifically, there is evidence that grazing livestock seasonally compete for protein-rich forbs (non-grasses) with browsing and mixed-feeding wildlife. While this has been attributed to protein needs, there are no experimental tests of whether grazers in such a context alter their diet selection when supplemented with protein. We compared forage selection between cattle supplemented with protein (cotton seedcake) and those not supplemented during dry and wet periods, in a semiarid African savanna rangeland where they have been demonstrated to compete with wildlife for forage. We further evaluated whether such dietary alteration affected the overall biting and movement behavior, nutrition, and performance of cattle, by comparing bite and step rates, diet quality (crude protein and digestible organic matter), forage intake, and live mass change between these treatment groups. During the dry period, relative consumption of forbs was 76% lower in supplemented cattle than in non-supplemented cattle. Notably, supplemented cattle significantly avoided forbs relative to their abundance in the environment, while non-supplemented cattle over-sampled this herbage type. Conversely, selection and relative use of *Brachiaria lachnantha*, the most abundant grass species, and *Bothriochloa insculpta*, a grass species otherwise avoided, increased following protein supplementation. These patterns were similar but nonsignificant during the wet period. Bite and step rates, diet quality, forage intake, and performance were not significantly affected by protein supplementation in either period. Our study shows that foraging cattle partially trade off protein-rich forbs for protein-poor grasses when supplemented with protein, without suffering detrimental behavioral, nutritional, or performance consequences. These results broaden our understanding of the role of non-grasses in the diets of "grazers" and suggest protein supplementation as a potential tool in managing coexistence between grazing livestock and browsing (forb-consuming) wildlife.

Key words: African savanna rangelands; browsers; competition; cotton seedcake; crude protein; forbs; grazers; livestock; ruminants; wildlife; wildlife–livestock coexistence.

Introduction

Ruminants can be categorized as grazers, browsers, or mixed feeders, based on the plant types they select (Hofmann 1989, Bodmer 1990, Robbins et al. 1995, Gordon 2003). Grazers primarily consume graminoid monocots (grasses and sedges), while browsers largely eat herbaceous non-grasses (forbs) and the leaves and twigs of woody plants. Mixed feeders are intermediate between grazers and browsers, selecting a mixture of grass and browse, often seasonally switching between these food types. Diet selection by ruminants of different feeding types corresponds with morphophysiological adaptations of their respective digestive systems (Schwartz and Ellis 1981, Van Soest 1996, Shipley 1999, Clauss et al. 2008, 2010). These adaptations are in turn driven by fundamental physicochemical differences between food types. Key among these dissimilarities is the well-established fact that browse plants contain higher levels of protein than grasses (Holecheck 1984, Boutton et al. 1988, Van Soest 1994, Codron et al. 2007). The presence of secondary compounds such as tannins in browse may inhibit the availability of protein, but this problem is more commonly associated with woody browses than with forbs (Clauss et al. 2008).

It is has been suggested that sustained coexistence between domestic and wild ungulates is possible in semiarid savanna rangelands because of the facilitative interactions that have been demonstrated between these herbivore guilds (Odadi et al. 2011*a*, *b*). However, this coexistence is threatened by intense competition for scarce nutritious forage resources such as forbs. Because of their high protein content, forbs can play a vital role in nutritionally enhancing the diets of ungulate species

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[5] E-mail: woodadi@yahoo.com

that utilize the herbaceous vegetation layer (Zimmermann 1980, McCollum and Galyean 1985). However, forbs are usually in short supply in most semiarid ecosystems, and it has been suggested that domestic stock, especially cattle, and wildlife seasonally compete for this forage class (Beck and Peek 2005, Fulbright and Ortega-S 2006, Odadi et al. 2007). Cattle are primarily grazers, but in many settings eat nontrivial amounts of forbs depending on season and locality, even competing with browsing and mixed feeding ungulates (Fulbright and Ortega-S 2006). For example, forbs can represent up to 15% of the bites of cattle in a semiarid African savanna system (Odadi et al. 2007). In blue gramma and desert grasslands in North America, year-round average contribution of forbs to cattle diets has been reported to range between 25% and 35% (Pieper and Beck 1980). High selection of forbs (10–68%) by cattle has also been reported on an aspen–sagebrush summer range in northeastern Nevada (Beck and Peek 2005). It has been suggested that forbs are included in the diets of grazing ruminants because of their high protein content (Pieper and Beck 1980, Holecheck 1984), but there is limited experimental confirmation of this.

It has been proposed that the nutritional status of a free-ranging herbivore influences its preference for various food types (Heady 1964). Whereas protein supplementation can alter an animal's nutritional status, there is limited scientific knowledge on the effect of such supplementation on botanical diet selection by any free-ranging grazing ruminant (Judkins et al. 1985). Such knowledge would be vital in managing coexistence between grazing domestic stock and wild ungulates, especially in biodiversity-rich savanna ecosystems where these herbivore guilds often co-occur. Specifically, if protein supplementation can lead to reductions in selection and use of forbs by grazing livestock, then such supplementation could potentially suppress competition for forbs between large grazing livestock and forb-dependent wild ungulates.

We investigated whether cattle alter their patterns of forage selection when supplemented with protein in a semiarid African savanna in central Kenya. We hypothesized that compared to non-supplemented cattle, supplemented cattle would select and use forbs less frequently (and select grasses more frequently). Among grasses, we predicted that supplementing cattle with protein would result in cattle selecting and consuming more of the species otherwise less preferred but relatively more abundant. We further posited that these effects would be greater during the dry season, when the response of cattle to supplementation is likely to be more pronounced, than during the wet season, because of greater protein limitation. Finally, we predicted that supplementation-driven alteration in forage selection pattern would be accompanied by positive changes in cattle biting and movement behavior, nutrition (forage intake and dietary digestible organic matter and crude protein contents) and performance (mass gain).

Materials and Methods

Study area

We conducted the study at Mpala Research Centre and Conservancy (0°17′ N, 37°52′ E, 1800 m above sea level) in Laikipia County, Kenya. The 20 000-ha property encompasses Mpala Ranch, with approximately 2000 head of Boran (*Bos indicus*) cattle. The area experiences a mean annual rainfall of 500–600 mm, which generally peaks in April–June, July–August, and October–November, with marked interannual variation (Young et al. 1998).

We sited our study in a semiarid savanna ecosystem dominated by black cotton soils (vertisols). The overstory vegetation is principally composed of *Acacia drepanolobium* Sjøstedt, while perennial grasses dominate the herb-layer vegetation, which also contains several species of forbs, albeit at much lower abundance (Young et al. 1998).

Large wild herbivores of varied feeding types occur in the study site. Primary grazers that frequent the area include plain's zebra (*Equus burchelli*), African buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus buselaphus*), and Grevy's zebra (*E. grevyi*). Primary browsers and mixed feeders are represented by giraffe (*Giraffa camelopardalis*), eland (*Tragelaphus oryx*), oryx (*Oryx gazella*), Grant's gazelle (*Gazella granti*), steinbuck (*Raphicerus campestris*), and elephant (*Loxodonta africana*). Cattle (*Bos indicus*) dominate among the domestic herbivores that forage in the study site, with sheep (*Ovis aries*) and camels (*Camelus dromedarius*) also present but in much smaller numbers.

Trial periods, experimental animals, and treatments

The study covered a period of 16 weeks between February and June 2007. The first six weeks of the study period (February–March) were dry (<10 mm of rainfall), while the following 10 weeks (April–June) were relatively wet (>90 mm of rainfall).

At the start of the experiment, we obtained eight test heifers aged 2.5–3.5 years and weighing 301 ± 26 kg (mean ± SD) from Mpala Ranch. We randomly selected four heifers for supplementation with cottonseed cake, and used the remaining four as controls. Heifers to be supplemented individually received 0.5 kg of the supplement in plastic bowls at 08:00 daily throughout the course of the experiment. The supplement contained 92% dry matter, 87% organic matter, and 32% crude protein.

All heifers receiving supplement became fully accustomed to the supplementation regimen within 1–2 weeks. Throughout the course of the experiment, an experienced herder herded all the experimental heifers together, starting at 08:00–09:00 and ending approximately eight hours later for an overnight stay at a boma located within the study site each day. Because herding is a common practice in this region, and the study animals were accustomed to being herded, the presence of the herder was expected to have minimal influence on the behavior of the experimental animals and their response to supplementation. The animals accessed drinking water daily at midday.

Focal observations and herb-layer vegetation surveys

We observed the test heifers during three to six consecutive days weekly. On each day, we observed each heifer in three or four nonconsecutive five-minute focal periods, during which we counted steps and the number of bites taken on each plant species. We randomized the order of sampling of individual heifers within each treatment group, carrying out the five-minute focal observations alternately between supplementation groups. We carried out all focal observations between 09:00–12:00 after allowing a settling period of 15–30 minutes prior to sampling each day.

We considered as bites the actual prehension of plant material and discerned them by both sound of prehension and visual criteria. A step was a forward movement of either front limb by the focal animal. We made all observations within 4 m of the focal animals to ensure accurate discernment of bites, steps, and plant species eaten.

We calculated step rate, bite rate, and percentage of bites on different forage species and categories for individual heifers per survey. In addition, we calculated Ivlev's (1961) selection indices for consumed plant species and categories for each heifer per survey using the formula

$$\text{Selection index} = (p_i - c_i)/(p_i + c_i)$$

where p_i is percentage of bites on species i and c_i is the relative cover of species i. The index ranges from -1 (total avoidance) through 0 (no selection) to 1 (total selection).

For the purpose of calculating selection indices, we measured relative cover of plant species along the grazing paths of the test heifers during focal observations. We did this by vertically placing a 1 m long pin at 25 locations at approximately 1-m intervals along four randomly originated transects, and recording first pin contacts with different species at each location. We calculated the relative cover of each species per survey by dividing the total number of pin contacts with that species by the total number of pin contacts with all species.

Live mass measurements

We measured the live masses of test heifers routinely at 07:00–08:00 after overnight starvation without feed or water every two weeks. For initial live mass measurements at the start of the trial, we used a fixed platform weighing machine located about 4 km from the study site. Subsequently, we used a hanging scale weighing system located next to the boma. We made all measurements to the nearest 1 kg.

Estimation of forage intake and diet quality

For supplemented heifers, we calculated forage intake by subtracting supplement organic matter intake (amount of supplement fed [0.5 kg] × supplement dry matter content [92%] × supplement organic matter content [87%]) from the total organic matter intake. We derived total organic matter intake from estimates of fecal output and digestibility (i.e., organic matter intake = organic matter fecal output/[1 − digestible organic matter]). To estimate fecal output, we manually collected all fecal material voided by each heifer on five consecutive days. Experimental heifers were kept in separate sections of the overnight enclosure for the purpose of collecting the dung voided at night. Forage intake was measured during the dry season, but could not be reliably measured during the wet period because dung was mostly too loose to be collected manually.

During the dry period, each fresh dung collection was weighed immediately and a grab sample randomly taken and placed in a sealable plastic bag. Fecal grab samples were then pooled for individual heifers each day (24 hours), weighed and air-dried for six weeks. Percent dry mass was then calculated for each pooled sample and the result multiplied by the fresh mass of dung collected over the day (24 hours) associated with that sample to estimate dry matter fecal output. The dried samples were analyzed for organic matter content at the Kenya Agricultural Research Institute (KARI) laboratory in Naivasha using standard procedures (AOAC 1990), to convert dry matter fecal output to organic matter basis. Mean daily organic matter fecal output during each fecal collection period was calculated for each heifer.

The dry season fecal samples together with additional samples obtained twice from each test heifer during the wet period were analyzed using the near infrared reflectance spectroscopy to estimate dietary crude protein and digestible organic matter contents for each heifer (Kidane 2005). Mean dietary crude protein and digestible organic matter contents were calculated for individual heifers per trial period.

Data analysis

We used the four individual heifers per treatment group ($n = 4$) as replicates and, for all dependent variables, averaged measurements for each individual heifer per trial period. We used two-way ANOVA to test for the effects of supplementation (supplemented vs. non-supplemented) and trial period (wet vs. dry) on mass change, bite and step rates, diet selection, and diet quality. The model included supplementation × trial period interaction and whenever this interaction was significant ($P < 0.05$) or tended to be significant ($P < 0.10$), we used Tukey's post hoc test to separate means. Because forage intake was measured only in the dry season, we analyzed the data for this variable using one-way ANOVA to test for the effect of supplementation. We performed a one-sample t test, with zero as the benchmark mean, to determine significant selection (selection index > 0) or avoidance (selection index < 0) of different forage species or classes. We analyzed relative cover of different herbaceous plant species and classes descriptively using means. Prior to statistical

TABLE 1. Availability, selection, and use of the major grass species by cattle during February–June 2007 (both time periods, combined).

Species	Relative cover (%)	Bites (%)	Selection index
Brachiaria lachnantha	27 ± 2	41 ± 3	**0.21 ± 0.02**
Themeda triandra	22 ± 1	30 ± 2	**0.14 ± 0.01**
Lintonia nutans	11 ± 1	9 ± 1	**−0.09 ± 0.03**
Setaria anceps	3 ± 1	3 ± 1	−0.01 ± 0.11
Pennisetum stramineum	17 ± 2	9 ± 1	**−0.32 ± 0.04**
Bothriochloa insculpta	3 ± 1	2 ± 1	**−0.33 ± 0.09**
Pennisetum mezianum	10 + 1	2 + 0	**−0.65 ± 0.04**

Notes: Data are means ± standard errors. Selection indices in boldface type indicate significant selection (positive values) or avoidance (negative values).

analysis, we arcsine transformed all percentage data derived from counts to meet assumptions of normality and homoscedasticity. However, as with all other data, we present these percentage data as untransformed estimates (mean ± SE). We performed all analyses using Systat 9 statistical software (SPSS 1998), and generated graphics in R version 2.15.0 (R Development Core Team 2012).

RESULTS

Herbaceous vegetation cover

Total herbaceous cover at the grazing sites averaged 90% ± 1% (mean ± SE). Grasses dominated the herb layer (relative cover 97% ± 0%), while forbs (3% ± 0%) were far less abundant. Among grass species, *Brachiaria lachnantha* (Hochst.) Stapf, *Themeda triandra* Forssk, and *Pennisetum stramineum* Peter were the most common. *Lintonia nutans* Stapf and *P. mezianum* Leeke were intermediate, while *Bothriochloa insculpta* (A. Rich.) and *Setaria anceps* (Shumach.) were the least common (Table 1). Several other plant species each comprised less than 2% of herb-layer vegetation cover.

Diet selection

Across both time periods, cattle ate primarily grasses (95–99% bites) and forbs (1–5% bites). Woody browses (shrubs) comprised a negligible proportion (<0.1%) of cattle bites (Appendix A: Table A1). Among grasses, *B. lachnantha* and *T. triandra* comprised the highest proportions of total bites, and were significantly selected (eaten in proportions greater than their representation in the environment) (Table 1; $t = 10.4$, $P < 0.001$ and $t = 12.2$, $P < 0.001$, respectively). In contrast, cattle ate *B. insculpta* and *P. mezianum* least frequently of the common grasses, and significantly avoided them (Table 1; $t = -3.7$, $P = 0.002$ and $t = -14.7$, $P < 0.001$, respectively). Although *L. nutans* and *P. stramineum* were consumed in moderate proportions (9% each), their selection indices indicated significant avoidance (Table 1; $t = -2.9$, $P = 0.01$ and $t = -9.2$, $P < 0.001$, respectively). *Setaria anceps* was selected in approximate proportion to its relative availability (Table 1: $t = -0.9$, $P = 0.365$). *Rhinacanthus ndorensis* Schweinf. was the most frequently eaten forb species, especially during the dry period when it comprised 2.6% ± 0.4% of the total bites taken by both supplementation groups combined. Several other plant species consumed by cattle individually comprised less than 1% of total bites (Appendix A: Table A1).

The relative consumption of forbs was 76% lower ($P < 0.01$) in supplemented cattle than in non-supplemented cattle during the dry period, but not ($P = 0.95$) during the wet season (Fig. 1a). Similarly, selection of forbs was lower ($P = 0.015$) in supplemented cattle only during the dry period (Fig. 1b). Notably, whereas forbs were significantly selected ($t = 7.3$, $P = 0.005$) by the control heifers during the dry period, they were significantly avoided ($t = -3.8$, $P = 0.033$) by the supplemented heifers (Fig. 1b). The major forb species driving these patterns was *R. ndorensis*, which comprised 86% of the total bites on forbs (Fig. 1c), and was strongly selected (selection index = 0.71, $t = 44.3$, $P < 0.001$) by the control heifers, but not (selection index = −0.07, $t = -0.3$, $P = 0.76$) by the supplemented heifers (Fig. 1d).

Brachiaria lachantha and *B. insculpta* were eaten more frequently ($P = 0.048$ and $P < 0.001$, respectively) by supplemented cattle than by control cattle during the dry period, but not during the wet period (both $P > 0.80$; Fig. 2a, c). Likewise, selection indices of these grasses were increased significantly following supplementation in the dry period (both $P < 0.01$), but not in the wet period (both $P > 0.70$) (Fig. 2a, d). Notably, during the dry period, *B. insculpta* was strongly avoided by non-supplemented cattle (selection index = −0.50, $t = -4.6$, $P = 0.019$), but not by supplemented cattle (selection index = 0.20, $t = 2.4$, $P = 0.098$; Fig. 2a, d). Selection and consumption of the other major grass species (*T. triandra*, *P. stramineum*, *P. mezianum*, and *S. anceps*) were not significantly affected by supplementation in either period (all $P > 0.10$).

Bite and step rates

Bite rate, step rate, and bites per step averaged 34.7–38.9 bites/minute, 11.3–13.4 steps/minute, and 2.9–3.2 bites/step, respectively. These behavioural parameters did not differ significantly between supplementation groups or between periods (all $P > 0.05$), with the exception of step rate, which was 13% higher in the wet season than in the dry season ($P < 0.01$; Table 2).

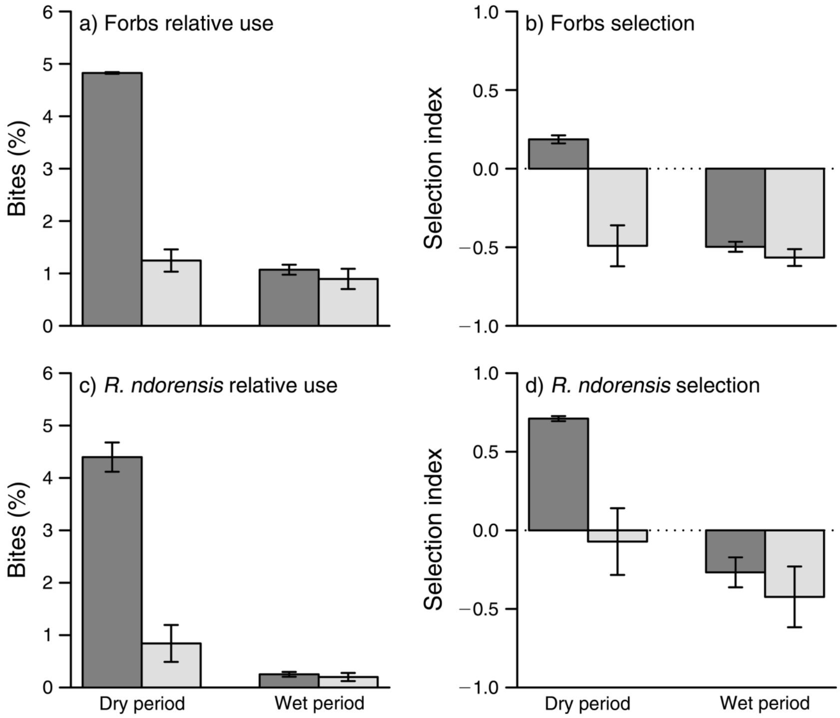

FIG. 1. Selection and consumption of forbs by control heifers (dark gray bars) and protein-supplemented heifers (light gray bars). Error bars represent one standard error ($n = 4$ replicates). Effects for forb use are: supplementation, $F_{1,12} = 32.2$, $P < 0.001$; period, $F_{1,12} = 36.0$, $P < 0.001$; supplementation × period interaction, $F_{1,12} = 23.4$, $P < 0.001$. Effects for forb selection are: supplementation, $F_{1,12} = 25.9$, $P < 0.001$; period, $F_{1,12} = 26.7$, $P < 0.001$; supplementation × period, $F_{1,12} = 17.2$, $P = 0.001$. Effects for *Rhinacanthus ndorensis* use are: supplementation, $F_{1,12} = 32.2$, $P < 0.001$; period, $F_{1,12} = 76.2$, $P < 0.001$; supplementation × period, $F_{1,12} = 24.4$, $P < 0.001$. Effects for *R. ndorensis* selection are: supplementation, $F_{1,12} = 9.6$, $P = 0.009$; period, $F_{1,12} = 19.2$, $P < 0.001$; supplementation × period, $F_{1,12} = 4.3$, $P = 0.061$.

Performance, food intake, and diet quality

Mass gain averaged 0.2–0.4 and 0.2–0.3 $\text{kg}\cdot\text{head}^{-1}\cdot\text{d}^{-1}$ for control and supplemented heifers, respectively, and did not differ significantly ($P = 0.53$) between these groups in either period (Table 3). However, mass gain was significantly higher ($P = 0.04$) in the wet than in the dry period (Table 3).

Daily forage intake did not differ significantly between groups (Table 3). The diets of both groups contained 57–60% digestible organic matter and 8–10% crude protein. Both diet quality parameters did not differ significantly between treatment groups ($P > 0.6$), but were 3% and 15% greater, respectively, in the wet than in the dry period (Table 3, $P < 0.01$).

DISCUSSION

Altered forage selection patterns

Decreased selection and relative consumption of forbs (Fig. 1a–d), and increased selection and relative consumption of *Brachiaria lachnantha* (the most abundant species) and *Bothriochloa insculpta* (a largely avoided species) (Fig. 2a–d) by cattle following protein supplementation were consistent with our predictions. Also consistent with our hypothesis was the fact that all the dietary selection changes associated with supplementation were pronounced and statistically significant during the dry period, but weak and nonsignificant during the wet period (Figs. 1 and 2).

We propose that these dietary alterations were driven by the need by cattle to select a diet with a favorable balance of protein to energy. In particular, the strong selection for forbs by the non-supplemented cattle (Figs. 1b and d), suggests that these cattle were actively seeking this protein-rich food type (Holecheck 1984, Boutton et al. 1988, Van Soest 1994, Codron et al. 2007) presumably to enhance their dietary crude protein levels. This was in sharp contrast to supplemented cattle, which avoided forbs (Fig. 1b, d). This avoidance may have been because selecting this herbage class in addition to protein supplement would have probably raised their protein intake beyond their requirements, and led to an unfavorable nutrient balance. Alternatively, because cattle are not primarily adapted to browsing, forbs may become undesirable to them once they meet their protein needs elsewhere.

The rejection by non-supplemented cattle of *B. insculpta* (Fig. 2d), a grass species known for its low protein content and poor palatability especially when mature (Todd 1956, Field 1976, Perrin and Brereton-Stiles 1999, Bowers 2006), suggests that these cattle were

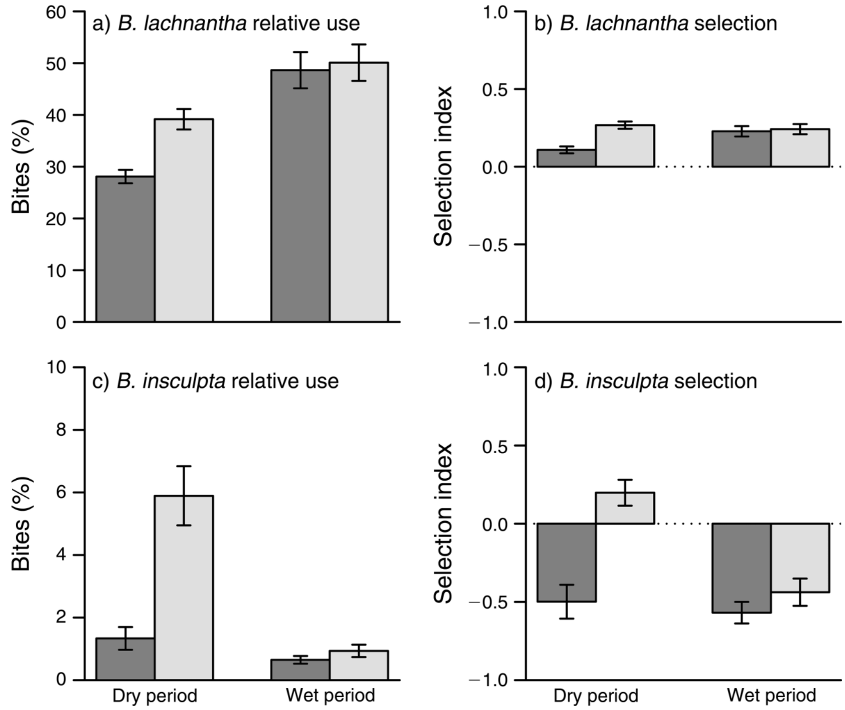

FIG. 2. Selection and consumption of *Brachiaria lachnantha* and *Bothriochloa insculpta*, by control heifers (dark gray bars) and protein-supplemented heifers (light gray bars). Error bars represent one standard error ($n = 4$ replicates). Effects for *B. lachnantha* use are: supplementation, $F_{1,12} = 5.6$, $P = 0.035$; period, $F_{1,12} = 33.9$, $P < 0.001$; supplementation × period, $F_{1,12} = 3.4$, $P = 0.089$. Effects for *B. lachnantha* selection are: supplementation, $F_{1,12} = 9.4$, $P = 0.009$; period, $F_{1,12} = 2.7$, $P = 0.124$; supplementation × period, $F_{1,12} = 6.6$, $P = 0.025$. Effects for *B. insculpta* use are: supplementation, $F_{1,12} = 24.4$, $P < 0.001$; period, $F_{1,12} = 37.0$, $P < 0.001$; supplementation × period, $F_{1,12} = 15.0$, $P = 0.002$. Effects for *B. insculpta* selection are: supplementation, $F_{1,12} = 22.1$, $P < 0.001$; period, $F_{1,12} = 16.1$, $P = 0.002$; supplementation × period, $F_{1,12} = 10.3$, $P = 0.007$.

avoiding species that would have, otherwise, lowered the overall protein–carbohydrate balance of their diet. In contrast, the tendency toward selection of this grass by protein supplemented cattle (Fig. 2d) provides further evidence that these supplemented animals were not selecting for protein.

The observed increased selection and use of *B. lachnantha*, the most abundant and most consumed forage species (Table 1; Fig. 2a, b), suggests that foraging cattle increase their focus on their major and most common grass species when supplemented with protein. In addition, there is evidence that increased protein intake may be critical for increased selection and use of *B. lachnantha* by cattle. In a previous study, cattle were found to consume this grass more in areas where they also consumed forbs more frequently, and apparently had higher protein intake, than in areas where forb consumption was impaired (Odadi et al. 2007).

TABLE 2. Biting and movement behavior of cattle under different supplementation treatments during February–June 2007.

Parameter	Control	Supplemented	Mean
Dry period			
Bite rate (bites/minute)	34.7 ± 1.4	37.3 ± 1.5	36.0 ± 1.1
Step rate (steps/minute)	11.3 ± 0.2	11.7 ± 0.4	11.5 ± 0.2
Bites per step	3.1 ± 0.1	3.2 ± 0.2	3.2 ± 1.1
Wet period			
Bite rate (bites/minute)	38.9 ± 0.7	37.7 ± 0.7	38.3 ± 0.5
Step rate (steps/minute)	13.4 ± 0.4	13.2 ± 0.4	13.3 ± 0.3
Bites per step	2.9 ± 0.1	2.9 ± 0.1	2.9 ± 0.1

Notes: Data are means ± standard errors. Effects for bite rate are: supplementation, $F_{1,12} = 1.9$, $P = 0.57$; trial period, $F_{1,12} = 20.8$, $P = 0.07$; supplementation × trial period interaction, $F_{1,12} = 14.6$, $P = 0.12$. Effects for step rate are: supplementation, $F_{1,12} = 0.6$, $P = 0.81$; trial period, $F_{1,12} = 25.7$, $P < 0.01$; supplementation × trial period interaction, $F_{1,12} = 0.7$, $P = 0.41$. Effects for bites per step are: supplementation, $F_{1,12} = 0.1$, $P = 0.77$; trial period, $F_{1,12} = 4.3$, $P = 0.06$; supplementation × trial period interaction, $F_{1,12} = 0.5$, $P = 0.50$.

TABLE 3. Performance and nutrition of cattle under different supplementation treatments during February–June 2007.

Parameter	Control	Supplemented	Mean
Dry period			
Mass gain ($kg \cdot head^{-1} \cdot d^{-1}$)	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
Forage intake ($g\ OM \cdot kg\ LM^{-1} \cdot d^{-1}$)	16.3 ± 1.8	16.5 ± 1.1	16.3 ± 0.1
DOM (%)	57.2 ± 0.4	57.3 ± 0.2	57.3 ± 0.2
CP (%)	8.2 ± 0.3	8.6 ± 0.3	8.4 ± 0.2
Wet period			
Mass gain ($kg \cdot head^{-1} \cdot d^{-1}$)	0.4 ± 0.2	0.3 ± 0.1	0.3 ± 0.0
Forage intake ($g\ OM \cdot kg\ LM^{-1} \cdot d^{-1}$)			
DOM (%)	59.5 ± 0.8	58.7 ± 0.4	59.1 ± 0.4
CP (%)	9.6 ± 0.4	9.7 ± 0.2	9.7 ± 0.2

Notes: Data are means ± standard errors. Abbreviations are: OM, organic mass; LM, live mass; DOM, digestible organic matter; CP, crude protein. Effects for mass gain are: supplementation, $F_{1,12} = 0.4$, $P = 0.53$; trial period, $F_{1,12} = 2.7$, $P = 0.04$; supplementation × trial period, $F_{1,12} = 0.0$, $P = 0.82$. Effects for forage intake (dry period) are: supplementation, $F_{1,6} = 0.0$, $P > 0.90$. Effects for DOM are: supplementation, $F_{1,12} = 0.6$, $P = 0.47$; trial period, $F_{1,12} = 14.4$, $P < 0.01$; supplementation × trial period, $F_{1,12} = 1.0$, $P = 0.34$. Effects for CP are: supplementation, $F_{1,12} = 0.8$, $P = 0.40$; trial period, $F_{1,12} = 13.6$, $P < 0.01$; supplementation × trial period, $F_{1,12} = 0.1$, $P = 0.74$.

It is critical for ruminants to maintain a favorable protein–energy balance (Van Soest 1994, Rutter 2010) because the energetic expense associated with metabolizing amino acids ingested in excess of protein requirement is usually very high (Reid 1974). For optimal performance, non-lactating cows require 24 g digestible protein for every 1000 kilocalories (1 kilocalorie = 4184 J) of metabolizable energy, a balance attained at a dietary protein level of approximately 9% (Prins and Beekman 1989). In the present study, the protein content of the diet selected by the non-supplemented heifers during the dry season was slightly below this level (8.2%, Table 3), suggesting why these animals selected forbs and avoided or reduced the selection of low-protein forage items.

On the other hand, had the supplemented cattle selected a diet similar to the diet of control heifers, their total daily crude protein (CP) intake (forage + supplement) per kg body mass (BM) would have equaled 2.06 g (Appendix B: Eq. B.1). This would have resulted in a CP content of 10.7% (2.06 g/19.2 g $DM^{-1} \cdot kg\ BM^{-1} \times 100$) (where DM is dry mass), which is well above the 9% level required for a balanced diet. However, the actual CP content of the diet of the supplemented heifers (including the supplement CP intake) was 8.6% (Table 3), suggesting that the altered diet selection by these animals (Figs. 1 and 2) was sufficient for attainment of a more favorable nutrient balance.

The dietary selection shifts associated with protein supplementation reported here have not been shown previously in any rangeland ecosystem. In one of the few studies that have investigated the effect of protein supplementation on cattle diet selection, Judkins et al. (1985) reported no significant change in the botanical composition of cattle diet following protein supplementation. However, in that study, cattle were able to select diets with much higher crude protein levels (>11%) than those reported in the present study. It appears that free-ranging cattle become less responsive to protein supplementation when the quality of the available forage is generally high. This logic is supported by the muted response of cattle to supplementation during the rainy season in the present study (Figs. 1 and 2), when the CP content of the diet of both supplemented and non-supplemented cattle was generally high (9.5%; Table 3).

Our results are consistent with the findings of Prins and Beekman (1989) who showed that the African buffalo, a species closely related to cattle, avoided food items containing too high crude protein levels in order to select a more balanced diet. Similarly, sheep supplemented with protein were shown to consume more of the otherwise less-preferred carbon-rich species (Golluscio et al. 1998). This change in selectivity was suggested to either result from the meeting of protein requirements (Lardy et al. 1999) or be the indirect consequence of an increase in ruminal fermentation and thus in herbage digestibility (Delagarde et al. 1999, Mathis et al. 1999). In the present study, forage intake did not change significantly following protein supplementation, further confirming that the dietary changes reported here resulted from the supplemented heifers meeting, and most likely exceeding, their protein requirements.

Unchanged behavior, nutrition, and performance

We did not find a statistically significant difference in bite rate between treatment groups (Table 2; but the nonsignificant 7% increase in bite rate following supplementation during the dry period is noteworthy). At first, this may appear counterintuitive because based on the observed supplementation-driven reduced selection of forbs and increased selection of grasses (Figs. 1 and 2), one would expect bite rate to be higher in the supplemented than in the control cattle. This is because forbs were relatively less abundant than grasses (Table 1) and their reduced selection (and concomitant increase in grass selection) would be expected to result in increased bite rate by the supplemented cattle through reduced need for more frequent movement in search of these scarce forage plants. However, step rate was similar between treatment groups (Table 2), suggesting that the frequency of movement within and between feeding patches was unaltered by supplementation.

We suggest that the non-supplemented cattle maintained similar bite and step rates as supplemented cattle possibly because of morphological characteristics and spatial distribution patterns of *R. ndorensis* (the principal forb species selected by cattle) that facilitate its location and cropping by foraging cattle. Specifically, this spreading, creeping and mat-forming forb forms randomly distributed distinct green patches in open spaces between perennial grass tufts, and is fairly easily accessible to large herbivores (Appendix C: Fig. C1). Once foraging cattle locate a patch containing this forb, they tend to settle and take several successive quick bites before moving on to the next feeding patch (personal observation).

The absence of significant effects of supplementation on cattle nutrition and performance (Table 3) was inconsistent with our predictions. We suggest that these unaltered nutritional and performance parameters were as a result of the demonstrated supplementation-driven diet selection shifts (Figs. 1 and 2). Specifically, because forbs maintain high crude protein content compared to grasses, the observed reduced selection and intake of forbs, and increased grass selection, by the supplemented heifers (Figs. 1 and 2) essentially fully compensated for any effect that supplementation may have had on the crude protein and digestible organic matter contents of selected diets. In addition, the increased selection of *B. insculpta*, a grass species that was otherwise highly avoided (Fig. 2c), and the dominant *B. lachnantha*, by supplemented cattle may have attenuated the effects of supplementation on diet quality. The absence of significant treatment effects on the measured nutritional and performance parameters (Tables 2 and 3) indicates that the observed supplementation-driven changes in diet selection (Figs. 1and 2) were fully compensatory.

Management implications

Our results show that when cattle are supplemented with protein during the dry period, they reduce selection and relative use of forbs, and increase selection and consumption of relatively less preferred (*B. insculpta*) or dominant (*B. lachnantha*) grass species. These dietary shifts may have important implications on cattle-wildlife interactions. In particular, because forbs are usually relatively scarce and are an apparent source of competition between cattle and browsing and mixed-feeding wild ungulates (Odadi et al. 2007), their reduced selection implies increased availability to these wild ungulates. Conversely, supplemented cattle are less likely to be competitively suppressed by wild browsers and mixed feeders (c.f. Young et al. 2005). Therefore, supplementation can potentially be used as a tool for moderating competition between cattle and wild ungulates. The fact that biting and movement behavior, nutrition and performance of cattle were unaltered despite the supplementation-driven dietary changes reported here, suggests that other than the cost of supplement, there are no other costs to cattle production associated with such dietary changes.

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Supplemental Material

Appendix A

Relative consumption (percentage of bites) of plant species individually comprising less than 1% of total bites by non-supplemented (CON; control) and supplemented (SUP) cattle at different periods (*Ecological Archives* A023-022-A1).

Appendix B

Estimation of crude protein intake by supplemented heifers, if they were to select diets with crude protein levels similar to diets selected by the non-supplemented heifers (*Ecological Archives* A023-022-A2).

Appendix C

A photograph showing a classic patch of *Rhinacanthus ndorensis*, a forb species most commonly consumed by cattle, amid dry grass tufts (*Ecological Archives* A023-022-A3).

Supplement

Data necessary to replicate statistical analyses of the effects of protein supplementation and sampling period on various measured parameters (*Ecological Archives* A023-022-S1).