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Original Research Article

Quantifying nutrient re-distribution from nutrient hotspots using camera traps, indirect observation and stable isotopes in a miombo ecosystem, Tanzania

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ABSTRACT

Nutrient hotspots strongly attract mammalian herbivores in nutrient-poor habitats such as savanna systems. However, little is known about their seasonal importance for mammalian herbivore species, particularly grazers. In addition, no study has fully quantified the potential re-distribution of nutrients into the surroundings of these hotspots. We assessed nutrient hotspot (i.e., grazing lawns and termite mounds) use by herbivores in a Miombo ecosystem of the Issa valley, Tanzania, using dung counts, camera traps and stable isotope analyses over a one year period, from May 2016 to October 2017. We conducted dung counts along four transects each radiating away from ten termite mounds and six grazing lawns as well as in 16 control sites 100 m away from each nutrient hotspot. In addition, we sprayed grasses around five termite mounds with urea and traced the isotopic signature back in grazing herbivore dung. Grazer dung deposition was twice as high in hotspot areas vs control sites. A total of 32 camera stations recorded 244 wildlife encounters, with mammalian herbivores using hotspot areas four times more frequently compared to control plots. Stable isotope analyses highlighted that dung deposited by mammalian grazers around hotspots likely originated from grasses within or close to hotspot areas, indicating that grazers are responsible for maintaining nutrient stability of these hotspots. We, therefore, emphasize the importance of grazing mammal species for the long-term persistence of hotspots and, thus, their contribution to the maintenance of a heterogeneous landscape within the Miombo ecosystem.

1. Introduction

Grazing ecosystems, that often host a large diversity and biomass of mammalian wildlife species, are increasingly threatened (Frank et al., 1998). These ecosystems often encompass savannas that are characterized by a continuous layer of

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palatable and unpalatable grass species (Grant and Scholes, 2006). Nutrient availability in grasses attract various mammalian herbivores (Frank et al., 1998; McNaughton, 1985; Treydte et al., 2011). A substantial amount of the nitrogen (N) and phosphorus (P) that is found in grasses is recovered back in the herbivore's dung and urine (Hobbs, 1996), further enhancing N and P in soils and, consecutively, grasses (van der Waal et al., 2011; Williams and Haynes, 1990). Nutrient rich sites produce palatable forage for both livestock and wildlife in savannas, highlighting the importance of patchiness for large mammalian herbivores (Muchiru et al., 2008; Porensky and Veblen, 2015).

Various factors such as climate, soil type, grass species and grazing can affect dynamics of nutrients (Silveira et al., 2012). In addition, dung mineralization, which is higher than that of plant litter, strongly fosters nutrient cycling (Tonn et al., 2019). Nutrient concentration is often high in areas of high grazer visitation (Sollenberger et al., 2009) such as grazing lawns (Cromsigt and Olff, 2008; McNaughton, 1985). Further, nutrients can also accumulate on and around termite mounds due to the termites' decomposition activities (Davies et al., 2016; Reid, 2012), thereby enhancing both soil and plant foliar nutrients (Porensky and Veblen, 2015).

At fine spatial scales, termites are responsible for inducing savanna heterogeneity due to their earth burrowing activities (Dangerfield et al., 1998; Moe et al., 2009; Odadi et al., 2018). The highly fertile soils on and around mounds promote nutrient-rich grass growth (Arshad, 1982; Fox-Dobbs et al., 2010). Further, one would expect that ungulates, grazers in particular, favorably forage on these sites (Augustine et al., 2003). In addition, their urine and dung depositions on or next to these hotspots might alter soil nutrient availability for plants via changes in soil nutrient cycling (van der Waal et al., 2011).

However, the spatial and temporal nutrient cycling around these hotspot areas, from soils via plants to herbivores and back into soils, is difficult to trace and has rarely been quantified (Jobbágy and Jackson, 2001). Further, decomposition of dead organic matter is a key process in nutrient recycling of terrestrial ecosystems, providing essential nutrient input for plant communities (Veldhuis et al., 2017a, 2017b). Grasses from nutrient-rich sites normally also possess high nutrient concentrations, which are particularly important for pregnant and lactating ungulates (Augustine et al., 2003).

The high soil nutrient concentrations of termite mounds (Carneiro et al., 2018; Holt and Lepage, 2000; Sileshi et al., 2010) are often not strongly re-distributed into the surrounding landscape through natural processes due to mound structure and termite behaviour (Holt and Lepage, 2000). Re-distribution extent to nearby soils depends on the nature of the mounds, soil erosion as well as nutrient leaching rates (Holt and Lepage, 2000). This re-distribution can sometimes happen via herbivores as agents, from foraging to resting or sleeping sites, where excretions take place (Frank and Evans, 1997; Jewell et al., 2007; Singer and Schoenecker, 2003; Veldhuis et al., 2016). However, tracing the origin of the forage and assessing whether the excreta belong to the ungulates in question has only been reliably studied for domestic herbivores (Bol et al., 2000). Little is known on the linkage between savanna vegetation quality and nutrient redistribution by wild herbivores as an important mechanism sustaining heterogeneity in savanna systems (van der Waal et al., 2011). Stable isotopes have been used for various ecological aspects with respect to food webs, trophic relationships and resource allocation (Boecklen et al., 2011; Finlay and Kendall, 2008; Frank and Evans, 1997; Werner et al., 2012), mostly focusing on trophic levels in aquatic systems (Finlay and Kendall, 2008). Little has been done in terrestrial systems using stable isotopes, particularly in Eastern Africa (but see Treydte et al., 2006b). Stable isotopes were also used in Kruger National Park, South Africa, to understand feeding patterns of elephants (*Loxodonta africana*), particularly when they switch between grass and browse (Codron et al., 2011). Herbivores have been studied for decades, yet debate still exists across Africa about their diet composition (Sponheimer et al., 2003). Among the challenges in many studies is to clearly set the connection between the herbivore species of interest foraging on a diet that differs in isotopic composition and choosing tissue that will yield the appropriate record of the past feeding location (Hobson, 1999). As natural tracers, stable isotopes can be used for showing plant-animal relationships and for truly reflecting food sources, habitat, distribution and movement in terrestrial ecosystems (Jianzhu et al., 2004). This technique also provides an ideal tool to understand food web relationships and herbivore community structure because of isotopic fractionation during the processes of nutrient assimilation by animals (Bouillon et al., 2011; Jardine et al., 2017).

We used indirect observations and camera traps to understand grazer utilization of nutrient hotspots such as grazing lawns and termite mounds across the year in a Miombo ecosystem of the Issa valley, Tanzania. We focused on selected grazing mammalian species that were expected to preferably graze on these hotpots. Further, we marked five termite mounds with labeled urea and traced stable N isotopes from grasses originating from the mounds to the grazer species' dung. We wanted to (i) assess if the dung deposited around termite mounds originated from grasses growing on these termite mounds and (ii) to understand whether the nutrient input through herbivore dung is accumulated around termite mounds or whether mammalian herbivores act as agents carrying the nutrients away from these nutrient hotspots back into the savanna landscape. We used urea as a tracer, marking grasses that can then easily be detected in herbivore dung based on their isotopic signature as well as camera traps and indirect observations to understand herbivore movements.

2. Methods

2.1. Study area

Our study was conducted in Issa valley, western Tanzania (05° 23 S 30° 35 E; Fig. 1), which consists of steep valleys and flat hill plateaus ranging from 900 to 1800 masl (Stewart, 2011). The area is composed by a mixture of swamps, dry grassland, wooded grassland, woodland, gallery forest, thicket forest and hill forest (Piel et al., 2015). Mean annual rainfall ranges from 900 to 1400 mm and there are two distinct seasons, wet (November–April) and dry (May–October) (Piel et al., 2015). Mean

Fig. 1. Map of Issa valley, western Tanzania, showing camera trap locations at termite mounds, grazing lawns and respective control sites.

annual temperature ranges from 11 °C to 38 °C (Piel, 2014). The grassland in the study area is dominated by *Hyparrhenia hirta, Andropogon gayanus, Digitaria* spp, *Themeda triandra, Panicum repens* and *Oryza longistaminata* (Mayengo et al., 2020) and woodlands are dominated by miombo (*Brachystegia*) and Julbernardia (*Fabaceae*) (Piel, 2014). The main large mammalian herbivores found in the study area are Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), Roan antelope (*Hippotragus equinus*) and reedbuck (*Redunca redunca*) (Mayengo et al., 2020; Piel et al., 2018).

2.2. Data and sample collection

We selected ten active termite mounds and six grazing lawns that were not close to water bodies or near big trees to avoid potential confounding factors (see supplementary information). We further selected ten and six respective control sites that were at least 100 m away from the mounds and from the edge of grazing lawns, respectively (Moe et al., 2009, Fig. 1). We established transects radiating away from each termite mound and grazing lawn centre in all four cardinal directions (N, S, E, W). Along these transects, we quantified dung depositions of the three main grazer species, i.e., hartebeest, Roan antelope, and reedbuck every month over a period of one year (Sept 2016—Oct 2017) in and around grazing lawns, termite mounds and their respective control sites (see supplementary information). The presence of different grazer species was determined by recording cumulative dung depositions (graded as 1-fresh, 2-recent, 3-old) (Curtis, 1995; Liebenberg, 1990). After recording, dung signs were removed to avoid re-counting. Identification of the dung was done according to Stuart and Stuart (2006) and together with the assistance from experienced Tanzanian field assistants. Moreover, two types of motion detecting, infrared triggered cameras (Reconyx HC600 Hyperfire and Bushnell) (Kolowski and Forrester, 2017; Schieltz, 2017), twelve in total, were randomly placed in pairs, with one camera on the hotspot and one in the control area of similar ground cover characteristics (Kolowski and Forrester, 2017, Fig. 1). All cameras were mounted 40 cm above the ground (Kelly and Holub, 2008; Kolowski and Forrester, 2017; Rendall et al., 2014) and about 5 m away from but facing towards the nutrient hotspot centre (Mann et al., 2015), (see supplementary information). About 1 m^2 of vegetation was cleared around each camera to avoid triggers caused by moving vegetation (Kelly and Holub, 2008; Rendall et al., 2014). The distance between camera locations was at least 100 m (Kolowski and Forrester, 2017). Generally, three cameras were placed on different grazing lawns, three on their control sites, three on termite mounds and three on their control sites, thereafter rotated every month to cover all ten termite mounds, six grazing lawns and their respective control sites. Cameras took one photograph per second after the object/animal passed in front of the camera within the field of view (Wearn and Glover-Kapfer, 2017). We recorded the total number of grazer images captured, counted as number of events per hour (Kelly and Holub, 2008), in a particular plot over the year (Zavaleta et al., 2014). If the same animal was photographed more than once by the same camera within 1 h, this was considered as one event (Tobler et al., 2009).

To test whether the isotopic $\delta^{15}N$ signature of dung deposited around termite mounds was more closely related to termite mound grass signatures than to non-termite mound grass signatures we used ^{15}N-Urea. We foliarly sprayed ^{15}N-Urea (Carlo et al., 2009) on grasses around five termite mounds within a quadrat of 2×2 m^2. As weak signatures and impurities might lead to confounding factors in our analyses (Werner et al., 2012) we decided not to rely on potential natural differences in stable N isotopes (Hobson, 1999) but rather to spray isotopically labeled urea. We aimed at retracing the urea back in the collected dung through corresponding $\delta^{15}N$ values. We placed a quadrat of 1 m^2 at a distance of 2 m away from the centre of each mound in all cardinal directions. Within this quadrat, we assessed the proportion of grass partially or fully eaten by herbivores (Treydte et al., 2010), (see supplementary information). We then collected all dung depositions found around termite mounds within a radius of 30 m^2 and recorded their distance away from the mound. About 4–6 fresh dung pellets from hartebeest only were collected for three weeks consecutively after spraying. Grass samples were collected from sprayed grasses near termite mounds and at a distance of 100 m away as a control. We collected a total of 32 dung pellet and 32 grass samples, air dried them (Carlo et al., 2009; Miranda et al., 2014), stored them in paper bags and analysed them at the Food Chemistry Institute, University of Hohenheim, Germany. Grass and dung samples were oven dried at 70 °C for 48 h (Carneiro et al., 2018), homogenized with a milling machine (Namiesnik and Zygmunt, 2003) and 2–3 mg were placed in a tin capsule (Reitsema, 2015). The $\delta^{15}N$ was determined by an Euro EA 3000 Elemental analyzer linked via Thermo FinniganConflo IV continous flow interface with an Delta XP Isotope Mass spectrometer (Ogawa et al., 2010; Reitsema, 2015). N isotope ratios were calculated as $\delta^{15}N$, where δ represents the proportional deviation in (‰) from the international standard (atmospheric N_2) (Qi et al., 2016): $\delta = 1000((R_{sample}/R_{standard}) - 1)$, where R is the ratio of heavy to light isotopes (Markow et al., 2000). For calibration and quality control of $\delta^{15}N$ values the international reference material USGS40 (δ15N −4.52‰) and glutamic acid laboratory working standard were used. Each sample was replicated once to avoid errors (Peters, 2001; Reitsema, 2015). Standard deviations for $\delta^{15}N$ were less than 0.1‰ (Rennie et al., 1975).

2.3. Data analysis

We averaged the presence of the three grazer species based on cumulative dung depositions over the ten termite mounds, six grazing lawns and their respective control sites and tested for normality. Camera trap data were grouped into months, and categorized into dry and wet season for both hotspot and non-hotspot areas. We used a Generalized Linear Mixed Model (GLMM) to assess the effect of dung deposition as dependent variable, with season (wet vs dry) and location, i.e., nutrient hotspot vs non nutrient hotspot, and their respective interactions. Further, isotopic signatures of urea sprayed grass and isotopic signatures of dung deposited within 30 m from the sprayed grass were compared using one-way ANOVA (Miranda et al., 2014). Tukey's Post-hoc test was used in all statistical tests, significance levels were set at $\alpha = 0.05$. Software used was Origin Pro 8 (Serrano et al., 2011) and SPSS version 20 (Treydte et al., 2007).

3. Results

Herbivore presence using indirect observation (dung) was about three times higher in hotspots vs control areas ($F_{1,22} = 34.51$, $P < 0.0001$), with twice as many dung depositions found at hotspots during the dry season than during the wet season ($F_{3,2\ 0} = 10.7$, $P = 0.0002$; Fig. 2). Of all dung depositions recorded, Roan antelope dung constituted 43%, hartebeest dung 40% and reedbuck dung 17%. Seasonal differences were mainly visible in hotspot areas but not in the respective control sites, highlighting the temporal importance of these hotspots (Fig. 2).

Our Generalized Linear Mixed Model (GLMM) showed that season alone had no significant effect on dung depositions ($F_{1,\ 48} = 0.01$, $P = 0.04$), while location, i.e., nutrient hotspot vs non nutrient hotspot, did ($F_{3,\ 48} = 27.37$, $P < 0.0001$) and the interaction of season and location was also significant ($F_{3,\ 48} = 5.55$, $P < 0.005$). Herbivore dung around termite mounds over the year differed significantly between grazer species using one way ANOVA ($F_{2,\ 9} = 4.84$, $P = 0.037$; Fig. 3 a), with Roan antelope highly preferring the termite mounds. Dung deposition frequencies did not differ significantly between the three grazer species for grazing lawns ($F_{2,\ 18} = 1.77$, $P = 0.198$; Fig. 3 b). The number of dung depositions was higher close to termite mounds compared to far away from mounds ($F_{1,\ 174} = 146.77$, $P < 0.0001$; Fig. 3 c), with the same patterns seen for grazing lawns ($F_{1,\ 1628} = 1382$, $P < 0.0001$; Fig. 3 d).

Herbivore presence based on camera trap data was four times higher in hotpots (both termite mounds and grazing lawns combined) vs control areas ($F_{1,\ 18} = 11.93$, $P = 0.0028$; Fig. 4 a). Around termite mounds only, animals were captured four times more frequently than in control sites ($F_{1,\ 18} = 10.23$, $P = 0.004$), and the same pattern was visible for grazing lawns ($F_{1,\ 18} = 6.05$, $P = 0.024$; Fig. 4 b). Herbivore images captured during the wet season were thirty two times higher around termite mounds ($F_{1,\ 8} = 16.71$, $P = 0.003$) and grazing lawns ($F_{1,\ 8} = 2.33$, $P = 0.16$; Fig. 4 b) compared to the respective control sites, (see Table 1). Herbivore images captured during dry season were not significantly different around termite mounds compared to controls ($F_{1,\ 12} = 0.09$, $P = 0.76$) and grazing lawns were six times higher than their controls ($F_{1,12} = 3.78$, $P = 0.07$; see also Table 1).

There was a statistical difference in $\delta^{15}N$ between urea sprayed grass, control grass and dung deposited within a 30 m radius around the termite mounds ($F_{2,\ 45} = 40.23$, $P < 0.0001$). Tukey's post hoc analysis showed no difference between urea sprayed grass and dung (Fig. 5). Urea sprayed grass around termite mounds had about twice as high values in $\delta^{15}N$ compared to unsprayed grass in controls ($F_{1,\ 28} = 39.07$, $P < 0.0001$). Further, there was a positive correlation between $\delta^{15}N$ of dung deposited close to the mounds than far away from mounds ($F_{1,\ 30} = 3.84$, $R^2 = 0.347$, $P = 0.059$; Fig. 6).

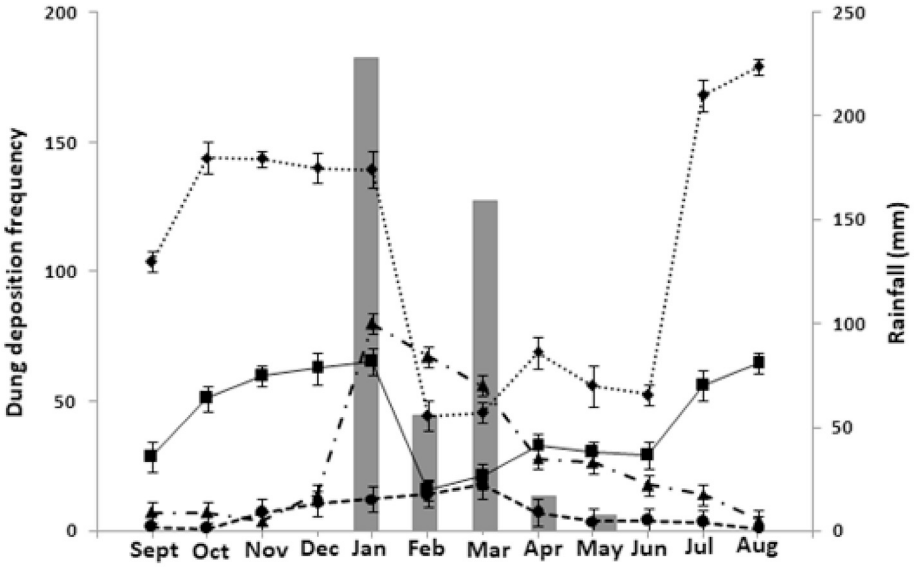

Fig. 2. Rainfall amount in mm (histogram) at the Issa valley in the year 2016–2017 and herbivore presence according to the average dung depositions frequency overall in numbers in grazing lawns (rhombus with round dotted line), non grazing lawns (rectangle with solid line), termite mounds (triangle with dash-dot line) and non termite mounds (circle with dashed line) across different months. Tips of the whiskers indicate standard deviation.

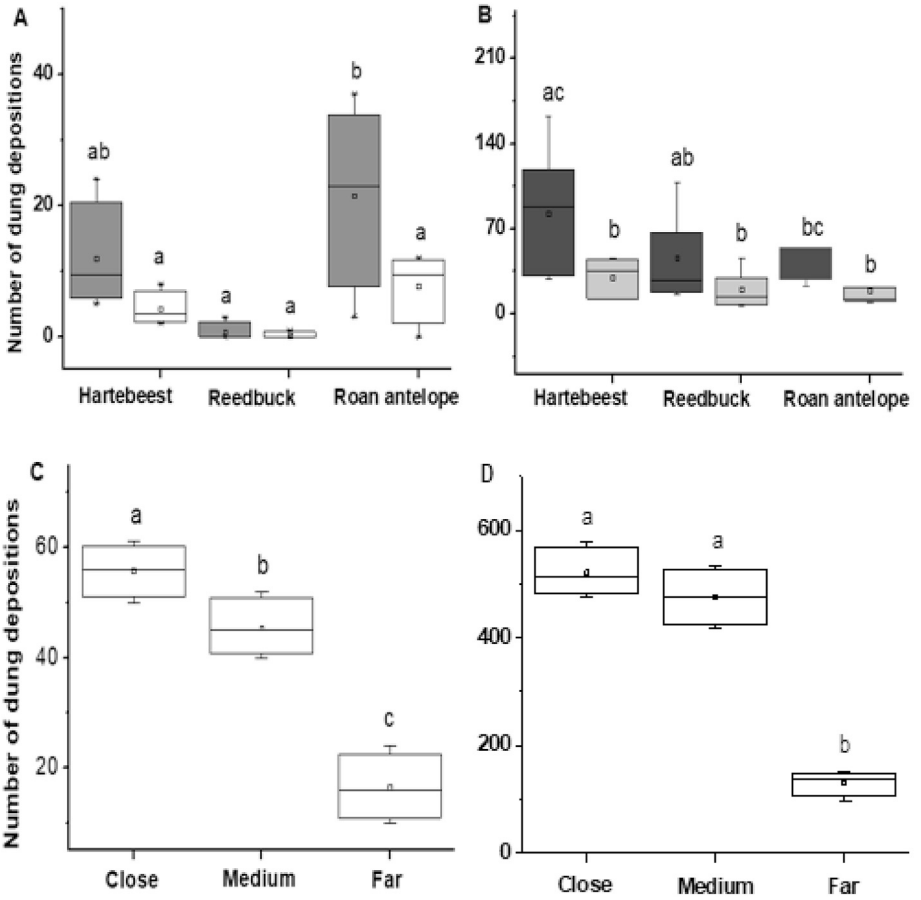

Fig. 3. (A) Mean (±SE) dung frequencies of hartebeest, reedbuck and Roan antelope around termite mounds (grey boxes) and controls (white boxes). (B) Mean (±SD) dung frequency of hartebeest, reedbuck and roan antelope around grazing lawns (black boxes) and controls (grey boxes) and dung deposition frequency against distance categories away from termite mounds (C) and grazing lawns (D), where 0–10 m = Close, 11–20 m = Medium, and 100 m = Far. Boxplots show the mean (a square within boxes) and ranges from 25% to 75% quartile, and the tips of the whiskers indicate standard deviation. Boxes with different letters are significantly different by Fisher *LSD* at $P < 0.05$.

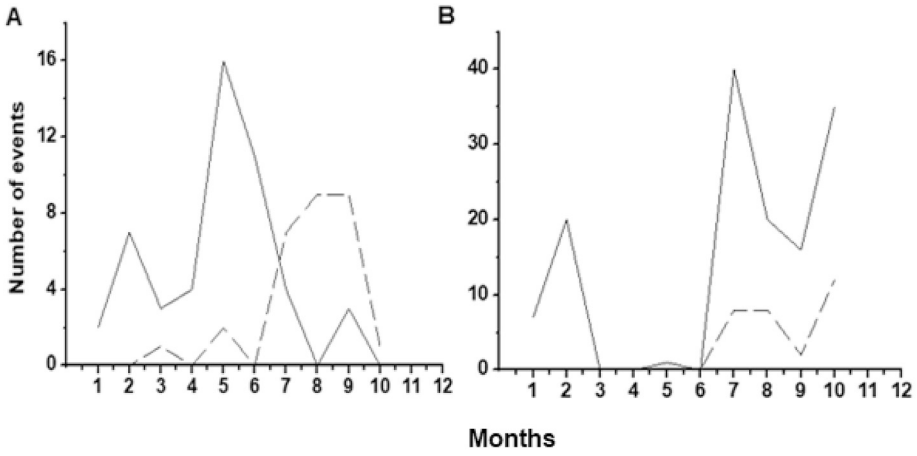

Fig. 4. Animal visitation as number of event per hour captured by camera traps (A) around termite mounds (solid line) vs non termite mounds (dashed line) and (B) around grazing lawns (solid line) vs non grazing lawns (dashed line). If the animal was photographed more than once by the same camera within 1 h, this was considered as one event. Animal visitation events did not differ significantly between night and day in hotspots ($F_{1,\ 30} = 0.42$, $P = 0.518$).

Table 1
Animal species that were captured by camera traps in hotspot areas from May 2016–October 2017. If the animal was photographed more than once by the same camera within 1 h, this was considered as one event.

			capture events	
Taxonomic group	Scientific name	Common name	Dry season	Wet season
Primates	*Papio cynocephalus*	Yellow baboon	2	3
	Pan troglodytes schweinfurthii	Chimpanzee	1	0
Ungulates	*Potamochoerus porcus*	Bushpig	2	2
	Tragelaphus scriptus	Bushbuck	0	10
	Alcelaphus lichtensteinii	Hartebeest	49	10
	Oreotragus oreotragus	Klipspringer	1	11
	Redunca redunca	Reedbuck	129	32
	Hippotragus equinius	Roan antelope	32	16
Carnivora	*Mellivoria capensis*	Honey badger	1	1
	Panthera pardus	Leopard	0	1
	Crocuta crocuta	Spotted hyena	1	0
	Civettictis civetta	African Civet	5	0
	Genetta angolensis	Miombo genet	6	0
	Herpestes ichneumon	Mongoose	1	0
Rodents	*Hystrix africae-australis*	Porcupine	7	0

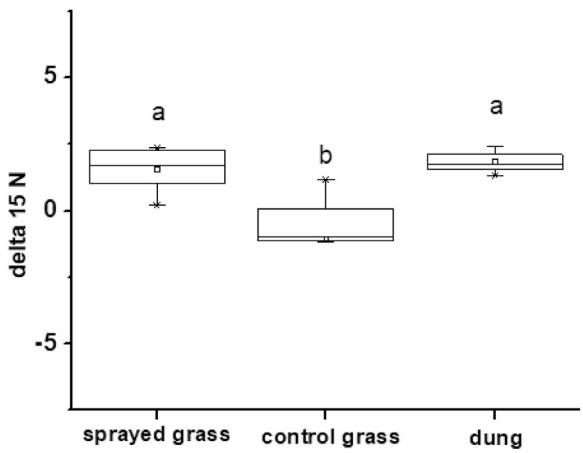

Fig. 5. Isotopic $\delta^{15}N$ plot of urea sprayed grass (termite mound grass) vs unsprayed grass in controls and vs hartebeest dung deposited within a 30 m radius from urea sprayed termite mounds. Boxplots show the mean (a square within boxes) and ranges from 25% to 75% quartile, and the tips of the whiskers indicate standard deviation. Boxes with different letters are significantly different by Fisher LSD at $P = 0.05$.

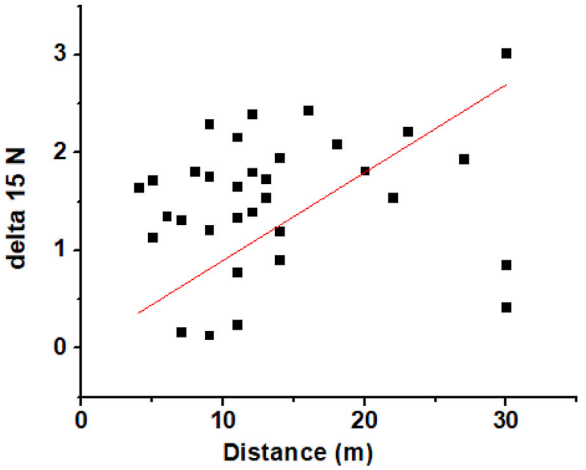

Fig. 6. A. Isotopic $\delta^{15}N$ in dung deposited with 30 m radius from urea sprayed termite mounds against the distance at which dung was deposited away from the termite mound centre ($F_{1,\ 30} = 3.84$, $R^2 = 0.347$, $P = 0.059$).

4. Discussion

Our results show that the high nutrients in and around termite mounds are likely enhanced through mammalian grazers via their dung deposition and grazing activity, as was the case for grazing lawns. We also showed that grazer dung deposited around termite mounds is isotopically similar to sprayed grasses around termite mounds, which, in combination with our other indirect and direct observations, indicates that dung deposited around termite mounds likely originated from grasses growing on these termite mounds. This would agree with findings by Treydte et al. (2006b), who concluded that ungulates might be responsible for maintaining stability of nutrient hotspots that had been created by former cattle bomas. Grazing herbivores normally deposit dung frequently at specific locations in nutrient rich sites (Veldhuis et al., 2017a, 2017b). Herbivores were found to highly use termite mounds based on their dung depositions (Brody et al., 2010) affecting spatial heterogeneity in soil across the landscape at large (Levick et al., 2010; Veldhuis et al., 2017a, 2017b) by creating islands of fertility. Experimental work has shown that urine patches can also alter $\delta^{15}N$ values in the short term (Tonn et al., 2019).

Grass species are generally low in $\delta^{13}C$ and $\delta^{15}N$ values as was found in various studies (Ehleringer, 1991; Wooller et al., 2007; Treydte et al., 2006b). We enriched our termite mound grasses in $\delta^{15}N$ by spraying urea, which marked these grasses with a higher isotopic value compared to the surrounding, unsprayed grasses. These higher $\delta^{15}N$ were likely reflected in the dung values of the hartebeest in our study. Higher isotopic levels of dung were also obtained by Treydte et al., (2006b), who concluded that this might indicate the location of foraging due to a different local isotopic signature. The hartebeest is a typical grazer (Schuette et al., 2006), and does generally not forage on legumes, which are more enriched with $\delta^{15}N$ (Wanek and Arndt, 2002). This highlights that the hartebeest in our study foraged on our sprayed termite mound grass rather than on forbs or leguminous tree species that might have shown higher $\delta^{15}N$ values naturally. However, we recommend future microhistological studies to identify the individual grass species eaten as well as direct foraging observation studies of grazer species to confirm origins of the dung as well as precise foraging locations and plant species. Further, DNA metabarcoding could be applied in addition to our approach as it provides the greatest resolution of dietary items (Garnick et al., 2018). While this was not possible due to time and financial constraints, we did combine our isotope work with camera traps, indirect observations and other experimental work (Mayengo et al., 2020), which supports our results and highlights the power of isotopic work for foraging ecology in African ungulates (see also Rysava et al., 2016) and other herbivores.

Further, we found that season had a strong effect on whether a nutrient hotspot was visited by mammalian herbivores or not. Since rainfall strongly affects vegetation quality (Okitsu, 2005) and, accordingly, distribution of foraging herbivores (Ogutu and Owen-Smith, 2003; Knape and de Valpine, 2011), we expected seasonal differences in nutrient hotspot use. Our results showed that dung depositions on the grazing lawns were highest during the dry season compared to the wet season, similar to results by Tate et al. (2003), who found highest depositions of cattle dung around hotspots during the dry season in Sierra Nevada foothills, California, USA. In their study, cattle dung distribution patterns were significantly associated with location of livestock attractants, slope, hydrologic position, and season (Tate et al., 2003). In another study conducted in Japan, Hirata and Higashiyama (1997) found higher concentrations of Japanese Black heifers' and steers' dung around resting sites but their study lacked a seasonal component. Further, our study showed higher herbivore dung depositions around termite mounds during the wet season (see also Mayengo et al., 2020), and concentrated close to the termite mounds, indicating that this was also the herbivores' feeding location. These findings are similar to (White-Leech et al., 2013), who found livestock dung concentrated around shade, water, and feeding locations.

We found that not only grazers but also mixed feeders were attracted by vegetation around termite mounds, in agreement with research conducted in Zimbabwe by Holdo and McDowell (2014), who found that elephants were highly using trees

growing around termite mounds due to their higher concentration of nutrients compared to surrounding vegetation matrix. Further, chimpanzees in Issa valley, western Tanzania, were found to use flexible fishing probes to fish termites in various termite mounds (Stewart and Piel, 2014). Hence, particularly termite mounds in Issa valley are likely to be attractive feeding and resting grounds for a large variety of iconic and endangered species. While it is known that different termite species built different mound types and influence soils in various ways (Enagbonma and Babalola, 2019), we were not able to investigate the influence of different species of termites on grass quality and how grazers respond towards them, which might be an interesting future topic for research.

Heterogeneity in African savannas is attributed by different abiotic and biotic factors (Odadi et al., 2018;). For example, precipitation, fire and herbivory affect savanna vegetation structure and composition (Odadi et al., 2018; Sankaran et al., 2005) as well as variation in topography and soil characteristics (Baldeck et al., 2014; Odadi et al., 2018). Our results confirmed that hotspots act as a key feeding resource for wild animals (Anderson et al., 2010). Our dung deposition results showed that the mammalian herbivores used hotspot areas up to four times more frequently than the control sites, which is in agreement with other studies on sites with highly nutritious forage, e.g., as can be found in areas of abandoned cattle grazing (Davies et al., 2016), or around termite mounds (Mayengo et al., 2020; White et al., 2016).

Further, as we expected, herbivores grazed more intensively around nutrient hotspots, and added more dung, and probably urine, around these hotspots. This is in contrast to (Gillet et al., 2010) who found low grazing intensity on nutrient hotspots compared to their surroundings in a temperate climate of the Jura Mountains of north-western Switzerland. The grazed nutrient hotspots in Issa valley might, thus, attract even more herbivores to visit the area (Moe and Wegge, 2008; Day and Detling, 1990). Since dung and urine depositions highly affect chemical composition of soil and grasses (Moe and Wegge, 2007) as well as plant productivity (Williams and Haynes, 1990) these nutrient hotspot areas strongly support mammalian herbivore species (Grant and Scholes, 2006), especially in nutrient poor areas like savanna soils.

We also found that roan antelope and hartebeest deposited more dung around hotspots than reedbuck did, which might be due to their relative numbers within our study area, which was confirmed by our camera trap events. However, data on the population estimates of different ungulate species in Issa valley are missing (Piel et al., 2018). Since Roan antelope and hartebeest are larger in size than reedbuck, they might need a higher amount of good quality food from nutrient rich areas (Shipley, 1999), and they were found to frequently return to previously visited areas (Morales et al., 2005). Large herbivore grazing is affected by abiotic factors such as slope and distance to water (Senft et al., 1996) as well as biotic factors such as forage quality and quantity (Bowyer et al., 1998; Senft et al., 1996; Treydte et al., 2006a). However, for large herbivores such as roan antelope and hartebeest, foraging velocity decreases and intake rate increases once they reach areas of abundant palatable grass (Senft et al., 1996), which was confirmed by our results.

In our study, we used a combination of animal presence estimates using dung depositions (Treydte et al., 2010) and camera traps (Rendall et al., 2014). The use of camera traps in ecological studies has increased (Wearn and Glover-Kapfer, 2017) and is an effective measure for monitoring wild animals in a non-invasive way (Ancrenaz et al., 2012; Kays et al., 2009; Rendall et al., 2014). Camera trap footage showed higher animal activity around grazing lawns during the dry season than during the wet season, and higher animal activity during the rainy season compared to the dry season around termite mounds, which might be due to the shifting quality of foraging resources (Anderson et al., 2010) around hotspots across different seasons. Camera trap images showed that reedbuck and hartebeest were frequently visiting the grazing lawns, which might be due to high nutrient availability in these areas (Cromsigt and Olff, 2008) or the lower susceptibility to predation (Anderson et al., 2010). Reedbuck strongly prefer flat, low lying land (Kingdon and Hoffmann, 2013), and hartebeest prefer short grasses (Schuette et al., 2006) in low lying areas, which were represented by and found on our grazing lawns.

Our stable isotope technique, a method rarely used for terrestrial ecological studies in eastern Africa, highlighted spatial distribution of foraging and defecating of wild animals with respect to plant nutrient distribution. Isotope Ratio Mass Spectrometry (IRMS) is a novel approach used to provide useful information on the chemical and biological origin of various components (Muccio and Jackson, 2009; Reitsema, 2015). Measurement of isotope ratios can effectively be used to differentiate samples, which otherwise share similar chemical signatures (Muccio and Jackson, 2009). However, uncertainty may occur over the relative contribution of diet and water to tissue (Jardine et al., 2017), which might cause isotopic differences locally and temporally. Hence, a strong initial spatial difference in isotopic composition is of high advantage as it shows the differences between herbivore species and their respective diet (Hobson, 1999). This fact made us use urea spray in order to clearly show the link between grazer and their forage.

Since we did not use an adhesive after spraying urea and because we conducted this study during the rainy season our results might have been affected and effects weakened due to rain events (Carlo et al., 2009). In addition, physiological and metabolic processes within herbivores after eating grass might also have affected our results, diluting potentially strong differences (Zanden et al., 2014). However, our results still show strong isotopic differences between sprayed and unsprayed grasses, and suggest similarities between dung and hotspot grasses, in combination with our other studies in the area (Mayengo et al., 2020). Hence, we claim that our isotopic data strength provided an important cue in highlighting spatially determined foraging resources (Ballantyne et al., 2011).

Understanding how nutrients are transferred from high nutrient areas to low nutrient areas is an important aspect in ecology (Holtgrieve et al., 2009). As dung depositions can be used as proxy for describing habitat use of feeding mammalian wildlife (Treydte et al., 2006a), patterns of nutrient cycling and impacts on forage quality can show the long-term maintenance of high fertility sites in these areas (McNaughton et al., 1997; Treydte et al., 2006a), promoting a positive feed-back loop (van der Waal et al., 2011).

We are aware that hotspot size can affect species diversity (Cook et al., 2014), and our results here provide only a snapshot of grazer activity, grass and soil properties as well as nutrient cycling. Our grazing lawns were about 1 ha in size (70 × 70 m), while the termite mound influence areas were about 30 × 30 m (Moe et al., 2009). However, we showed that termite mounds, despite being small in size, still can act as small grazing lawns that grazers preferably feed on, hence, increasing nutrient cycling through their dung depositions (Cromsigt and Olff, 2008). These results were confirmed by our camera trap data, revealing that herbivores frequently used hotspot sites. Hence, our combination of various data assessment methods proved to be an effective and efficient way in understanding how wild mammalian herbivores use hotspot areas.

With our study we could show that herbivores enrich nutrient hotspots even more (Augustine et al., 2003), highlighting the importance of these feeding grounds, and, thereby, ensuring long-term persistence of the latter in savanna ecosystems. Furthermore, the extent to which these feeding grounds, i.e., termite mounds and grazing lawns, are important to grazers will depend on the their density and distribution patterns in a particular habitat (Holdo and McDowell, 2014).

Declaration of competing interest

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01073.

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