Cattle don’t care: Animal behaviour is similar regardless of grazing management in grasslands

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ABSTRACT

It is well known that rangelands lose productivity and ecosystem function under excessive rates of livestock stocking, however the role of the spatio-temporal distribution of grazing density remains debated. Multiple studies show that managing grazing for high livestock density has little effect on plant and livestock productivity, yet fewer explore animal behaviour as a mechanism that would explain these observations. We hypothesised that increasing cattle grazing densities under equivalent stocking rates will cause animals to concentrate more, spend more time grazing and thereby increase utilisation of forage, and reduce selection for palatable vegetation patches and species. We compared season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) over three years in an experimental trial in a mesic grassland of South Africa reflecting a range of grazing densities (SLG < FCG < HPG). We measured the spatio-temporal patterns of cattle behaviour, dietary composition, dung trampling, animal productivity, and normalised difference vegetation index (NDVI). The management approach did not change the time allocated to different animal behaviours, trampling of dung, nor the selection for particular plants. HPG cattle grazed at closer distances to one another than SLG but not FCG, and herds were equally concentrated when resting and walking. HPG cattle spent less time in patches of high vegetation NDVI compared to SLG, thereby reducing the spatial heterogeneity of NDVI over time. Cattle gained 0.2 ± 0.02 kg day⁻¹ ha⁻¹, and this did not differ between management approaches. The HPG approach is costly to set up and is predicted to take twice as long as FCG and SLG to become profitable. Depending on the management goal, HPG could reduce selection for palatable patches, possibly preventing overgrazing and formation of bare patches over the long term. Alternatively, SLG could increase selection for palatable patches and initiate the formation of grazing lawns and, in combination with fire, commonly used in FGC, might enhance biodiversity.

1. Introduction

Globally, livestock grazing is one of the most widespread land uses, occupying 26% of the terrestrial earth surface (FAO, 2014). After fire, wild and domestic herbivores (vertebrate and invertebrate) are the most prevalent consumers of biomass globally (Bond and Keeley, 2005; Estes et al., 2011; Archibald and Hempson, 2016), and can alter ecosystem function, for example, through reducing competition for invasive unpalatable herbs (Milton, 2004) and woody plants (O’Connor et al., 2014; Venter et al., 2018). New paradigms in rangeland management identify the importance of managing the spatial and temporal distribution of ungulate herbivory for maintaining ecosystem services and biodiversity conservation (Fuhlendorf et al., 2017). In ecosystems relatively untransformed by human impact, the movement patterns of grazing herbivores track seasonal or ephemeral patterns of resource availability (McNaughton, 1993). This is evident from the seasonal migrations of wildebeest in the African Serengeti (McNaughton, 1985) or the way bison herds concentrate on post-fire vegetation regrowth in North American prairies (Fuhlendorf et al., 2009). Grazing management approaches in rangelands have drawn from these ecological observations and developed methods to reintroduce periods of rest from grazing (Briske et al., 2008).

Reviews of rangeland management literature over the last century have found that manipulating grazing densities via grazing management systems is of minor importance relative to stocking rate in determining vegetation and animal production (Sampson, 1951; Heady, 1961; Van Poollen and Lacey, 1979; O’Reagain and Turner, 1992; Briske et al., 2008). Stocking rate refers to the number of large stock...
units (LSUs) per hectare of available rangeland, whereas grazing density (sometimes referred to as ‘stock density’) is the number of LSUs per subunit of area at any point in time on that rangeland so that two farms may have the same stocking rate but different densities depending on the number of defined camps or paddocks in which stock are held per unit time. Grazing management approaches such as rotational grazing attempt to manipulate grazing densities by altering the duration of vegetation exposure to livestock with the aid of fencing or herding (Heitschmidt and Taylor Jr, 1991) and even fire (Andrew, 1986; Fuhlendorf et al., 2009). Such approaches exist on a continuum of grazing density ranging from season-long continuous, where animals are moved once a year, to high- or ultra-high-density grazing, where animals are moved daily or multiple times a day. Season-long continuous grazing was traditionally and remains to some extent the conventional approach in the USA (Briske et al., 2008) and is very similar to the ‘rotational rest’ approaches adopted in Middle-East, African and Asian rangelands based on transhumance (seasonal rotation) (Makarewicz and Tuross, 2012; Aryal et al., 2014; Morokong, 2016). At the other end of the grazing density spectrum are practices such as short duration grazing and holistic planned grazing (Savory, 1978; Tiedeman, 1986; Tainton, 1999; Savory and Butterfield, 2016). These approaches move animals using electric fencing or herding between small paddocks at high frequencies based on an adaptive management framework.

Despite the theory, the balance of experimental studies show little effect of rotational grazing practices (Briske et al., 2008) or high density practices in particular (Hawkins, 2017) on vegetation basal cover, biomass, or animal gain compared to season-long grazing. The debate about rotational grazing effects persists due to a mismatch between experimental evidence and anecdotal experiences of practitioners (Briske et al., 2011), and possibly, a lack of nuanced research that captures less obvious consequences of rotational grazing. For example, assumptions about animal behaviour under different grazing densities have been largely ignored. Testing the assumptions implicit in arguments for high density grazing is important given that it has been advocated to policy makers as a solution to climate change (Sherron et al., 2012; Briske et al., 2014). High density grazing approaches, including holistic planned grazing, are based on the assumption that animals concentrated in space and time will behave differently resulting in (1) increased proportion of available plants that are grazed, (2) homogenization of grazing severity across species and vegetation patches, and (3) increased distribution of plant litter, dung and urine into the soil via hoof trampling (Savory and Butterfield, 2016). In lower density management approaches, overgrazing of highly palatable plants leads to mortality and may cause the competitive release of less palatable species that may consequently encroach or become invasive (Anderson and Briske, 1995). The loss of palatable species can also increase soil exposure and reduce overall vegetation basal cover (Thurow, 1991; Fuls, 1992; Ash and Smith, 1996; Teague et al., 2011). This is predicted to feedback negatively into animal production and farm profitability. While the causal links between increasing animal numbers (i.e. stocking rates) and the loss of ecological function and species richness (degradation) on rangelands have been corroborated (Briske, 2017), few studies have investigated the changes in animal behaviour induced by increasing grazing densities at the same stocking rate. This might be important in explaining farm productivity responses, or lack thereof, to rotational grazing.

The primary behavioural mechanism assumed to be distinctive in high density grazing practices is the spatial utilisation of and selectivity for palatable plants and forage patches within a defined area (Barnes et al., 2008; Bailey and Brown, 2011). In a comprehensive review of the literature (Hawkins, 2017), only one study compared forage utilisation under rotational and continuous grazing management (Hart et al., 1993) and they found no difference in the proportional grazing of available plants. A few studies have found that increasing grazing densities with fencing that breaks large scale grazing movement patterns can prevent animals from selecting for palatable vegetation patches (Smith and Owensby, 1978; Charles et al., 1985; Volesky, 1994), however, qualitative reviews of the literature have also argued that rotational grazing has no consistent effect (Launbaugh and Howery, 2005; Soder et al., 2009; Bailey and Brown, 2011). Rather, other factors such as watering points, topography and stocking rates are stronger determinants of selection at the patch scale. Similarly, selection at the plant-scale is largely unaffected by rotational grazing management (Kirby et al., 1986; Kreuter and Tainton, 1988; Olson and Malechek, 1988) because animals choose to eat plants based on nutritional status and digestibility regardless of how tightly they are concentrated (Bailey and Brown, 2011). However, recent work has found exceptions in African rangelands where active herding reduces selection for palatable taxa in cattle (Odadi et al., 2018) and sheep/goat (Samuels et al., 2016) systems. Thus, grazing management apparently has no effect on dietary selection at the patch scale while results are contradictory at the plant scale.

A second behavioural mechanism potentially triggered by concentrating animals under high density grazing is the allocation of time and energy to grazing, walking and resting. Typically, herbage quality and availability determine the time livestock spend grazing (Ungar and Noy-Meir, 1988), however the literature also highlights the potential trade-offs between energy savings and adverse effects of herd concentration and frequent moving. In wild ungulates such as Alaskan moose, increasing herd size and density can promote foraging efficiency by reducing vigilance for predators, but may also reduce time spent grazing due to inaspecific competition for forage resource (Molvær and Bowyer, 1994). In African rangelands, increasing cattle herd size can reduce foraging efficiency due to inaspecific competition (Odadi and Rubenstein, 2015), yet this effect may be counteracted by forcing herds to concentrate more closely and thereby prevent energy losses from walking longer distances to search for preferred forage (Odadi et al., 2018). Experimental trials show that frequent movements between fenced areas can cause animal agitation and stress and, combined with reduced ability to select for palatable forage that meets animal requirements and a sudden decline in forage availability (Cox et al., 2017), can lead to declines in animal performance and conception rates (Worthington, 1984; McCollum III et al., 1999; Badgery et al., 2017). The time animals allocate to walking has consequences for step rates and trampling behaviour. Rotational grazing management has been shown to increase the density of cattle walking trails (Walker and Heitschmidt, 1986), but has also been found to have little effect on step rates and distances walked (Hart et al., 1993). Understanding the effect of management on trampling behaviour and consequent hoof impact has important implications for soil hydrology and nutrient cycling and may conceivably promote or inhibit plant growth and consequently animal production (Byrnes et al., 2018).

The effects of rotational grazing, particularly holistic planned grazing, on animal behaviour has been identified as a research gap (Hawkins et al., 2017). We set up an experimental trial on a working farm in a mesic grassland of the Eastern Cape, South Africa, to test the effects of a range of grazing densities on animal responses, implemented via three management approaches including season-long grazing, four-camp rotation and holistic planned grazing. We predicted that increasing animal grazing density using fencing would cause (1) tighter concentration of animal herds; (2) altered time spent grazing, resting and walking; (3) increased utilisation of available forage; (4) reduced selectivity for palatable patches and plants; (5) increased trampling of dung; and (6) increased animal production per unit area and farm profitability.

2. Methods

2.1. Study site

The Merino Walk experimental trial was located approximately 5 km north of Cedarville, Eastern Cape, South Africa (30° 21′ 8″ S; 29° 3′
29° E) at an altitude of 1440 m above sea level. Half of the trial was located on north-facing slopes covered by East Griqualand Grassland and the other half was located on low-lying flats covered by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands (Mucina and Rutherford, 2006). Dominant grasses include Themeda triandra and Eragrostis plana, respectively. The area is underlain by mudstones and sandstones of the Elliot and Molteno Formations (Mucina and Rutherford, 2006). Flats consist of poorly-drained and nutrient-rich haplic luvisols with high clay contents whereas slopes contain relatively nutrient-poor haplic airesols (Hengl et al., 2014). Long-term (1960–2000) mean annual rainfall and temperature is 760 mm and 15°C (Hijmans et al., 2005), with most rainfall occurring during austral summer months.

2.2. Experimental design

Three grazing management treatments, occupying 219 ha of land on the Merino Walk farm, were initiated as an experimental trial in December 2015. Prior to this, the land had been managed under conservative stocking rates as a commercial cattle and sheep farm. Initial vegetation and soil measurements allowed us to determine how management legacy affected variation across the treatments prior to commencement of the trial (Table A.1), and to express changes relative to these initial measures.

Treatments included season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG) and were deliberately assigned non-randomly to control for watering points, topography and vegetation as far as possible (Fig. A.1). Each treatment had one replicate on a sloped and flat area of the farm respectively, where the sloped area was more suitable for cattle during winter due to reduced frost and lack of flooding. Our study, like many other experimental trials was limited to one treatment replicate due to limited resources. For this reason, we sampled intensively across the farm prior to and during the study. A regularly-spaced sampling grid of points 90 m apart was generated over the farm producing 209 sampling locations which were revisited over time for dung and vegetation sampling. The treatments differed primarily in the number of camp divisions, and consequently the relative grazing densities (Table 1). In SLG grazing, one camp is grazed for an entire growing-season and then cattle are moved to a second camp, with accumulated biomass, for the non-growing season. In FCG, cattle are rotated amongst three camps while one camp is left to rest for an entire year. In subsequent years, the camp allocated to annual rest is the first camp to be grazed, and conventionally this is proceeded by burning (Venter and Drewes, 1969). We chose to exclude burning from this system because of difficulties in distinguishing and comparing fire and grazing behaviour effects across treatments. We recognized that this could bias against plant productivity in the FCG approach relative to working farms using this approach. For this study, HPG refers to a high intensity grazing approach similar to short duration (Tiedeman, 1986), cell grazing (McCosker, 2000), and holistic planned grazing (Savory and Butterfield, 2016). We followed the adaptive management protocol of Holistic Management (HM; Savory and Butterfield, 2016) for the duration of the study and across all treatments. In HM a flexible grazing plan is constructed outlining animal movements between multiple small camps based on forage availability, seasonal temperature and flooding, with the aim of increasing animal densities and thereby increasing even utilisation and reducing overgrazing while increasing animal gain. The farm manager and research team undertook an intensive 3 d training course by an accredited HM trainer familiar with the South African context. This was done in order to adhere to HM principles and follow the correct HM planning procedure. The same trainer oversaw the development and implementation of grazing plans in the first year of the study. Portable electric fencing was employed to construct grazing strips of between one and two hectares in size. All treatments were stocked with year-old Bonsmara-Boran steers at a moderate stocking rate of 0.53 LSU ha\(^{-1}\) yr\(^{-1}\), i.e. similar to the government recommended rate of 0.55 LSU ha\(^{-1}\) yr\(^{-1}\) (Avenant, 2016).

The trial stocked cattle destined for the meat market and was managed as a commercial operation. Stock remained on the trial between 12 and 18 months depending on market-related factors and animal weight gains. Over the duration of the trial, three sets of cattle were introduced and at each intake, individual cattle were randomly allocated to management treatments. Ten of each new herd intake were tagged and monitored for weight gain over the course of their occupancy. Cattle were managed according to livestock agricultural best practices and national guidelines for the care and use of animals (University of Cape Town ethical clearance certificate no. 2016/v14/ HH).

2.3. Herb observations

During Jun 2017 and Jan 2018 we performed behavioural sampling to identify how concentrated or spread-out herds were during grazing, resting and walking behaviours. Grazing behaviour was considered as the act of searching (movement of less than 5 m between bites) for and consuming grass. Walking was defined as a continuous forward movement without grazing. Resting was defined as standing or lying down without consuming food. Observations took place over 2 d in summer and 2 d in winter. Three observers concurrently monitored cattle in a treatment for 2 h recording behaviour every 5 min, and rotated between all treatments. Observers recorded the behaviour and proximity to nearest neighbour of ten individuals in the herd. Proximity to nearest neighbour was estimated at five intervals between 0, 5, 10, 15, 20, > 25 m.

2.4. Triaxial accelerometers

We deployed triaxial accelerometers (Fig. A.2) on randomly selected cattle for 30 d during Jun 2017 and Jan 2018. MicroPython pyboards with triaxial accelerometers were programmed to take recordings of movement along the X-, Y- and Z-axes every 0.5 s. The monitors weighing 464 g were attached alongside the GPS devices (see below) to nylon collars of 7 cm in width, fastened with an adjustable buckle. We

<table>
<thead>
<tr>
<th>Variable</th>
<th>Season-long grazing (SLG)</th>
<th>Four-camp grazing (FCG)</th>
<th>Holistic planned grazing (HPG)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stocking rate (LSU ha(^{-1}) yr(^{-1}))</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
</tr>
<tr>
<td>Number of camp divisions</td>
<td>2</td>
<td>4</td>
<td>70</td>
</tr>
<tr>
<td>Grazing density (LSU ha(^{-1}) d(^{-1}))</td>
<td>1</td>
<td>2.1</td>
<td>36.8</td>
</tr>
<tr>
<td>Grazing period (d camp(^{-1}))</td>
<td>180</td>
<td>21-28</td>
<td>1</td>
</tr>
<tr>
<td>Recovery period (d camp(^{-1}))</td>
<td>180</td>
<td>15-180</td>
<td>60</td>
</tr>
<tr>
<td>Between season rest</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Within season rest</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Adaptive management</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Table 1

Characteristics of three grazing management treatments implemented at the Merino Walk experimental trial. Stocking rate refers to the number of livestock units (LSUs) per hectare of available rangeland, whereas grazing density refers to the number of LSUs per fenced subunit area at any point in time on the rangeland.
successfully retrieved data from 18 of the 22 devices deployed, resulting in an average of 3 replicates per treatment per sampling occasion. At each sampling occasion, the devices collected data for a mean of 15 ± 1 d. During the Jun 2017 deployment, observational measurements of grazing, resting and walking took place to calibrate the accelerometer readings (see below). A mobile phone with a clock synchronous to the triaxial accelerometers was used to record exact timestamps for switches between grazing, resting and walking using CyberTracker (https://www.cybertracker.org/). Each collared individual was observed for at least 120 contiguous seconds in each behavioural state. The post-processing of the raw accelerometer data and calibration with observational data was conducted in R (R Core Team, 2017) following methods outlined in Alvarenga et al. (2016). Briefly, a machine learning Random Forest (RF) model (Liaw and Wiener, 2002) was developed to classify behavioural states from the accelerometer data. The raw X, Y and Z axis values were used to calculate feature vectors specifically designed to classify animal behaviour from accelerometer readings (Campbell et al., 2013). The feature vectors included the signal magnitude, movement variation, energy, entropy, pitch, roll and inclination using formulae described in Alvarenga et al. (2016) for each 5 s epoch. Along with the mean values we also calculated the standard deviation, minimum and maximum for each epoch. This produced forty-four explanatory variables which were used in the RF model to predict the observed behaviour. This data subset was split into 70% for training the model using calibration data (evaluation) and 30% for testing the predictions of the model. The accuracy of the model was assessed by calculating a confusion matrix of the observed and predicted behavioural classes. Finally, the trained model was used to predict behavioural states over the duration of the accelerometer readings.

2.5. Dung counts

At each sampling location (Fig. A.1) trampled and untrampled dung pats were counted in a 10 x 2 m belt transect every six months from January 2016 to January 2018. A dung pat was defined as any intact dung with a diameter greater than 10 cm. Old dung pats which had disintegrated and had no clear boundary were excluded. A trampled pat was considered as one with clear evidence of a cattle hoof print.

2.6. Vegetation patch selectivity

GPS collars were deployed on randomly selected cattle for 60 d on two summer (Jan 2017 and 2018) and two winter (June 2016 and 2017) sampling occasions. GPS devices (Perthold Engineering LCC, Richardson, Texas, USA) were set to log a position every 5 min and attached to nylon belts fastened around the animal’s necks. We deployed enough collars to obtain an average replication of 3 collars per treatment per sampling date. Three devices were placed at a known distance of 10 m to each other and at a range of distances defined by the extent of the point pattern. We used Monte Carlo simulations to derive confidence intervals around the \( L(r) \) curve for a completely random point process (Wiegand and Moloney, 2004). We then plotted the observed \( L(r) \) curve for a GPS point pattern and quantified the deviation of this pattern from randomness as the area between the \( L(r) \) curve and the upper confidence envelope for a random point pattern (Fig. A.4).

Satellite-derived estimates of vegetation quality were obtained using the Google Earth Engine cloud computing platform (Gorelick et al., 2017). The normalized difference vegetation index (NDVI, Tucker, 1979) has been widely used as an indicator of vegetation productivity, quality and vigour in rangelands (Svobay et al., 2013; Ali et al., 2016). We extracted the median NDVI values over the farm from the Landsat 7 Enhanced Thematic Mapper Plus (ETM+ ) dataset at 30 m resolution for the three years prior to the start of the trial. This served as a spatial template of the forage quality distribution. To establish the association between cattle and vegetation quality, we related the kernel ("gaussian") smoothed density of locations to the farm NDVI. For each 30 m Landsat pixel we calculated the GPS point density per animal replicate. To assess how the heterogeneity in vegetation NDVI changed through time under the management treatments, we created annual median mosaics of NDVI for 2015 – 2018. For each annual mosaic, we estimated heterogeneity by assigning to each pixel the standard deviation of the eight neighbouring pixels (Fig. A.5). The initial (2015) measure was calculated from Landsat 7 ETM+ and Landsat 8 Operational Land Imager data after correcting for inter-sensor discrepancies using published calibration coefficients (Roy et al., 2016). For 2016, 2017 and 2018 we used Sentinel 2 Multi Spectral Instrument, Level-1C data (Drusch et al., 2012) because this has a higher spatial resolution (10 m) and would thus capture vegetation heterogeneity in more detail. To compare treatments whilst accounting for the initial or baseline heterogeneity, we calculated the trend in heterogeneity as the slope of the linear trend line between 2015 and 2018 for each pixel over the farm. We then sampled this trend image at each of the 209 sampling locations.

2.7. Vegetation utilisation

After clipping GPS locations to camp boundaries and isolating those defining grazing behaviour, we extracted a random subset of 1000 points per GPS collar. To estimate the percentage of forage space utilized by the cattle we created a 5 m buffer around each location (Fig. A.4), representing the potential ‘footprint’ of the animal’s consumption at that point. Cattle that repeatedly visit the same grazing patch will use less of the available forage space than cattle that seldom return to the same grazing patch. Given that the cattle in different treatments occupied camps of slightly different sizes, we standardized the number of randomly extracted points to equal 66 points per hectare. This value was the maximum number of random points per hectare that could be extracted across all collars based on the available sample sizes. We calculated utilisation as the percentage of the camp covered by the footprint of buffered GPS points.

2.8. Dietary selection

Vegetation in camps occupied by cattle within the preceding 6 months were sampled in Jan (2017 and 2018) and Jun (2016 and 2017) for bite marks. At each sampling location (Fig. A.1), a Levy Bridge (Levy and Madden, 1933) was used to sample ten descending points spaced 25 cm apart. At each point, the plant species were identified and height, basal cover, and percentage of leaves with bite marks
Table 2

Animal responses (means ± standard errors) for three grazing management treatments, season-long grazing (SLG), four-camp grazing (FCG) and holistic planned grazing (HPG), implemented at the Merino Walk experimental trial. Results from linear mixed-effects models are reported for individual treatment, season, and vegetation type terms, along with interaction terms, where they applied. Vegetation types constitute flats and slopes characterised by low-lying Eragrostis plana dominated by Mabela Sandy Grassveld and Eastern Temperate Freshwater Wetlands, and higher-lying Themeda triandra dominated by East Griqualand grasslands, respectively. The integrated measure of complete spatial randomness is the area between the L(r) curve for observed GPS point pattern and the upper confidence envelope for a random point pattern, where L(r) is a transformed Ripley’s K-function. The larger the area, the greater the deviation from randomness. The change in NDVI heterogeneity is the slope of the linear trend line between 2015 and 2018 and is represented in heterogeneity units per decade instead of year to reduce decimal values.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>SLG</th>
<th>FCG</th>
<th>HPG</th>
<th>Significance (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to neighbour (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>6.8±</td>
<td>± 0.5</td>
<td>5.0±</td>
<td>± 0.5</td>
</tr>
<tr>
<td>Resting</td>
<td>7.5 ±</td>
<td>± 0.5</td>
<td>6.2±</td>
<td>± 0.5</td>
</tr>
<tr>
<td>Walking</td>
<td>7.6±</td>
<td>± 1.3</td>
<td>6.2±</td>
<td>± 1.3</td>
</tr>
<tr>
<td>Activity budget (% day)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazing</td>
<td>36.4±</td>
<td>± 0.7</td>
<td>36.8±</td>
<td>± 0.7</td>
</tr>
<tr>
<td>Resting</td>
<td>54.5±</td>
<td>± 1.0</td>
<td>53.1±</td>
<td>± 0.8</td>
</tr>
<tr>
<td>Walking</td>
<td>8.9±</td>
<td>± 0.5</td>
<td>10.6±</td>
<td>± 0.5</td>
</tr>
<tr>
<td>Spatial forage utilisation (%)</td>
<td>15.6±</td>
<td>± 0.1</td>
<td>16.0±</td>
<td>± 0.9</td>
</tr>
<tr>
<td>Forage bite mark utilisation (%)</td>
<td>30.1±</td>
<td>± 11.6</td>
<td>33.1±</td>
<td>± 5.5</td>
</tr>
<tr>
<td>Selectivity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Patch scale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Integrated spatial</td>
<td>1514.0</td>
<td>± 366.1</td>
<td>2068.0</td>
<td>± 284.5</td>
</tr>
<tr>
<td>randomness score</td>
<td></td>
<td></td>
<td></td>
<td>± 1218.1</td>
</tr>
<tr>
<td>Change in NDVI heterogeneity</td>
<td>0.9±</td>
<td>± 0.8</td>
<td>0.2±</td>
<td>± 0.3</td>
</tr>
<tr>
<td>(units decade⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td>± 1.0</td>
</tr>
<tr>
<td>Plant scale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bite marks (% of plants)</td>
<td>21.8±</td>
<td>± 5.7</td>
<td>18.7±</td>
<td>± 6.0</td>
</tr>
<tr>
<td>Avoided</td>
<td>4.4±</td>
<td>± 4.4</td>
<td>5.6±</td>
<td>± 2.2</td>
</tr>
<tr>
<td>Faecal DNA (% of plants)</td>
<td>60.3±</td>
<td>± 25.8</td>
<td>60.6±</td>
<td>± 9.7</td>
</tr>
<tr>
<td>Avoided</td>
<td>4.8±</td>
<td>± 3.1</td>
<td>6.1±</td>
<td>± 4.3</td>
</tr>
<tr>
<td>Dung trampling (pats ha⁻¹)</td>
<td>407.9±</td>
<td>± 212.5</td>
<td>347.1±</td>
<td>± 63.1</td>
</tr>
<tr>
<td>Dung produced (pats ha⁻²)</td>
<td>913.8±</td>
<td>± 109.3</td>
<td>900.2±</td>
<td>± 78</td>
</tr>
<tr>
<td>Step counts (steps m⁻¹)</td>
<td>8.9±</td>
<td>± 1.2</td>
<td>14.3±</td>
<td>± 3.8</td>
</tr>
<tr>
<td>Animal production (kg day⁻¹ ha⁻¹)</td>
<td>0.2±</td>
<td>± 0.02</td>
<td>0.2±</td>
<td>± 0.0</td>
</tr>
</tbody>
</table>

Significance is indicated at p < 0.05a and p < 0.001a. For direct treatment effects, significant differences are indicated with letters.

recorded. To assess diet selectivity, we first established a forage palatability rating for the available plant species. We used Jacob’s (1974) index of selection, Dr = (n − p) / [(n + p1) − 2np], where n and p are the proportions of plant species i in diet (from bites) and in vegetation, respectively. Each forage species was assigned an index score which immediately frozen at 20 °C. Samples for summer (Jan to Mar) and winter (Apr to Jun) were then blended together, oven dried at 60 °C, milled to a fine powder and sent to Inqaba Biotechnical industries (Pretoria, South Africa) for DNA extraction and sequencing. The genomic DNA was extracted from samples using the ZymoBIOMICS (Zymo Research, USA) extraction kit. A portion of the chloroplast trnL intron was amplified from each DNA sample using the c and h trnL intergenic primers. Amplicons libraries were purified using the Agencourt AMPure XP bead (Beckman Coulter, USA) protocol. Library concentration was measured using the NeoBx Library quant kit (New England Biolabs, USA) and quality validated using Agilent 2100 Bioanalyzer (Agilent Technologies, USA). The samples were pooled in equimolar concentrations and diluted to 4 nM based on library concentrations and calculated amplicon sizes. The library pool was sequenced on a MiSeq using a MiSeq Reagent kit V2 300 cycles PE (Illumina, USA). The final pooled library was at 9 pM with 30% PhiX (nucleotide library derived from the well-characterized bacteriophage PhiX genome) as a control for run quality. The DNA sequence data was analysed by Jonah Ventures (Colorado, USA) following methods outlined in Craine et al. (2016) yielding operational taxonomic unit (OTU) counts from the GenBank database. The top 50 OTU counts per sample were converted to proportions of total count and the selectivity index calculated using the same protocol outlined for animal bites.

2.9. Animal production and profitability

The ten randomly tagged cattle per treatment were weighed monthly. Auction sales records and purchase invoices for set up infrastructure (fencing and water) and running costs (labour, feed, fuel and electricity) were used to calculate gross income and expenditure for each management treatment. The gross income and expenditure from the first two years was used to forecast annual net profits over a five-year time horizon. Using the forecast figures, we calculated the 5-year return on investment (ROI) as the net returns as a percentage of the cumulative cost of investment (E): $ROI = \frac{\text{Net returns}}{E} \times 100$, where G is the cumulative gross income.
2.10. Statistical tests

To establish whether grazing management approach was a significant predictor of cattle behaviour, we used linear mixed-effects modelling (Harrison et al., 2018) with the ‘lme4’ package in R (Bates et al., 2014). Grazing management treatment was considered a fixed effect and variables designating non-independence of replicates (e.g. repeated measures) were considered random effects. In animal location, behaviour and production data each animal was considered a replicate. The GPS point complete spatial randomness statistics were calculated for each season, and thus season index was considered as the random intercept. For the model explaining time spent under different behavioural states, we calculated the proportion of each 24-hour day spent in each behavioural state and, in this case, day index was assigned to a random intercept. Proportional response variables were left untransformed if the distribution of model residuals met the assumptions of linear models. The animal production data were collected monthly, and thus month was assigned to the random intercept.

For dung trampling and plant selectivity data, camp-level averages were calculated and added to a model that included season and camp (Fig. A1) as random effects. Data from scan sampling of herd behaviours were aggregated into morning and afternoon samples which were treated as pseudo-replicates and assigned to a random intercept in the model.

3. Results

3.1. Cattle behaviour

Cattle remained at an average distance of 4.8 ± 2.6 m (mean ± SE) from one another regardless of treatment and behaviour (p = 0.658, data not shown). We found HPG cattle grazed closer together than SLG but not FCG cattle (Table 2), whereas management did not affect herd densities during resting or walking. Cattle were more dispersed when walking during winter compared to summer (Table 2). The RF model correctly classified the activities grazing, resting and walking from triaxial accelerometer readings 91%, 95%, and 84% of the time (Table A2). Grazing management did not affect how much time was spent on each behaviour (Table 2). Cattle spent more time grazing under HPG than FCG but not SLG in winter, while in summer there were no differences between treatments (Table 2). Grazing behaviour followed a diurnal pattern across all treatments (Fig. 1). Grazing commenced at ca. 06h00 and ceased at ca. 20h00 with a small grazing bout, exaggerated during winter, around 23h00. A short cessation of grazing at mid-morning during summer and at midday during winter coincided with observed rumination activity. Cattle spent more time grazing and less time resting during summer compared to winter (Table 2) and cattle appeared to walk in between grazing and resting throughout the day (Fig. 1).

Based on behavioural observations, cattle took an average of 11 ± 2 steps per minute and trampled 23% (378 ± 114) of the 1658 ± 115 dung pats found per hectare. There was no difference in the step rate, the number of dung pats produced or trampled between grazing management treatments (Table 2). This was corroborated by accelerometer recordings of walking and grazing behaviour which showed no management effect on the time allocated to these behavioural states (Fig. 1, Table 2). Both walking and grazing require steps and thus one would expect no difference in dung trampling between treatments.

3.2. Vegetation utilisation and selectivity

The percentage of available plant foliar cover with evidence of grazing bite marks, a proxy for forage utilisation, was 33% overall and did not differ between treatments (Table 2). The alternative measure of spatial forage utilisation using GPS points revealed that cattle utilised only 0.5% more of their grazing camps in summer (16.3 ± 0.06) relative to winter (15.8 ± 0.06%) and that cattle utilized more of available forage area under FCG compared to SLG, but HPG was not different from either (Table 2). Treatment and season both affected the clustering of cattle GPS points, measured by the integrated spatial randomness score (SRS), at the patch scale (Table 2). The clustering of GPS points during in winter was lower under HPG (1125 ± 270 SRS) relative to FCG (2590 ± 392 SRS) but not SLG (1189 ± 832 SRS), and in summer there was no treatment effect (Table 2). Thus, assuming that the clustering of GPS points is a good proxy for selective grazing behaviour, we found that HPG had no effect on reducing patch selectivity relative to SLG but was more effective than FCG. In addition, when accounting for the existing spatial variation in forage NDVI, we found a treatment effect on selection for patches of high NDVI. In both summer and winter, SLG cattle GPS point densities were positively correlated to vegetation NDVI (Fig. 2). This correlation was less apparent in FCG and HPG grazing treatments. Consistent with the increased selection for patches of high NDVI under SLG, we found that SLG increased the spatial heterogeneity of NDVI, whereas HPG reduced it (Fig. 3). The effect of HPG on reducing NDVI heterogeneity was significantly different to SLG but not to FCG (Table 2). FCG and HPG reduced heterogeneity in 2016 relative to the baseline (see dip in Fig. 3) presumably due to homogenous grazing patterns at the trial outset, whereas SLG further entrenched existing baseline heterogeneity in 2016. The large variation in SLG heterogeneity is itself a further indication of heterogeneity at the landscape scale.

At the plant scale, the extent to which cattle selectively grazed species did not differ between treatments (Table 2). Cattle displayed positive selection for a variety of forbs and grasses including *Eragrostis capensis*, *Andropogon appendiculatus*, *Harpochloa laxa*, *Sporobolus africanus* and *Setaria incrassata* (Fig. A.6). Some of the strongly avoided species included *Elionurus muticus*, *Heteropogon contortus* and *Aristida junceiformis*. The proportion of available preferred and avoided plant species bitten or found in faecal DNA did not differ between treatments (Table 2). Indeed, when expressed as a continuous variable, the selectivity index of forage species was positively correlated to the proportion utilised across all treatments (Fig. 4). This was true for data from both bite mark sampling and faecal DNA.

3.3. Animal production and profitability

Average daily weight gain for all cattle was 0.2 ± 0.02 kg day⁻¹ ha⁻¹. Animal weight fluctuations tracked the seasonal vegetation productivity cycle (Fig. 5), differing significantly between seasons (Table 2). In summer cattle gained 0.4 ± 0.02 kg day⁻¹ ha⁻¹ whereas in winter they lost 0.1 ± 0.02 kg day⁻¹ ha⁻¹. Over the duration of the trial weight gain did not differ between management treatments (Table 2), although HPG cattle from the first intake underperformed relative to FCG and SLG cattle during the winter months (Fig. 5). During the second intake, SLG cattle outperformed HPG and FCG cattle over summer months. These group-specific differences disappeared when averaging across all groups. Revenue generated from two years of auction sales was 81, 80 and 79 $ ha⁻¹ yr⁻¹ for SLG, FCG and HPG treatments, respectively. The HPG approach was the most expensive to set up (Fig. 6A). Fencing and water infrastructure exceeded that of FCG and SLG. The excess running costs under HPG relative to SLG and FCG constituted fuel, labour and electric fencing. After accounting for expenses, we forecast SLG, FCG and HPG management approaches to start making a net profit after 20, 24 and 48 months, respectively (Fig. 6B). The return of investment for SLG (116%) over five years is predicted to be substantially higher than that for FCG (70%) and HPG (9%).

4. Discussion

Increasing animal densities with rotational grazing management practices (i.e. FCG and HPG) did not increase cattle productivity or
profitability relative to low-density SLG in a mesic grassland of South Africa. We found that HPG did not affect cattle herding proximities, time spent grazing, forage utilisation, forage species selection, or dung trampling. We did, however, find evidence to support the hypothesis that increasing animal densities reduces the selection for palatable vegetation patches within a grazing camp, and that this can reduce the spatial heterogeneity in vegetation vigour over time.

A striking finding was that constraining cattle with electric fencing did not cause cattle to concentrate more tightly relative to cattle that are allowed to range freely in a camp when averaging across all behavioural states. This is a key assumption of high density grazing practices (Brunson and Burritt, 2009; Savory and Butterfield, 2016). SLG and FCG cattle performed all activities at similar distances to neighbours compared to HPG cattle although HPG cattle did graze at greater proximities than SLG cattle. These results might vary considerably over time depending on the shape and size of grazing camps occupied and thus more intensive sampling effort might yield different outcomes. Studies on wild herbivore sociality have found that intraspecific competition for forage increases with herd density (Molvar and Bowyer, 1994). This competition may drive individuals to spend more time grazing or increase intra-specific aggression and thereby reduce time spent grazing (Krebs and Davies, 2009). In African rangelands, when animal densities were increased through active herding, cattle benefitted through enhancing foraging efficiency because they spent less time actively searching for forage and thereby expending energy (Odadi et al., 2018). Given that there was no difference in observed herding densities in our study, it follows that there were unlikely to be differences in time allocated to grazing behaviour. Indeed, data from triaxial accelerometers revealed no management effect on time allocated to grazing, resting or walking. A study testing Holistic Resource Management (Savory, 1983), an earlier version of holistic planned grazing, also found no effect on cattle behavioural patterns on an experimental range in Wyoming, USA (Hart et al., 1993). Consequently, grazing management approach produced no effect on the cattle utilisation of available forage and confirming this, animal weight gain was unaffected. Similarly, cattle in our study spent similar time grazing, utilized the same amount of available forage and gained similar weight across all three management approaches. Other studies have even
reported declines in animal production (Worthington, 1984; Anderson, 1988; McCollum III et al., 1999; Badgery et al., 2017) and conception rates (Worthington, 1984) under high density grazing due to increased stress from continuous movements and the rapid depletion of pasture and restrictions in diet quality associated with mature forage at the time of grazing. Our results show no such effect possibly because all cattle spent the same proportion of time walking.

Another mechanism through which walking was proposed to
influence animal production is hoof impact on soil and vegetation (Savory and Butterfield, 2016). Trampling of dung and urine into soil is predicted to enhance nutrient and water cycling, vegetation cover and consequently animal production. The number of trampled dung pats, steps taken, and time spent walking under HPG did not differ to FCG or SLG in our trial. Previous experimental trials in the USA have found that increasing paddock numbers may reduce (Hepworth et al., 1991), increase (Walker and Heitschmidt, 1986) or have little effect (Hart et al., 1993) on distances walked and ground trampled by cattle. Despite the diverse grazing management effects on trampling, rotational grazing enhances soil organic carbon and reduces bulk density relative to year-long continuous grazing (Byrnes et al., 2018), although whether the same is true for season-long continuous grazing is not clear. Practitioners of holistic planned grazing suggest that increased hoof impact and trampling can be induced by placing supplemental feed cubes in a field or using active herding with horses and dogs (Savory and Butterfield, 2016), although whether this will be beneficial for soil hydrological processes has been debated in the literature (Briske et al., 2008). It is possible that rotational grazing may enhance the trampling effect when a threshold grazing density is exceeded, highlighting the scope for testing a broader range of animal densities.

A common criticism of experimental trials is that they do not have sufficient herd sizes or densities to induce the “herd effect” (see comments in Venter, 2017). Discerning what grazing densities or herd sizes constitute high density grazing is difficult because it varies across socio-ecological contexts depending on factors like vegetation productivity and decision-making paradigms (Mann and Sherren, 2018). Further, there are virtually no recommendations for specific grazing densities in training materials produced by well-known holistic planned grazing organisations apart from phrases like “Maximum density for minimum time.” (The Global Savory Network, 2015; Savory and Butterfield, 2016). A global meta-analysis found that no studies on variants of high density grazing implemented grazing densities exceeding 12 LSU ha$^{-1}$ (Hawkins, 2017). Our trial took place on a working farm and implemented HPG with average grazing densities of 36 LSU ha$^{-1}$. This was characteristic of high density grazing practitioners in the area according to the local farmer (Nel, G. pers comm 2016) and accredited Holistic Management trainer (Lambrechts, J. pers comm 2016).

The animal behaviour most commonly associated with high density grazing in the literature is reduced selective foraging under high animal density. Our results support this proposition that concentrating animals and rotating grazing pressure over the farm reduces the selection for palatable vegetation at the camp scale. Although HPG did not distribute grazing pressure more randomly than SLG in summer or winter, HPG cattle were restrained from focussing on more palatable (or more green) vegetation patches relative to SLG. SLG cattle were able to spend more time in areas of high vegetation greeness/vigour. A rotational grazing trial in Australia also found that high intensity rotations prevented sheep from selecting quality forage and in this case it resulted in a decline in per head productivity (Badgery et al., 2017). In European
Fig. 5. Monthly cattle weights for three grazing management treatments over the duration of the Merino Walk experimental trial. Each group of lines (differentiated by line styles) represents a set of ten oxen which were bought onto the farm and monitored for weight gain before being sold. Lines and ribbons reflect a loess regression and 95% confidence intervals. Mean monthly normalised difference vegetation index (NDVI) values over the farm, derived from Landsat satellites, are plotted above to indicate the seasonality of vegetation production.

Fig. 6. Farm expenses (A) and profitability (B) of the Merino Walk experimental trial. Expenses are separated into set up costs incurred at the initiation of the trial, and running costs, incurred on an annual basis. Using cattle sales records from the first two years of the trial, combined with cumulative expenses, we forecast the return on investment over five years for each management treatment.
(Probo et al., 2014) and American (Charles et al., 1985) pastures rotational grazing has also been shown to reduce the patchiness of grazing behaviour, however others have found that the location of watering points, topography and stocking rates override any effect of rotational grazing (Launchbaugh and Howery, 2005; Soder et al., 2009; Bailey and Brown, 2011). Because we controlled for these variables in our trial, we were able to detect the effect of manipulating animal densities. To our knowledge, our study is the first experimental trial to report on changes in the heterogeneity of vegetation in response to high density grazing. Using satellite data, we provided evidence that even over three years, high density grazing reduced the spatial heterogeneity of vegetation vigour (NDVI), probably because cattle were prevented from over-grazing palatable patches and further entrenching existing patchiness. The land allocated to HPG had higher NDVI heterogeneity at the commencement of the trial compared to FCG but not SLG (Table A.1). Thus, the magnitude of treatment differences might have been reduced or increased given equal starting points, nevertheless, assuming the trends persist, over the long-term HPG could possibly prevent bare patch formation (Throw, 1991; Fuls, 1992). Alternatively, homogenizing vegetation might open up a niche vulnerable to invasion by non-palatable herbaceous (Milton, 2004) and woody (O’Connor et al., 2014; Venter et al., 2018) species.

Recent advances in the understanding of natural disturbance patterns in rangelands suggest that managing for patchiness and heterogeneity is beneficial for biodiversity and productivity (Fuhlendorf et al., 2017). The use of fire and herbivory to create diversity in vegetation structure and function over the landscape is known as pyric herbivory (Fuhlendorf et al., 2009). This heterogeneity can provide niches for a greater variety of species to occupy, thereby increasing the resilience of rangeland to stress such as drought (Briske et al., 2017), and benefitting ranchers that enter into incentive-based land stewardships where the maintenance of biodiversity is desired (Reed et al., 2015). Furthermore, the repeated grazing of burned patches can, along with nutrient import from dung, maintain grass in palatable vegetative states that constitute grazing lawns (Hempson et al., 2015; Porensky and Veblen, 2015), a common occurrence in African savannas. Here grass communities can convert within a few years to stoloniferous, low-growth forms with low C:N ratios, sustaining palatable forage for livestock (Donaldson et al., 2017) and wild herbivores. Although fire was not included as a factor in our trial, GPS collar and satellite NDVI data showed that SLG cattle repeatedly visited palatable patches over the grazing camp. This appeared to increase the patchiness of vegetation vigour over time, a result possibly akin to that achieved with pyric herbivory. Further, allowing cattle to select for palatable, more nutritious forage may explain why SLG cattle gained more weight than HPG cattle over several months of the year.

The influence of management practice on cattle selection for palatable vegetation at the patch scale was not mirrored at the plant scale. Both bite mark sampling as well as faecal DNA analysis revealed that cattle actively selected for palatable forbs and grasses, and that increasing grazing densities did not reduce this selectivity. Assuming this remains consistent over time, HPG is not projected to result in a more favourable species composition (more palatable species) over the long term compared to forms of low density grazing. Indeed, a 24-year simulated rotational grazing trial showed no effect of grazing treatment on floristic composition in South Africa (Morris and Tainton, 1996). Thus, this contradicts a central tenant in high intensity rotational grazing (Briske et al., 2008). However, Odadi et al. (2018) found that increasing animal densities through herding (instead of fencing) reduced the selectivity for palatable grass species in savanna. Similarly, a study in more arid rangelands of the Karoo, South Africa, found that herded sheep consumed less annual herbs and more non-succulent shrubs than free-ranging sheep (Samuels et al., 2016). Herding at large spatial scales moves animals across a range of vegetation communities and prevents them from lingering in any one type. It is possible that the vegetation species communities on our farm, a grassland, are more evenly distributed over space relative to those in Karoo and savannas and thus forcing animal movements over space did little to change the diversity of their dietary intake. This may also be the case for other experimental trials revealing no rotational grazing effects on plant species selectivity (Kirby et al., 1986; Kreuter and Tainton, 1988; Olson and Malechek, 1988). Herbivore dietary choices will always be largely determined by factors intrinsic to plant physical and chemical structure that characterise nutritional status and digestibility (Bailey and Brown, 2011), however distributing grazing across plant communities at the landscape scale can reduce over utilisation of palatable species vulnerable to overgrazing.

It is important to note that the dynamics of cattle behaviour change over spatial scales (Bailey et al., 1996; Soder et al., 2009) and the results of our study might not be directly applicable to other management contexts. For example, in more arid rangelands where stocking rates are lower and grazing areas are larger, the effect of fencing on increasing spatial forage utilisation and reducing overgrazing of patches may be enhanced. Furthermore, our study included only steers. Social hierarchies are important determinants of grazing patterns (di Virgilio and Morales, 2016d) and our results may have differed with herds constituted of breeding animals or a diversity of age classes. Cow-calf operations, where conditioning to electric fencing is maintained through multiple generations, as opposed to fattening operations, where new animals are bought onto the farm every year might prevent possible drops in production caused by stress (Brunson and Burritt, 2009). Incorporating mixed herds with a diversity of functional guilds may diversify the utilisation of available plant taxa (Hempson et al., 2017; Venter et al., 2017). For example, introducing browsers such as goats with grazers in savannas can mitigate woody plant encroachment (Venter et al., 2018). Finally, replicating this study in both similar and different vegetation types will improve the scope of our findings, based as they are on a large-scale trial on a working commercial farm with associated limitations on replication and randomization in the design. Despite this we find that our conclusions here are well founded because our results agree with the literature where there was commonality and we reduced limitations on experimental design by having similar vegetation and soil characteristics between treatments at the start of the trial, by sampling intensively, and by accounting for pseudoreplication using a mixed modelling approach.

5. Conclusion

Our results suggest that adopting rotational grazing practices or variants of high density grazing do not enhance animal productivity relative to season-long continuous grazing in mesic grasslands over the short term. This has significant economic consequences given the capital investment in setting up electric fencing and watering infrastructure for high density grazing. An economic analysis, although context-specific, revealed that conventional approaches like SLG and FCG will become profitable after one to two years, whereas HPG will take around four years to offset the higher setup and maintenance costs. Over the long term this may change, especially if vegetation heterogeneity becomes so entrenched under SLG that it leads to rangeland degradation and declines in animal production. Managers who wish to homogenize grazing over space by adopting rotational grazing might consider reducing infrastructure costs by replacing the function of fencing with active herding, especially in rural African rangelands where traditional herding activities have played a functional role in savanna ecosystems for millennia (Marshall et al., 2018). Alternatively, managers who wish to enhance vegetation heterogeneity and possibly initiate the formation of grazing lawns might consider adopting SLG which, in combination with fire, commonly used in FCG, may enhance biodiversity.
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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.11.023.

References

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