Rangeland Ecology & Management 71 (2018) 481–491

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Tightly Bunched Herding Improves Cattle Performance in African Savanna Rangeland☆

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ARTICLE INFO

Article history:
Received 16 November 2017
Received in revised form 16 March 2018
Accepted 28 March 2018

Key Words:
close herding
grazing management
grazing selectivity
habitat heterogeneity
livestock nutrition
rotational grazing

ABSTRACT

Rotational grazing management approaches are regarded as strategies for sustaining rangeland productivity and continue to be applied across many parts of the world. In Africa, livestock farmers implementing rotational grazing often switch from traditional loosely bunched herding (LBH), in which animals within a herd are allowed to spread out naturally when foraging, to tightly bunched herding (TBH) with limited herd spread to increase animal impact on the range. However, there is little scientific information on the actual direct (short-term) effects of this altered herding strategy on livestock productivity. We investigated the direct effects of TBH versus LBH on foraging behavior, nutrition, and performance (weight gain) of cattle in a semiarid savanna rangeland in central Kenya. We conducted the study across two habitat types: a heterogeneous red soil habitat and a relatively homogeneous black cotton soil habitat. Across both habitats, cattle traveled 9–15% less, foraged 10–29% more efficiently, and put on 14–39% more weight when managed with TBH as compared with LBH. These changes occurred despite the fact that stock densities were double to several times higher under TBH, and cattle under this herding regime foraged less selectively, consuming preferred plants less (especially in the black cotton soil habitat) and consuming diets with lower crude protein content (in the red soil habitat). Financial projection showed that the benefit of increased cattle performance under TBH could sufficiently outweigh increased cost of additional labor required to implement this herding strategy. These findings suggest that TBH, as practiced here, can be implemented without livestock production or financial losses. Further, the research demonstrated reduced grazing selectivity under TBH indicates that this herding strategy could potentially be used to reduce grazing pressure on preferred forage plants and maintain herbaceous species diversity without sacrificing cattle performance.

Introduction

Rangelands provide habitats for wildlife and livestock and support the livelihoods of millions of people globally. However, many rangeland ecosystems, especially those in the developing world, are under threat of degradation and associated negative environmental, social, and economic consequences (Narjisse, 2000; Millennium Ecosystem Assessment, 2005; Bedunah and Angerer, 2012; Mussa et al., 2016). The way that grazers are managed in rangelands can influence their productivity and ability to provide ecosystem services desired by society presently and in the future. Therefore, understanding the effects of different grazing management approaches is vital in finding ways of maintaining and/or improving ecological and socioeconomic sustainability of rangeland ecosystems.

Rotational grazing (or stocking) management approaches are regarded as strategies that can sustain or enhance the productivity of rangeland systems (Savory and Butterfield, 1999; US Department of Agriculture, Natural Resources Conservation Service [USDA-NRCS], 2003; Barnes and Hibbard, 2016; but see Briske et al. [2008, 2011] and Hawkins [2017] for opposing views). Rotational grazing involves strategies that use recurring periods of grazing and rest among two or more paddocks in a grazing management unit throughout the period when grazing is allowed (Society for Range Management [SRM], 1998). This grazing management approach contrasts markedly with continuous grazing where herbivores have unrestricted and uninterrupted access to a specific unit of land throughout the time period when grazing is allowed (SRM, 1998). Rotational grazing approaches are generally applied with a view to achieving one or more environmental and livestock

☆ The study was funded by Princeton University's Grand Challenges and Class of 1877 Research Fund.

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https://doi.org/10.1016/j.rama.2018.03.008
1550-7424/

production objectives including 1) enhancing forage species composition and productivity by ensuring rest periods for key plant species, 2) reducing grazing selectivity by increasing stock density to minimize patch grazing, 3) improving forage quality and quantity for improved animal health and productivity, and 4) improving soil condition, water quality and quantity, and riparian watershed function (USDA-NRCS, 2003). A continuum of management intensities can be used, ranging from simple deferred rotation (moderate intensity) to short-duration, high-intensity rotational grazing (Briske et al., 2011). Different stocking density levels are applied both within and among these broad categories of management intensity. The choice of management intensity and stocking density levels is generally dictated by economic constraints and goals of the landowner (Sollenberger et al., 2012).

Implementing rotational grazing typically necessitates fencing the land into paddocks to facilitate grazing rotation. However, such fencing can be expensive and thus economically unfeasible for many livestock farmers, especially those in developing countries. Moreover, for livestock-dominated landscapes that also host wildlife, as is the case in many parts of Africa, fencing is usually unsuitable, particularly when the goal is to manage for both livestock production and wildlife conservation. This is because fenced paddocks can be detrimental to wild animals by impeding their movement and access to critical resources and causing their mortality through entanglement (Boone and Hobbs, 2004; Harrington and Conover, 2006). When economic and conservation considerations preclude fenced paddocking, active herding (by herders) can be used to implement rotational grazing (Vallentine, 2001). An additional advantage of active herding across landscapes that also harbor large predators is that it can help lower predation on livestock (Ogada et al., 2003). In general, livestock can be herded using two methods: loosely bunched herding (LBH) in which individual animals within a herd are allowed to spread out naturally when foraging and tightly bunched herding (TBH) in which herd spread is limited (SRM, 1998; Vallentine, 2001).

In many African rangelands, livestock have traditionally been managed with LBH. Due to the nature of habitats and presence of predators in these rangelands, herders and livestock are accustomed to staying together in a loose formation, which markedly contrasts with unherded grazing management commonly applied in many other parts of the world. Where stocking rates are moderate, as is the case in many commercial ranches in these rangelands, livestock within a given property are typically herded across a specific general grazing area for a period of time depending on forage availability and desired level of utilization, then moved to a new area while forage regenerates in the previous grazing area (Veblen et al., 2016). This traditional grazing approach results in some form of rotational grazing, which contrasts with conventional (continuous) grazing commonly employed in many other parts of the world. However, it is worth noting that the traditional loosely bunched rotational grazing practices have been altered in many communal rangelands where livestock numbers are too high to enable rest from grazing (Odadi et al., 2017). In East Africa, some livestock farmers implementing rotational grazing often switch from the traditional LBH to TBH with the intent of increasing positive aspects of animal impact (e.g., reduced grazing selectivity, enhanced distribution of dung and urine) on the range (Odadi et al., 2017).

By concentrating grazing animals within small areas for short periods, TBH effectively increases stock density, which can affect individual animal performance both directly through altered foraging patterns (Barsila et al., 2015; Brunsvig et al., 2017), and indirectly through cumulative long-term effects on the range (Derner and Hart, 2007; Derner et al., 2008). Whereas farmers adopt TBH anticipating long-term improvement in rangeland health (e.g., enhanced nutrient cycling, forage productivity and nutritional quality), they are also often concerned that it may directly depress livestock performance in the short run. Previous studies have largely compared rotational grazing with continuous (season-long or year-long) grazing, especially using free-ranging (unherded) livestock. At present, there is limited information on the direct short-term effects on livestock productivity of TBH versus the traditional LBH. Yet such information could be useful for better understanding the ecological and economic implications of implementing one herding approach as opposed to the other.

Here, we investigated differences between the direct (short-term) effects of TBH versus LBH in cattle foraging behavior, nutrition, and performance in a semiarid savanna landscape in central Kenya. We conducted the study across two habitat types—a spatially heterogeneous sandy red soil habitat with high plant species diversity and low herbage biomass and a spatially homogenous clayey black cotton soil habitat with relatively low plant species diversity and high herbage biomass. We hypothesized that TBH would reduce grazing selectivity by cattle, thereby negatively altering cattle nutrition and performance as measured by weight gain. We also hypothesized that these effects would be less pronounced under more homogeneous forage distribution conditions where the postulated effects of TBH on grazing selectivity by cattle might be muted.

Materials and Methods

Study Area

We conducted the study at Mpala Research Centre (0°17′N, 36°52′E; 1 800 m above sea level) in Laikipia County, Kenya. The research center is located within Mpala Conservancy, a 200-km^2 livestock ranch that is also managed for wildlife conservation. The mean annual rainfall is 625 mm based on a long-term (1999–2014) average. Generally, there are three rainy periods: April–June ("long" rains), August ("continental" rains), and October–November ("short" rains). The study area comprises two distinctive habitat types, a black cotton soil habitat (hereafter called "black soil") and a red soil habitat ("red soil"). Soil in the black soil habitat is black colored, clayey (42–62% clay), and imperfectly drained and has relatively high cation exchange capacity (CEC; 26–28 meq/100 g), while soil in the red soil habitat is dark (or reddish) brown, well-drained sandy loam (~66% sand) with relatively low CEC (~11 meq/100 g) (Ahn and Geiger, 1987). Vegetation on the black soil is fairly homogenous (Sensenig et al., 2010), comprising a relatively continuous herb layer dominated by six perennial grass species, namely *Setaria anceps* Stapf, *Themeda triandra* Forssk., *Lintonia nutans* Stapf, *Brachiaria lachnantha* (Hochst.) Stapf, *Pennisetum stramineum* Peter, and *P. mezianum* Leeke. The tree and shrub layers are dominated by *Acacia drepanolobium* Sjøstedt (whistling thorn) and few other woody species (Young et al., 1998). By contrast, the herbaceous vegetation layer on the red soil habitat is relatively heterogeneous and is characterized by higher plant diversity and a mosaic of grass-dominated patches with varying levels of biomass interspersed with bare ground patches of varying sizes (Augustine, 2003). In general, herbage biomass is higher in the black than red soil. Dominant grasses in the red soil include *Cynodon plectostachyus* (K. Schum.) Pilg., *Enteropogon macrostachyus* (Hochst.) Munro, *Eragrostis papposa* (Roem. & Schult.) Steud., and *C. dactylon* (L.) Pers., while common woody species include *Acacia etbaica* Schweinf., *A. mellifera* (Vahl) Benth., *A. brevispica* Harms, and *Grewia tenax* (Forssk.) Fiori.

Eighty-five mammal species occur on Mpala Conservancy, among them large wild herbivores including elephant *(Loxodonta africana)*, giraffe *(Giraffa camelopardalis)*, eland *(Tragelaphus oryx)*, plains zebra *(Equus burchelli)*, Grevy's zebra *(E. grevyi)*, African buffalo *(Syncerus caffer)*, oryx *(Oryx gazella beisa)*, impala *(Aepyceros melampus)*, Grant's gazelle *(Gazella granti)*, and Jackson's hartebeest *(Alcelaphus buselaphus)*. The major large carnivores in the area include African lion *(Panthera leo)*, African leopard *(Panthera pardus pardus)*, spotted hyena *(Crocuta crocuta)*, and African wild dog *(Lycaon pictus)*. Cattle *(Bos indicus)* is the primary livestock species at Mpala Conservancy (and similar properties in our study region) and occurred at moderate stocking rates (0.1–0.2 head ha^{-1} yr^{-1}; Odadi et al., 2007) by the time we conducted the present study.

To facilitate livestock grazing management at Mpala Conservancy (and similar properties), the range is usually partitioned into several unfenced grazing zones. Cattle are normally herded within a radius of 2–3 km from a camp positioned approximately centrally within each grazing zone. Each camp comprises one or more cattle *bomas* (night enclosures). A given grazing zone is typically used by two to five distinct cattle herds, each comprising 80–120 head of cattle. Each herd is typically herded separately in a loosely bunched manner by one experienced herder, although some farmers in this region are currently switching to TBH executed by more than one herder. Potential for cattle theft and depredation by wild carnivores necessitate active herding of livestock during the day and corralling them at night. Notably, only a subset (approximately one half) of the total number of grazing zones is used at any one given time, which enables grazing rotation among zones. Herding proceeds in a given grazing zone until the leaf table height of key forage species is reduced by 50–60%, based on visual approximation. Leaf table height is considered in accordance with O'Reagain (1993) as the height below which 80% of the plant's leaves are subjectively judged to occur. When the desired forage utilization level is reached, cattle and herders migrate to another grazing zone with sufficient forage and the procedure continues.

Experimental Design, Attributes Measured, and Test Steers

We compared cattle forage species composition and selection, diet quality, forage and nutrient intake, travel distance, foraging efficiency, and performance (weight gain) between LBH (control) and TBH treatments. In addition, we measured herbaceous vegetation foliar cover, grass height, herbage greenness, and botanical composition at the foraging sites of the experimental herds. We also estimated instantaneous and daily stock densities of differently grazed herds as they foraged. All measurements were made across both habitats (black and red soil).

We conducted the study across Mpala Conservancy grazing zones during three grazing periods: August–September 2011, January–February 2012, and March–April 2012. At the start of each grazing period, we obtained 200 "Boran" steers (age 1.5–2.0 yr; live weight 241.1 kg ± 19.3 standard deviation) from Mpala Conservancy, composed two herds of 100 steers each, and randomly assigned them to the two herding treatments. We then randomly assigned both herds to one grazing zone in one habitat (red or black soil) for 20–26 d and then moved them to a grazing zone in the other habitat for the same amount of time. Overall, we used two separate grazing zones in each habitat during the study. Experimental herds were restricted to grazing only a section (one half) of the grazing zone during each grazing period. Because there were three grazing periods, one grazing zone in each habitat was used twice (i.e., shared between two grazing periods). However, a separate section of each repeated grazing zone was used for each grazing period. Hereafter, we refer to grazing zone sections used by experimental herds as "prescribed grazing areas." Overall, the study comprised a randomized block design with six prescribed grazing areas ("blocks"; three per habitat type) and 12 herd locations ("plots"; two per prescribed grazing area).

Steers in the LBH treatment were allowed to spread naturally when foraging, while those in the TBH treatment were kept relatively close to one another to prevent natural spread. For each TBH herd, herding was performed by three herders: one in front, one on the left side, and the other on the right side of the herd. The front herder slowed down the herd "leaders," while the flank herders prevented the spread sideways and also ensured that the "laggards" kept pace with the rest of the herd. Each LBH herd was manned by one herder, who watched over the herd but did not in any way attempt to prevent its natural spread.

Apart from herding method, all other aspects of cattle management were identical between the two herding treatment groups. Within each prescribed grazing area, the two groups were penned at night in separate sections of the same *boma*. They both left the *boma* by 0800 hours for grazing and returned by 1700, in accordance with the general practice in our study region. Both groups were watered once daily and shared the same water sources. Experimental herds were sprayed once weekly for tick control.

Estimation of Stock Densities

We estimated instantaneous and daily stock densities by assessing the extent to which LBH and TBH herds spread out (herd spread) when foraging. To assess herd spread, we measured the length and width of each herd using a range finder 6–12 times daily for 3 consecutive d during each grazing period in each habitat. Herd length was considered as the distance between the herd leader and the straggler, while herd width was the distance between the outermost animals on the opposite flanks. These measurements were taken at 30-min intervals between 8:30 am and 4:00 pm. We calculated herd spread as the product of herd length and herd width. We calculated instantaneous stock density (mean area per individual animal) as herd spread divided by herd size (100 steers) and daily stock density as the product of herd width and daily distance traveled divided by herd size.

Live Weight Measurements and Global Positioning System Tracking

We randomly selected 10 steers (out of 100 steers) in each of the two treatment herds allocated to a given prescribed grazing area and used them as focal animals for performance estimation. We measured live weights of these focal steers once every 7–11 d during the period herds accessed the prescribed grazing area, after allowing an acclimatization period of 4–5 d to minimize any carryover effects. In total, focal steers were weighed three times during the period herds accessed the prescribed grazing area. Focal steers from both treatment herds were weighed on the same days. The focal steers were weighed between 0700 and 0800 hours after overnight stay in the *boma* with no access to food or water. Live weight was measured to the nearest 1 kg using a platform weighing scale. We calculated the average daily gain for each focal steer by dividing live weight change for each weighing interval (i.e., the period between two successive weight measurements) by the number of days corresponding to that change and averaging gains across weighing intervals. We then estimated the average daily weight gain per head for each herd by averaging weight gains of individual focal steers in that herd.

To estimate the daily travel distance, we tracked the movement of experimental herds using a global positioning system (GPS) navigation device (i-gotU GT-120 GPS Travel Logger, Mobile Action Technology, Inc., New Taipei City, Taiwan) set to capture location data every 5 sec. Within each prescribed grazing area, we tracked each herd for 3 consecutive d using a subset of 5 of the 10 focal steers used for performance estimation. In the morning of each tracking day, just before the steers headed out for grazing, we randomly selected (with replacement) one of five focal steers used for foraging observations (see later) and fitted it with the GPS device. We removed the device in the evening when the steers returned from grazing and downloaded the tracking data. From the GPS data, we calculated the mean daily distance covered by each herd.

Foraging and Vegetation Surveys

We estimated cattle diet selection and composition using scan-sampling in accordance with Dumont et al. (2007). Each treatment herd in each prescribed grazing area was observed for 3 consecutive d using 5 focal steers randomly selected from the 10 focal steers used for performance estimation. On each of these days, we scan-sampled each of the five focal steers every 5 min and, if it was grazing, recorded the plant species it cropped. These recordings were carried out between 0830 and 1630 hours. All observations were made as close to the focal steer as possible without disturbing it. To make this possible, test steers were habituated to close-range observation for approximately 1 wk before sampling began. Using these foraging observation data, we estimated percentage of bites by cattle on individual forage species and functional types (grasses and grasslike plants [sedges] combined, forbs and shrubs) and dietary breadth. We calculated percentage of bites for each forage species or functional type. We calculated diet breadth according to Levins (1968) as $B = 1/\sum p_i^2$, where B = Levins' measure of niche breadth and p_i = proportion of bites on forage species i. We standardized this measure of niche breadth on a scale of 0 (strong specialization in one species) to 1 (opportunistic foraging on all species) according to Hurlbert's (1978) formula $B_s = (B - 1)/(n - 1)$, where B_s = standardized food niche breadth and n = total number of forage species. The total number of forage species eaten at least once within a given prescribed grazing area was used to calculate the index for each herd within that prescribed grazing area.

Concurrent with the foraging observations, we sampled herbaceous vegetation at the grazing sites of the experimental herds using the point-intercept method. On each sampling day, we randomly located four transects along the grazed path of the herd under observation. We paced each transect and dropped a 1-m-long pin perpendicular to the ground at one-pace intervals for a total of 25 pin locations per transect. At each pin location, we recorded the first pin hit on vegetation by plant species and measured the height of the highest grass leaf that touched the pin. Pins not touching vegetation were recorded as bare hits. Whenever the pin hit more than one species at any given pin location, one hit was recorded for each species. Using these pin hit data, we estimated herbage foliar cover, percentage herbage greenness, percentage (relative) cover by herbaceous plant species and functional type (grasses [including sedges] and forbs), species richness, and Shannon's species diversity index. Herbage foliar cover was estimated as total number of pin hits on herbage divided by total number of pins dropped, multiplied by 100. Relative cover by each plant species or functional type was calculated as total number of pin hits on that species or functional type divided by the total number of pin hits on all species.

Using foraging and vegetation survey data, we estimated cattle diet selection for each treatment herd within a given prescribed grazing area. Diet selection was estimated using Jacobs' (1974) index of selection $D_i = (p_i - c_i)/(p_i + c_i - 2p_ic_i)$, where p_i and c_i are the proportions of plant species (or functional type) i in diet (bites) and available herbaceous vegetation, respectively. The index ranges from –1 (total avoidance) through 0 (neutral selection) to 1 (total selection). Selection indices could not be calculated for woody plants (shrubs) because we did not measure their relative availabilities. For each habitat, we categorized species on the basis of their mean selection indices according to Lamoot et al. (2005) as preferred (positively selected; $D > 0.08$), neutrally selected ($-0.08 < D < 0.08$), and avoided (negatively selected; $D < -0.08$) species. For each herd within a given prescribed grazing area, we calculated each preference category's relative cover and percentage bites by pooling data across species in that category.

Forage Intake, Diet Quality, and Foraging Efficiency Estimation

For each treatment herd within a given prescribed grazing area, we estimated forage intake (dry matter intake [DMI]) according to Stuth and Lyons (1995) as DMI (kg DM day^{-1}) = (fecal output [FO; kg DM day^{-1}])/(diet indigestible fraction [IDM; kg^{-1} DM]), where IDM = 1 – (% total digestible nutrients [TDN] × 0.01) and TDN = 1.05 × digestible organic matter (DOM). We used the five focal steers used for foraging observations in each treatment herd to estimate FO and DOM (for DMI estimation) and dietary crude protein (CP). We estimated FO using granulated polyamide (PA; Akulon F223-D PA6, DSM, Heerlen, Netherlands), a hard, physiologically inert plastic particle (~2 mm diameter), as the external marker. We orally administered a single dose containing 75 g (August–September and January–February) and 45 g (March–April) of PA granules (15 g per capsule) to each test steer using gelatin capsules size 7 and a compatible plastic balling gun (Torpac Inc., Fairfield, NJ). After dosing, the steers were followed for 4 consecutive d, during which samples of freshly dropped feces were collected and collection time was recorded. We physically recovered the PA marker from individual samples according to Odadi and Rubenstein (2015).

The recovered markers were weighed to the nearest 1 mg, and marker concentration (mg PA kg^{-1} fecal dry matter) was calculated. For each test steer, we plotted marker concentration against time (h) after dosing and calculated the area under the resulting curve using the trapezium method (Mayes and Dove, 2000). We then calculated FO by dividing the amount of marker administered by the area under the marker concentration versus time curve and multiplying by 24 h. For each test steer, we analyzed a subsample of its pooled ground fecal samples for dietary DOM and CP using the near infrared reflectance spectroscopy technique (Kidane et al., 2008). We multiplied DOM and CP by DMI to estimate digestible organic matter intake (DOMI) and crude protein intake (CPI), respectively. We pooled these data across individual test heifers in each treatment herd within a given prescribed grazing area. We indexed foraging efficiency as the ratio of mean daily DOMI (proxy for energy gained) to mean daily distance traveled (proxy for energy expenditure during locomotion). We estimated foraging efficiency for each treatment herd within each prescribed grazing area.

Statistical Data Analysis

For all measured attributes other than relative cover, relative bites, and selection indices of individual forage species, we performed linear mixed-effects models with herding treatment (TBH and LBH), habitat type (black and red soil) and their interaction as fixed factors, and prescribed grazing area as a random factor. Because the two habitats have distinct plant communities, we ran linear mixed-effects models for individual forage species' attributes separately for each habitat type, with herding treatment and prescribed grazing area as fixed and random factors, respectively. Species that individually comprised <1% of total bites in a given habitat type were not analyzed. We used simple linear regression to test the relationship between cattle foraging efficiency and performance.

We executed the linear mixed-effects models using the package *nlme* (Pinheiro et al., 2016). For models performed for the two habitat types jointly, we conducted Tukey's post hoc tests using the package *multcomp* (Hothorn et al., 2008) to separate means for significant ($P <$ 0.05) or nearly significant ($P < 0.1$) herding treatment by habitat type interactions. All percentage data derived from counts were arcsine square root transformed, while logarithmic or square root transformations were applied to nonpercentage data when necessary, to meet normality and homoscedasticity assumptions. We performed all statistical analyses in R (R 3.3.0; R Core Team, Vienna, Austria, 2016; R code for full models and associated statistical outputs are presented in Appendix S1, available online at https://doi.org/10.1016/j.rama.2018.03.008). We report all data as untransformed estimates.

Results

Stock Densities

Both instantaneous and daily stock densities were influenced by interaction between herding treatment and habitat type (both $P <$ 0.041, $F > 8.9$; Fig. 1a and b). Overall, instantaneous and daily stock densities were 5–11 times and 2–4 times, respectively, higher for TBH than LBH steers (see Fig. 1a and b). But while both stock density attributes were similar for TBH cattle in both habitats, they were both significantly lower in the red soil than in the black soil habitat for LBH cattle (see Fig. 1a and b).

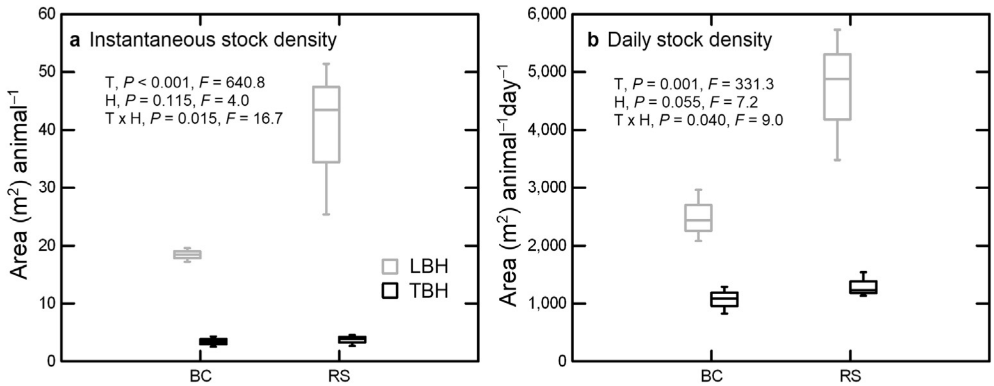

Figure 1. Stock densities of cattle managed under loosely bunched herding (LBH) and tightly bunched herding (TBH) across black soil (BC) and red soil (RS) habitats. T, H, T × H are herding treatment, habitat, and herding treatment by habitat interaction effects, respectively.

Vegetation Attributes

Overall, we encountered a total of 70 herbaceous plant species across the sampled cattle foraging sites. Foliar cover was significantly lower, while plant species richness and diversity were significantly higher, in red soil than black soil (Table 1). However, these attributes did not differ significantly between the foraging sites of the differently herded (LBH and TBH) cattle. Grass leaf height and herbage greenness did not differ by habitat or herding treatment (see Table 1). The cover of grass (including sedge) relative to forbs did not differ between black soil and red soil habitats (87.1% ± 0.7 [SE] vs. 83.1% ± 2.0; $P = 0.210$, $F = 2.2$) or between the foraging sites of LBH and TBH herds (85.5% ± 1.8 vs. 84.7% ± 1.7; $P = 0.634$, $F = 0.3$).

Dominant grass species at cattle foraging sites included *T. triandra* and *S. anceps* in the black soil habitat and *E. papposa* and *C. plectostachyus* in the red soil habitat (Table 2). There were no differences across herding treatments in terms of relative availability of different herbaceous plant species other than *T. triandra* and *Bothriochloa insculpta* (A. Rich.) A. Camus, which were significantly less common in TBH than LBH foraging sites across black and red soil habitats, respectively (see Table 2). Analysis of relative cover of forage species preference categories showed that positively selected species tended to be less common at foraging sites of TBH than LBH herds ($P = 0.058$, $F = 6.9$; Fig. 2a). Relative cover of neutrally selected species tended to follow a reverse but statistically nonsignificant pattern ($P = 0.135$, $F = 3.4$; Fig. 2b). Relative cover of negatively selected species did not differ significantly between foraging sites of the two herding treatments ($P = 0.258$, $F = 1.7$; Fig. 2c). Neutrally selected species were significantly more common, while negatively selected species were significantly less common, in black soil than red soil habitat. Relative cover of positively selected species was similar between habitats.

Cattle Behavior, Nutrition, and Performance

Overall, we identified 66 plant species in the diet of cattle across sampled foraging sites. The total number of species eaten by cattle was higher in the red than black soil (57 vs. 35). Cattle ate 17 grasses, 17 forbs, and 1 shrub (*Cadaba farinosa* Forssk.) in the black soil and 28 grasses, 2 sedges (*Cyperus* L. sp. and *Kyllinga* sp.), 26 forbs, and 2 shrubs (*A. brevispica* and *C. farinosa*) in the red soil. Diet breadth was greater in red soil than black soil (Levins' index 0.24 ± 0.03 [SE] vs. 0.37 ± 0.01; $P = 0.040$, $F = 9.0$) but did not differ significantly between LBH and TBH cattle (0.31 ± 0.03 vs. 0.30 ± 0.04; $P = 0.907$, $F < 0.1$).

Overall, cattle primarily ate grasses (89.4% ± 1.5 [SE]) and forbs (10.6% ± 1.5) and rarely consumed shrubs (0.4% ± 0.2) across both habitats. Cattle generally neutrally selected grasses and avoided (negatively selected) forbs relative to their availability (Jacobs' selection index = 0.07 ± 0.38 vs. –0.22 ± 0.08). Total grass consumption relative to forbs and shrubs did not differ between black soil and red soil habitats (90.6% ± 2.2 vs. 88.2% ± 2.0; $P = 0.515$, $F = 0.5$) or between TBH and LBH cattle (91.4% ± 1.4 vs. 87.5% ± 2.5; $P = 0.128$, $F = 3.6$). Likewise, grass selection index was similar between black soil and red soil habitats (0.23 ± 0.13 vs. 0.20 ± 0.12; $P = 0.914$, $F < 0.1$) or between TBH and LBH cattle (0.29 ± 12 vs. 0.15 ± 0.12; $P = 0.190$, $F = 2.5$). Analysis of individual species showed that cattle diet was dominated by *S. anceps* and *T. triandra* in the black soil and *E. papposa, C. plectostachyus,* and *E. macrostachyus* in the red soil (see Table 3). The grasses *T. triandra, B. insculpta, E. papposa,* and *Panicum maximum* Jacq. were among species with the highest selection indices, while the grass *Ischaemum afrum* (J. F. Gmel.) Dandy and forbs *Aspilia* sp. and *Rhynchosia* sp. were among those with the lowest selection indices (Table 4). The relative consumption and selection of most species did not differ between herding treatments, with a few exceptions (see Tables 3 and 4). Across the black soil habitat, relative consumption of *T. triandra* was lower ($P = 0.009$, $F = 116.3$), while that of *E. papposa* tended to be lower ($P = 0.059$, $F = 15.5$) among TBH than LBH cattle. Conversely, TBH cattle consumed more *Aspilia* sp. ($P = 0.019$, $F = 52.2$) and tended to consume more *Rhynchosia* sp. ($P = 0.087$, $F = 10.0$) than did LBH cattle. Selection index of *Rhynchosia* sp. was also higher among TBH cattle ($P = 0.029$, $F = 33.5$). In the red soil habitat, relative consumption of *P. maximum* was lower among TBH than LBH cattle ($P = 0.025$, $F = 39.1$).

Table 1
Herbaceous vegetation attributes (means ± SE) at foraging sites of cattle managed with loosely bunched herding (LBH) and tightly bunched herding (TBH) across different habitats.

Attributes	Black soil		Red soil		Significance (*P* value)		
	LBH	TBH	LBH	TBH	T	H	T × H
Cover (%)	86.8 ± 1.4	86.7 ± 2.7	73.3 ± 2.0	70.4 ± 1.4	0.538	0.003	0.515
Leaf height (cm)	18.2 ± 2.0	19.1 ± 1.7	13.4 ± 1.2	15.4 ± 2.9	0.315	0.180	0.676
Greenness (%)	40.6 ± 16.4	37.0 ± 9.1	57.5 ± 7.0	58.1 ± 5.7	0.752	0.254	0.652
Species richness	21.7 ±3.8	17.7 ± 2.0	31.7 ± 2.2	35.0 ± 3.5	0.616	0.030	0.157
Species diversity	1.9 ± 0.1	1.9 ± 0.1	2.6 ± 0.1	2.7 ± 0.1	0.738	0.007	0.353

T, H, T × H are herding treatment, habitat, and herding treatment by habitat interaction effects, respectively.

Table 2
Forage species relative cover (%; means ± SE) at foraging sites of loosely bunched (LBH) or tightly bunched (TBH) cattle across different habitats.

Species	Black soil		Red soil	
	LBH	TBH	LBH	TBH
Setaria anceps	25.2 ± 10.0	32.0 ± 6.0		
Themeda triandra	$17.3^{a} \pm 3.6$	$10.5^{b} \pm 1.7$	2.7 ± 1.2	1.5 ± 0.3
Lintonia nutans	8.9 ± 2.6	12.4 ± 1.4		
Pennisetum mezianum	8.8 ± 1.0	10.2 ± 0.8	5.1 ± 0.6	2.8 ± 0.6
Pennisetum stramineum	7.2 ± 2.5	6.9 ± 0.8	5.3 ± 1.7	4.4 ± 1.3
Brachiaria lachnantha	3.4 ± 1.8	5.2 ± 1.0		
Rhynchosia sp.	5.1 ± 1.2	6.4 ± 0.8		
Ischaemum afrum	4.6 ± 1.4	3.4 ± 0.4		
Aspillia sp.	2.4 ± 0.5	2.4 ± 0.6		
Bothriochloa insculpta	1.6 ± 0.3	0.9 ± 0.6	$2.0^{a} \pm 0.7$	$1.1^{b} \pm 0.3$
Eragrostis papposa	1.4 ± 1.0	0.6 ± 0.4	12.1 ± 1.9	11.6 ± 1.8
Brachiaria lersoides	2.9 ± 0.7	3.0 ± 0.6		
Aristida kenyensis	0.8 ± 0.8	0.1 ± 0.1	6.1 ± 3.3	10.0 ± 4.7
Cynodon plectostachyus			17.0 ± 3.3	13.0 ± 2.0
Enteropogon macrostachyus			7.9 ± 0.5	9.9 ± 0.5
Cynodon dactylon			6.0 ± 1.0	5.3 ± 1.2
Tragus berteronianus			6.9 ± 2.4	7.7 ± 3.5
Chrysopogon plumulosus			0.4 ± 0.4	0.1 ± 0.1
Aristida congesta			2.3 ± 2.0	3.4 ± 1.6
Panicum maximum			0.6 ± 0.6	0.5 ± 0.2
Eragrostis rigida			0.5 ± 0.4	0.8 ± 0.6
Microchloa kunthii			1.1 ± 0.4	0.3 ± 0.2
Commelina sp.			2.5 ± 0.4	2.9 ± 0.6
Cyperus sp.			0.1 ± 0.1	0.0 ± 0.0
Cenchrus ciliaris			2.3 ± 1.4	1.3 ± 0.6
Justicia sp.			2.6 ± 1.3	3.6 ± 0.9
Monechma sp.			0.1 ± 0.1	0.1 ± 0.1
Chloris virgata			2.1 ± 1.2	2.1 ± 0.4
Indigofera spp.			3.8 ± 1.3	1.5 ± 0.5
Phyllanthus sp.			0.2 ± 0.2	0.2 ± 0.2
Chloris gayana			0.1 ± 0.1	0.4 ± 0.3
Baleria spp.			1.3 ± 0.4	2.6 ± 1.1

For each habitat type, only species comprising at least 1% of cattle bites are included.
Blank spaces imply species absent or comprised <1% of total bites.
Within habitats, means with different superscript letters (a,b) differ significantly ($P < 0.05$).

Table 3
Percentage of bites (means ± SE) taken on different forage species by loosely bunched (LBH) or tightly bunched (TBH) cattle across different habitats.

Herbage species	Black soil		Red soil	
	LBH	TBH	LBH	TBH
Setaria anceps	22.2 ± 9.4	30.4 ± 7.1		
Themeda triandra	$22.1^{a} \pm 1.9$	$16.7^{b} \pm 0.6$	3.3 ± 0.8	2.5 ± 0.3
Lintonia nutans	10.8 ± 4.2	12.4 ± 1.3		
Pennisetum mezianum	11.3 ± 1.5	8.7 ± 1.0	6.6 ± 2.1	6.6 ± 1.5
Pennisetum stramineum	6.5 ± 1.5	6.2 ± 1.0	6.6 ± 1.6	4.9 ± 1.1
Brachiaria lachnantha	5.2 ± 1.5	4.5 ± 1.6		
Rhynchosia sp.	3.4 ± 1.0	6.0 ± 0.7		
Ischaemum afrum	1.7 ± 0.3	3.3 ± 0.9		
Aspillia sp.	$2.0^{a} \pm 0.6$	$2.8^{b} \pm 0.1$		
Bothriochloa insculpta	2.5 ± 0.6	1.7 ± 0.8	3.2 ± 1.3	1.6 ± 0.9
Eragrostis papposa	3.1 ± 1.5	1.1 ± 0.6	11.4 ± 3.7	10.7 ± 4.1
Brachiaria lersoides	1.8 ± 0.3	1.9 ± 0.5		
Aristida kenyensis	2.5 ± 1.8	0.6 ± 0.4	6.2 ± 2.4	7.3 ± 2.7
Cynodon plectostachyus			8.9 ± 2.3	8.4 ± 1.1
Enteropogon macrostachyus			6.7 ± 0.8	8.0 ± 1.0
Cynodon dactylon			6.2 ± 0.7	7.9 ± 1.2
Tragus berteronianus			5.3 ± 0.1	4.0 ± 0.9
Chrysopogon plumulosus			3.8 ± 0.8	4.3 ± 2.0
Aristida congesta			2.7 ± 1.7	4.3 ± 0.9
Panicum maximum			$3.8^{a} \pm 1.7$	$1.7^{b} \pm 0.8$
Eragrostis rigida			2.1 ± 0.9	2.8 ± 1.2
Microchloa kunthii			2.2 ± 2.2	2.3 ± 2.3
Commelina sp.			1.7 ± 0.2	2.3 ± 0.7
Cyperus sp.			1.2 ± 0.7	2.1 ± 2.0
Cenchrus ciliaris			2.2 ± 1.8	1.0 ± 0.7
Justicia sp.			1.5 ± 1.0	1.6 ± 0.1
Monechma sp.			1.8 ± 1.0	1.2 ± 0.8
Chloris virgata			1.6 ± 0.9	0.6 ± 0.6
Indigofera spp.			1.3 ± 0.5	1.3 ± 0.5
Phyllanthus sp.			0.8 ± 0.5	1.6 ± 0.8
Chloris gayana			1.6 ± 0.9	1.2 ± 0.6
Baleria spp.			0.4 ± 0.3	1.7 ± 0.8

For each habitat type, only species comprising at least 1% of cattle bites are included.
Blank spaces imply species absent or comprised <1% of total bites.
Within habitats, means with different superscript letters (a,b) differ significantly ($P < 0.05$).

Analysis of preference categories revealed that herding treatment by habitat interaction influenced relative consumption of preferred (positively selected) species ($P = 0.026$, $F = 11.9$; Fig. 2d) and neutrally selected species ($P = 0.057$, $F = 7.0$; Fig. 2e). Specifically, across the black soil (but not across red soil) habitat, relative consumption of preferred species was 32% lower ($P < 0.001$), while relative consumption of neutrally selected species was 16% higher ($P = 0.009$) among TBH than LBH cattle. Relative consumption of avoided (negatively selected) species did not differ significantly between herding treatments but was significantly higher in red than black soil (Fig. 2f).

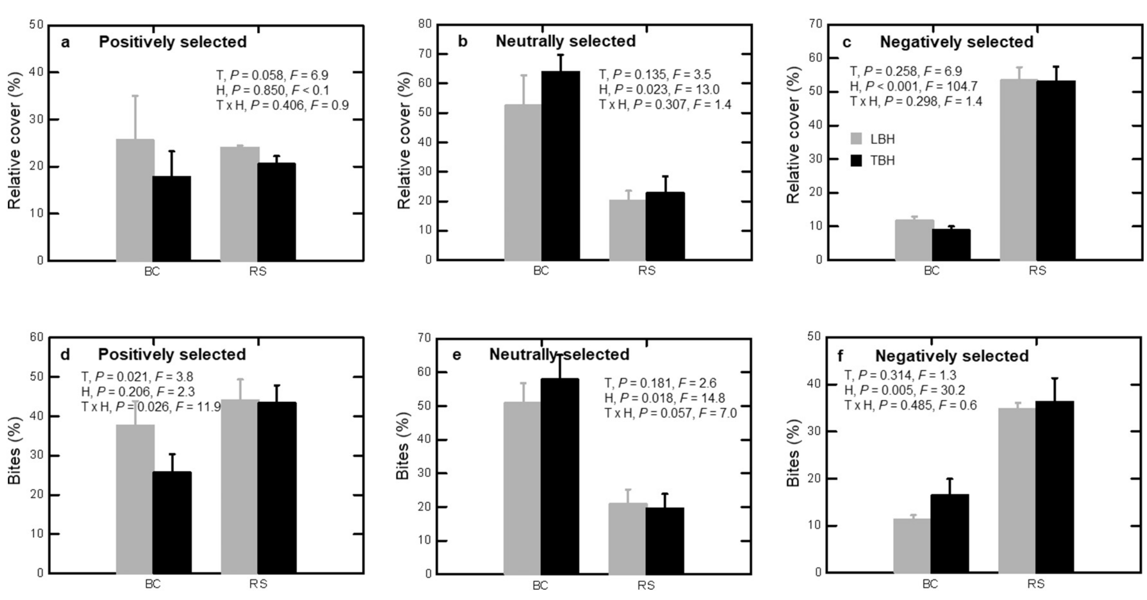

Figure 2. Relative availability (cover) of different forage preference and percentage of bites taken on these categories by loosely bunched (LBH) and tightly bunched (TBH) cattle across black soil (BC) and red soil (RS) habitats. T, H, T × H are herding treatment, habitat, and herding treatment by habitat interaction effects, respectively.

Table 4
Jacobs' selection indices (means ± SE) of forage plants consumed loosely bunched herding (LBH) or tightly bunched herding (TBH) cattle across different habitats.

Herbage species/class	Black soil		Red soil	
	LBH	TBH	LBH	TBH
Setaria anceps	−0.07 ± 0.08	−0.05 ± 0.04		
Themeda triandra	0.19 ± 0.13	0.30 ± 0.16	0.19 ± 0.14	0.23 ± 0.12
Lintonia nutans	0.07 ± 0.23	0.00 ± 0.01		
Pennisetum mezianum	0.14 ± 0.09	−0.09 ± 0.06	0.06 ± 0.20	0.43 ± 0.06
Pennisetum stramineum	−0.02 ± 0.11	−0.06 ± 0.08	0.16 ± 0.12	0.08 ± 0.22
Brachiaria lachnantha	0.26 ± 0.16	−0.10 ± 0.08		
Rhynchosia sp.	−0.24[a] ± 0.11	−0.06[b] ± 0.03		
Ischaemum afrum	−0.39 ± 0.20	−0.06 ± 0.18		
Aspillia sp.	−0.18 ± 0.17	0.01 ± 0.18		
Bothriochloa insculpta	0.20 ± 0.16	0.36 ± 0.17	0.14 ± 0.31	−0.06 ± 0.49
Eragrostis papposa	0.61 ± 0.25	0.31 ± 0.12	−0.06 ± 0.19	−0.10 ± 0.11
Brachiaria lersoides	−0.22 ± 0.07	−0.24 ± 0.14		
Aristida kenyensis	0.72 ± 0.28	0.85 ± 0.15	0.08 ± 0.08	−0.05 ± 0.19
Cynodon plectostachyus			−0.34 ± 0.16	−0.24 ± 0.07
Enteropogon macrostachyus			−0.10 ± 0.09	−0.12 ± 0.06
Cynodon dactylon			0.03 ±0.14	0.22 ± 0.03
Tragus berteronianus			−0.05 ± 0.22	−0.25 ± 0.13
Chrysopogon plumulosus			0.78 ± 0.23	0.98 ± 0.02
Aristida congesta			−0.09 ± 0.51	0.28 ± 0.25
Panicum maximum			0.88 ± 0.12	0.24 ± 0.63
Eragrostis rigida			0.74 ± 0.15	0.49 ± 0.39
Microchloa kunthii			−0.44 ± 0.56	0.28 ± 0.64
Commelina sp.			−0.18 ± 0.03	−0.14 ± 0.07
Cyperus sp.			0.73 ± 0.27	1.00 ± 0.00
Cenchrus ciliaris			−0.20 ± 0.16	−0.40 ± 0.40
Justicia sp.			−0.38 ± 0.33	−0.37 ± 0.08
Monechma sp.			0.33 ± 0.67	0.75 ± 0.25
Chloris virgata			−0.39 ± 0.39	−0.31 ± 0.28
Indigofera spp.			−0.46 ± 0.15	−0.08 ± 0.04
Phyllanthus sp.			0.33 ± 0.67	0.33 ± 0.67
Chloris gayana			0.59 ± 0.42	−0.17 ± 0.83
Baleria spp.			−0.61 ± 0.20	−0.30 ± 0.42

For each habitat type, only species comprising at least 1% of cattle bites are included.
Blank spaces imply species absent or comprised <1% of total bites.
Within habitats, means with different superscript letters (a,b) differ significantly ($P < 0.05$).

Dietary digestible organic matter (DOM) was significantly higher in red soil than black soil but did not differ significantly between herding treatments (Table 5). Dietary crude protein (CP) was significantly lower in TBH than LBH cattle in the red soil but not in the black soil (herding treatment by habitat interaction $P = 0.063$, $F = 6.5$; see Table 5). Crude protein intake (CPI) tended to be lower ($P = 0.091$) in TBH than LBH cattle across the red soil but not black soil habitat (herding treatment by habitat interaction $P = 0.062$, $F = 6.6$; see Table 5). Dry matter intake (DMI) and digestible organic matter intake (DOMI) did not differ significantly between herding treatments or habitats (see Table 5).

Overall, cattle traveled 7.2 km ± 0.5 (SE) and 7.5 km ± 0.5 daily in black and red soil, respectively. Travel distance did not differ significantly between the two habitats (Fig. 3a). Across both habitats, cattle in TBH covered significantly shorter distance than those in LBH (see Fig. 3a). Cattle foraging efficiency (nutrient intake per unit distance traveled) was 480 g DOMI km^{-1} ± 29 in the black soil habitat and 434 g DOMI km^{-1} ± 51 in the red soil habitat. Foraging efficiency was significantly higher in TBH than LBH cattle across both habitats, although the magnitude of this difference was larger in the black soil (29%) than red soil (10%) (herding treatment by habitat interaction $P = 0.012$, $F = 18.7$; Fig. 3b).

Cattle weight gain was 377 ± 68 (SE) and 328 ± 111 g $head^{-1}$ day^{-1} in black soil and red soil, respectively. Weight gain was significantly higher in TBH than LBH herds but did not differ significantly between habitats (Fig. 3c). Herding treatment by habitat interaction was not statistically significant ($P = 0.231$, $F = 0.2$; see Fig. 3c). There was a significant positive relationship between cattle weight gain and foraging efficiency (Fig. 3d).

Discussion

This study quantified the short-term effects of tightly bunched herding (TBH) versus loosely bunched herding (LBH) on cattle foraging behavior, nutrition, and performance (weight gain) across a heterogeneous red soil habitat and a homogeneous black soil habitat for the first time in an African savanna rangeland. We found that, across habitats, cattle traveled less, foraged more efficiently, and performed better

Table 5
Diet quality, forage and nutrient intake attributes (means ± SE) of cattle managed with loosely bunched herding (LBH) or tightly bunched herding (TBH) across different habitats.

Attribute	Black soil		Red soil		Significance (*P* value)		
	LBH	TBH	LBH	TBH	T	H	T × H
DOM (%)	54.7 ± 0.6	55.8 ± 0.8	59.8 ± 1.4	60.1 ± 0.4	0.442	0.007	0.688
CP (%)	6.3 ± 0.1	6.3 ± 0.3	7.3 ± 0.9	6.6 ± 0.3	0.649	0.478	0.063
DMI (kg d^{-1})	6.0 ± 0.3	6.4 ± 0.3	5.4 ± 1.1	5.3 ± 0.9	0.347	0.454	0.181
DOMI (kg d^{-1})	3.3 ± 0.1	3.6 ± 0.2	3.2 ± 0.7	3.2 ± 0.5	0.368	0.764	0.229
CPI (g d^{-1})	373 ± 24	398 ± 23	402 ± 127	353 ± 92	0.627	0.748	0.062

T, H, T × H are herding treatment, habitat and herding treatment by habitat interaction effects, respectively.

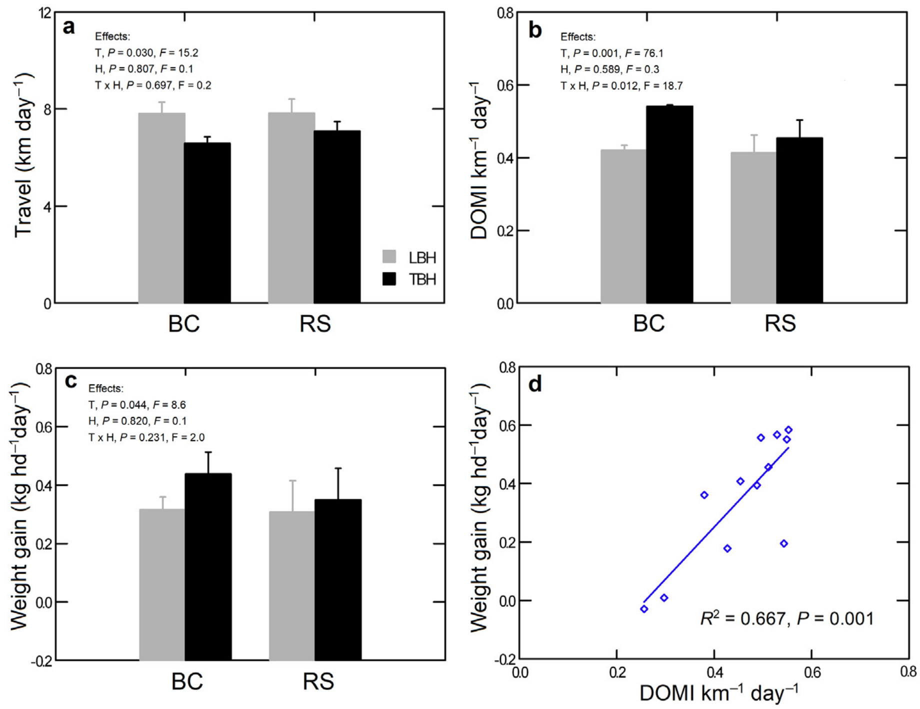

Figure 3. Daily travel distance, foraging efficiency and performance of cattle managed under loosely bunched herding (LBH) and tightly bunched herding (TBH) across black soil (BC) and red soil (RS) habitats. T, H, T × H are herding treatment, habitat, and herding treatment by habitat interaction effects, respectively. Digestible organic matter intake (DOMI).

(i.e., put on more weight) when managed with TBH than when allowed to spread naturally during herding. These changes occurred despite the fact that tightly bunched cattle grazed at much higher stocking densities across both habitats, reduced consumption of preferred forage plants while increasing consumption of less preferred plants (in black soil), and consumed diet with lower crude protein content (in red soil).

The observed positive effect of TBH on cattle does not support our hypothesis that this herding approach depresses cattle performance. Normally, increased stock density as was observed under TBH would be expected to depress individual cattle performance through increased interindividual competition and reduced grazing selectivity and forage intake (Odadi and Rubenstein, 2015). However, we observed a converse pattern, suggesting that the benefits of TBH overshadowed any deleterious effects of increased stock density. We attribute the improved performance to the steers' increased foraging efficiency under TBH, primarily driven by reduced travel distance. Animals forage more efficiently and perform better when they consume more energy in relation to energy spent foraging (Sevi et al., 1999; Howery and DeLiberto, 2004).

That cattle traveled less when managed with TBH is attributable to the fact that this herding method restricted cattle to foraging within much smaller areas, thereby minimizing their freedom to range more widely in search of higher-quality food items. On average, tightly bunched steers traveled 1 km day^{-1} less than their loosely bunched counterparts. Assuming energy spent in locomotion averaged 0.5 kcal kg BW^{-1} km in line with Hart et al. (1993), tightly bunched steers should have saved approximately 120.5 kcal day^{-1} (i.e., 0.5 kcal × 241 kg × 1 km) from reduced daily travel. Tightly bunched steers gained 82 g day^{-1} more weight than loosely bunched steers. On the basis of the model developed for cattle grazing under tropical conditions (Valente et al., 2013), the energy retained in this weight gain difference equates to 125 kcal day^{-1}, which roughly matches the energy (120.5 kcal day^{-1}) that steers under TBH saved from reduced travel.

TBH is often used by livestock farmers with the belief that it improves range condition through increased animal impact, but farmers are normally concerned about its perceived short-term negative effects on cattle performance. This concern possibly stems from previous reports indicating that grazing livestock perform better when allowed to range freely across the landscape than when herded (El Aich and Rittenhouse, 1988; Vallentine, 2001; Odadi and Rubenstein, 2015). For herded livestock, however, little is known about how altering herding method affects animal performance in the short term. Our findings indicate that, under the conditions of our study, TBH does not directly depress cattle performance; it actually improves it. A previous study in northern Kenyan pastoral lands reported positive responses of cattle to an altered grazing management regime, which involved TBH among several other practices (Odadi et al., 2017). However, that study did not separate short-term direct effects of altered grazing management regime on livestock performance from long-term cumulative effects of grazing management on vegetation conditions. Such effects of altered grazing management on vegetation were not present in our study because both herding treatment groups accessed the same grazing areas. Therefore, the effects observed here are primarily attributable to altered herding method rather than cumulative changes in vegetation conditions. Our study highlights the difference between testing TBH and testing grazing systems such as rotational versus continuous grazing, which could have different effects on forage conditions over the long term. While our study did not attempt to test whether tightly bunched grazing improves the rangeland, it did show that this grazing strategy itself may be good for cattle production at least in the short term, contrary to predictions indicating otherwise.

The observed positive relationship between foraging efficiency and cattle performance is consistent with studies in other rangelands (Olson and Malecheck, 1988; Hart et al., 1993; D'Hour et al., 1994). Notably, Hart et al. (1993) attributed improved cattle performance to reduced nongrazing travel, especially travel to water by cattle in smaller pastures. In our study, however, the observed reduced travel by cattle when managed with TBH appears to be largely related to reduced travel during grazing as opposed to nongrazing travel. This is because cattle under both herding treatments shared camps (*boma* locations) and drank water from the same sources at the same frequency (once) daily and were therefore unlikely to differ in distance traveled to water or camp. Also consistent with our findings, Parker et al. (1996) and Sevi et al. (1999) reported increased body mass change with increasing foraging efficiency in Sitka black-tailed deer *(Odocoileus* *hemionus sitkensis)* in Alaska and sheep *(Ovis aries)* in southern Italy, respectively. Cattle can shift from foraging more extensively to an energy conservation foraging strategy depending on forage conditions (Clark et al., 2017). Our study shows that an altered herding regime can also trigger such a shift in cattle foraging strategy.

The positive effect of TBH on cattle performance observed here appears to contradict our previous work (Odadi and Rubenstein, 2015), which showed depressed cattle performance when herd size was increased. In that study, however, cattle were not actively tightly bunched and their performance was primarily determined by forage intake rather than by distance traveled, which was unaltered by herd size. In the present study, TBH reduced the distance cattle traveled but did not influence forage or nutrient intake. These discrepancies suggest that herd size and TBH have contrasting effects on cattle performance unless managed appropriately. It is important to understand that increasing herd size could erode the positive effects of TBH on cattle performance.

Cattle reduced or tended to reduce use of preferred forage plants (*T. triandra* and *E. papposa* and all positively selected species combined) and increased use of less preferred plants (*Rhynchosia* sp., *Aspilia* sp., and all neutrally selected species combined) when tightly bunched in the black soil, indicating reduced grazing selectivity. These patterns were generally associated with lower relative availability of preferred forage plants at the foraging sites of cattle under TBH, suggesting that this herding method reduced the ability of cattle to select foraging sites with high concentrations of preferred forage species. Diet composition changes were, however, not quite evident in the red soil habitat, except for the positively selected *P. maximum,* which was consumed less by cattle when tightly bunched. Because the relative availability of *P. maximum* did not differ significantly between foraging sites of the differently herded cattle across the red soil habitat, it is unclear why cattle consumed this grass species less frequently when managed with TBH. We posit that increased stock density under TBH prevents individual cattle from seeking preferred but relatively rare forage species, reducing the relative consumption of such species.

The observed effects of TBH on cattle diet composition generally support our hypothesis that this herding approach reduces forage selectivity by cattle. However, the fact that these changes were more evident in the black soil habitat would at first glance appear to contradict our prediction of muted effects of TBH in this relatively homogeneous habitat. It is noteworthy, however, that these diet composition shifts had negligible effects on cattle diet quality in the black soil habitat; cattle diet CP and DOM contents did not differ between herding treatments in this habitat. Our findings suggest that when forage is relatively abundant and homogeneously distributed across the landscape, as is the case in the black soil habitat, tightly bunched cattle are able to obtain sufficient leaf material and attain diet quality levels similar to those attained by loosely bunched cattle, despite foraging less selectively at plant species or preference group level. In addition, TBH did not alter cattle diet CP in the black soil habitat, possibly because of the observed increased use or selection of the forbs *Aspilia* and *Rhynchosia* by tightly bunched cattle. Because forbs contain higher CP than grasses (Pieper and Beck, 1980), we posit that the observed increase in their relative use by cattle when managed with TBH canceled out any effects of reduced consumption of preferred forage on cattle diet CP content.

The observed negative effect of TBH on cattle diet CP content in the red soil but not in the black soil supports our hypothesis of muted negative effects of this herding method under relatively homogeneous conditions. This disparity between habitats in the effects of TBH on diet CP suggests that the effects of TBH on cattle diet quality is context dependent (i.e., dependent on forage availability and distribution pattern). Reduced dietary CP under TBH in the red soil habitat indicates reduced grazing selectivity. Because the effects of TBH on cattle diet composition were less evident in the red soil habitat, the difference in dietary CP between herding treatments possibly resulted from differential consumption of plant parts rather than differential consumption of plant species or groups. Despite reduced dietary CP under TBH in the red soil habitat, tightly bunched cattle still put on more weight, suggesting that their CP requirements for maintenance and growth were met. Growing steers require a minimum of 6% CP in their diet for maintenance (Zimmermann, 1980), a threshold that was surpassed in the present study.

Despite the fact that TBH triggered diet composition shifts in cattle, it did not influence their diet breadth, contrary to our expectation. According to the concept of density-dependent resource selection, animals should expand their dietary niche breadth with increasing population density if they have 1) ideal knowledge of the distribution of resources in their habitat and 2) free access to all resources (Pianka, 1988; Nicholson et al., 2006). In the present study, both tightly bunched and loosely bunched cattle were herded and were therefore limited in the extent to which they could freely access forage resources across the landscape. However, this limitation was likely greater for tightly bunched cattle, which may explain why they were unable to increase dietary breadth in response to increased stock density.

One major knowledge gap in grazing management has been whether high-density grazing actually alters animal behavior to limit selective grazing and whether such reduced grazing selectivity depresses livestock performance (Hawkins et al., 2017). In our study where TBH increased the stock density of cattle by more than 100%, we observed reduced grazing selectivity by cattle when managed with this herding method. However, our study shows that the effects of reduced grazing selectivity under TBH were outweighed by the benefit of reduced travel and improved foraging efficiency, resulting in improved cattle performance. Our study demonstrates that TBH slows the herd down and prevents individual cattle from wasting energy wandering away from the herd. Under LBH, individual cattle continually switch from investigating areas peripheral to the herd to keeping up with the rest of the herd when they become stragglers, which appears to be energetically costly. When grazing cattle are tightly bunched, they resort to nonselective foraging while moving slowly across the landscape apparently in a more linear pattern (less weaving), which is energetically more efficient.

The differences in dietary differences between black soil and red soil are attributable to differences in herbaceous vegetation species composition and diversity. These herbaceous vegetation differences are in turn related to differences in topography, soil properties, woody vegetation, and native ungulate communities between the two habitats (Young et al., 1998; Augustine et al., 2010; Bergstrom, 2013). The higher cattle diet digestible organic matter (DOM) in the red soil habitat indicates that forage quality is generally higher in this habitat. Despite the higher dietary DOM content in red than black soil, digestible organic matter intake (DOMI) was similar between these habitats, which could explain the observed lack of habitat difference in cattle performance.

The increased steer performance under TBH seen here appears financially beneficial even when the increased cost of labor associated with implementing this herding approach is considered. On average, TBH increased steer weight gain by 82 g $head^{-1}d^{-1}$, which would translate to approximately 3 000 kg annually for a herd of 100 steers. Currently, a mature steer (live weight 450 kg) sells at approximately US $800 (or US$ 1.8 kg^{-1} live weight) in our study region. Therefore, the observed increased steer performance would earn US$ 5 400 $herd^{-1}$ yr^{-1}. Implementing TBH with a herd of 100 steers requires two more herders when compared with LBH. Going by the current herding labor cost in our study region of approximately US$ 1 500 $herder^{-1}$ yr^{-1}, the total increase in labor cost for TBH would be US$ 3 000 yr^{-1}. Therefore, this herding approach would increase the profitability of raising a herd of 100 steers by US$ 2 400 yr^{-1} after accounting for the cost of additional labor requirements. This margin might appear somewhat modest, especially in a developed world context. However, commercial ranchers tend to minimize risk and maintenance costs by making beef cattle attain the target market weight as quickly as possible (Odadi et al., 2011). Therefore, the observed faster growth of cattle under TBH may reinforce the economic benefits and attractiveness of this herding strategy to many ranchers, especially in a developing world context.

Management Implications

Our study demonstrates that TBH as practiced here does not depress, but actually improves cattle performance (weight gain), contrary to predictions otherwise. In addition, the financial benefit of improved cattle performance more than offsets the increased cost of additional labor required to implement TBH. Therefore, this herding approach can be implemented without having negative livestock production and financial implications. In addition, the fact that cattle foraged less selectively when managed with TBH suggests that this herding method could potentially be used to prevent overuse of preferred forage plants and maintain herbaceous species diversity without sacrificing animal performance. However, these findings should be interpreted with caution. First, our study was conducted under moderate cattle stocking rate and adequate forage availability. It is possible that these findings might not hold in heavily stocked rangelands with relatively poor forage conditions. Secondly, cattle herd size was controlled (i.e., herd size was equal between herding treatments [100 animals herd^{-1}]) in this study. Implementing TBH with larger herd sizes relative to herd sizes of loosely bunched herds could erode or even reverse the positive effects reported here. Thirdly, we used only steers in our study and therefore did not evaluate the effects of TBH on the reproductive performance of cattle. Concentrating cattle within small areas can increase interference with breeding activities and reduce conception rates (Olson and Malecheck, 1988). Fourthly, because herding treatments were replicated in time, we do not know whether and how the positive effects of TBH reported here could vary temporally, and especially between wet and dry seasons. Further investigations would be worthwhile to unravel any such temporal variations, and the thresholds of forage availability, stocking density, and herd size at which TBH might begin to depress both production and reproductive performance of cattle. Lastly, the value of any grazing management regime should be judged on not only its short-term effects on livestock performance but also its long-term impacts on the range. We recommend further investigations into the effects of TBH as applied here on rangeland health dynamics in the long run.

Acknowledgments

We are grateful to Mpala Conservancy and Mpala Research Centre for experimental animals and sites, research facilities, and logistics. Field assistance was provided by Robert Kibet, Peter Ekai, Wilson Longor, Martin Sisanya, and Boniface Kirwa. We thank David J. Augustine and two anonymous reviewers for valuable comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.03.008.

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