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Effects of Plant Species Diversity and Biomass on Grazing Patch Selection by Semi Free-Ranging Cattle

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Abstract

Studies examining forage selection by large herbivores have generally focused on single herbivore-plant relationships and few studies link plant species diversity with large herbivore feeding preferences, particularly in species-rich ecosystems. A study was therefore conducted to examine how herbaceous plant biomass, species richness, diversity and evenness, together with elevation and distances to houses, agricultural fields and cattle holding-pen areas (kraals), predict cattle grazing intensity at small (0.5 x 0.5 m) and large (20 x 50 m) patches by semi free-ranging indigenous cattle in Kilombero Valley Floodplain wetland Tanzania. Results showed that cattle grazed patches with high species richness and intermediate level of biomass at a small spatial scale, suggesting that selection of small patches is a trade-off between food quality and quantity. On a larger scale, cattle grazed patches with a higher abundance of palatable plant species with high biomass, but with less plant species diversity. Moreover, grazing intensity in large patches was positively related to elevation and distance from agricultural fields. Overall, this study shows that considering both plant community properties and physiographic variables in forage selection studies facilitates a better understanding of grazing ecology of large domestic herbivores in species-rich ecosystems. Thus, maintenance of plant species richness and biomass in wetland rangelands is important to improve domestic herbivore production and conservation of biodiversity.

Keywords: Domestic herbivore; Forage selection; plant-animal interaction; Rangelands; Species richness.

Introduction

Large herbivores utilize food resources unevenly by feeding more intensively in some areas than others in heterogeneous environments (Bailey 1995, Bailey et al. 1998, Wang et al. 2010a, Milligan and Koricheva 2013). Several theories have been proposed to describe foraging behaviour and associated grazing patterns among herbivores. According to optimal foraging theory, diet selection is a trade-off between benefits of ingesting a particular food resource and the cost of obtaining it (Stephens and Krebs 1986). Thus, for herbivores to meet their optimal nutritional requirements, diet selection must focus on a variety of plant species with different nutritional quality and quantity, and diet choices therefore operate at different spatial and temporal scales. Since a single plant species will not meet the nutritional demands of animals, large herbivores usually switch between alternative plant species to diversify their diet during foraging (Simpson et al. 2004, Wiggins et al. 2006). According to the nutrient balance hypothesis, dietary diversity allows individual herbivores to balance the intake of different nutrients (Westoby 1978), which consequently improves their performance and growth (Simpson et al. 2004, Unsicker et al. 2008). Switching among plant species during foraging may also buffer the animal against accumulation of digestion-inhibiting compounds or toxic secondary metabolites that could be present in the consumed foliage (Freeland and Janzen 1974, Milligan and Koricheva 2013).

For small invertebrate herbivores (e.g. arthropods), changes in plant community properties, particularly reduced species diversity, may negatively affect their abundance, diversity and performance (Scherber et al. 2006, Unsicker et al. 2008). Okullo et al. (2013) found that diversity of small savannah mammals increased with herbaceous species evenness and diversity, and that their biomass increased when few plant species dominated the herbaceous species assemblage. Moreover, the maintenance of plant species richness is critical to improve nutritional status, performance and overall production of large herbivores (Gordon and Prins 2008, Wang et al. 2010b, Milligan and Koricheva 2013). This suggests that plant community properties affecting forage quality and quantity, such as plant biomass, species richness, diversity and evenness, may determine feeding site selection by large herbivores.

Besides plant community properties, physiographic factors, such as slope and distance to congregation areas, may also influence feeding site selection by large herbivores (Bailey et al. 1998). In general, domestic herbivores tend to avoid steep slopes and feeding sites far away from congregation areas, such as camp sites and water sources (Bailey et al. 1996, Tarhouni et al. 2010). Moreover, the synthesis of mechanisms behind the grazing distribution patterns of large herbivores, Bailey et al. (1996) pointed out that plant community properties associated with forage quality and quantity is the main determinant of grazing patterns at small spatial scales, while physiographic factors predict grazing patterns at large scales. Overall, this suggests that the two sets of factors (plant community properties and physiographic variables) potentially explain the spatial variations in grazing intensities, and that large herbivores are more likely to visit species-rich patches and sites close to their congregation points more frequently than species poor patches and distant sites (Bailey 1995, Bailey et al. 1998, Tarhouni et al. 2010).

Studies on forage selection by large herbivores have generally focused on relationships of single species of herbivores and plants and studies linking plant species diversity with large herbivore feeding preferences are only starting to emerge. Two notable exceptions are the study by Milligan and Koricheva (2013), who found that browsing moose (*Alces alces*) preferred species-rich sites, and Wang et al. (2010b), who documented an asymptotic relationship between sheep (*Ovis aries*) food intake and plant species richness. In this study, the determinants of foraging decisions by bulk feeding semi-free ranging cattle were investigated in the Kilombero wetlands in Tanzania. Specifically, plant community properties (biomass, species richness, evenness and diversity) and physiographic variables (elevation, distances to houses, agricultural fields and kraals) were related to cattle grazing intensity at large (20 x 50 m) and small (0.5 x 0.5 m) feeding sites. It was predicted that: (a) plant community properties would be important for grazing intensity at a small spatial scale, while physiographic variables explain variations in grazing intensities at large patch sizes; consistent with Bailey et al. (1996); (b) since plant species richness offers an opportunity for large herbivores to optimize their nutrient balance (Wang et al. 2010b), grazing intensity at small spatial scale would be explained best by species richness, evenness and diversity, and (c) since biomass is significant important to bulk feeding cattle (Belovsky 1997), it would be an important determinant of spatial variations in grazing intensities at the small spatial scale.

Materials and methods

Location of the study area

The study area, Kilombero Valley Floodplain wetland, is situated in the Morogoro Region in Ulanga and Kilombero Districts, in the south-central Tanzania and found between longitude 8° 32′ 0″ S and latitude 36° 29′ 0″ E (Figure 1). The Kilombero wetland is the largest lowland freshwater wetland in East Africa rich in biodiversity that made it be declared a Ramsar site in 2002 (Ramsar 2020). The wetland is also ecologically important as it adjoins the Great Selous Ecosystem, a World Heritage Site. It covers an area of 7,967 km^2 at an elevation of 210-400 meters (Ramsar 2020). The area experiences sub-humid tropical climate with a mean annual temperature of 26 °C and a mean annual rainfall of 1200-1400 mm (Kangalawe and Liwenga 2005). At Kilombero, light and sporadic rainfall occurs usually between December and February, while heavy and regular rainfall occurs between March and June. The Kilombero wetland supports diverse livelihood activities, including agriculture, fisheries and livestock keeping (Kangalawe and Liwenga 2005). Among the livestock (cattle, sheep, goats and donkeys), cattle is the most abundant (about 300,000 individuals in an area of 37,058 km^2), with the indigenous Tanzania shorthorn zebu cattle (Sukuma and Maasai strains) being dominant. Cattle are released in the morning as semi free-ranging livestock and are herded back to kraals every evening. A more detailed description of the study area was given by Andrew et al. (2012).

Although the actual number of plant species is not known in the Kilombero wetland, at least 350 plant species are documented from the area comprising riverside, papyrus (*Cyperus papyrus* L.) swamps, low-lying valley grasslands, tall grasslands, marginal grasslands, marginal woodlands, combretaceous wooded grasslands and miombo woodlands plant communities (Starkey et al. 2002). The marginal grasslands, with intensively grazed short herbaceous vegetations, were the focus of this study because they form a substantial portion of the wetland. Agro-pastoralists have grazed their cattle in these grasslands at least over the last two decades. The marginal grasslands contain a large number of plant species which is 33% of all species reported in the wetland including economically important fodder species (Andrew et al. 2012).

Vegetation sampling and physiographic variables

Following a preliminary survey conducted in 2009/2010, 60 plots of 20 x 50 m each from different areas of the marginal grasslands were randomly selected to assess the livestock grazing pattern in relation to plant community properties and physiographic variables. Using a table of random numbers and compass bearings (1–360°), twenty 0.5 x 0.5 m quadrats were established in each plot. In each quadrat, species cover and identities were recorded using the point intercept method (Bråthen and Hagberg 2004). A point intercept table 0.5 m long, 0.5 m wide and 0.5 m high was placed above each quadrat and a 0.003 m diameter and 0.8 m long pin inserted vertically through 25 points spread uniformly on the grid. All contacts each species made with the pin (i.e. even when the same individual was in contact with the pin more than once) was recorded to estimate the cover of each species (Frank and McNaughton 1990). In addition, all grazed foliar parts that contacted the pin were recorded. Plant species were identified at the National Herbarium of Tanzania in Arusha, where all voucher specimens are deposited. Elevation of plots was estimated at the centre by a hand held calibrated global positioning system (GPS). The distances between plots and the three closest kraals were measured by GPS and the mean distance was used in the analyses. Distances between a plot and nearest agricultural field and house were estimated visually.

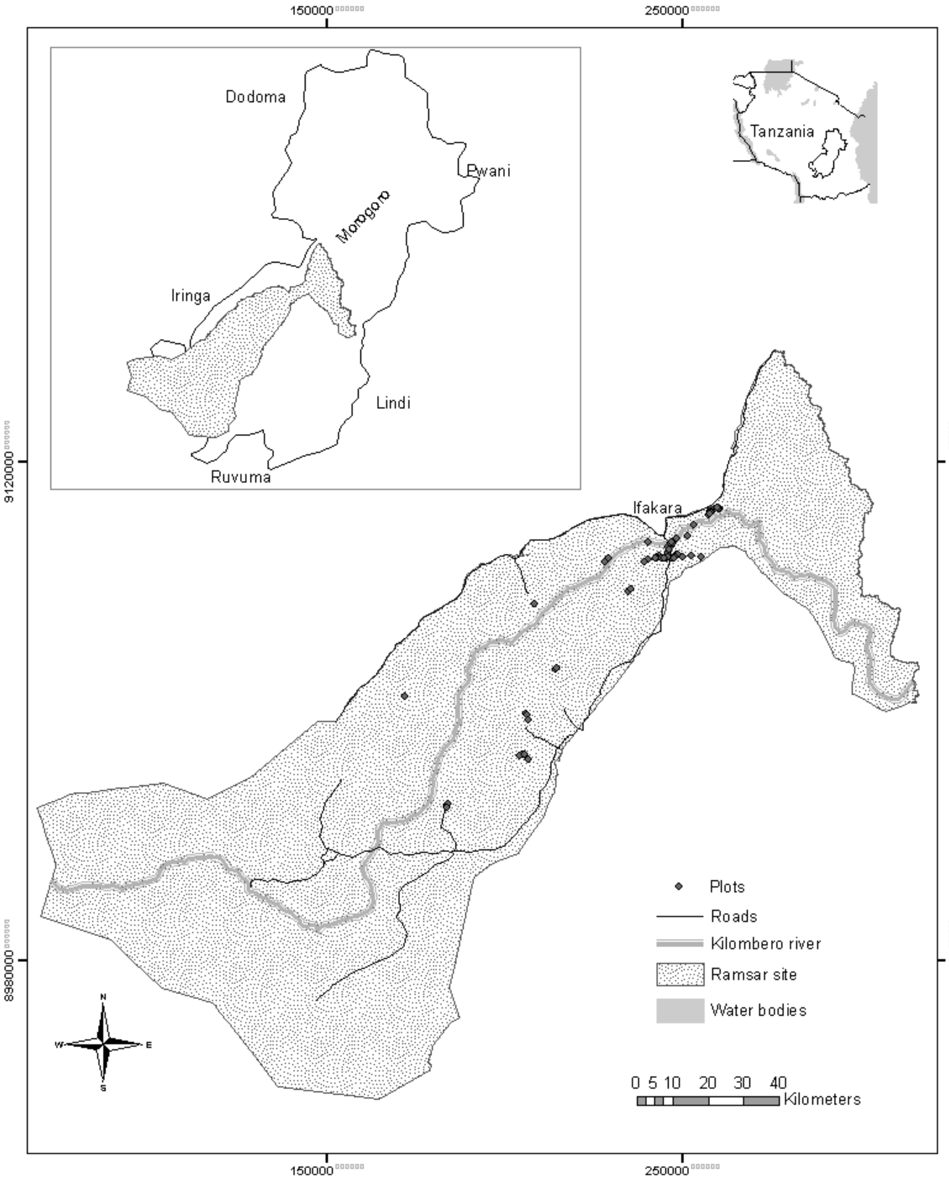

Figure 1: Map showing location of Kilombero Valley wetland in Morogoro Region, Southern-central Tanzania.

Data analyses

To obtain vegetation data for plots, the total number of contacts per species over all quadrats was used. Data matrices of plant biomass, species richness, evenness, diversity, elevation and distances to house, kraal and agricultural field and grazing intensity for quadrats (small patches) and plots (large patches) were created. In this case, all the plant species were considered in the computation of community properties in each patch type. A separate data matrix of community properties and physiographic variables for large patches where only grazed plant species were considered was also created. Finally, using the three matrices (i.e. all species together in small and large patches, and all grazed species in large patches), a relationship between livestock grazing and within-patch plant community properties and physiographic variables was established. Richness was obtained by adding the total number of species that made contacts with the pin. The Shannon diversity index was computed with *Biodiversity R* package (Kindt and Coe 2005) and evenness as $E = H'/\ln S$ where S is the number of species (Magurran and McGill 2011). Grazing intensity was obtained from the total number of grazed leaves. The sum of the number of pin hits was used as a measure of biomass in each data matrix (Bråthen and Hagberg 2004).

Information-theoretic model selection and multi-model procedure (Burnham et al. 2011) was used to examine how community properties and physiographic variables may influence the grazing patterns of animals. Multi-model inferences avoid overlooking alternative models that could have nearly equivalent fit to the single most parsimonious model (Burnham and Anderson 2002). To determine the most parsimonious model therefore, a set of candidate models were developed (for each patch type) using a linear combination of non-correlated (Pearson Product Moment Correlation, $r < 0.50$), quadratic (second order) and interaction terms of community properties and physiological variables, and the grazing intensity. Some of the plant community properties, such as species richness and diversity were strongly correlated at the small ($r = 0.87$, $p < 0.05$) and large ($r = 0.70$, $p < 0.05$) patch scales when all the species were considered. Moreover, species evenness was strongly correlated with species diversity at the small ($r = 0.68$, $p < 0.05$) and large ($r = 0.85$, $p < 0.05$) patch scales when all the species were analysed. Consequently, these variables (species richness, diversity and evenness) were not included in the same candidate models. The standard model-fitting and adequacy checking procedures to fit each model was adhered to. Backward elimination was used to find the best model for each response variable by removing first the interaction terms, then quadratic and lastly linear terms (Crawley 2007). After fitting each of the candidate models, change in Akaike information criterion (ΔAICc) and Akaike weight (*W*i) for all the models was computed using *AICcmodavg* package in R (R Development Core Team 2017). Final model with the lowest ΔAICc or the highest *W*i was selected as the most parsimonious (Burnham and Anderson 2002, Burnham et al. 2011). Finally, simple linear regressions were used for large patches on the most parsimonious models to establish the relationship between grazing intensity and community properties and physiographic variables. Because of the nesting structures of the data on small patches, generalized linear mixed models (GLMMs) analysis was employed on the most parsimonious model to establish the relationships between grazing intensity and community properties and physiographic variables at this spatial scale (Crawley 2007). In the GLMMs analysis, function *lmer* was used in the package *lme4* (Bates 2005) and plot was used as a random effect. All the statistical analyses were performed using R statistical software (R Development Core Team 2017).

Results

Herbaceous community composition

A total of 115 plant species were recorded in the Kilombero grasslands. Of these, only twenty-two species (Table 1) were grazed by cattle. *Echinochloa colona*, *Paspalum scrobiculatum*, *Digitaria velutina*, *D. ternata*, *Panicum maximum*, *Brachiaria deflexa*, *Sporobolus pyramidalis* and *S. ioclados* (all Poaceae) were the most intensively grazed species (Figure 2) and together they comprised more that 53% of the total cover of all the species in the area.

Table 1: Herbaceous plant species grazed by cattle at Kilombero wetland, Morogoro, Tanzania

Scientific name	Grazing intensity level (%)	Growth form	Functional group	Family
Brachiaria comata (A. Rich.) Stapf	0.7	Grass	Graminoid	Poaceae
Brachiaria deflexa (Schumach) Robyns	7.5	Grass	Graminoid	Poaceae
Crotalaria spp.	0.2	Shrub	Shrub	Fabaceae
*Cynodon nlemfuensis*Vanderyst	2.8	Grass	Graminoid	Poaceae
Digitaria ciliaris (Retz.) Koel.	1.9	Grass	Graminoid	Poaceae
Digitaria longiflora (Retz.) Pers.	2.3	Grass	Graminoid	Poaceae
Digitaria ternate Stapf.	3.4	Grass	Graminoid	Poaceae
Digitaria velutina (Forssk) P. Beauv.	5.9	Grass	Graminoid	Poaceae
Echinochloa colona (Linn.) Link	32.7	Grass	Graminoid	Poaceae
Echinochloa haplocloda (Stapf.)	2.7	Grass	Graminoid	Poaceae
Eragrostis cilianensis (All.) Lutati	0.3	Grass	Graminoid	Poaceae
Hygrophila auriculata (Schumach) Heine	0.3	Forb	Forb	Acanthaceae
Mellinis minutiflora P. Beauv.	1.9	Grass	Graminoid	Poaceae
Oryza punctata Steud.	2.0	Grass	Graminoid	Poaceae
Panicum maximum Jacq	4.8	Grass	Graminoid	Poaceae
Paspalum scrobiculatum L.	19.6	Grass	Graminoid	Poaceae
Pavonia flavoferruginea (Forssk.) Hepper and J.R.I. Wood	0.4	Shrub	Shrub	Malvaceae
Pynostachys ruandensis Del. Wild	0.2	Forb	Forb	Labiatae
Sida rhombifolia L.	0.2	Forb	Forb	Malvaceae
Sporobolus iocladus (Trin.) Nees	3.4	Grass	Graminoid	Poaceae
Sporobolus pyramidalis P. Beauv.	4.7	Grass	Graminoid	Poaceae
Urochloa mossambicensis (Hack.) Dandy	2.2	Grass	Graminoid	Poaceae

Grazing intensity level is the ratio between number of grazed leaves of individual species and the total number of grazed leaves for all the grazed species (22) in percentages.

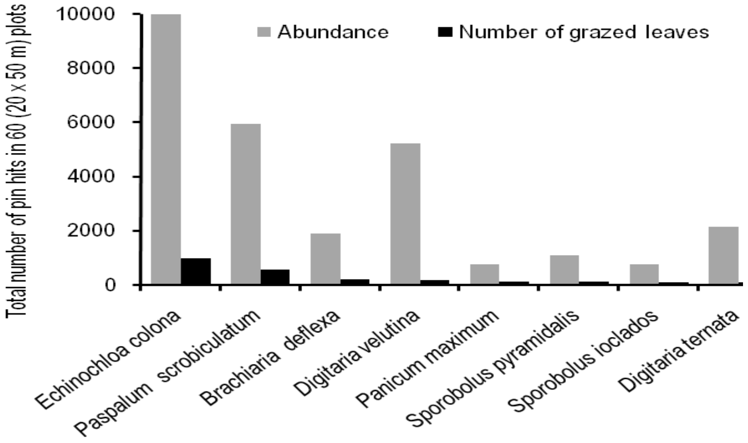

Figure 2: Herbaceous plant species most grazed by cattle in the Kilombero wetlands, Morogoro Tanzania.

Grazing intensity in small patches

Grazing intensity in small patches had no relationship with physiographic variables, while plant community properties were important for grazing intensity when all the species were considered (Table 2). The best two candidate models included plant biomass, species richness and evenness (models 4 and 5, Appendix 1), while models with species diversity had relatively poor fit (model 1) in explaining grazing intensity on small patch level (Appendix 1). The most parsimonious model explaining grazing in small patches included biomass, species richness and their interactions (Table 2). All the remaining models (models 1-4), with ΔAICc between 3.96 and 717.24, explained less of the variations in selection of small patches when all the plant species were considered (Appendix 1). Grazing intensity in small patches increased with biomass and species richness when all the plant species were analysed (Table 2). However, grazing intensity was highest in small patches with an intermediate level of biomass (unimodal relationship, Table 2). Thus, there was a negative relationship between biomass and species richness in explaining variations in grazing intensity at small spatial scale (Table 2).

Table 2: The most parsimonious model explaining the relationships between grazing intensity and plant community properties and physiographic variables within small patches for all species at the Kilombero wetland, Morogoro, Tanzania

Effects	Estimate	SE	*t*-value	*P*-value
Intercept	–19.140	0.320	–5.976	< 0.001
Biomass	0.057	0.004	13.160	< 0.001
Biomass^2	–0.001	0.0001	–7.853	< 0.001
Species richness	0.210	0.051	4.136	< 0.001
Biomass: species richness	–0.006	0.001	–5.239	< 0.001

Grazing intensity in large patches

Both plant community properties and physiographic factors significantly explained variations in grazing intensity in large patches when all the plant species were combined (Table 3). The most parsimonious model explaining grazing in large patches included species diversity, elevation and distance to agricultural fields (model 5; Appendix 2). All other models (models 1-4), with ΔAICc between 2.78 and 10.25, explained less of the total variations in grazing intensity in large patches (Appendix 2). Grazing intensity decreased significantly with species diversity, whereas it increased with elevation and distance to agricultural fields (Table 3). There was no significant interaction among biomass, species richness, evenness, diversity, elevation and distances to agricultural fields, house or kraal in explaining variations in grazing intensity in large patches when all the plant species were considered (Table 3).

Table 3: The most parsimonious model explaining the relationships between grazing intensity and plant community properties and physiographic variables within large patches for all species at the Kilombero wetland, Morogoro, Tanzania

Effects	Estimate	SE	*t*-value	*P*-value
Intercept	23.600	22.080	1.069	0.290
Elevation	64.730	25.650	2.524	0.015
Diversity	–81.990	23.250	–3.527	< 0.001
Distance to agricultural field	52.240	22.060	2.368	0.021

When only grazed plant species (22) were analysed in large patches, plant community properties and physiographic variables were included in the best two candidate models explaining grazing intensity (Appendix 3). Plant species richness explained a marginal significant variation in grazing intensity in large patches (Table 4). Grazing intensity was positively related to plant biomass, elevation and the three-way interactions of biomass, richness and evenness when grazed plant species were separately analysed (Table 4). However, grazing intensity in large patches was negatively related with the interaction of biomass and richness, as well as with richness and evenness when only grazed plant species were considered (Table 4).

Table 4: The most parsimonious model explaining the relationships between grazing intensity and plant community properties and physiographic variables within large patches, considering only grazed plant species at the Kilombero wetland, Morogoro, Tanzania

Effects	Estimate	SE	*t*-value	*P*-value
Intercept	–102.45	77.76	–1.317	0.194
Biomass	443.04	191.77	2.310	0.025
Richness	330.27	170.49	1.937	0.059
Evenness	203.47	161.02	1.264	0.213
Elevation	65.86	27.12	2.429	0.019
Biomass: richness	–935.94	367.70	–2.545	0.014
Richness: evenness	–635.55	310.86	–2.045	0.046
Biomass: richness: evenness	1816.58	687.86	2.641	0.011

Discussion

This study showed that cattle grazed patches with high plant species richness and moderate biomass at a small spatial scale. On a larger scale, cattle grazed on patches with low diversity, at high elevations, and at longer distances from agricultural fields. Moreover, cattle selected many palatable plant species with high biomass at larger spatial scale, and richness had less influence on the selection of these palatable species at large scale. Therefore, it appears that community properties are important for cattle foraging decisions both at small and large spatial scales. In addition to species diversity, physiographic variables were also important for variations in the grazing intensity at large spatial scale. Thus, the first prediction that plant community properties would be important for grazing intensity at a small spatial scale, whereas physiographic variables would be important in explaining variations in grazing intensity at larger patch sizes, is not fully supported.

A positive relationship between grazing intensity and plant species richness has also been documented for moose (Milligan and Koricheva 2013) and sheep (Wang et al. 2010b). Since a single plant species will not meet animal's optimal energy and nutritional requirements, diet switching is important for large domestic herbivores, such as cattle as pointed out by Westoby (1978) and Wiggins et al. (2006). By foraging in patches with high species richness, cattle increase chances to secure palatable and nutrient-rich materials (Westoby 1978). Moreover, a high species richness offers the opportunity for cattle to change species preferences and thereby stimulating intake of more food (Early and Provenza 1998) which leads to higher energy and protein gains (Belovsky 1997). In addition, experimental studies suggest that daily nutrient intake by large domestic herbivores (sheep) increases chances not only for selecting the most palatable species in patches, but also from complementary effects of specie richness (Wang et al. 2010b). In particular, taking a mixed diet from several plant species (i.e. from a species-rich patch) facilitates intake of both low and different classes of plant secondary metabolites (PSMs; although generally low in grasses) (Cheeke 1995, Provenza et al. 2003, Marsh et al. 2006) in addition to the instantaneous intake of balanced nutrients. Therefore, feeding in species-rich patches provides the animal with nutritional benefits and reduces toxic effects of PSMs (Gordon and Prins 2008). Thus, feeding in species-rich patches saves energy that cattle would expend on searching and travelling, which is not the case when the herbivore feeds in species-poor patches (WallisDeVries 1996, Milligan and Koricheva 2013).

Grazing intensity related positively to plant biomass at a small spatial scale, and grazing intensity reached maximum at an intermediate level of biomass where species richness is predicted to be highest in grasslands (Oba et al. 2001, Bhattarai et al. 2004). Moreover, grazing intensity increased with biomass of grazed species at a large spatial scale. Large bulk feeders, such as cattle, can tolerate low nutrient content of plants but need a greater abundance of foliage to maintain energy demands (Bell 1970, Bell 1971, Jarman 1974, Belovsky 1997). Thus, at small spatial scale in the study area cattle appear to prefer patches with intermediate biomass and high species richness, whereas at a larger scale they appear to prefer individual species with high biomass. Moreover, using cafeteria and field experiments, Wang et al. (2010b) demonstrated that species richness enhanced overall nutrient intake of sheep and that the benefit of higher species richness came from the greater abundance of foliage consumed and not a higher quality of foliage. This suggests that biomass is also important to sustain energy in addition to species richness, for large domestic herbivores (Belovsky 1997, Gordon and Prins 2008). Since grazing was at maximum at moderate amounts of biomass, the third prediction that cattle selected patches with high plant biomass at small spatial scale is not fully supported. Instead, the selection of patches at small scales seems to be based on a trade-off between food quantity and quality (i.e. a varied diet).

This study showed that grazing intensity was positively related to distance to agricultural fields, i.e. grazing intensity increased away from agricultural fields. A likely explanation for this is that herders often release cattle away from the agricultural fields to avoid cattle feeding on crops (e.g. rice and vegetables) under semi free-ranging system. The progressive change in grazing intensity with elevation at a large spatial scale implies that patches located at relatively high elevations are more preferred by livestock than lower floodplain landscapes. Although differences in elevation are small, many nutrient- and energy-rich plant species, such as *Echinochloa colona* and *Paspalum scrobiculatum* cannot tolerate prolonged inundation (Phillips et al. 2003, CABI 2020) and these species therefore potentially occur mostly on higher elevations. Moreover, it is possible that vegetation patches at relatively high elevations are more accessible and available to cattle and thus often selected and grazed (Bailey et al. 1996, Bailey et al. 1998).

The physiographic variables, such as distance to kraal sites, were not important in explaining variations in grazing intensity at large spatial scale in the study area. This agrees partly with a study that related grazing intensity to droppings, distance from pastoral camp sites and pika burrows by Dorji et al. (2013). They found that distance from camp sites predicted only a small variation (30%) in grazing intensity, suggesting that other physiographic variables (e.g. elevation and distance to agricultural fields) may be more important for foraging choices by herbivores at large spatial scales.

Conclusion

In general, few studies examine the combined effects of plant community properties and physiographic variables on grazing intensity by free-ranging large herbivores in plant species-rich ecosystems. This study therefore, adds to our understanding of grazing ecology in such systems, particularly the role of plant community properties and physiographic variables in shaping grazing intensity of large domestic herbivores. This study suggests that foraging by cattle is driven by different factors at different spatial scales. At small scale, cattle appear to select and graze small vegetation patches with high species richness and intermediate level of biomass; presumably to achieve nutritional balance and maximize energy gains (Westoby 1978, Belovsky 1997). On a larger scale, cattle appear to select and graze patches with relative low plant diversity, but with a higher abundance of palatable plant species with high biomass. Moreover, at a large scale cattle seem to graze mostly at high elevations and at longer distances from agricultural fields. These results have important implications for improvement of livestock production and rangelands management strategies. In particular, maintenance of plant species richness and biomass is important to improve rangelands conditions and domestic herbivore production.

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Conflict of interest: None.

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Appendix 1: Comparison of the candidate models following information-theoretic model selection and multi-model procedure in explaining the relationship between grazing intensity and community properties and physiographic variables within small patches for all species at Kilombero wetland, Morogoro, Tanzania

Model Code	Candidate model(s)	*K*	AICc	ΔAICc	*W*i	*Cum.Wt*
5	Grazing intensity = Biomass + Species richness - Biomass^2- Biomass: richness	6	2595.20	0.00	0.88	0.88
4	Grazing intensity = Biomass + Species richness + Evenness + Biomass: richness + Biomass: evenness + Richness: evenness + Biomass: richness: evenness	9	2599.16	3.96	0.12	1.00
3	Grazing intensity = Species richness + Evenness + Richness^2 +Evenness^2 + Species richness: evenness	7	2773.65	178.45	0.00	1.00
2	Grazing intensity = Biomass + Species evenness + Biomass^2 + Evenness^2 + Biomass: evenness	7	3305.07	709.87	0.00	1.00
1	Grazing intensity = Biomass + Diversity + Biomass^2 + Diversity^2 + Biomass:Diversity	7	3312.44	717.24	0.00	1.00

K: the number of parameters in the regression model, AICc: Akaike information criterion, *W*i: Akaike weight, ΔAICc: change in Akaike information criterion, *Cum.Wt*: cumulative Akaike weight and ":" show interaction terms. Only a few candidate models are presented for illustration purposes.

Appendix 2: Comparison of the candidate models following information-theoretic model selection and multi-model procedure in explaining the relationship between grazing intensity and community properties and physiographic variables within large patches for all species at Kilombero wetland, Morogoro, Tanzania.

Model Code	Candidate model(s)	*K*	AICc	ΔAICc	*W*i	*Cum.Wt*
5	Grazing intensity = Elevation + Distance to agricultural field - Shannon diversity	5	599.39	0.00	0.69	0.69
4	Grazing intensity = Elevation + Distance to agricultural field - Species richness - Evenness	6	602.17	2.78	0.17	0.87
3	Grazing intensity = Elevation + Distance to agricultural field - Species evenness	5	603.18	3.79	0.10	0.97
2	Grazing intensity = Elevation + Distance to agricultural field - Species richness	5	606.19	6.80	0.02	1.00
1	Grazing intensity = Biomass + Species richness + Evenness + Elevation + Distance to agricultural field - Distance to house + Distance to kraal - Biomass: richness- Biomass: evenness - Richness: evenness + Biomass: richness: evenness	13	609.64	10.25	0.00	1.00

K: the number of parameters in the regression model, AICc: Akaike information criterion, *W*i: Akaike weight, ΔAICc: change in Akaike information criterion, *Cum.Wt*: cumulative Akaike weight and ":" show interaction terms. Only a few candidate models are presented for illustration purposes.

Appendix 3: Comparison of the candidate models following information-theoretic model selection and multi-model procedure in explaining the relationship between grazing intensity and community properties and physiographic variables within large patches considering only grazed species at Kilombero wetland, Morogoro, Tanzania.

Model Code	Candidate model(s)	*K*	AICc	ΔAICc	*W*i	*Cum.Wt*
5	Grazing intensity = Biomass + Species richness + Evenness + Elevation - Biomass: richness- Richness: evenness + Biomass: richness: evenness	9	604.52	0.00	0.51	0.51
4	Grazing intensity = Biomass + Species richness + Evenness + Elevation - Distance to house + Distance to agricultural field + Distance to kraal - Biomass: richness- Biomass: evenness - Richness: evenness + Biomass: richness: evenness	13	606.16	1.64	0.22	0.73
3	Grazing intensity = Biomass + Elevation - Distance to house	5	606.67	2.15	0.17	0.90
2	Grazing intensity = Elevation + Distance to agricultural field	4	608.91	4.39	0.06	0.96
1	Grazing intensity = Elevation - Evenness - Distance to house	5	609.45	4.93	0.04	1.00

K: the number of parameters in the regression model, AICc: Akaike information criterion, *W*i: Akaike weight, ΔAICc: change in Akaike information criterion, *Cum.Wt*: cumulative Akaike weight and ":" show interaction terms. Only a few candidate models are presented for illustration purposes.