

When less is more: heterogeneity in grass patch height supports herbivores in counter-intuitive ways

Rina CC Grant^{1,2*}, Judith Botha², Thelani C Grant³, Mike JS Peel^{4,5,6} and Izak PJ Smit^{2,7}

¹ Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa

² Scientific Services Kruger National Park, South African National Parks, Skukuza, South Africa

³ Faculty of Animal and Wildlife Science, University of Pretoria, Pretoria, South Africa

⁴ Agricultural Research Council–Animal Production, Nelspruit, South Africa

⁵ School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

⁶ Applied Behavioural Ecology and Ecosystem Research Unit, University of South Africa, Florida, South Africa

⁷ Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

* Corresponding author, email: Rinagrants@gmail.com

Abstract

Herbivores are an integral part of the African landscape and have evolved with the vegetation to create the savanna landscape. Managers of these landscapes can benefit from a better understanding of how indigenous herbivores use the landscape to which they are adapted. In this study we observed which patches were frequently utilised, by doing regular monthly road counts, grass height observations and dung counts on selected short grass patches in the Kruger National Park. Smaller-framed impala and blue wildebeest (meso-herbivores) were most regularly seen on these nutritious patches, while from dung deposits it was clear that the even larger-framed buffalo (mega-herbivores) spent time there. This preference can be explained by considering the nutritional needs and food intake of the herbivores. Smaller-framed herbivores seem to be able to satisfy their dietary requirements on the high-quality forage patches, while larger-framed herbivores seem to supplement the quality forage by also spending foraging time on areas of higher grass biomass. From this insight we propose that range management should take herbivore preferences into account and allow herbivores to select and concentrate their foraging on the most nutritious forage. This approach is likely to decrease inputs while allowing animals to maintain or increase production.

Keywords: diet selection, grazing management, forage quality, nutrition

Introduction

Africa is home to a large variety of herbivores, where the rangelands and herbivores have evolved and adapted together in their responses to system changes, with grazers increasing with an increase in grasslands and decreasing with an increase in woody vegetation (Du Toit and Cumming 1999). It is well known that wild grazers utilise these landscapes heterogeneously both in space and time, often concentrating on short grass areas as long as grazing is available. This is illustrated in the Serengeti system where animal migration is linked to forage quality (Hopcraft et al. 2014; Bukombe et al. 2018). A similar pattern of adaptive herbivory of the heterogenous landscape is seen with the seasonal migration between wetlands and uplands in Botswana (Fynn et al. 2014, 2015b). Even on a much smaller scale grazers show an unexpected preference for low biomass short grass patches (Grant and Scholes 2006; Owen-Smith et al. 2015), with many of these patches being maintained over long periods (Novellie and Gaylard 2013; Marshall et al. 2018).

There are several possible reasons for grazers to prefer shorter grass:

(1) Higher nutritional quality: several authors have shown a link between forage nutrients and utilisation, both in East

Africa (McNaughton 1979, 1984, 1988, 1990; Murray 1995; Voeten et al. 1999; Owen-Smith 2002b) and in southern Africa (Grant and Scholes 2006; Verweij et al. 2006; Archibald 2008; Novellie and Gaylard 2013; Treydte et al. 2013; Hempson et al. 2015)

(2) Higher digestibility: short, green, growing grass has less lignin with lower carbon to nitrogen ratios, which makes it more palatable (Heady 1964) and digestible (Milchunas et al. 1995; Wilmshurst et al. 1999) and thus more nutritious per individual bite (Van de Vijver et al. 1999; Hempson et al. 2015).

(3) Higher bite rates: a higher percentage of green leaf in the forage allows higher bite rates with less time required to search for suitable forage (Drescher et al. 2006; Van Langevelde et al. 2008).

(4) Predator avoidance: herbivores in the presence of predators must balance their nutritional needs with predator avoidance, and open patches with short growing grass provide areas of high visibility (Frank 2008; Burkepile et al. 2013; Weterings et al. 2018).

Rangeland management is very complex and many different grazing systems have been implemented, from exploitation, through steady-state management to

ecosystem management, now moving towards implementing resilience-based management (Briske 2017). Varying management approaches has been used for production of cattle and sheep on rangeland. Most of these approaches opt for a homogenous utilisation of the biomass to support herbivores, using available biomass as an indicator to recommend stocking density (Coe et al. 1976; Fritz and Duncan 1994; Peel et al. 1999; Fynn and O'Connor 2000; Peel 2005; Fynn et al. 2015a). However, many of these systems have not delivered the expected results (Briske et al. 2008; Hawkins 2017), and areas of short well-utilised grasses are often casually classified as degraded. Fuhlendorf and Engle (2001), Fuhlendorf et al. (2017) and Fynn et al. (2017) suggested that allowing animals to utilise the rangeland heterogeneously could improve production. As stated by Fuhlendorf et al. (2017: 191), 'Perhaps the greatest challenge for applying heterogeneity-based science in rangeland management is overcoming a century-old vision of rangelands as simple ecosystems that sustainably provide forage for domestic livestock'.

Some wild and domestic grazers have similar body sizes and thus probably bite sizes (Pretorius et al. 2015); one may thus expect that they would have similar foraging preferences in a heterogenous landscape under similar circumstances. Understanding how the indigenous grazers utilise the landscape could thus contribute to resilience-based management of rangelands. For example, the mass of a buffalo cow of 410 kg is comparable to that of a similar-sized medium-framed beef cow of 450 kg, while an impala ewe of 44 kg has similar mass to sheep of the same age of 40 kg (Meissner et al. 1981). They seem to also have similar nutrient requirements, with Prins and Beekman (1987) estimating that herbivores require 7%–8% dietary protein and at least 0.24% phosphorus in the forage. Energy requirements vary according to the reproductive state and size of the animal, with pregnant and lactating individuals having higher nutrient requirements. A lactating adult buffalo cow, for example, requires approximately 101 MJ energy d^{-1} , which is the same as that of a lactating medium-framed beef cow (Meissner et al. 1981), and is approximately 25% more energy than the energy required by non-lactating animals of the same size.

Food intake is the product of mouth type, bite size and biting rate (Owen-Smith 2002a), and one would thus expect herbivores to concentrate on patches where bite rate can be optimised. On short grass patches, bite size will be smaller due to low biomass, but higher bite rates can compensate for smaller bite size (Drescher et al. 2006). One would thus expect grazing herbivores to concentrate on patches with high concentrations of green leaf. As buffalo (and cattle) use their tongues to obtain forage, they cannot increase bite rates on very short grass patches and one would thus expect these animals to rely on higher bite rates on the lower-quality taller grasses to obtain sufficient nutrients (Prins and Beekman 1987).

The aim of this study was to determine how wild grazers utilise a heterogenous landscape over space and time. We classified the foraging landscape into two types of forage patches: short grass patches described as frequently utilised patches (FUPs) and the taller grass areas that made up the remainder (non-FUPs). FUPs generally occur at very

small spatial scales and at this stage it is very difficult to evaluate herbivore distribution over time using aerial counts or other remote sensing systems. Thus, we decided to use road counts to examine herbivore distribution at these small spatial scales.

We proposed the following hypotheses:

- (1) wild grazers prefer short grass patches and utilise these as long as there are sufficient green leaves available to enable effective foraging;
- (2) wild grazers move to areas with higher forage biomass during the hot dry season, when available forage biomass is depleted on the short grass patches;
- (3) soil type and geology influence how wild grazers utilise the rangeland, with higher nutrient soils, such as gabbro and basalts, showing a weaker selection for short grass patches;
- (4) the size of the grazer will influence how they utilise FUPs.

Materials and methods

We used three different approaches to address the question of whether certain patches are more frequently utilised by wild herbivores, and in each case by which species.

- (1) Repeat road counts using a pre-determined route covering FUPs and non-FUPs and across different soils and geology. These counts yielded important individual observations during every monthly trip from which localised density estimates were derived but did not give any indication of the time animals spent on a specific patch, which was determined using grass surveys and dung counts (see following points).
- (2) Grass surveys used grass height and tuft utilisation as an indicator of herbivore presence. These surveys explored whether FUPs were indeed more heavily utilised than patches identified as non-FUPs.
- (3) Dung counts on FUPs and non-FUPs were used to give a better indication of the presence of herbivores over a longer time period than that provided by the single observations of the road counts.

Road counts

Animal sightings from a vehicle were recorded on a monthly, one- to two-day trip over 21 months from April 2013 to July 2015, using the same route. Observations were done in central Kruger National Park (KNP); the road transect between Orpen gate and Nwanetsi picnic site covered four of the main geological areas of the KNP: granites, ecca shale, gabbros and basalt (Venter 1990; Venter et al. 2003). To account for the role of water as an attractant to areas, transect paths were as far as possible selected to cover the variation in distance from rivers to ensure a sample representative of varying water availability (see Figure 1).

Sightings of some common herbivores were recorded. These included impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Transect widths were 50 m from the road verge on both sides; 50 m was used as the cut-off point as counts of animals further than 50 m became very inaccurate in the denser vegetation types. Each animal sighting was classified into distance bands following the Distance procedure (Buckland et al. 1993). Visibility of animals was

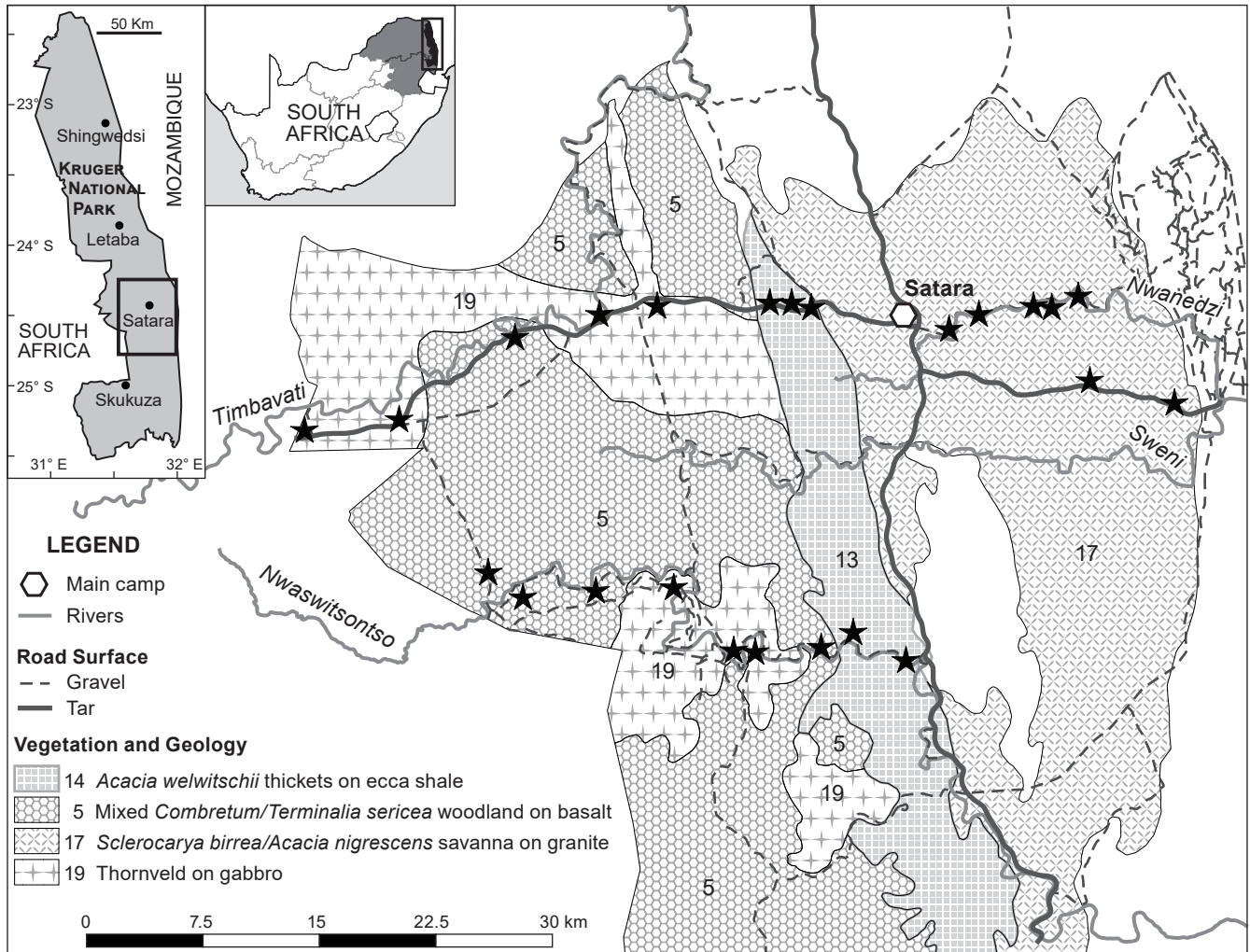


Figure 1: Route for monthly and sample sites for both grass surveys and dung counts in relation to geological areas: granites, ecca shale, gabbros and basalt. Stars indicate the transect sites

estimated (always with the same main observers) according to the vegetation density (Table 1). For each sighting we recorded whether the animals were on a FUP dominated by short grass, or not (see later in the text for criteria used to classify FUPs). The distances travelled through each route as indicated in the map and the length of the area covered by habitats classified as FUPs and non-FUPs in each route as well as the geological area is presented in Table 2.

Grass surveys

Grass surveys were done during the growth season in January, March, April and May as well as during the hot dry season in September, October and November. Surveys were performed along 100 m × 2 m belt transects. Grass height was measured in centimetres at the level of the bulk of the leaves and the utilisation of the grass was estimated by evaluating the percentage of tufts that showed blunt cutting edges within the transect line.

After five months, small-scale patches that were observed to be frequently utilised were identified as FUPs taking the following criteria into account:

Table 1: Estimation of visibility at each class of vegetation density

Vegetation density	Distance band (distance from the road edge)	Estimated visibility
1 Very open	A (0–2 m)	100
	B (2–15 m)	100
	C (15–30 m)	90
	D (20–50 m)	75
2	A (0–2 m)	100
	B (2–15 m)	95
	C (15–30 m)	70
	D (20–50 m)	50
3	A (0–2 m)	100
	B (2–15 m)	90
	C (15–30 m)	60
	D (20–50 m)	15
4 Very dense	A (0–2 m)	100
	B (2–15 m)	80
	C (15–30 m)	15
	D (20–50 m)	10

Table 2: Distance covered in each part of the study route in either frequently utilised patches (FUPs) or non-FUPs in each of the main geological areas along the route (distance allocated for each geological type along the route) and a comparison of the total distance covered for each habitat in the main geological areas

Route number	Geology	FUP (km)	Non-FUP (km)	Geological area	FUP (km)	Non-FUP (km)	Total distance (km)	Percentage of areas covered
1	Basalt	7.35	43.35	Basalt	8.65	49.45	58.1	37
2	Ecca shale	1.51	8.89	Gabbro	7.00	16.60	23.6	15
3	Gabbro	2.90	5.40	Granite	4.60	24.60	29.2	19
4	Granite	5.80	19.60	Ecca shale	13.81	31.69	45.5	29
5	Gabbro	6.90	22.40	Total	34.06	122.34	156.4	
6	Granite	3.10	8.00					
7	Gabbro	2.60	20.40					
8	Ecca shale	4.60	8.60					

- herbivore distribution
- the presence of stands of *Euclea divinorum* and *Sporobolus iocladis*, which are indicators of sodic sites, especially in the granites; sodic sites form the only FUPs in the granites
- grass height of less than 15 cm
- extent and regularity of utilisation by all herbivores
- sparse tree cover and mean tree height less than 2 m
- presence of *Urochloa mosambicensis* patches.

Dung counts

The number of dung heaps per species within 1 m on both sides of the transect line was counted and recorded at every 20 m mark and added to form one survey sample for 100 m. Dung counts were done during the growth season in January, March, April and May as well as during the hot dry season in September, October and November.

Data processing and statistical analysis

Monthly animal counts were expressed as densities (corrected for visibility) in the 100 m area next to the road (50 m both sides of the road) per 1 km of FUP or non-FUP per route. Each of the FUP and non-FUP blocks were scaled to density per 1 km² for analysis. Monthly observations were grouped into seasons as follows: wet season December to March; cold, dry season April to July; and hot, dry season August to November. To correct for density of the vegetation the number of animals was adjusted according to the estimated visibility, as presented in Table 1. Thus, in the A band and on FUPs up to 15 m all animals were assumed to have been seen and numbers were not adjusted, while with a class 3 density, which was the most common in the granites, the number of animals seen at 15–30 m (C band) were corrected for the fact that only 60% of animals were assumed to have been counted.

The adjusted count data per species were tested as response variables in a mixed-effects model using the lme function in the nlme package for R (R Core Team 2013). The predictor variables FUP/non-FUP, season and geology were included separately and month was included as a random variable to take into account native differences in months.

Dung counts of different species were included as response variables in a mixed-effects model using the lme function in the nlme package for R (R Core Team 2013). FUP and geology were predictor variables and month was once again included as a random variable. Grass height

Table 3: Differences in density of animals observed per 100 m × 1 km scaled blocks of 137 frequently utilised patches (FUPs) vs 152 non-FUPs, over 21 months with repeat measures ANOVA

Species	Factor	Chi-square	Significance
Impala	FUP	32.87	<0.001
	Season	12.13	0.0023
	FUP:Season	7.79	0.02
	FUP	30.9	<0.001
	Geology	4.35	ns
Blue wildebeest	FUP:Geology	4.26	ns
	FUP	17.08	<0.001
	Season	0.69	ns
	Season:FUP	1.27	ns
	FUP	17.3	<0.001
Buffalo	Geology	7.62	0.05
	FUP:Geology	6.04	ns
	FUP	0.11	ns
	Season	0.14	ns
	FUP:Season	1.43	ns
	FUP	0.08	ns
	Geology	4.34	ns
	FUP:Geology	5.66	ns

ns = non-significant

was normally distributed, and comparisons between FUPs and non-FUPs were performed using a Student's *t*-test.

Results

Road counts

Impala and blue wildebeest densities were significantly higher on FUPs than on non-FUPs in all seasons (Table 3). Season influenced how impala utilised FUPs, and impala selected FUPs significantly more in the wet season (Figure 2). Impala selected for FUPs in all geological areas, but the selection for FUPs was not significantly influenced by the geological substrate. Blue wildebeest utilisation of FUPs was not significantly influenced by season or geology. There was no indication that buffalo selected FUPs above non-FUPs from the road counts.

Grass surveys

The mean grass height, as proxy for utilisation, was significantly lower on FUPs ($p < 0.001$) with an average grass height of 10.8 cm on 101 FUP sites and 37.26 cm on

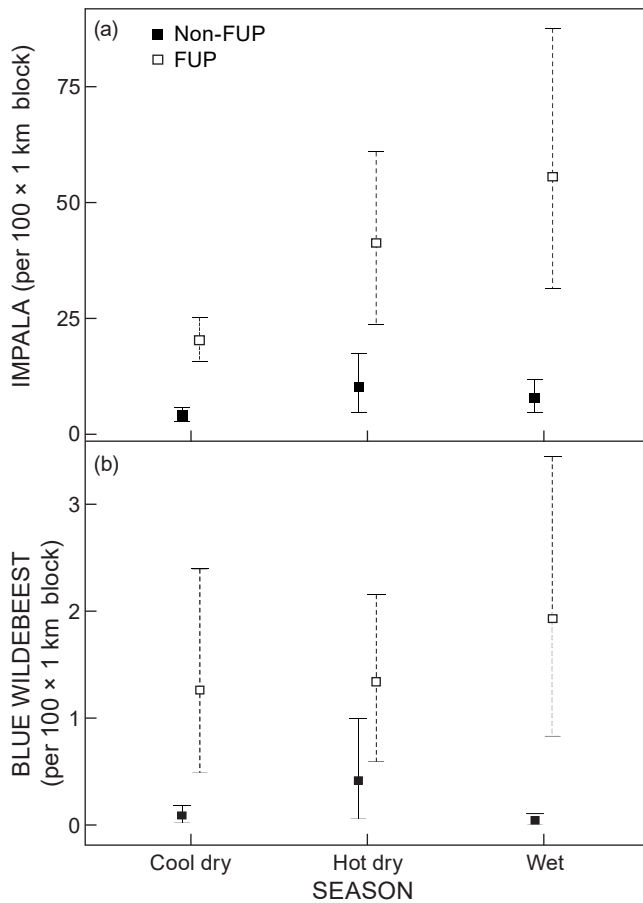


Figure 2: Average utilisation of frequently utilised patches (FUPs) and non-FUPs by (a) impala and (b) blue wildebeest in cool dry, hot dry and wet seasons. Error bars indicate the SE

51 non-FUP sites. On the FUP sites most of the tufts showed clear signs of utilisation within the transect. Grass tended to be taller on the eccla shales for the non-FUPs (interaction between habitat and geology $p = 0.06$) (Figure 3).

Dung counts

The dung count data for impala and blue wildebeest showed similar trends to that of the road counts (i.e. preference for FUPs), with geology influencing the number of blue wildebeest dung heaps observed (Figure 4). Buffalo dung heaps showed a preference of buffalo for FUPs contrary to the findings from the road count data, although the preference was not influenced by geology. There was also a lot of variation in the number of dung heaps recorded in these sites as animals tended to move between sites (Table 4).

Discussion

The observations from road counts showed that smaller-framed impala and wildebeest showed a significant preference for short grass patches even in the hot dry season when forage on these patches is limited. We could not, however, show the hypothesised movement

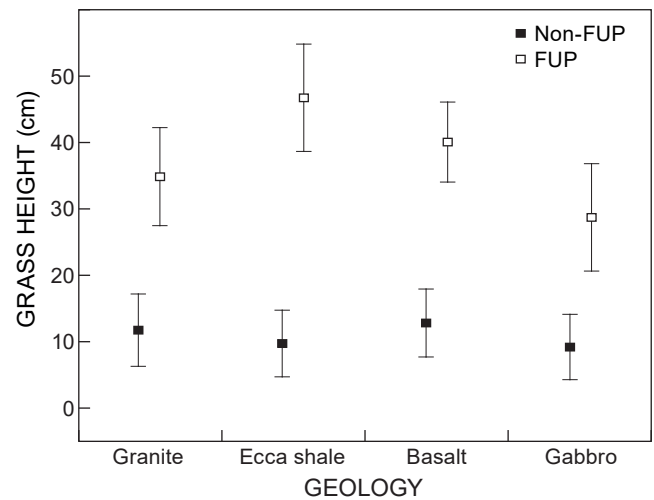


Figure 3: Average grass height in different geological areas. Error bars indicate the SE

toward areas with higher forage biomass during the dry season. However, fewer impala were observed in the cool dry season when they would have been more inclined to utilise browse (Whyte 1985; Pietersen et al. 1993) and the highest number of blue wildebeest on non-FUPs were recorded during the hot dry season when they tend to move away from the short grass areas (Owen-Smith et al. 2015). Although from the road count observation, the larger-framed buffalo did not show any preference for FUPs, dung counts indicated that buffalo showed a significant preference for FUPs over a longer time period. This selection for FUPs by buffalo is likely a sign of individual animals spending time on these short grass patches during the night to avoid predators (Burkepile et al. 2013).

Contrary to our expectation, road count data indicated that the underlying geology did not influence the preference of blue wildebeest and impala for FUPs. The dung count data indicated that, again contrary to expectation, blue wildebeest showed a stronger preference for FUPs on the higher nutrient soils of the basalts and gabbros where higher number of wildebeest occur.

The size of the animal did influence how the grazers utilised the heterogenous landscape. Animals have to accumulate the nutrients they need from the available forage. One could predict which animals would be able to obtain sufficient forage from FUPs by taking the nutrients required by different species and sizes of herbivores into account. Analysis of green leaves from an additional part of this study (Grant 2018) showed that forage on FUPs had an average of 0.28% phosphorus, 15.5% protein and contained 8.8 MJ kg⁻¹ energy. In contrast, the non-FUPs had an average of 0.24% phosphorus, 13.1% protein and contained 7.9 MJ kg⁻¹ energy. For example, a blue wildebeest would need about 3.7 kg of forage per day on the FUPs and 4.1 kg of forage per day on the non-FUPs to address their energy needs. In the same environment a non-pregnant buffalo cow would need 12 kg on FUPs and 13 kg forage per day on non-FUPs. Blue wildebeest, and similar or smaller domestic herbivores (Meissner et

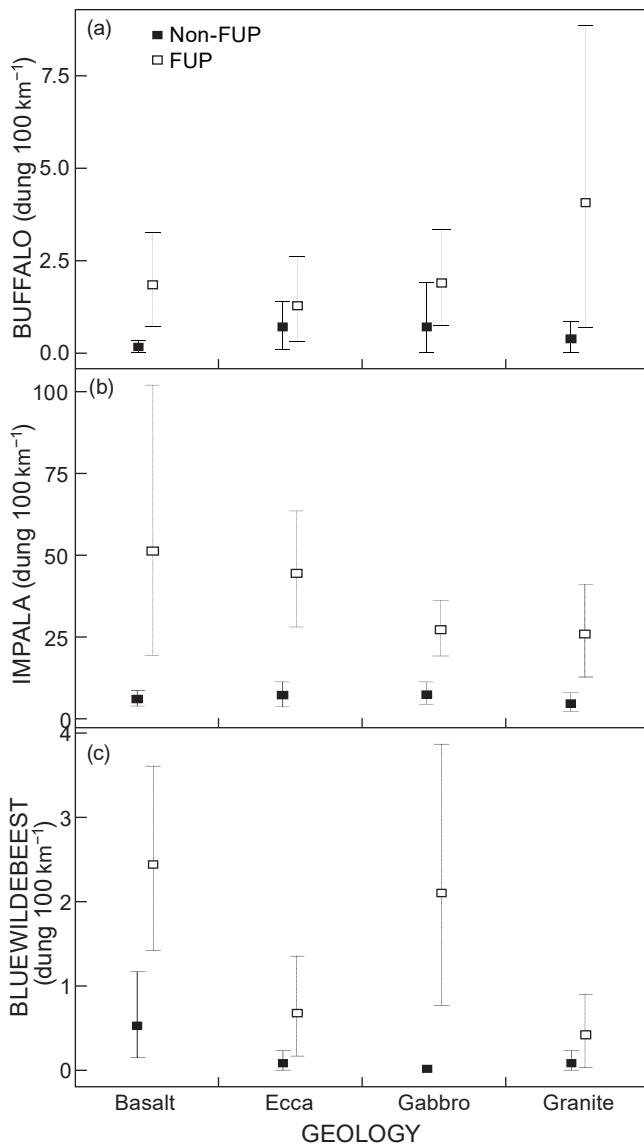


Figure 4: Average (a) buffalo, (b) impala and (c) blue wildebeest dung heap counts per 2×100 m transects in different geological areas. Error bars indicate the SE

Table 4: Repeated-measures ANOVA for seven dung surveys between September 2013 and July 2014 covering 99 frequently utilised patch (FUP) and 51 non-FUP sites

Species	Factor	Chi-square	Significance
Impala	FUP	12.31	0.0005
	Geology	0.63	ns
	FUP:Geology	0.32	ns
Wildebeest	FUP	8.05	0.0005
	Geology	12.22	0.0005
	FUP:Geology	4.32	0.038
Buffalo	FUP	4.91	0.02
	Geology	1.82	ns
	FUP:Geology	1.02	ns

ns = non-significant

al. 1981), are thus likely to obtain sufficient forage from FUPs, while larger-framed herbivores such as buffalo would probably have to forage on non-FUPs to obtain sufficient biomass. This is reflected in our results, with blue wildebeest showing much stronger associations with FUPs than buffalo do, although both species utilise FUPs.

This would suggest that animals could optimise their daily nutrient intake by foraging on FUPs while they are able to access sufficient quality forage effectively. For species such as impala and wildebeest, these open short grass patches provide very efficient foraging opportunities as they would not have to spend time selecting for more nutritious green leaves with higher quality (Collinson and Goodman 1982; Peel et al. 1999). Larger herbivores such as buffalo (and likewise, medium-sized cattle breeds) are unlikely to obtain sufficient forage on these short grasses and could reduce their foraging time by including tall grass patches (Wilmshurst et al. 1999; Owen-Smith 2002; Provenza et al. 2003; Arsenault and Owen-Smith 2008). This explains why buffalo were not recorded on the FUPs as often as the smaller herbivores, although they also seemed to utilise these areas.

As long as animals are able to return to grazed patches frequently they can maintain a heterogeneous foraging area with FUPs as well as non-FUPs. Such a heterogeneous landscape can provide the necessary nutritional resources in terms of maximising energy and nutrient intake (Fynn et al. 2017) and minimising foraging time (Fuhlendorf et al. 2017).

From our observations it seems that various factors can lead to the formation of a FUP, but all involve regular utilisation of grass tufts to maintain them in a short growing state with dense leaf cover of high quality. This is often the case around waterpoints and animal paths. Other factors can also act to attract herbivores to create FUPs, such as regular small fires (Donaldson et al. 2018), areas of higher sodium concentration in the soil and hence in the forage (Noy-Meir 1973) and old cattle kraals (Marshall et al. 2018). It is important to note that we cannot exclude the possible effect of predator avoidance in this study on the selection of short grass patches, as suggested by Burkepille et al. (2013), and it is highly likely that this is an important contributing factor to the selection of these patches.

Conclusion

This study confirms that wild grazers utilise the available forage heterogeneously, concentrating on certain preferred short grass patches over time. Smaller grazers, such as blue wildebeest and impala, seem to be able to largely satisfy their nutritional requirements on these higher nutrient, low biomass patches. Larger grazers such as buffalo that need more bulk to satisfy their needs have to utilise the non-FUPs in addition to the short grass patches. In an African environment, where many grass species are adapted to grazing, rangelands could become more resilient and sustainable by managing for this natural heterogeneity and adaptability of the grassland (Fynn et al. 2017; Fuhlendorf et al. 2017). Rangeland management for conservation of wildlife and for the production of domestic stock should provide sufficient heterogeneity to provide forage of different heights and leaf density to supply the

nutrients required by different sized grazers. In the case of domestic grazers this could be achieved by allowing animals to utilise larger, more heterogeneous landscapes where animals are able to reutilise grazed patches, rather than moving them regularly to more homogeneous tall grass pastures. Such a 'more' heterogeneous management system was already suggested by Venter and Drewes (1969) for domestic stock, and for larger systems by Fynn (2012) for wild herbivores. We conclude that on the basis of our observations of the preference for short grass patches by wild grazers in KNP, we should consider creating similar heterogeneity in commercial rangelands to provide quality forage for domestic animals as well as wildlife in smaller conservation areas. Small fires, or other attractants (e.g. waterpoints) could possibly concentrate grazers on specific areas in order to create, and maintain through positive feedbacks, FUPs (see e.g. Donaldson et al. 2018).

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