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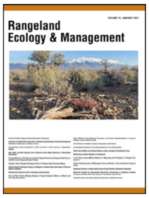

Original Research

Informing the Grazing Debate With Empirical Data on Black Wildebeest (*Connochaetes gnou*) Patch Use

Steven McGregor[1,*], Joris P.G.M. Cromsigt[1,2], Mariska te Beest[1,3], Graham I.H. Kerley[1]

[1] *Centre for African Conservation Ecology, Nelson Mandela University, Gqeberha, 6031, South Africa*
[2] *Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, 901 83, Sweden*
[3] *Utrecht University, Copernicus Institute of Sustainable Development, 3584 CB, Utrecht, the Netherlands*

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ABSTRACT

High-density short-duration grazing (SDG) is widely suggested to increase productivity. Among various SDG practices, the most widespread and popular, “holistic grazing,” claims to mimic the movement patterns of wild African ungulate herds to improve rangeland health and promote biodiversity. However, this claim has rarely been empirically tested. Focusing on Karoo Escarpment Grasslands in the eastern Karoo, South Africa, we compared patch use patterns of black wildebeest (*Connochaetes gnou*) in a continuously grazed wildlife system with cattle paddock use on farms implementing SDG management in the same landscape. Camera trap data revealed heterogeneous wildebeest patch use over the 26-mo sampling period, with wildebeest consistently using some patches more intensely than others. Mean intensity of patch use by wildebeest varied with a factor of 10, from 0.05 LSU · ha^{-1} · day^{-1} to 0.51 LSU · ha^{-1} · day^{-1} across patches. The relative difference in mean intensity of paddock use among farms ranged across a similar magnitude from $<$ 0.01 to 0.18 LSU · ha^{-1} · day^{-1} for least to most intensely grazed paddocks, respectively. Grazing durations in wildebeest patches ranged from 3-15 d (mean = 8 d), compared to the range of 3-60 d (mean = 18 d) for cattle. Intense grazing periods in wildebeest patches ranged from 0 to 2 d (mean = 1 d) and from 1 to 30 d (mean = 7 d) across cattle farms. The greatest difference was between rest intervals, lasting from 1 to 5 d on average across wildebeest patches, compared to 60–365 d across cattle farms. Our findings suggest that SDG systems prevalent in Karoo Escarpment Grasslands differ from the patch use patterns of black wildebeest in most aspects. These findings add to growing literature on grazing behavior of wild herbivores, and effectively contrasts these patterns with SDG cattle farming practices in the same landscape.

Introduction

There is much debate globally over the efficacy of various grazing strategies with respect to improving rangeland heath and forage quality (Briske et al., 2011; Roche et al., 2015; di Virgilio et al., 2019). Recently there has also been an increasing emphasis on grazing strategies that promote soil carbon sequestration and reduce greenhouse gas (GHG) emissions in the face of climate change (Godde et al., 2020; Wang et al., 2021). This has become vital as grassland transformation and overstocking to meet the rising demands of a growing human population have caused further land degradation, including soil erosion (Neke and Du Plessis, 2004), and may contribute to increased GHG emissions (Wang et al., 2021).

Since the start of the century there has been rising interest in managing livestock herds such that their grazing patterns resemble those of wild herbivores (Fuhlendorf and Engle, 2001; Cingolani et al., 2014; Gordon et al., 2021). This approach is motivated by evidence that the dynamic grazing by wild herbivores promotes soil health, grass productivity, and carbon storage (Schmitz et al., 2014; Cromsigt et al., 2018; Schmitz et al., 2018). It is also motivated by a sense that rangeland plant communities have co-evolved with indigenous grazers and that mimicking these grazer-vegetation relationships will maintain or improve rangeland biodiversity and functioning (Cingolani et al., 2014). Holistic management (HM), a form of rotational grazing management developed by Allan Savory, seeks to do just that (Savory and Butterfield, 1999). Globally embraced as a ’silver bullet’ for rangeland management, HM

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[*] Correspondence: Steven McGregor, MSc, Centre for African Conservation Ecology, Nelson Mandela University, Gqeberha, 6031, South Africa
E-mail address: s214045560@mandela.ac.za (S. McGregor).

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employs high-density short-duration grazing (Savory and Butterfield, 2016; Franke and Kotzé, 2022; Hawkins and Cramer, 2022). Although other terms like holistic planned grazing and regenerative grazing management are used to describe HM, along with different types of rotational grazing that closely resemble HM practices (e.g., cell grazing, mob grazing, adaptive multi-paddock grazing and high-density short-duration grazing, amongst others), the underlying philosophy remains consistent. Both HM and these other high-density short-duration rotational grazing practices aim to mimic the spatiotemporal dynamics of wild herbivore grazing patterns (Franke and Kotzé, 2022). This involves stocking paddocks at high livestock densities to facilitate intense, nonselective grazing pressure over a short time period, followed by an extended rest interval where vegetation is allowed to recover (Lawrence et al., 2019). Throughout this manuscript, we collectively refer to these forms of rotational grazing management as "short-duration grazing" (SDG).

It has been well-documented that the densities of wild ungulates are highly variable in space and time, with large-scale movement across the landscape being either a seasonal migration (i.e., movement between widely separated seasonal ranges) or a nomadic movement in search for better forage (i.e., an opportunistic response as resource availability changes) (Skinner, 1993; Owen-Smith et al., 2020). While migrations and nomadic movements are limited to specific regions globally, occurring at the scale of hundreds of kilometers (Owen-Smith et al., 2020), most ungulates exhibit dynamic spatiotemporal variations in patch use at a much smaller scale. These smaller-scale movements and patch use patterns are prevalent in wild herbivore-dominated systems globally, unlike contemporary migrations (Morrison et al., 2021). These smaller-scale movements and patch use patterns are largely driven by a range of abiotic and biotic factors, including thermoregulation, distance to water, food quality and quantity, competition, and predator avoidance (Valeix et al., 2008).

Principles underlying short-duration grazing originated from observations of natural ecosystems such as migratory herds of ungulates in tropical and subtropical African grasslands and savannas (Savory and Parsons, 1980; Savory, 1983). The best-known example is the mass migratory herds of blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), and Thomson’s gazelle (*Eudorcas thomsonii*) that migrate across the Serengeti-Masai system in East Africa seasonally (Franke and Kotzé, 2022). These (and other) ungulate migrations happen over large distances (100s of km), where there is a distinct difference in precipitation and productivity between wet and dry season ranges of the migrating species (Owen-Smith et al., 2020) – a scale at which it is not feasible to rotate livestock across paddocks in short bouts. It should therefore be more important to compare the spatiotemporal grazing patterns of wild ungulates at a finer scale than these migrations, more specifically at a realistic livestock farm scale, and use this to inform grazing management practices in the same landscape.

In regions where large migratory herds are absent, landowners could potentially use the dominant free-roaming ungulate species’ patch use patterns to guide their livestock management practices. Here we use the black wildebeest (*Connochaetes gnou*), an endemic southern African ungulate, as a model system to illustrate this point. Historically black wildebeest ranged across much of the South African interior - in contrast to the blue wildebeest (*C. taurinus*). The latter was historically distributed across savannas in the north-east of South Africa and further north into Africa, with some overlap of the two species in the Free State (Boshoff and Kerley, 2013). Throughout their distribution range, black wildebeest (hereafter referred to as wildebeest) are restricted to open grassland habitats (Von Richter, 1971). In the eastern Karoo region where the present study was conducted, black wildebeest are (and has historically been) a dominant grazer in high-altitude open grassland systems (Boshoff and Kerley, 2015). Because of their similarities with cattle, including digestive morphology (Voeten and Prins, 1999) and reliance on the same food and space resources, black wildebeest serve as a model species for comparison with short-duration cattle grazing regimes in the same region. Many farmers in the region are adopting short-duration grazing in an attempt to increase grassland productivity and livestock production (Keay-Bright and Boardman, 2007; McManus et al., 2018), but it remains unclear if these practices do indeed reflect the grazing patterns of wild ungulates in the region.

To our knowledge, there are no studies that have directly compared short-duration grazing practices of livestock with the spatiotemporal grazing patterns of wild grazers, particularly in the same system. To that extent, the claim that short-duration grazing mimics wild grazer patterns of use remains unsubstantiated by empirical data (Franke and Kotzé, 2022). The aim of this study was to explore the extent to which short-duration grazing mimics wild grazer patterns. Specifically, we compare the spatiotemporal grazing patterns (intensity and duration of use and rest periods) of black wildebeest with those of short-duration cattle grazing regimes within the same habitat and landscape. Due to the selective grazing nature of wildebeest (Mariotti et al., 2020) and the abundance of grasses that remain palatable throughout the year in our study system (De Fortier et al., 2014), we hypothesized that wildebeest use the same patches of vegetation throughout the year. This creates a range of intensity of use, where favored patches are expected to have a higher proportion of intensely-used days compared to less favored patches. If short-duration grazing patterns in the region mimic the dominant wild grazers, farmers should rotate their cattle through paddocks in similar ways.

Materials and Methods

Study area

The study area was located in the eastern Karoo of South Africa, between the towns of Murraysburg in the west, Middelburg to the north, Cradock to the east and Pearston in the south. Within that study area, we focused on Karoo Escarpment Grasslands – occurring at elevations over 1 100 m (Mucina et al., 2006). Average daily temperature ranges between 11.5 and 23.5°C, with the warmest days occurring between December and February (Van Cauter et al., 2005). Karoo Escarpment Grasslands receive between 300 and 580 mm of precipitation on average each year, experiencing two peaks in rainfall during early austral autumn (March) and late spring/early summer (November–December). Rainfall increases from the west towards the east, and with increasing altitude (Mucina et al., 2006). Karoo Escarpment Grasslands typically have shallow soils and the geology consists of sand- and mudstones of the Beaufort Group (Karoo Supergroup), with doleritic intrusions (Mucina et al., 2006).

Livestock production, particularly cattle and sheep, is the dominant land-use in the study area (Masubelele et al., 2015), with recommended stocking rates ranging between 0.07 and 0.08 LSU $\cdot$ ha^{-1} (DAFF, 2018). These high-altitude Karoo Escarpment Grasslands are dominated by grasses from the genera *Aristida*, *Eragrostis*, *Elionurus*, *Helictotrichon*, *Melica*, *Tetrachne*, *Tribolium* (formerly *Karroochloa*), *Themeda* and *Tragus* on top of plateaus, in addition to low shrubs, and the grass *Merxmuellera disticha* on the slopes (Mucina et al., 2006).

Study site

Black wildebeest patch use data were collected at the Kondoa Plateau of Samara Karoo Reserve (SKR) (32°23’S, 24°55’E),

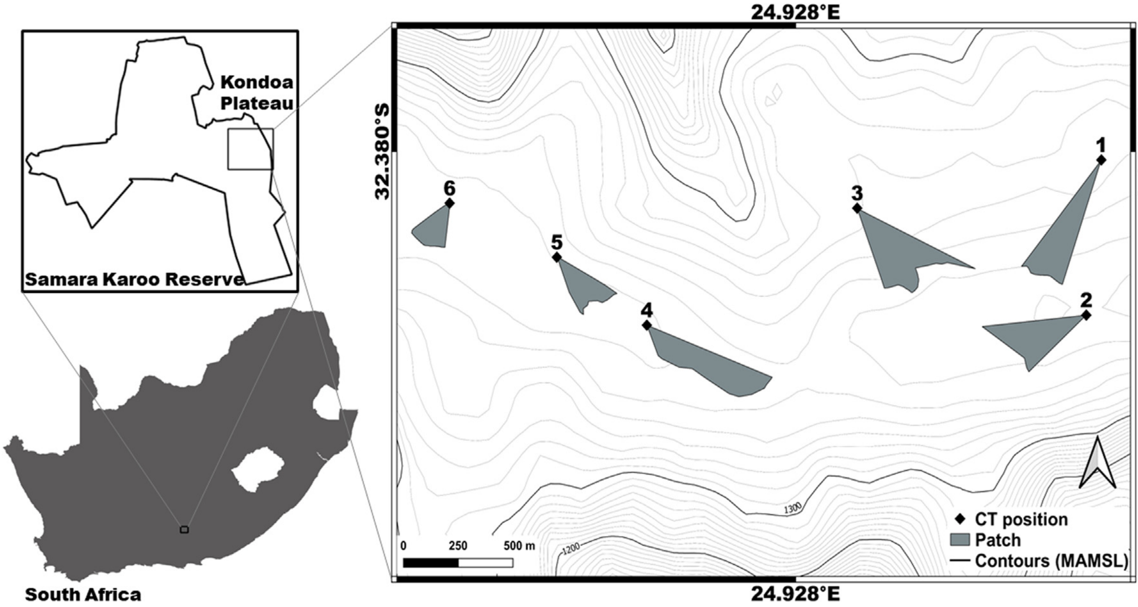

Figure 1. Geographical location of six camera trap monitored patches on the Kondoa Plateau within the Samara Karoo Reserve, South Africa. Black numbered diamonds (1–6) represent the position of each camera trap, and grey polygons depict the respective field of view for each.

situated approximately 30 km to the southeast of Graaff-Reinet within the eastern Karoo (Fig. 1). The Kondoa Plateau is classified as a Karoo Escarpment Grassland (Mucina et al. 2006), covering an area of approximately 1650 ha with an elevation range of 1200 to 1 400 m. The SKR supports a diversity of medium- and large-sized mammalian herbivores (Van Cauter et al., 2005), in addition to an established guild of predators. This region of the Karoo was historically home to a number of large ungulate grazer species, including, amongst others, the extinct quagga *Equus quagga quagga*, red hartebeest *Alcelaphus buselaphus*, buffalo *Syncerus caffer*, springbok *Antidorcas marsupialis* and black wildebeest (Boshoff et al., 2016). While many wild grazer herds have disappeared from the Karoo region due to habitat loss and overhunting (Von Richter, 1971; Skinner, 1993), the SKR has rewilded large portions of their 28 000 hectare property which is now home to more than 60 mammal species (De Fortier et al., 2014). Prior to the founding of SKR in 1997, the land was used for agricultural purposes and livestock farming as part of multiple farms (De Fortier et al., 2014). The Kondoa Plateau hosted a livestock farm before SKR started operating, and until that time the plateau was divided up into multiple paddocks used for rotating livestock.

The vegetation on the Kondoa Plateau is dominated by the perennial tussock grasses *Themeda triandra* and *Eragrostis lehmanniana,* as well as the stoloniferous lawn-forming *Cynodon dactylon*. While *M. disticha* is present on the cooler slopes of the Kondoa Plateau within a temperate thicket mosaic (Van Cauter et al., 2005), it is not found in any significant abundance on the plateau itself where wildebeest patch use was sampled.

We surveyed 11 livestock farms situated within 65 km of SKR, with comparable geology and elevations, and supporting Karoo Escarpment Grasslands (Mucina et al., 2006). All 11 farmers surveyed informed us that they had *T. triandra* (red grass) as one of their dominant grasses, with six also having *Eragrostis spp*. (white grass) as a dominant component. Following this, and although no formal vegetation surveys were conducted on the livestock farms, we assumed that the vegetation was comparable to that of the wildebeest-dominated Kondoa Plateau. Five of the farmers surveyed also indicated that *M. disticha* was relatively abundant in their grassland paddocks.

Field sampling

Black wildebeest intensity of use

We monitored black wildebeest patch use within six separate patches distributed across the Kondoa Plateau, using 6 camera traps (Bushnell Trophy Cam HD Aggressor) over a 26-mo period from February 2020 to March 2022. Each monitored patch was at least 2 hectares (ha) in size. The camera traps were strategically placed in different parts of the plateau so that they offered the widest possible field of view to cover as much of the Kondoa Plateau as allowed by the natural relief and topography. The camera traps were positioned at a height of 1.5–2 m, either secured to available trees or fixed to metal stakes.

Camera traps were serviced (had their images downloaded and batteries replaced) every 3 mo. The area covered by each camera trap (i.e., field of view) was measured after each service by having an observer stand at each camera trap, holding a printed color image of the camera's field of view, from which they would direct a field assistant carrying a Garmin GPSMAP 62s GPS to map out the field of view. This was done after each service, because the position and angle of the cameras could slightly change during servicing. The GPS data were then imported into QGIS (Development Team, 2022) to estimate a patch area measurement in hectares for each sampling period (Table A.1).

Camera traps were set to capture images using the timelapse setting, with the interval between images set to 15 min between sunrise and sunset. Some of the camera traps were periodically out of service and failed to record images. As a result, a total of 2128 camera trap days were recorded across all cameras, with the lowest number of days recorded by an individual camera being 267 and the highest 480 (mean = 355 d) (Table A.1). Images that were obscured by animals or poor weather conditions (such as fog) were excluded. For each image, the total number of wildebeest within the patch were counted and recorded. A total of 97 145 images of the patches were recorded successfully, in which 338 710 records of wildebeest were counted.

Livestock farm surveys

Ethics approval to conduct surveys was obtained from the Nelson Mandela University Research Ethics Committee: Human (permit H22-SCI-ZOO-001). The surveys (Table A.2) were conducted using a snowball sampling approach (Naderifar et al., 2017) which involved contacting an initial livestock farmer to participate in the study. Each participating farmer was asked to provide referrals to other potential participants in the same geographic area. This process continued iteratively, until the final survey was completed on 15 May 2023. A total of 11 participants meeting the criteria (i.e., managing Karoo Escarpment Grasslands for short-duration cattle grazing) were included in the study. Data collected in the surveys included the number of grassland paddocks available for grazing, average paddock size and range of paddock sizes, average stocking densities, average grazing and intense grazing durations, as well as the average duration of rest periods in between grazing cycles for each farmer (Table A.2).

Statistical analyses

The number of wildebeest in each camera trap image was counted and divided by the patch area (in ha) covered by the respective camera trap during the time of recording to estimate the number of wildebeest per ha for each patch. This was divided by the number of images captured by that camera on that day to estimate an average number of wildebeest per hectare per day (WB $\cdot$ ha^{-1} $\cdot$ day^{-1}), which is representative of daily wildebeest patch use. The same was done for all other ungulates observed on images taken throughout the study period. Wildebeest made up 88.6% of all animals recorded over the study period, with the second and third most abundant grazers (Cape mountain zebra and blesbok) making up 4% (15 474 individual counts in the patches) and 3.7% (14 026 counts), respectively.

Our main objective was to compare the wildebeest and livestock grazing systems in terms of grazing patterns, including the length of resting periods and the duration of less intense and intense grazing periods. The reason to look at these grazing intensity patterns is that holistic management suggests that it mimics natural grazing in terms of the duration of intense grazing in a patch and the subsequent resting duration. To be able to compare wildebeest and livestock grazing patterns in this way, we had to first define "less intense" and "intense" grazing for the wildebeest. We used the following binning method to establish these distinct levels of patch use intensity for wildebeest. We generated a segmented accumulative frequency curve using the wildebeest patch use data (number of wildebeest $\cdot$ ha^{-1} $\cdot$ day^{-1}) from all six camera traps throughout the study using R software (R Core Team, 2023) with the packages "vegan" (Oksanen et al., 2022), "tidyverse" (Wickham et al., 2019) and "segmented" (Muggeo, 2003). The segmented curve resulted in two clear data breakpoints (0.44 and 1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}) that we used to categorize each day into four levels of grazing intensity: "rest day" (0 WB$\cdot$ ha^{-1} $\cdot$ day^{-1}), "low intensity of use" (0.01-0.44 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}), "moderate intensity of use" (0.45-1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}) and "high intensity of use" ($>$ 1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}). Following this, we tallied the count of days within each month sampled for unique resting, low, moderate, and high intensity grazing events for each of the six monitored patches. This was subsequently averaged across the sampling period for each patch and expressed as the average number of days per month of each of the four different intensities of use.

The wildebeest intensity of use data were not normally distributed, even after transformation, and therefore nonparametric tests were used for comparisons. The Kruskal-Wallis test was used to compare whether there were differences in the four levels of wildebeest patch use intensity (rest, low, moderate, and high) among the six monitored grazing patches. The Mann-Whitney *U* test with the Bonferroni correction was then used for post-hoc analysis where the Kruskal-Wallis test returned a significant result ($P < 0.05$).

Both wildebeest patch use intensity data and cattle grazing management data were then converted into comparable units. The average number of WB $\cdot$ ha^{-1} $\cdot$ day^{-1} was transformed to Large Stock Unit (LSU) equivalents, which were obtained from Bothma (2002), where 2.17 black wildebeest are equivalent to one LSU. For cattle use intensity, the average stocking density (number of LSUs per hectare) was divided by the number of days in one average grazing cycle (i.e., the average number of days spent grazing in a paddock plus the average number of rest days before cattle are returned to the same paddock). Rest days were included in the intensity of use calculations for both the livestock and wildebeest systems for standardization. Both wildebeest and cattle intensity of use were thus represented as LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}.

We then compared the average duration of rest, grazing, and intense grazing periods between the wildebeest and cattle grazing systems. To do this, we counted the number of consecutive days of rest (0 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}), grazing (0.01 to 1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}) and high-intensity grazing ($>$ 1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}) throughout the study period and averaged each of these three categories for each camera trap. For the livestock farms, we did not use a binning method and instead asked the farmers about their average duration of grazing and intense grazing events, as well as rest periods. Due to these different modes of data collection, we took a conservative, descriptive approach towards comparing the livestock and wildebeest grazing patterns, using boxplots and descriptive statistics to compare the intensities and duration of wildebeest patch use with that of cattle paddocks.

Results

Black wildebeest patch use intensity and duration

The average field of view was 5.14 ha across the six monitored patches (range = 2.04–7.29 ha) (Table A.1). The size of the smallest paddocks on six of the 11 farms surveyed were less than 7 ha (mean of smallest paddocks across all 11 farms = 39 ha). Therefore, the sizes of the monitored wildebeest patches were similar in scale to the smaller paddocks found in almost half of the cattle grazing systems.

Black wildebeest intensity of use varied by a factor of 10 across the six monitored patches. The average intensity of use was 0.54 WB $\cdot$ ha^{-1} $\cdot$ day^{-1} (equivalent to 0.25 LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}) per patch, with a range of 0.1–1.1 WB $\cdot$ ha^{-1} $\cdot$ day^{-1} (or 0.05–0.51 LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}) across patches. Overall, wildebeest tended to use patches more at low and moderate intensities of use rather than resting (no use) or high use intensity (Fig. 2).

Rest days varied from 0.2 to 9 d/mo on average across wildebeest patches. Here, monitored patches 1, 3, and 4 had a significantly lower number of rest days per month ($P < 0.01$ for all; Mann-Whitney *U-test*) compared to the others. The average number of low use intensity days ranged from 7.9 to 14.6 d/mo, with no significant differences among patches. Moderate use intensity ranged from 0.9 to 12.8 d/mo on average, with patches 1, 3, and 4 having significantly more moderate use intensity days per month than the other patches ($P < 0.001$ for all; Mann-Whitney *U-test*). High use intensity days were the least common, with an average spanning from 0 to 4.3 d/mo across patches. Both patches 1 and 3 had more high use intensity days per month on average compared to the other patches ($P < 0.01$ for all; Mann-Whitney *U-test*), and patch 6 had no occurrence of high-use intensity days.

Cattle paddock-use intensity

The total number of paddocks per farm ranged from 7 to 160 (mean = 72), with average paddock sizes ranging from 10 to 250

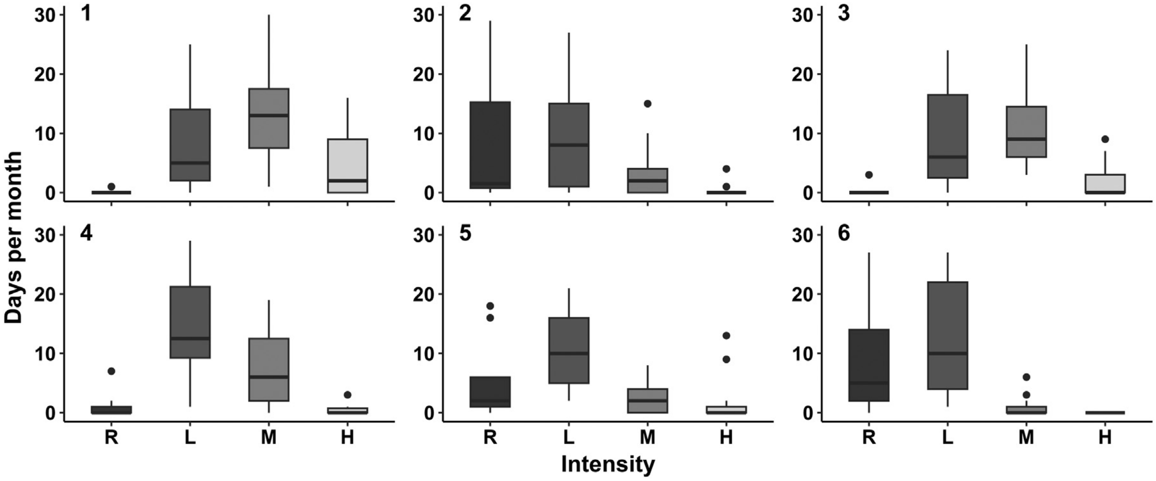

Figure 2. Black wildebeest intensity of use across six camera trap sites (1–6) on the Kondoa Plateau, represented as the average number of days per month at four different intensities of use: Rest (R): 0; Low (L): < 0.44; Moderate (M): 0.45 - 1.97; High (H): > 1.97 WB $\cdot$ ha^{-1} $\cdot$ day^{-1}.

ha (mean = 92 ha) across the 11 livestock farms surveyed. Paddock size was inversely proportional to the number of paddocks on a farm. Reported average intensity of use by cattle across the 11 livestock farms over one grazing cycle (grazed plus consecutive rest days) was 0.04 LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}, with a range of < 0.01 to 0.18 LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}. Only two farmers had stocking rates higher than 0.1 LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}.

Comparison of wild black wildebeest and cattle grazing durations

The duration of rest periods was far shorter across wildebeest patches (mean = 2 d, range = 1–5 d), compared to that implemented on cattle farms which ranged from 60 to 365 d, with an average of 180 d across the 11 livestock farms (Fig. 3). The average grazing duration was 8 d in the wildebeest system (range = 3–15 d) and 18 d across livestock farms (range = 3–60 d). The intense grazing period for wildebeest averaged 1 d (range = 0–2 d), while intense grazing periods averaged 7 d (range = 1–30 d) across livestock farms.

Discussion

Our study is among the first to compare the grazing patterns of wild grazers with those of cattle in short-duration grazing regimes for the same habitat and region. This topic is highly relevant to current debates in rangeland management with respect to the use of short-duration grazing to mimic grazing patterns of free-living ungulates (Cingolani et al., 2014; Franke and Kotzé, 2022). The wildebeest in our study had short grazing bouts of 3 to 15 d, and in the case of intense grazing only 1–2 d, followed by resting periods of less than a week. In contrast, the cattle grazing systems had much more variable grazing durations of a few days to months, with intense grazing bouts typically lasting a week or more, but followed with much longer resting periods of at least several months. Wildebeest also exhibited a more consistent use of certain patches while using others less regularly. Therefore, the hypothesis that wildebeest use the same favored patches more intensely and consistently than others was supported. Moreover, our results showed that wildebeest grazing patterns differed quite significantly from the short-duration cattle grazing systems applied in these Karoo Escarpment Grasslands, although there were also some similarities.

Intensity of use patterns

In the wildebeest-dominated Kondoa Plateau grassland system, intensity of patch use leaned more toward low and moderate use with short rest periods compared to livestock grazing patterns, where cattle were grazed at high densities followed by long rest intervals. Interestingly, the average intensity of patch use (LSU $\cdot$ ha^{-1} $\cdot$ day^{-1}) by wildebeest was higher than that of cattle in the livestock grazing systems when averaged over one grazing cycle (i.e., average number of days spent grazing in a paddock plus rest days). However, the main difference is that livestock are rotated through paddocks in pulses, with intense short grazing periods followed by long rest periods, whereas wildebeest show high site fidelity and regularly use the same preferred patches more intensely than other patches.

It is evident that cattle farmers surveyed in the region predominantly implement short-duration grazing systems, although these practices (here and globally) are not yet backed by evidence of wildlife patterns of use (Franke and Kotzé, 2022). The prevalence of short-duration grazing in our study region is evident by the large number of paddocks through which relatively high densities of livestock are rotated for short periods. This is supported by earlier research in the same (Sneeuberg) region of the Karoo by Keay-Bright and Boardman (2007) who found that farmers, at the time of surveying, had substantially increased both their number of paddocks and the rate at which livestock were rotated between paddocks compared to their predecessors. These trends are likely a result of increased availability of fencing (Archer, 2000) as well as the growing popularity of the short-duration grazing practices linked to holistic management and regenerative agriculture, both locally (Hawkins and Cramer, 2022) and globally (Gosnell et al., 2019; Gordon et al., 2022; O'Donoghue et al., 2022; Gordon et al., 2023).

Rest periods

A key tenet of short-duration grazing (and rotational grazing systems in general) is that long intervals of no grazing (rest or deferment) are essential for the recovery of vegetation in-between grazing cycles (Zhang et al., 2018; Lawrence et al., 2019; Augustine et al., 2020). However, many wild ungulate species display a high degree of site fidelity (such as mule deer *Odocoileus hemionus* and moose *Alces alces*) and return to the same patches frequently in landscapes with predictable resources and vegetative phenology

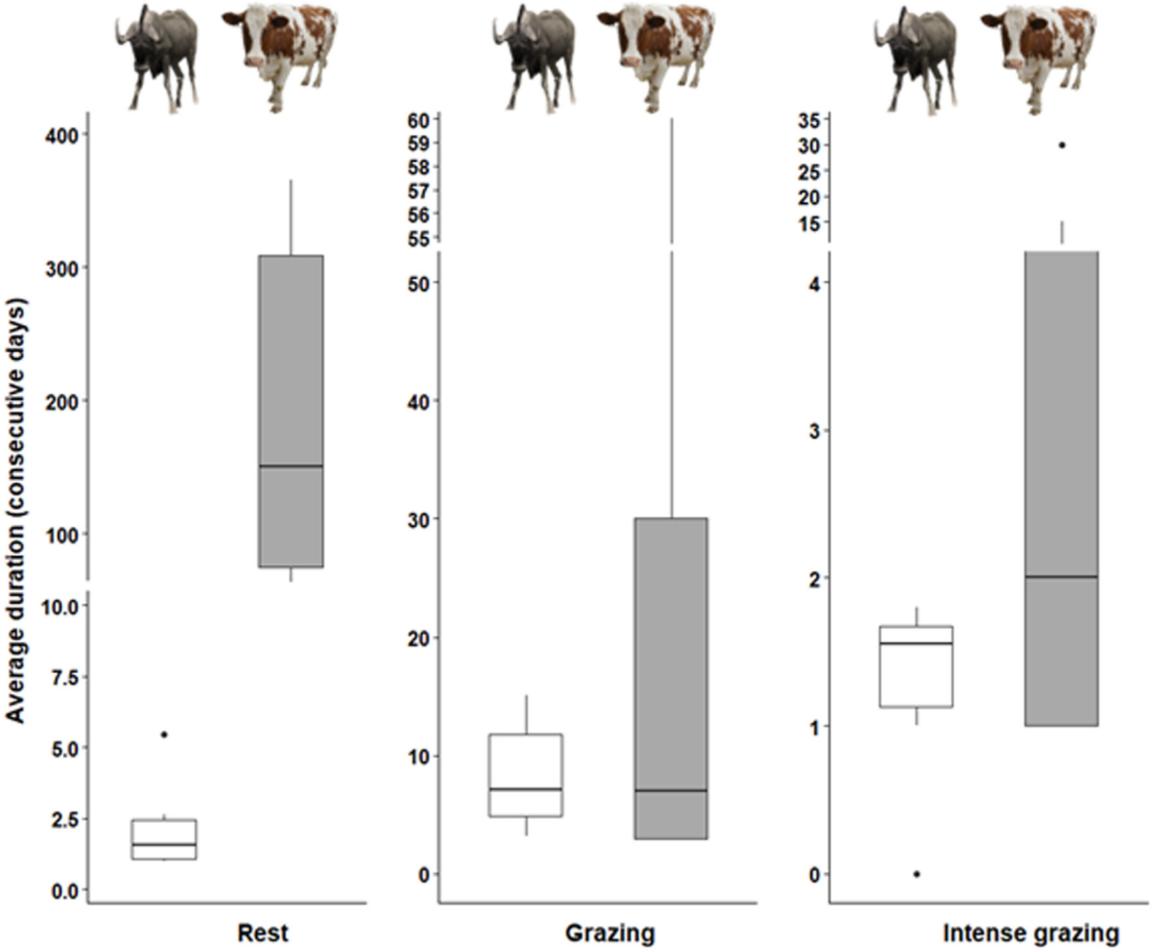

Figure 3. Average rest, grazing and intense grazing durations of black wildebeest patches and cattle grazing practices in Karoo Escarpment Grasslands. Rest refers to days with no grazing for both cattle and wildebeest. Grazing and intense grazing categories for cattle were derived from farmer survey data. For wildebeest, grazing duration represents the average number of consecutive days within each patch where the intensity of use ranged from 0.01 to 1.97 WB · ha^{-1} · day^{-1}, while intense grazing duration indicated the average number of consecutive days with an intensity of use exceeding 1.97 WB · ha^{-1} · day^{-1}.

(Morrison et al., 2021), and in some cases in response to predation risk (Anderson et al., 2010). As such, most wild ungulates use certain preferred patches almost all the time, some patches less frequently, while some patches are almost always avoided. This creates highly dynamic spatial variation on the landscape across a range of scales. These patterns were clear for wildebeest on the Kondoa Plateau too, where rest periods were brief and lasted only a few days in favored patches, while rest periods were longer in less preferred patches. These patterns align with the findings of other studies on black wildebeest, which show that they avoid long moribund grasses and frequently return to the same green short grass patches (typically less than 10 cm). This behavior suggests a high degree of patch selectivity and site fidelity within their favored patches on the landscape (Von Richter, 1971; Novellie, 1990; Mariotti et al., 2020).

Similar behavioral patterns have been described for other grazers, including bison (*Bison bison*) in North American tallgrass prairies (Knapp et al., 1999), and a range of short-grass specialists in African grasslands and savannas. This group includes warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus* (Kleynhans et al., 2011), white rhinoceros *Ceratotherium simum* and hippopotamus *Hippopotamus amphibius* (Hempson et al., 2015). These grazers all exhibit a preference for short grass patches, leading them to use the same preferred patches more frequently while using others infrequently. The consistent use of specific patches contributes to maintaining heterogeneity in the grass sward, creating highly palatable short grass patches within the bunch grass mosaic (Cromsigt and Olff, 2008). This repetitive use, coupled with the addition of nutrients via the excretion of dung and urea (Ruess and McNaughton, 1984; Day and Detling, 1990), creates a positive feedback loop that encourages sustained utilization of the same favorable short grass patches on limited parts of the landscape (Cromsigt and Olff, 2008). While livestock also forage selectively to some degree (Venter et al., 2019), selective grazing by livestock is often considered undesirable due to concerns that repeated selective herbivory can reduce the abundance of palatable species in the vegetation (Kemp, 1999; Bailey and Brown, 2011).

The frequency of rest periods remains one of the key differences between short-duration livestock grazing and patterns observed in wild herbivore-dominated systems. In systems dominated by wild grazers, rest periods are far shorter in limited preferred patches than in rotational grazing systems that claim to be based on migratory ungulate herds in the East African Serengeti-Masai system (Franke and Kotzé, 2022). The migratory herds here concentrate in the southern plains during the wet season (December–May), and in the northern woodlands during the dry season (August–November), covering a straight-line distance of over 650 km – although the actual distance covered is likely close to double this (Thirgood et al., 2004; Torney et al., 2018). These annual migrations are driven by rainfall and fertility gradients, as are all seasonal ungulate migrations (Holdo et al., 2009; Owen-Smith et al., 2020; Abraham et al., 2022). As such, there is huge variation in the scale and intensity of patch use across the landscape, with patches being used unequally in space and time and not homogenously as promoters of short-duration grazing suggest (Hoffman, 2003).

Moreover, short rest periods have been observed in preferred patches even in these large migratory systems. This is due to significant populations of the migratory ungulates remaining behind as sedentary populations when the rest of the herd migrates, in addition to other resident herbivores that do not undergo mass migrations (Ottichilo et al., 2001; Owen-Smith et al., 2020; Franke and Kotzé, 2022). These patterns are consistent throughout most African savanna and grassland ecosystems where ungulate migrations still occur (Owen-Smith et al., 2020). Herbivore pressure is therefore rarely absent from preferred patches on the landscape, although the intensity of use within these patches will decrease after the bulk of the migratory herds commence their migration. While the number of migrants versus residents fluctuates depending on resource availability and competition, Ndibalema (2009) partially quantified this by assessing various demographic components of resident and migratory blue wildebeest populations in the Serengeti during an 18-mo study. The estimate by Ndibalema (2009) suggested that 38 432 wildebeest (or 37.1% of all individuals counted) were residents. In addition to the resident populations of migratory species, the Serengeti-Masai system also hosts vast herds of nonmigratory species, with buffalo being the most abundant (Booth, 1988). Competition for food resources exists between the wildebeest and buffalo here, meaning resident populations of wildebeest and nonmigratory buffalo exhibit dietary overlap in some areas (Dublin and Ogutu, 2015). The consequence of these use patterns is that preferred patches, even in migratory systems, will seldom be rested at the scale implemented in short-duration grazing systems.

Our findings emphasize the short rest duration inherent to a wild grazer-dominated system. While this pattern exhibited some variation within patches at the scale of a few days, it pales in comparison to the range of rest periods implemented by the various livestock farmers in the same region. In the previous study in the Sneeuberg region of the Karoo by Keay-Bright and Boardman (2007) it was found that landowners were resting their paddocks in the region of 100–150 d, which is shorter than that recorded in the present study. These large variations in rest periods in the same climatic region support the notions of other authors internationally, who acknowledge that there remains much debate around which grazing management strategies work best in different landscapes, particularly when it comes to the duration and frequency of grazing periods and rest intervals (Briske et al., 2011; Roche et al., 2015; di Virgilio et al., 2019). However, long rest periods (often at the scale of a year or more) are generally promoted as a rangeland management tool for vegetation recovery in rangelands worldwide – particularly in regions with a history of degradation and/or limited precipitation (Li et al., 2014; Scanlan et al., 2014; Fedrigo et al., 2018).

What does this contribute to the grazing debate?

According to Fynn (2012) there are a number of conceptual and theoretical flaws on which the principles of rotational grazing systems are based. These include the short time animals spend in a paddock followed by a prolonged rest interval, exposing them to low-quality mature grasses with low nutritional value. This practice is antagonistic to natural herbivore movements and optimal foraging theory (Fynn, 2012). Additionally, there are variations in spatial herbivore intensity of use patterns across the landscape at multiple scales. At the landscape scale, certain hectares are consistently used, while others are less frequently utilized by free-living ungulates (McNaughton, 1984), as evidenced by our results for wildebeest. This spatial variation also occurs at finer scales within these larger patches; at the hectare scale, specific patches at the meter scale are repeatedly used while others are avoided (Grant and Scholes, 2006). Similar patterns exist on the individual bite scale (Shipley, 2007). It is this heterogeneity in grazing intensity at different spatial scales that facilitates biodiversity, and which stands in stark contrast to most cattle grazing systems, including short-duration grazing.

Our findings align with the idea that wild ungulates intensely use certain patches on the landscape, akin to the principles advocated by Savory and supporters of short-duration grazing management (Savory and Parsons, 1980; Savory and Butterfield, 2016; Lawrence et al., 2019). But unlike short-duration grazing management where all patches are intensely used at some point, wild ungulates consistently use preferred patches without extended rest intervals – as our results show. However, it is important to note that wild ungulates return frequently and intensely use only specific patches on limited parts of the landscape, such as grazing lawns in the case of grazers like wildebeest and bison (McNaughton, 1983; Knapp et al., 1999; Hempson et al., 2015) and nutritious browsing lawns in the case of browsers (Fornara and du Toit, 2007). These patterns contrast the conceptual basis of short-duration grazing, which posits that all patches are at some point used intensely (Hoffman, 2003; Franke and Kotzé, 2022).

Our research contributes to the growing literature on wild herbivore patch use patterns within their native range and effectively contrasts these patterns with cattle farming practices in the same landscape. It is clear that the short-duration cattle farming practices implemented in Karoo Escarpment Grasslands differ from the intensity of use patterns of black wildebeest within the same habitat and landscape in most aspects, with the duration of rest periods being the biggest difference between the two systems. Wildebeest only used certain patches intensely, while rest periods within these patches were far shorter than those implemented in the cattle grazing systems. Our data suggests that wildebeest use the landscape selectively, likely in response to patch quality. On the other hand, wildebeest use of some patches was limited and with longer rest intervals. As a result, the grazing and trampling pressure of wildebeest is not equal across all parts of the landscape, contradicting the homogenous use patterns promoted by short-duration grazing practices (Savory and Parsons, 1980; Hoffman, 2003; Lawrence et al., 2019). While farmers would have to reduce the duration of rest intervals to truly mimic wild herbivore spatiotemporal patch use patterns, this may not be practically feasible.

Future studies would benefit by including different wild and domesticated ungulate species in the same habitat and landscape, expanding the study area, and assessing vegetation impacts along a gradient of intensities of use between both systems. Empirical data on livestock patch use within paddocks, as obtained for our wildebeest-dominated system using camera trap imagery, would also benefit future comparisons because larger paddocks within livestock systems could comprise numerous patches of varying quality. Consequently, the intensity of use of specific patches within these larger paddocks may exhibit significant variability that we did not look at in our study. Given ongoing rangeland degradation and biodiversity crises due to the ever-growing human population, development, and associated resource requirements, it is imperative to learn from natural systems where consumers and their forage have co-evolved. By exploring these patterns we can gain insights into the sustainable grazing, vegetation productivity and nutrient cycling processes that have naturally developed in evolutionary time. This understanding can inform the design and implementation of effective nature-based grazing strategies, ensuring that these align with the ecological processes that have stood the test of time.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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