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Herd Size-Dependent Effects of Restricted Foraging Time Allowance on Cattle Behavior, Nutrition, and Performance☆,☆☆

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ABSTRACT

We tested the influence of herd size on the effects of restricted foraging time on cattle *(Bos indicus)* foraging behavior, nutrition, and performance in a Kenyan savanna rangeland. Using a randomized block design, we compared weight gain, forage intake, diet selection, dietary crude protein (CP) and digestible organic matter (DOM), bite and step rates, distance travelled, and activity time budgets between steers allowed unlimited foraging time (DNG) in predator-free areas with those herded diurnally in predator-accessible areas in large (200 steers; LDG), medium (150 steers; MDG), or small (100 steers; SDG) herds and corralled at night. Daily weight gain was greater ($P < 0.01$) in DNG (0.61 kg) or SDG (0.56 kg) than in LDG (0.19 kg) or MDG (0.29 kg) but did not differ ($P = 0.591$) between DNG and SDG. Likewise, daily organic matter intake was greater ($P < 0.05$) in DNG (6.2 kg) or SDG (5.4 kg) than in LDG (3.7 kg) or MDG (3.7 kg) but did not differ ($P = 0.288$) between DNG and SDG. Grazing time was lower ($P < 0.01$) in DNG (42.2%) than in LDG (71.3%), MDG (72.2%), or SDG (69.5%), while the reverse was the case for ruminating and/or resting time (47.1%, 12.1%, 11.9%, and 10.3% in DNG, LDG, MDG, and SDG, respectively). Bite rate was lower in DNG (13.1 bites · min^{-1}) than LDG (21.0 bites · min^{-1}; $P = 0.068$), MDG (27.7 bites · min^{-1}; $P = 0.13$) or SDG (26.2 bites · min^{-1}; $P = 0.007$). However, diet selection, CP, DOM, step rate, and distance travelled did not differ among treatments. Our findings demonstrate subdued negative effects of restricted foraging time when cattle are herded diurnally in small-sized herds. Application of this strategy could reduce the need for eliminating wild carnivores to facilitate unrestricted foraging time for cattle.

Introduction

Night corralling is a common animal husbandry practice in tropical rangelands worldwide. In African savanna rangelands, this practice serves various purposes, including protection of livestock from predators or theft, and collection of manure in integrated crop-livestock systems. In addition, corralling has been suggested to be a key driver of heterogeneity across pastoral savanna landscapes through accumulation of nutrients and subsequent emergence of lush, nutritious, and palatable forage at abandoned corralling sites (Young, 1995; Augustine, 2004; Veblen, 2012; Donihue et al., 2013). Notably, on the basis of this latter function, the use of temporary livestock corrals in restoring degraded land and improving wildlife habitats is fast gaining prominence in African rangelands, especially in parts of eastern Africa.

Although corralling can be advantageous in many ways, its downside is that it effectively limits the amount of time animals can access forage resources, thereby potentially suppressing livestock productivity. Indeed, several studies have shown that allowing livestock unlimited foraging time enhances weight gain through increased forage intake (Joblin, 1960; Khombe et al., 1992; Ayantunde et al., 2000a, 2000b; Ayantunde et al., 2002). Therefore conflict often arises between the need for corralling for protection from predators and/or manure collection and the need for livestock to have unrestricted grazing time allowance for improved production performance. This conflict is often heightened in rangelands where manure is needed for crop production or where livestock predation risk is high.

In east African savanna rangelands where livestock and wildlife often share land, the conflict between the need for corralling and unrestricted foraging is primarily driven by relatively high risk of predation of nocturnally foraging livestock. This is because the benefit of enhanced livestock performance associated with additional foraging at night can be negated by increased predation losses (Wigg and Owen, 1973). Therefore many livestock owners seeking to improve livestock productivity and profitability through unrestricted 24-h grazing time consider elimination of wild carnivores as a key prerequisite (King, 1983; Bayer, 1986; Lamarque et al., 2009). Although some ranchers adopt a more wildlife-friendly approach by creating predator-free zones for nighttime

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livestock grazing, leaving the rest of their properties accessible to wildlife, others are less accommodating and entirely exclude predators and other wildlife. This latter approach is not consistent with biodiversity conservation and maintaining multiple value principles of sustainable rangeland management. Consequently, there is a need to explore grazing management techniques that enhance livestock performance without compromising the conservation of predators and other wildlife. One such strategy could involve manipulating the livestock stocking rate to minimize intraspecific competition among diurnally foraging livestock and lessen the need for extended grazing during nighttime. However, such an intervention requires a thorough understanding of the effects of a restricted foraging time allowance on livestock nutrition and performance and whether such effects are modulated by stocking rate.

While the impacts of restricted foraging time on livestock behavior, nutrition, and productivity have been extensively investigated (Joblin, 1960; Smith, 1961; Wigg and Owen, 1973; King, 1983; Nicholson, 1987; Fernandez-Rivera et al., 1996; Ayantunde et al., 2000a, 2000b; Ayantunde et al., 2002), little is known about the role of herd size in moderating such impacts. In this study, we investigated the effects of restricted foraging through nighttime corralling on cattle nutrition and production performance and whether such effects depend on herd size. Working in a semiarid savanna rangeland in central Kenya, we compared foraging behavior, nutrition, and performance between cattle herds allowed unlimited access to forage in predator-free areas with those herded diurnally in small-sized (100 steers$\cdot$herd^{-1}), medium-sized (150 steers$\cdot$herd^{-1}), and large-sized (200 steers$\cdot$herd^{-1}) herds that were corralled at night in predator-accessible areas. We controlled the overall stocking rate while maintaining the different herd sizes, and thus the different herd sizes represent different stocking rates (low, moderate, and high, respectively) in the landscape. We hypothesized that because intraspecific competition should become less intense with decreasing herd size, food intake and performance of cattle with limited foraging time would be greatest in small-sized herds and lowest in large-sized herds. We further predicted that the negative effects of restricted foraging time allowance would be less pronounced in small than in large herds.

Materials and Methods

Study Area

The study was conducted at Ol Pejeta Conservancy (OPC; lat 00°00′15″N, long 36°57′49″E) in Laikipia County, Kenya. The conservancy covers an area of 370 km^2 within the Laikipia plateau, which is bounded by Mt. Kenya to the east and the Aberdare Range to the west. Rainfall averages approximately 700 mm annually and is generally bimodally distributed, with peaks from March to May (long rains) and October to December (short rains). The mean annual maximum and minimum temperatures are 28°C and 12°C, respectively.

Black cotton soil is the dominant soil type. Four distinct vegetation types are discernible: a mosaic of grassland, *Acacia drepanolobium* Sjøstedt (whistling thorn) mixed woodland, *Euclea divinorum* Hiern (magic guarri) bushes, and riverine woodland dominated by *Acacia xanthophloea* Benth. (yellow fever tree). Several other plant species such as *Carissa edulis* (Forssk.) Vahl (Egyptian carissa), *Psiadia punctulata* (DC.) Vatke, and *Scutia myrtina* (Burm. f.) Kurz (cat-thorn) comprise the woody vegetation layer. The herbaceous layer is dominated by the perennial grasses, *Themenda triandra* Forsk. (red oat grass), *Cynodon* spp. Rich., *Pennisetum stramineum* Peter (Masai grass), and *Pennisetum mezianum* Leeke (bamboo grass).

Ol Pejeta Conservancy hosts approximately 68 species of mammals and carries one of the highest wildlife densities in Kenya. The major wild mammalian herbivores include plains zebra *(Equus burchelli)*, African buffalo *(Syncerus caffer)*, hartebeest *(Alcelaphus buselaphus)*, eland *(Tragelaphus oryx)*, oryx *(Oryx gazella beisa)*, waterbuck *(Kobus ellipsiprymnus)*, impala *(Aepyceros melampus)*, Thompson's gazelle *(Gazella thompsonii)*, Grant's gazelle *(Gazella granti)*, African elephant *(Loxodonta africana)*, and giraffe *(Giraffa camelopardalis)*. Notably, OPC also hosts some of the most endangered animals in the world, including black rhino *(Diceros bicornis)*, white rhino, and Grevy's zebra *(Equus grevyi)*. Several species of large carnivores are also present, including African lion *(Panthera leo)*, spotted hyena *(Crocuta crocuta)*, cheetah *(Acinonyx jubatus)*, leopard *(Panthera pardus)*, and African wild dog *(Lycaon pictus)*.

Cattle *(Bos indicus)* are the primary livestock species. The conservancy currently hosts the largest herd of pure Boran cattle in the world (5 500 head). Two other indigenous cattle breeds have also been introduced into the conservancy viz. "Ankole" from Uganda (100 head) and the Jiddu Boran from Somalia (40 head). In addition, there are 750 head of cattle of mixed local breeds purchased from pastoral communities in Kenya's northern rangelands. In addition to cattle, 300 sheep of the Dorper breed are reared in OPC.

Experimental Design and Animals

We took advantage of the fact that OPC cattle are managed under two different grazing regimens. The first regimen involves daytime herding of cattle in groups of varying sizes during daytime followed by nighttime corralling. Cattle herding is practiced in the conservation area (30 351 ha), which is also accessible to other livestock species (primarily sheep) and all guilds of wild mammals. Under the second grazing regimen, cattle are allowed to forage freely in predator-free areas throughout day and night (24 h) without herding or corralling. At the time of our study, there were three predator-free areas (total area = 4 047 ha)—Sirima (2 833 ha), Loidien (809 ha), and Maili Saba (405 ha)—all created in 2005–2006 using predator-proof barriers. These areas also contain several wild herbivores that were enclosed during predator-proof fencing. However, megaherbivores (elephants, giraffes, and rhinos) are excluded from these areas. To determine whether this exclusion affected woody vegetation cover, we used Google Earth to estimate tree/shrub canopy intercept survey along forty-eight 1-km transects randomly distributed equally across the conservation and predator-free areas and found no significant difference ($P = 0.695$, $F = 0.2$, $n = 48$) between these areas (data not shown). As such, the absence of megaherbivores in the predator-free areas was unlikely to influence our results. On the basis of the tropical livestock unit (TLU; 1 TLU = 290 kg live weight), the combined stocking rate of livestock and wild grazers and intermediate feeders is approximately equal between the conservation area (2.7 ha $\cdot$ TLU^{-1}) and predator-free areas (2.8 ha $\cdot$ TLU^{-1}).

Taking advantage of the existing setup at OPC comprising distinct management areas and grazing regimens, we created a randomized block design with four grazing treatments replicated across three time blocks. The blocks were the sampling periods starting from 21 February to 15 April 2010, 26 October to 30 November 2010 and 31 January to 9 March 2011 (Table 1). Weather conditions varied among these periods,

Table 1
Location of treatment herds in Ol Pejeta Conservancy at different sampling periods (experimental blocks) during the experiment.

Treatments	Time periods (experimental blocks)		
	21 February to 15 April 2010	26 October to 30 November 2010	31 January to 9 March 2011
[1]DNG	Loidien	Sirima	Maili Saba
[2]LDG	Sedai	Loirugrug	Morani
[3]MDG	Gatune	Ngerenyi	Kambi Punda
[4]SDG	Gatune	Kona Mbaya	Kambi Punda

[1] Day and night grazing.
[2] Day grazing, large-sized herd.
[3] Daytime grazing, medium-sized herd.
[4] Daytime grazing, small-sized herd.

with February to April 2010 being wet, October to November 2010 moderately wet, and January to March 2011 dry. This time-based blocking was appropriate because given that the OPC landscape is fairly homogenous in terms of soil, vegetation, and topography (Sensenig et al., 2010), we expected less variation among experimental units within, than between, time blocks.

The first of the four treatments involved unrestricted (day and night) foraging in the predator-free areas by approximately 175 steers without herding (DNG). The other three treatments comprised daytime herding of different-sized steer herds in the conservation area, followed by nighttime keeping in "bomas" (corals). These latter three treatments were large-sized herd (200 steers, LDG), medium-sized herd (150 steers, MDG), and small-sized herd (100 steers, SDG). These are the typical herd sizes used in OPC and most other ranches in these rangelands and were thus ideal for the purposes of our study.

Although the DNG steers were considered as a single herd, they naturally formed several distinct subgroups typically comprising fewer than 30 steers per subgroup (personal observation). This was not the case with the daytime-only foraging herds in which individual animals tended to stay relatively close to each other. We used a separate steer herd for each treatment during each sampling period, resulting in a total of 12 different treatment herds. Treatment herds were randomly assigned to new boma locations at the start of each sampling period to ensure that observed treatment differences were attributable to treatment effect rather than to any inherent differences among boma locations.

Experimental herds belonged to OPC and comprised Boran steers aged 2 to 3 yr and weighing 276 kg $\pm$ 59 standard deviation (SD) at the start of each sampling period. Before commencement of data collection in each sampling period, we randomly selected 10 test steers per treatment herd for live weight measurements and used five of these for behavioral and nutritional measurements during the entire sampling period. The experiment was carried out under the typical grazing management routines used in OPC and most other livestock ranches across the Laikipia region. Specifically, all daytime grazing steers left their bomas at 0800 to 0900 hours each morning for herding by experienced local pastoral herdsmen, and returned at 1600 to 1700 hours for overnight corralling. This foraging time allowance regimen is practiced to reduce chances of predation, especially during late afternoon when predators such as lions tend to be relatively active. All experimental herds were watered once daily. In addition, all experimental animals were sprayed once every week for tick control using Ticatraz, an amitraz-based acaricide.

Foraging Behavior and Vegetation Surveys

During each sampling period, we conducted daytime focal observations for bite-and-step counts and scan sampling for activity time budgets using five test steers in each treatment herd. We carried out these observations 3 to 6 d consecutively in each treatment herd, sampling the herds in a randomly determined sequence to minimize any sampling time-lag biases among herds. The sampling interval between treatment herds was 1 to 3 d. On each sampling day, we observed each focal steer within a treatment herd for bite-and-step counts in six (February to April 2010) or four (October to November 2010 and January to March 2011) nonconsecutive 5-min focal periods, with the order of sampling being randomized among individual focal steers.

We counted and recorded all bites taken by focal steers on different plant species and steps moved during each focal period, considering a bite as the actual prehension of plant material and a step as a forward movement of either front limb. All focal observations were made within 4 m of the focal steers to ensure accuracy in discernment of bites, plant species eaten, and steps. This observation distance has been used previously in similar environments with minimal interference with normal cattle behavior (Odadi et al., 2007, 2009, 2013). We calculated bite-and-step rates, bites per step, and percentage of bites on different plant species for individual focal steers. We further calculated Ivlev's (1961) selection indices of plant species for each focal steer as:

$$\textit{Selection index} = (p_i - c_i)/(p_i + c_i) \quad (1)$$

where p_i and c_i are the proportions of species i in bites and herb-layer vegetation, respectively. This index scales from -1 (total avoidance) through 0 (no selection) to 1 (total selection).

For the purpose of calculating selection indices, we estimated the relative covers of different herbage species at the grazing sites during foraging behavior observations. On each foraging behavior day, we vertically placed a 1-m-long pin at 25 locations approximately 1 m apart along four (October to November 2010 and January to March 2011) or six (February to April 2010) randomly located transects at the grazing sites and recorded the total number of pin contacts with different plant species at each location. Pins not in contact with vegetation were recorded as bare hits. We calculated the relative cover of each herbage species at the grazing sites as the total number of pin contacts with that species divided by the total number of pin contacts on all species. We considered this approach reliable in estimating the relative availabilities of different plant species given that pin hits correlate positively with biomass in this system (Sensenig et al., 2010).

Concurrent with focal observations, we scan-sampled the five focal steers in each treatment herd and recorded their activities every 5 min. The activities were grazing, graze-walking, walking, resting or ruminating, grooming and vigilance, with any other activities being categorized as "other." We defined grazing time as time spent cropping and chewing food, graze-walking as time spent walking with the head in a lowered position, walking time as time spent walking with the head in a raised position, and resting or rumination time as time spent lying down or standing idle and/or ruminating. We calculated the percentage of daytime spent on different activities for each individual focal steer.

GPS Tracking

We tracked the movement of treatment herds on foraging behavior observation days using i-gotU GT 120 GPS Travel Logger (Mobile Action Technology, Inc., New Taipei City 23143, Taiwan) tracking devices fitted on the five focal steers in each treatment. To fit the devices, we tied dog chains loosely around the focal steers' necks and attached the devices to the chains. For treatments LDG, MDG, and SDG, our research crew routinely fitted devices in the morning just before the steers left the boma for grazing and removed them when the animals arrived back each day. For the DNG treatment, the crew gathered and walked the focal steers to a handling facility within the designated grazing location for fitting and removal of the devices. During the February to April 2010 sampling period, the devices were fitted on the DNG steers in the morning and removed in the evening. However, in the subsequent sampling periods, the devices were fitted on these steers in the morning and removed the following morning. Fitting devices tended to cause some disturbance to steers, especially during the first few days, but this was short-lived (less than 10 min) with test steers being mostly settled and calm during all behavioral observations.

The devices captured data on the geo-reference location of the steers every 5 s. However, there were incidences when the devices did not function properly, switching off intermittently, and thereby gathering data for only a portion of the total time they were attached to the animals. We downloaded GPS data from the devices onto the computer each day and calculated the mean distance walked every hour.

Forage Intake and Diet Quality

We estimated forage intake and diet quality (digestible organic matter and crude protein contents) using the same five test steers used for foraging behavior observations in each treatment herd. Sampling for forage intake and diet quality ran concurrently with foraging behavior observations. We estimated forage intake by determining fecal output and diet digestibility and applying the relationship between these variables and intake (forage intake = fecal output/(1-digestibility); Mayer and Dove, 2000). To estimate fecal output, we used granulated polyamide (PA) as an external marker. Polyamide granules are hard, physiologically inert plastic particles of approximately 2 mm diameter. This marker has been shown to provide reliable estimates of fecal output of *Bos indicus* cattle foraging in extensive systems (Mahler et al., 1997). In the present study, we specifically used Akulon F223-D PA6 (DSM, 6401 JH Heerlen, Netherlands) as the external marker.

Using gelatin capsules size 7 and a compatible plastic balling gun (Torpac Inc. 333 Route 46, Fairfield, NJ 07004, USA), we orally administered a single dose containing 150 g (February to April 2010) and 60 g (October to November 2010 and January to March 2011) of PA granules (15 g per capsule) to each test steer. Subsequently, we followed the steers for 4 consecutive days and collected grab samples of freshly dropped feces, recording the time of collection in each case. Treating fecal grab samples individually, we air dried them to constant mass before analyzing them for PA marker content. We physically recovered the marker from individual grab samples by carefully grinding the samples using a household coffee grinder, sifting the ground material through a 1-mm sieve, and removing any fecal particles resting on the sieve by hand.

We then weighed the recovered marker to the nearest 1 mg and calculated marker concentration (mg PA/kg fecal dry matter) at each time of fecal grab sample collection. To convert marker concentration to organic matter basis, we pooled all ground fecal samples per individual test steer and obtained a subsample, which we then analyzed for organic matter content. For each test steer, we plotted marker concentration (mg PA $\cdot$ kg^{-1} of fecal organic matter) against time (h) after dosing and calculated the area under the resulting curve using the trapezium method (Mayer and Dove, 2000). Subsequently, we calculated daily fecal organic matter output by dividing the amount of marker administered by the area under the marker concentration versus time curve and multiplying by 24 h. The trapezium approach was appropriate under the field conditions of our study because it does not necessitate identical timing for postdosing fecal sample collection (Mayer and Dove, 2000).

To determine digestibility, we analyzed a subsample of the ground fecal samples pooled per test steer for dietary digestible organic matter (DOM) content using the near infrared reflectance spectroscopy (Kidane et al., 2008). We also analyzed these fecal subsamples for dietary crude protein (CP) content using the same technique. For each sampling period, we averaged forage intake, DOM, and CP values across test steers to obtain treatment herd means.

Statistical Data Analysis

Our study design was a randomized block design consisting of four grazing treatments (DNG, LDG, MDG, and SDG) replicated across three time blocks (n = 3), resulting in a total of 12 different treatment herds. In each of these treatment herds, we used 10 focal steers for live weight measurements, with 5 of these being used for all other animal measurements. For vegetation measurements, we had 3 to 6 d of sampling for each treatment herd during each sampling period. We used treatment herds as the experimental units, with individual focal steers within herds or vegetation sampling days being used as subsamples. Specifically, for all dependent animal variables, we calculated means for a given treatment herd by averaging measurements across individual focal steers within that herd. Similarly, for all dependent vegetation variables, we calculated means associated with each treatment herd by averaging measurements across vegetation sampling days for that herd.

Using analysis of variance (ANOVA) with block effects, we tested for differences in the measured animal and vegetation parameters among grazing treatments, accepting significant differences at $P < 0.05$. We used Tukey's honest significant difference post hoc test to separate means. To determine whether different herbaceous plant species were significantly selected (selection index > 0) or avoided (selection index < 0), we used a one-sample Student's t-test with zero as the hypothetical mean. We performed all these analyses using the SYSTAT 9 (SPSS, 1998) software.

Because weight gain and food intake were key to testing our hypotheses, we additionally calculated effect sizes (Cohen's d) and respective 95% confidence intervals for nonsignificant ($P > 0.05$) pairwise comparisons involving these two parameters. We calculated effect size as:

$$\text{Cohen's}\, d = (m_1 - m_2)/s_{\text{pooled}} \quad (2)$$

where m_1 and m_2 are means of groups 1 and 2, respectively, and s_{pooled} is the pooled standard deviation of the two groups calculated as:

$$\sqrt{\left[\left(s_1^{\,2} + s_2^{\,2}\right)/2\right]} \quad (3)$$

To calculate effect size confidence interval, we estimated the effect size standard deviation as:

$$s_d = \sqrt{\left[\{(n_1 + n_2)/(n_1 \times n_2)\} + \left\{d^2/2(n_1 + n_2)\right\}\right]} \quad (4)$$

where n_1 and n_2 are sample sizes of groups 1 and 2, respectively, and d is the effect size. Subsequently, we calculated a 95% confidence interval for each effect size as:

$$\text{Confidence interval} = d - 1.96 \times s_d \text{ to } d + 1.96 \times s_d \quad (5)$$

We interpreted effect size confidence intervals according to Coe (2002), with an interval containing zero indicating that the difference is nonsignificant at the 5% level. In addition, we retrospectively calculated statistical power associated with detecting differences in food intake and weight gains among grazing treatments.

Results

Herbaceous Vegetation Cover

Absolute herbaceous vegetation cover averaged 6.1, 5.8, 6.2, and 6.0 hits per pin at grazing sites of DNG, LDG, MDG, and SDG steers, respectively, with no significant differences among treatments (SE = 0.7, P = 0.97, F = 0.1). Herbaceous vegetation predominantly comprised grasses (mean relative cover ~94%) and forbs (~6%), with sedges (<1%) being much less common (Table 2). *Themeda triandra* (relative cover = 49.2–57.4%) was the most common species, followed by *P. stramineum*

Table 2
Relative cover (means ± SEs %) of different herbaceous vegetation species and classes in sites used by cattle under different foraging treatments. Only species comprising > 1% of total herbaceous cover included.

Herbage species or class	[1]DNG	[2]LDG	[3]MDG	[4]SDG	SE	F	P
Themeda triandra	49.2	57.4	53.0	50.1	3.4	1.1	0.425
Pennisetum stramineum	16.1	9.6	15.6	16.6	2.5	2.4	0.245
Cynodon spp.	14.8	6.8	10.3	9.8	1.8	3.5	0.091
Pennisetum mezianum	5.3	7.3	6.3	6.7	0.9	1.0	0.438
Bothriochloa insculpta	3.0	3.3	1.5	1.5	1.0	0.9	0.496
Eragrostis tenuifolia	2.7	2.8	1.3	1.9	0.9	0.6	0.613
Setaria anceps	0.0	2.4	2.3	1.6	1.1	1.1	0.406
Digitaria sp.	1.3	0.9	1.3	1.6	0.8	0.1	0.946
Commelina spp.	1.6	1.1	1.4	1.4	0.3	0.6	0.614
Total grass	93.7	93.6	93.3	93.7	0.5	0.2	0.916
Total forbs	5.6	5.9	5.8	5.6	0.3	0.2	0.884

[1] Day and night grazing.
[2] Day grazing, large-sized herd.
[3] Daytime grazing, medium-sized herd.
[4] Daytime grazing, small-sized herd.

(9.6–16.6%), *Cynodon* spp. (6.8–14.8%), and *P. mezianum* (5.3–7.3%) (Table 2). Other frequent species were *Bothriochloa insculpta* (Hochst. ex A. Rich) A. Camus (Sweetpitted grass; relative cover = 1.5–3.3%), *Eragrostis tenuifolia* (A. Rich.) Hochst. ex Steud. (elastic grass; 1.3–2.8%), *Setaria anceps* Stapf (African bristlegrass; 0.0–2.4%), *Digitaria* sp. Haller (finger grass; 0.9–1.6%), and *Commelina* spp. L. (1.1–1.6%) (Table 2). Several other species were also present but in trace proportions (<1%). The relative covers of all herbaceous species or classes did not differ among grazing sites (all $P > 0.05$, $F \leq 4$; Table 2).

Diet Selection and Quality

Cattle primarily ate grasses, which comprised 97–99% of their total bites (Table 3). Forbs and sedges were also consumed but in much lower proportions (<3%), while woody species were not consumed at all. Overall, grasses were selected (selection index = 0.02, $t = 6.8$, $P < 0.001$) while forbs (selection index = -0.46, $t = -8.9$, $P < 0.001$) and sedges (selection index = -0.70, $t = -5.7$, $P < 0.001$) were avoided. *Themeda triandra* was the most frequently eaten species and comprised 53–66% of total bites across all treatment groups (Table 3). Notably, this grass was consumed in higher proportion than its relative representation in the herb-layer vegetation (selection index = 0.06, $t = 4.2$, $P = 0.002$).

Other commonly eaten species were *P. stramineum* (8–19%), *Cynodon* spp. (6–14%), and *P. mezianum* (6–8%). These grasses were consumed in direct proportions to their relative availabilities, with no significant selection or avoidance (*P. stramineum* $t = -1.7$, $P = 0.120$, *Cynodon* spp. $t = -0.1$, $P = 0.942$, and *P. mezianum* $t = -0.4$, $P = 0.720$, Table 3). Other grass species individually comprising more than 1% of total bites were *B. insculpta, E. tenuifolia, S. anceps,* and *Digitaria* sp. (Table 3). These grasses were all consumed in direct proportion to their relative availabilities, with the exception of *E. tenuifolia,* which was significantly avoided ($t = -3.5$, $P = 0.007$). Percentage bites and selection indices of all herbage species or classes did not differ significantly among treatment groups (all $P > 0.1$, all $F \leq 3.0$; Table 3).

Dietary CP content averaged 6.9%, 6.6%, 6.5%, and 6.2% (SE = 0.3%), while DOM averaged 56.8%, 56.7%, 57.8%, and 56.6% (SE = 0.3%) in DNG, LDG, MDG, and SDG steers, respectively. Notably, both diet quality parameters did not differ significantly among treatment groups (both $P > 0.1$, $F < 3.0$).

Weight Gain

Across all treatment groups, live weight gain averaged 0.19 to 0.61 kg · d^{-1}. Weight gain differed significantly among treatment groups ($P = 0.002$, $F = 39.4$), being 68% and 52% lower in LDG ($P = 0.001$) and MDG ($P = 0.004$) than in DNG (Fig. 1). In addition, weight gain was 65% and 47% lower in LDG ($P = 0.002$) and MDG ($P = 0.010$) than in SDG (Fig. 1). However, weight gain did not differ significantly between SDG and DNG ($P = 0.752$) or between LDG and MDG ($P = 0.319$). These nonsignificant differences were consistent with the observed small effect sizes and their respective zero-containing confidence intervals (Fig. 1). In addition, retrospective analysis showed high statistical power (0.999) for detecting differences in weight gain among grazing treatments (Fig. 1).

Forage Intake

Forage organic matter intake averaged 3.7 to 6.2 kg · d^{-1}. Forage intake differed ($P = 0.003$, $F = 15.8$) among treatment groups, being approximately 40% lower ($P = 0.006$) in LDG or MDG than in DNG, and 31% lower ($P = 0.033$) in LDG or MDG than in SDG (Fig. 2). However, like weight gain, forage intake did not differ between SDG and DNG ($P = 0.288$) or between LDG and MDG ($P > 0.99$). These nonsignificant differences were consistent with the observed small to medium effect sizes and their respective confidence intervals containing zero and high statistical power (0.999) for detecting treatment differences (Fig. 2).

Bite, Step, and Travel Rates

Bite rate differed by treatment ($P = 0.007$, $F = 11.2$) and was higher in SDG ($P = 0.007$) or MDG ($P = 0.013$) but not LDG ($P = 0.068$) than in DNG (Table 4). There were no significant treatment differences in step rate ($P = 0.631$, $F = 0.6$). However, the bites-per-unit step was significantly lower ($P = 0.044$) in DNG than in MDG but not in SDG ($P = 0.139$) or LDG ($P = 0.221$). The mean travel rate was 0.8, 0.9, 0.9, and 1.0 km · h^{-1} (SE = 0.1) among DNG, LDG, MDG, and SDG steers, respectively. Consistent with step rate, travel rate did not differ significantly among treatment groups ($P = 0.760$, $F = 0.4$).

Table 3
Relative bites (%) and selection indices (in parentheses) of herbage species individually comprising > 1% of total bites taken by cattle under different grazing time allowance and herd size regimens. Data are means ± SEs.

Herbage species or class	[1]DNG	[2]LDG	[3]MDG	[4]SDG	SE	*F*	*P*
Themeda triandra	53.4	66.3	60.7	54.9	5.4	1.2	0.400
	(0.03)	(0.07)	(0.07)	(0.04)	(0.03)	(0.4)	(0.746)
Pennisetum stramineum	18.8	8.0	11.4	16.3	3.1	2.4	0.162
	(0.08)	(-0.13)	(-0.15)	(-0.03)	(0.06)	(2.9)	(0.122)
Cynodon spp.	13.2	6.0	11.3	13.7	2.5	2.0	0.217
	(-0.13)	(-0.07)	(0.04)	(0.14)	(0.09)	(1.6)	(0.277)
Pennisetum mezianum	6.1	7.8	6.8	6.7	1.5	1.4	0.893
	(0.03)	(-0.10)	(0.02)	(-0.04)	(0.05)	(1.3)	(0.350)
Bothriochloa insculpta	3.0	3.3	1.1	1.1	1.0	1.6	0.294
	(-0.15)	(0.23)	(0.12)	(0.11)	(0.24)	(0.6)	(0.659)
Eragrostis tenuifolia	1.7	2.3	1.1	1.2	1.0	3.3	0.804
	(-0.33)	(-0.17)	(-0.13)	(-0.35)	(0.21)	(0.4)	(0.765)
Setaria anceps	0.0	2.2	3.2	1.1	1.0	1.8	0.246
	(-0.10)	(0.28)	(0.52)	(0.19)	-	-	-
Digitaria sp.	3.3	0.4	1.1	1.1	0.9	0.8	0.546
	(0.27)	(-0.42)	(-0.14)	(-0.07)	-	-	-
Total grasses	98.9	97.7	98.1	98.2	0.9	0.3	0.815
	(0.02)	(0.02)	(0.02)	(0.02)	(<0.01)	(0.2)	(0.860)
Total forbs	1.8	2.5	1.9	1.7	0.3	1.8	0.200
	(-0.47)	(-0.38)	(-0.48)	(-0.51)	(0.05)	(1.3)	(0.359)

[1] Day and night grazing.
[2] Day grazing, large-sized herd.
[3] Daytime grazing, medium-sized herd.
[4] Daytime grazing, small-sized herd.

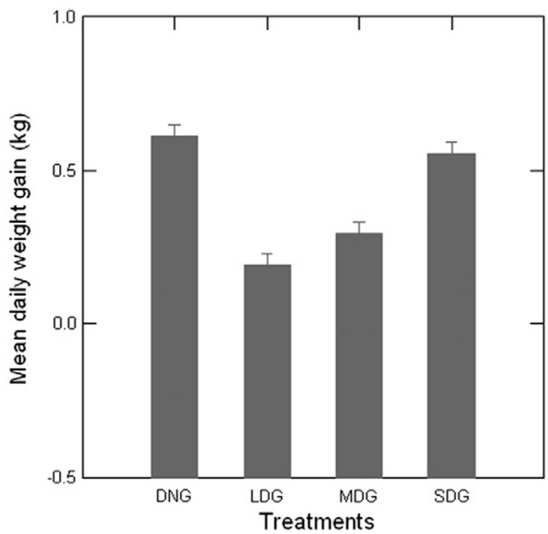

Fig. 1. Weight gain (mean ± SE, $n = 3$ replicates) of cattle under different grazing regimens. Grazing treatments were day and night foraging with no herding (DNG) and daytime foraging with herding in large (LDG), medium (MDG), and small (SDG) herds. Effect sizes for DNG versus SDG and MDG versus LDG were 0.16 (95% confidence interval -1.45 to 1.76) and 0.25 (-1.36 to 1.86), respectively. Statistical power for detecting treatment differences was 0.999.

Activity Time Budgets

The bulk of daytime was spent grazing by all treatment groups (Table 5). However, while steers with restricted foraging time spent 69.5–72.2% of their time foraging, those with unrestricted foraging time spent only 42.2% of their time on this activity (Table 5). Consequently, proportion of daytime spent grazing differed significantly among treatment groups ($P = 0.002$, $F = 18.4$), being lower in DNG than in LDG ($P = 0.004$), MDG ($P = 0.003$), or SDG ($P = 0.005$) (Table 5). The remaining time was spent on resting or rumination (10.3–47.1%), walking (5.2–8.2%), graze-walking (3.7–8.8%), grooming (1.5–3.0%), and vigilance (0.0–0.5%). In contrast to percentage grazing time, percentage of time spent resting and/or ruminating was significantly lower in LDG, MDG, or SDG than in DNG (all $P < 0.001$; Table 5). There were no significant treatment differences in percentage of time spent walking ($P = 0.409$, $F = 1.1$), graze-walking ($P = 0.144$, $F = 2.6$), grooming ($P = 0.170$, $F = 2.4$), or being vigilant ($P = 0.185$, $F = 2.2$) (Table 5).

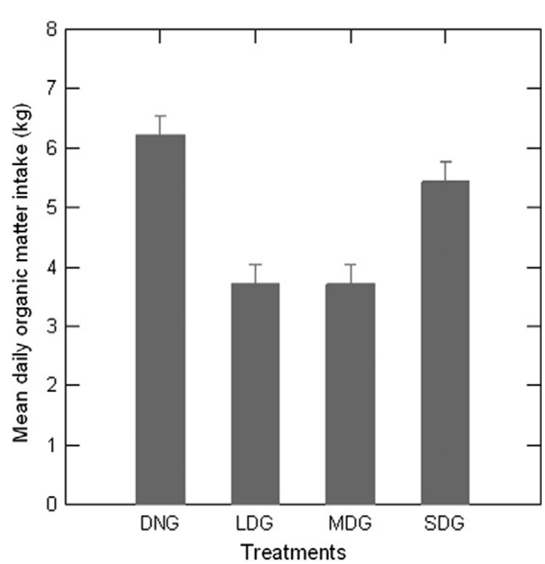

Fig. 2. Forage intake (mean ± SE, $n = 3$ replicates) by cattle under different grazing regimens. Grazing treatments were day and night foraging with no herding (DNG) and daytime foraging with herding in large (LDG), medium (MDG), and small (SDG) herds. Effect sizes for DNG versus SDG and MDG versus LDG were 0.52 (95% confidence interval -1.11 to 2.14) and < 0.01 (-1.60 to 1.60), respectively. Statistical power for detecting treatment differences was 0.988.

Table 4
Bite and step rates of cattle under different grazing time allowance and herd size regimens.

Parameter	[1]DNG	[2]LDG	[3]MDG	[4]SDG	SE	*F*	*P*
Bites · min^{-1}	13.1^{a}	21.0^{ab}	24.7^{b}	26.2^{b}	1.7	11.2	0.007
Steps · min^{-1}	15.6	16.5	17.8	19.1	2.0	0.6	0.631
Bites · step^{-1}	1.2^{a}	1.6^{ab}	1.8^{b}	1.5^{ab}	0.1	4.6	0.054

Row means with different superscript letters (a, b) differ significantly ($P < 0.05$).
[1] Day and night grazing.
[2] Day grazing, large-sized herd.
[3] Daytime grazing, medium-sized herd.
[4] Daytime grazing, small-sized herd.

Discussion

The mean values of the measured performance, nutritional, and behavioral parameters observed in this study are generally consistent with those previously reported for Boran cattle in a similar black cotton soil savanna ecosystem (Odadi et al., 2007, 2009, 2011a, 2011b, 2013). Consistent with our predictions, cattle under unrestricted foraging regimen (DNG) had higher forage intake and performed better than cattle herded during daytime in large (LDG) or medium-sized (MDG), but not small (SDG), herds (Figs. 1 and 2), suggesting that herd size influenced the strength of the effects of restricted foraging time. The zero-containing small effect size confidence intervals for pairwise comparisons of intake rate and weight gain between DNG and SDG, as well as the high statistical power for detecting treatment differences (Figs. 1 and 2), further confirm the validity of our findings of nonsignificant differences between these treatments. Also in line with our predictions were the observed lower food intake and weight gain in LDG or MDG than in SDG (Figs. 1 and 2). Notably, the patterns of treatment differences in weight gain (Fig. 1) were generally similar to the patterns of treatment differences in forage intake (Fig. 2), suggesting that food intake primarily influenced cattle performance, as has also been reported by other studies (Zimmermann, 1980; Meissner, 1995; Odadi et al., 2011b).

The higher weight gain and forage intake in DNG than in LDG and MDG is consistent with the findings of several studies that have shown that extending grazing increases food intake and performance of ruminants (Joblin, 1960; Khombe et al., 1992; Fernandez-Rivera et al., 1996; Ayantunde et al., 2000a, 2000b, 2001, 2002). However, our findings differ from the findings of Smith et al. (2006) who reported that extending grazing time allowance for cattle did not significantly affect food intake and weight gains of cattle in the southern-central highlands of Ethiopia. This discrepancy could possibly have arisen due to differences in the diet quality. Specifically, cattle in our study

Table 5
Proportion of daytime spent on various activities by cattle assigned to different grazing time allowance and herd-size regimens.

Activity	[1]DNG	[2]LDG	[3]MDG	[4]SDG	SE	*F*	*P*
Grazing (%)	42.2^{a}	71.3^{b}	72.2^{b}	69.5^{b}	3.4	18.4	0.002
Graze-walking (%)	3.7	6.1	4.7	8.8	1.4	2.6	0.144
Walking (%)	5.2	7.8	8.1	8.2	1.3	1.1	0.403
Resting/ruminating (%)	47.1^{a}	12.1^{b}	11.9^{b}	10.3^{b}	2.7	43.0	<0.001
Grooming	1.5	2.0	2.2	3.0	0.4	2.4	0.170
Vigilance	0.0	0.1	0.5	0.1	0.1	2.2	0.185

Row means with different superscript letters (a, b) differ significantly ($P < 0.05$).
[1] Day and night grazing.
[2] Day grazing, large-sized herd.
[3] Daytime grazing, medium-sized herd.
[4] Daytime grazing, small-sized herd.

selected less digestible diets (DOM < 57%) compared with those in the study of Smith et al. (2006), where dry matter digestibility exceeded 67%. Therefore we propose that when forage quality is generally high across the range, cattle are able to meet their daily nutrient requirements much faster and thus increasing grazing time allowance under such conditions may be less effective in altering their food intake and performance. In addition, our findings differed from the findings of Muller et al. (2011), who found no beneficial effect of 24-h grazing on food intake and performance of sheep in a Mongolian grassland system. However, it is important to note that daytime grazing duration was much longer (14–16.5 h) in the study of Muller et al. (2011) than in our study (8–9 h).

Although several studies have demonstrated the negative effects of restricted foraging time on ruminants, our study shows that these effects can be minimized or even eliminated by reducing herd size. The demonstrated herd size–dependent effects of restricted foraging time allowance on food intake and performance of cattle (Figs. 1 and 2) suggest stronger intraspecific competition in large than in small herds. In general, intraspecific competition can arise through exploitation where individuals are affected by resource depletion or through interference where a dominant individual prevents a less dominant individual from accessing a resource (Begon et al., 2006). Interference competition among conspecifics is often occasioned by increased aggressiveness, leading to reduced foraging efficiency measured, for example, as percentage time spent actively foraging (Molvar and Bowyer, 1994). Our scan samples did not reveal differential percentage foraging time among daytime grazing herds (Table 5), suggesting that the observed differences in food intake and weight gain (Figs. 1 and 2) likely resulted from exploitative rather than interference competition.

Although we did not measure forage depletion rates at sites used by different treatment herds, the observed lower food intake in large than in small herds (Fig. 2) is indicative of increased grazing pressure and higher forage depletion in large than in small herds. Intake rate is a function of bite rate, grazing time, and bite size. Because bite rate and percentage grazing time did not differ significantly among daytime-only foraging treatment groups (SDG, MDG, and LDG), we propose that the observed difference in food intake resulted from differential bite mass. The observed lower food intake in LDG and MDG than in SDG (Fig. 2) contradicts the findings of Sevi et al. (1999) in a Mediterranean rangeland showing that increasing group size led to increased food intake in sheep. However, it is important to note that in that particular study, group sizes were much smaller (6–12 animals per flock) than group sizes in our study. Under such conditions of small group sizes, increasing group size may increase food intake through enhanced social facilitation (Tribe, 1950; Penning et al., 1993).

The higher proportion of grazing time, lower proportion of ruminating or resting time, and higher bite rate in daytime-only foraging herds than in DNG (Tables 4 and 5) indicate that cattle increase grazing activity at the expense of other activities when foraging time is limited. These findings are consistent with the findings of several studies conducted on domestic ruminants elsewhere (Smith, 1961; Bayer, 1986; Ayantunde et al., 2000b; Kristensen et al., 2007; Moyo et al., 2012; Chen et al., 2013). Increased focus on grazing by daytime-only foraging cattle is necessary if they are to offset decreased forage intake due to restricted foraging time. Our findings suggest that the observed increased grazing activity among daytime herds was more effective in minimizing the effects of restricted foraging time on food intake among SDG but not LDG and MDG steers.

Because DNG steers had unrestricted foraging time allowance, we expected them to select a higher-quality diet compared with the time-restricted LDG, MDG, and SDG steers, but this was not the case. This result is consistent with the findings of Fernandez-Rivera et al. (1996) and Ayantunde et al. (2002) but contrasts with the findings of Ayantunde et al. (2000b) showing higher dietary protein content and lower digestibility in daytime-grazing cattle than in nighttime-grazing cattle. These differences in this study were associated with differential ingestion of woody forage, which are known to be rich in protein but relatively less digestible due to their high concentrations of secondary compounds. Notably, the fact that cattle did not consume woody forage in our study system probably explains this discrepancy.

The lack of significant differences in diet selection among treatment herds (Table 3) was somewhat unexpected because increased herd size should lead to reduced selectivity (Fortin and Fortin (2009). However, the large but statistically nonsignificant differences (30–58%) in relative frequency of bites on *Pennisetum stamineum* or *Cynodon dactylon* between NDG or SDG steers and LDG or MDG steers (Table 3) are worth noting. We suspect that the small sample size we used may have been ineffective in detecting species-level diet selection differences among herds. Therefore we propose further investigation with large sample size to conclusively determine occurrence of any such differences.

Management Implications

We have demonstrated that whereas restricted foraging time allowance negatively affects forage intake and performance of steers when herded during the day in large (200 steers per herd) or medium-sized (150 steers per herd) herds, these effects become subdued when cattle are herded in small herds (100 steers per herd). Therefore the need to fence off or eliminate wildlife from livestock properties for the purpose of enabling nocturnal foraging could be reduced by herding cattle diurnally in small herds. This could go a long way in enhancing compatibility between livestock production and wildlife conservation in such semiarid savanna rangelands.

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