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# Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment

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## Abstract

Understanding the spatial dynamics of landscape use by free-ranging herbivores is integral for successful ecosystem management. We used binary logistic regression analyses to determine the relative importance of biotic, abiotic and human factors in influencing the distribution (presence/absence) of wild grazers on two Maasai ranches in Kenya's Amboseli-Tsavo ecosystem. Both ranches had low grass biomass and suffered from regular droughts. We found that grazers consistently located themselves where grass biomass was highest, usually irrespective of grass quality, suggesting that forage quantity may be the limiting factor where grass biomass is generally low. The availability of surface water had no significant effect on the likelihood of grazers being present, even in the dry season.

*Key words:* abiotic factors, arid, biotic factors, grass biomass, herbivores, savannah

## Résumé

La bonne compréhension de la dynamique spatiale de l'utilisation du paysage par les herbivores qui paissent en liberté fait partie intégrante de la gestion réussie d'un écosystème. Nous avons employé des analyses de régression logistique binaire pour déterminer l'importance relative des facteurs biotiques, abiotiques et humains dans l'influence sur la distribution (présence/absence) d'herbivores sauvages sur deux ranches masai de l'écosystème Amboseli-Tsavo, au Kenya. Les deux ranches avaient une faible biomasse herbeuse et souffraient de sécheresses régulières. Nous avons découvert que les herbivores brouteurs se trouvaient de façon constante là où la biomasse herbeuse était la plus grande, sans tenir compte, d'habitude, de la qualité de l'herbe; ceci suggère que la quantité de fourrage pourrait être le facteur imitant là où la biomasse herbeuse est généralement faible. La dispo-

nibilité de l'eau de surface n'avait pas d'effet significatif sur la probabilité de la présence des herbivores, même en saison sèche.

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## Introduction

Understanding the spatial dynamics of landscape use by free-ranging grazers is integral to ecosystem management (Senft *et al.*, 1987; Bailey *et al.*, 1996). Regression models of grazing behaviours can help identify the environmental factors by which animals select preferred feeding areas (Senft, Rittenhouse & Woodmansee, 1983; Redfern *et al.*, 2003), providing important information about the factors determining the observed distribution patterns of species or guilds of species. Many landscape-scale models of herbivore distributions focus primarily on the role of biotic factors such as forage quality and quantity (Redfern *et al.*, 2003). However, Bailey *et al.* (1996) suggested that abiotic factors, such as slope and distance to water, are equally as important and can act as the primary determinants of large scale distribution patterns.

Theoretically, in an environment entirely free of constraints, one would expect herbivores to locate themselves where they are able to maximize their energy gain in the shortest possible time (see Bergman *et al.*, 2001). For example, Bailey *et al.* (1996) suggested that large herbivores should spend most time in areas where the available quantity and quality of forage is highest. However, where the land is shared by humans and their livestock, human activities may interfere with animal distributions and preempt access by wildlife to critical habitats (Corfield, 1973; Williamson, Williamson & Ngwamotsoko, 1988). Additionally, there may be natural restrictions on distributions, such as an overall scarcity of forage, the availability of water, competitive interactions with other wildlife or livestock and the effects of predation (Sinclair, 1985; Fryxell, 1991).

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Whilst Redfern *et al.* (2003) argue that a combination of both biotic and abiotic factors may be particularly important in determining the distribution patterns of large herbivores in African savannah ecosystems, the relative importance of these factors has not been quantified, particularly in arid ecosystems that are also subjected to heavy human pressure. In this study, we use logistic regression analyses to investigate the relative influence of biotic, abiotic and human factors in determining the landscape-scale distribution patterns of wild grazers on two Maasai ranches in southern Kenya. Grass biomass was low throughout the area, which was also prone to frequent droughts; it was therefore a resource-stressed environment.

## Materials and methods

### Study area

Mbirikani (c. 1300 km<sup>2</sup>) and Merueshi (183 km<sup>2</sup>) Group Ranches are located in the Amboseli-Tsavo ecosystem in southern Kenya. Both are in Agroclimatic Zones V and VI (Bekure *et al.*, 1991), that is, arid to semi-arid, with annual rainfall averaging between 350 and 500 mm (Worden, Reid & Gichohi, 2003). Severe droughts have occurred at least once every decade since 1930 (Campbell, 1999). Median grass biomass on Mbirikani was 68 and 136 g m<sup>-2</sup> in the dry and wet season, respectively, while on Merueshi it was 68 and 82 g m<sup>-2</sup> (Groom, 2007). Livestock farming was the dominant land use for the resident Maasai pastoralists, but wildlife also used both ranches, especially for wet season dispersal from Amboseli National Park.

Water availability on both ranches was widespread during wet seasons, but restricted during dry seasons. For example, dry season water availability on Mbirikani was restricted to a water pipeline in the western quarter, a swamp in the south-west, a river running along the southern boundary and the safari-lodge water hole in the east of the ranch (c. 5–10 km from the major concentrations of wild grazers). On Merueshi, wells dug in the riverbed, the pipeline on the neighbouring ranch and a few boreholes provided the only dry-season water. All waterholes were used by both cattle and people as well as wildlife. The safari lodge water hole was used by livestock illicitly at night. The area around all permanent waterholes was virtually denuded of vegetation for at least a 25-m radius, with grass and, to a lesser extent browse, considerably reduced for up to a 1-km radius.

The focus of this study is on the distributions of wild grazers, mainly zebra (*Equus quagga burchellii*, Gray 1824) and wildebeest (*Connochaetes taurinus albojubatus*, Burchell 1823), but also Thomson's gazelle (*Gazella thomsoni*, Günther 1884), Coke's hartebeest (*Alcelaphus buselaphus cokii*, Pallas 1766) and oryx (*Oryx beisa callotis*, Rüppell 1935). We focus on the wild grazer guild because they formed the majority of the herbivore population in the study area (74% on Mbirikani and 68% on Merueshi), and the quality and quantity of the grass resource was more easily investigated than browse. Furthermore, wild grazers are the species most likely to be in competition with livestock due to the shared forage resource (e.g. Ego, Mbuvi & Kibet, 2003) and, therefore, displaced by human activities. The majority of the grazers were zebra and wildebeest (60% and 34% of grazers, respectively). Thomson's gazelle constituted 5% of the overall grazer density, oryx 1%, and hartebeest <1%. On Mbirikani, zebra and wildebeest were present in fairly equal densities (45% and 49% of the total, respectively), whilst on Merueshi, zebra constituted the greatest proportion of grazers (73% as compared with 22% for wildebeest).

### Data collection

During 2005 density estimates of these and of cattle were obtained from monthly population counts using belt and point transects. On Mbirikani, 22 randomly located belt transects 4 km in length were driven each month, stratified by habitat size (Krebs, 1999). On Merueshi, the private land ownership and the abundance of fences precluded driving belt transects, and so 50 point transect counts were conducted monthly. Transect area varied according to visibility and was calculated independently for each transect. Both approaches are area counts; to test their comparability, 72 pairs of belt and point transects in two habitats (open grassland and thinly bushed grassland) on Mbirikani were compared using Mann–Whitney tests. Only 2/72 (2.8%) of comparisons were significantly different, and so the density estimates (numbers of grazers km<sup>-2</sup>) derived from these two methods were directly comparable (Groom, 2007). For each transect, all animals of Thomson's gazelle size or above within the specified area were counted. The number of individuals of each species of grazer counted in a transect were summed and the result divided by the area of the transect to give a density of wild grazers per transect.

For each transect, wild grazers were coded as 1 for presence (density >0) and 0 for absence. This was used as the dependent variable in the logistic regressions, with seven independent variables included in the models (see Table 1). Four biotic, grass-related variables were included because these are frequently the most important factors determining the distribution of wild grazers within a landscape (Fryxell, 1991; Wilmshurst, Fryxell & Bergman, 2000). Grass quality was represented by percentage crude protein (%CP) and percentage digestible organic matter (%DOM), as well as percentage greenness. The former two were determined by near-infrared spectroscopy of cattle faeces (Lyons & Stuth, 1992), thus representing the best quality grazing as selected by cattle. This was considered to be a good proxy for the quality of grass available to grazing herbivores since dietary overlaps between wildebeest, hartebeest and cattle were found to be over 75% in another study in Kenya (Ego *et al.*, 2003).

Data were collected for each of seven major habitats on Mbirikani (boulder field; dense bush; thinly bushed grassland; drained grassland; poorly drained grassland; woodland; whistling thorn scrub). However, the habitat on Merueshi was much patchier and it was not possible to define specific habitat types. Thus five areas were defined by Dirichlet tessellations centred on the five randomly selected bomas (Maasai homesteads) used to collect cattle faecal samples to assess forage quality. Dirichlet tessellations use a mathematical rule to construct borders at the midpoints between all neighbouring points, in this case bomas (see Blackwell & Macdonald, 2000). These borders then run perpendicular to the straight line between the neighbouring bomas, until they meet another border (from an adjacent tessellation). The resulting pattern is a matrix of convex polygons that contain all the points which are

nearer to the boma in the centre of the polygon than to any other neighbouring boma (Johnson *et al.*, 2001). The forage quality data from that boma were then applied to all point transect counts within the appropriate tessellation.

We were confident that the cattle faeces collected within the seven habitats provide a representative sample of the grass quality in that habitat for the following reasons. The bomas at which the faecal samples were collected were in the middle of each habitat type, with maximum grazing distances from the boma still being well within the habitat type in question. Moreover, we had Etrex GPSs attached to some of the cattle during their grazing rotations so we knew exactly where they went. We also made sure that the cattle had been in the boma for at least three full days prior to collection of the faecal samples, to avoid any problems arising from long digestive through time.

Grass greenness and biomass were recorded every 500 m along each belt transect and twice within the area of each point transect (Total  $n = 3735$ ) using a calibrated pin-frame (Mwangi & Western, 1998). The nine measurements per belt transect and two per point transect were averaged to give an estimate of grass biomass and greenness.

The most important abiotic factors are thought to be water availability and slope (Bailey *et al.*, 1996). However, since the majority of this landscape is flat, the only abiotic variable considered was distance to water. The effect of human influences on the distribution of grazers was investigated by including livestock density and distance to the nearest permanent boma as predictors. The GPS position of all available surface water and all permanent bomas were recorded in both the 2005 dry and wet seasons by Maasai assistants who knew their local areas intimately. The GPS position of every transect was

**Table 1** Summary statistics (means  $\pm$  SE) of the variables included in the regression models

Variables	Mbirikani		Merueshi	
	Wet season	Dry season	Wet season	Dry season
Biomass (g m <sup>-2</sup> )	145.26 $\pm$ 4.89	104.86 $\pm$ 3.95	121.14 $\pm$ 7.21	91.18 $\pm$ 4.00
CP (%)	10.66 $\pm$ 0.03	7.43 $\pm$ 0.09	11.57 $\pm$ 0.09	7.54 $\pm$ 0.07
DOM (%)	59.13 $\pm$ 0.10	57.76 $\pm$ 0.11	57.63 $\pm$ 0.05	54.70 $\pm$ 0.08
% Green (%)	35.44 $\pm$ 1.96	1.11 $\pm$ 0.22	47.41 $\pm$ 1.83	0.06 $\pm$ 0.04
Livestock (no km <sup>-2</sup> )	53.02 $\pm$ 7.60	31.05 $\pm$ 4.42	73.58 $\pm$ 9.04	44.75 $\pm$ 7.17
Distance to boma (m)	3224.73 $\pm$ 164.70	3066.33 $\pm$ 194.35	904.99 $\pm$ 37.87	1113.25 $\pm$ 50.41
Distance to water (m)	1745.95 $\pm$ 61.45	4905.84 $\pm$ 234.63	1488.82 $\pm$ 45.02	4515.37 $\pm$ 162.09

also recorded, and the nearest-features extension in ArcView GIS (v3.2) used to calculate the distance of each transect to the nearest surface water or permanent boma. All data were split into dry and wet seasons for analysis, because different variables may be important in affecting the distribution of grazers in the two seasons. Seasons were defined on the basis of grass greenness and percentage biomass deviations from the overall biomass mean (Mose, 2005).

#### *Binary logistic regressions*

Logistic regressions were carried out in SPSS v12.0 using the enter method. This was preferred to the stepwise methods (forwards, backwards and stepwise) because there is sound theoretical literature on which to base the model, precluding the need to rely on the computer to select variables based on mathematical criteria (Field, 2006). In addition, this method consistently produced the best model with regard to several different criteria.

Having selected the enter method, Akaike's Information Criterion (AIC) scores and Delta AIC were calculated for all possible models although, ultimately, the global model is presented in all cases. The global model is the most complex model of the set, that is, the one which includes all the variables of interest (Mazerolle, 2006). For all scenarios, the global model was close to the 'best' model on the basis of the lowest AIC score, and significant variables were so strong that they remained consistent in all the different models. In addition, the global model provides most information by including information on the direction and strength of non-significant variables, which can be just as interesting as significant variables (Field, 2006).

The case summaries of the final models (including Cook's distance values, Leverage values, standardized residuals and DFBeta values) were examined to ensure there were no individual points which were having an especially strong influence on the model. Treatment of individual outliers is discussed in the relevant section of the Results.

## Results

#### *Distribution of wildlife*

The distribution of wildlife between different habitats on Mbirikani was significantly different from that which

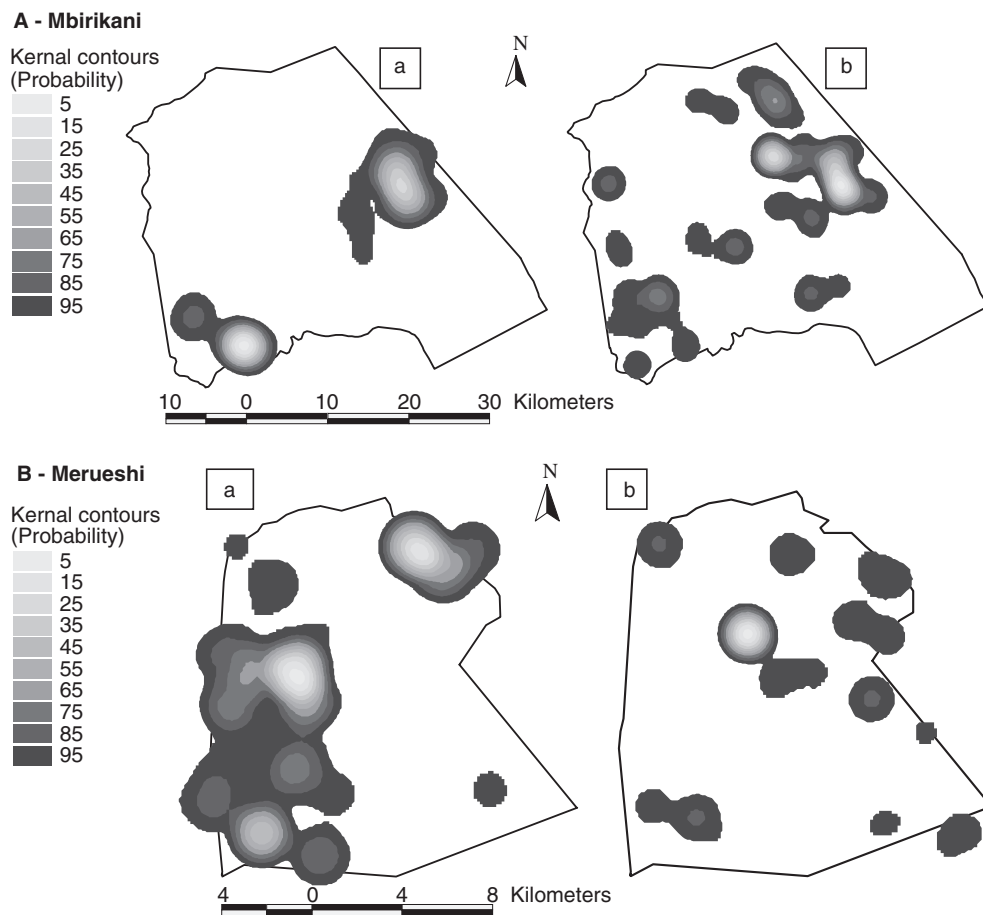
would be expected if the animals distributed themselves evenly with respect to the size of the habitat in both dry and wet seasons ( $\chi^2_6 = 7898.55$ ,  $P < 0.001$  and  $\chi^2_6 = 7787.17$ ,  $P < 0.001$  respectively), when grazers congregated in certain areas (Fig. 1).

Patterns within the distribution of wild grazers on Merueshi were tested using an index of dispersion against a null hypothesis that animals distributed themselves randomly on the ranch. Merueshi was divided into 65 grids using ArcView v3.2 and calculated wildlife densities standardized for sampling effort by dividing the number of wild grazers in each grid by the number of transects in that grid. This showed that the distribution of wildlife was significantly different from random ( $\chi^2_{64} = 655.66$ ,  $P < 0.001$ ) and could be classified as clumped (variance/mean ratio = 10.25) (Fowler, Cohen & Jarvis, 1998). This was the same for wet and dry seasons independently (Fig. 1).

#### *Logistic regressions*

*Wet season logistic regressions.* The Mbirikani wet season model produced a significant result overall ( $\chi^2_7 = 106.80$ ,  $P < 0.001$ ) and had a good fit (Hosmer & Lemeshow;  $\chi^2_8 = 6.60$ ,  $P = 0.580$ ). Three variables emerged as significant in explaining the likelihood of grazers being present (Table 2); a greater biomass and a greater percentage greenness of the grass both significantly increased the odds of grazer presence, whereas a higher %DOM significantly decreased the odds of grazer presence.

For the Merueshi wet season model, Cook's distance influence statistics and an anomalously high standardized residual for one case suggested an outlier. The case was examined and found to have a very high biomass value, although this was not a data input error. Even so, the point was excluded from the model because it was a statistical outlier and biologically unrepresentative of the vast majority of the known biomass values. Nonetheless, the overall outcome was the same with and without this point and the final model produced a highly significant result ( $\chi^2_7 = 27.80$ ,  $P < 0.001$ ) and had a good fit (Hosmer & Lemeshow;  $\chi^2_8 = 4.27$ ,  $P = 0.832$ ). Only one variable had a significant effect on the distribution of wild grazers on Merueshi in the wet season; a higher grass biomass significantly increased the odds of grazer presence (Table 3).



**Fig 1** Maps (using Kernel home ranges) showing the distribution of wild grazers on Mbirikani Group Ranch (A) and Merueshi Group Ranch (B) in (a) the dry season and (b) the wet season in 2005. Higher concentrations of grazers are indicated by paler tones

**Table 2** Results of the binary logistic regression model investigating Mbirikani wet season grazer densities ( $n = 333$ ); all are continuous variables

Independent variables	Description	B $\pm$ SE	Wald	Sig.	Exp(B)	95% CIs for Exp(B)
Livestock densities	No. of livestock per km <sup>2</sup>	0.000 $\pm$ 001	.013	0.910	1.000	0.998–1.002
Distance to boma	Distance to nearest permanent boma (m)	0.000 $\pm$ 000	.269	0.604	1.000	1.000–1.000
Biomass	Above ground grass biomass (g/m <sup>2</sup> )	0.014 $\pm$ 002	32.798	0.000	***	1.014 1.009–1.019
%CP	Crude protein content of grass (%)	-0.419 $\pm$ 291	2.068	0.150		0.658 0.372–1.164
%DOM	Dry organic matter digestibility of grass (%)	-0.156 $\pm$ 072	4.693	0.030	*	0.855 0.743–985
% green	Percentage greenness of grass (%)	0.015 $\pm$ 004	14.908	0.000	***	1.015 1.007–1.022
Distance to water	Distance to nearest available surface water (m)	0.000 $\pm$ 000	2.942	0.086		1.000 1.000–1.000
Constant		10.552 $\pm$ 4.483	5.540	0.019	38246.641	

\* $P < 0.05$ ; \*\*\* $P < 0.001$ ; Nagelkerke  $R^2 = 0.368$ .

*Dry season logistic regressions.* For the Mbirikani dry season data, %CP had to be removed because of collinearity issues with both biomass and %DOM. The model was highly significant ( $\chi^2_6 = 91.34$ ,  $P < 0.001$ ) and had a good fit (Hosmer & Lemeshow;  $\chi^2_8 = 25.01$ ,  $P = 0.002$ ). Only biomass had a significant relationship with the probability of wild grazers being present (Table 4).

With the Merueshi dry season data, Cook's distance influence statistics and an anomalously high leverage value for one case suggested an outlier. However, on inspection of the data, it was unclear why this was so and there was no valid reason for removing it. Nonetheless, the model was run both with and without the point to clarify its influence, but the overall model outcome was the same; the results in Table 5 include all data points. The model

**Table 3** Results of the binary logistic regression model investigating Merueshi wet season grazer densities ( $n = 320$ ); description of variables as in Table 2

Independent variables	B $\pm$ SE	Wald	Sig.	Exp(B)	95% CIs for Exp(B)
Livestock densities	0.000 $\pm$ 001	0.233	0.629	1.000	0.999–1.002
Distance to boma	0.000 $\pm$ 000	0.548	0.459	1.000	1.000–1.001
Biomass	0.005 $\pm$ 001	17.121	0.000***	1.005	1.003–1.008
%CP	-0.090 $\pm$ 100	0.798	0.372	0.914	0.751–1.113
%DOM	-0.245 $\pm$ 202	1.461	0.227	0.783	0.527–1.164
% green	0.002 $\pm$ 005	0.271	0.603	1.002	0.993–1.011
Distance to water	0.000 $\pm$ 000	0.337	0.561	1.000	1.000–1.001
Constant	12.611 $\pm$ 12.057	1.094	0.296	299946.855	

\*\*\* $P < 0.001$ ; Nagelkerke  $R^2 = 0.129$ .

**Table 4** Results of the binary logistic regression model investigating Mbirikani dry season grazer densities ( $n = 235$ ); description of variables as in Table 2

Independent variables	B $\pm$ S.E	Wald	Sig.	Exp(B)	95% C.I.s for Exp(B)
Livestock densities	0.001 $\pm$ 003	0.065	0.799	1.001	
Distance to boma	0.000 $\pm$ 000	0.038	0.845	1.000	1.000–1.000
Biomass	0.025 $\pm$ 005	24.675	0.000***	1.025	1.015–1.035
%DOM	0.028 $\pm$ 113	0.060	0.807	1.028	0.824–1.283
% green	0.064 $\pm$ 049	1.708	0.191	1.066	0.969–1.173
Distance to water	0.000 $\pm$ 000	0.261	0.609	1.000	1.000–1.000
Constant	-4.943 $\pm$ 6.665	0.550	0.458	0.007	

\*\*\* $P < 0.001$ ; Nagelkerke  $R^2 = 0.445$ .

**Table 5** Results of the binary logistic regression model investigating Merueshi dry season grazer densities ( $n = 294$ ); description of variables as in Table 2

Independent variables	B $\pm$ SE	Wald	Sig.	Exp(B)	95% CIs for Exp(B)
Livestock densities	0.000 $\pm$ 001	0.011	0.916	1.000	0.997–1.003
Distance to boma	0.000 $\pm$ 000	2.693	0.101	1.000	1.000–1.001
Biomass	0.006 $\pm$ 002	7.048	0.008**	1.006	1.001–1.010
%CP	0.107 $\pm$ 229	0.219	0.640	1.113	0.710–1.745
%DOM	-0.234 $\pm$ 210	1.243	0.265	.791	0.524–1.194
% green	0.101 $\pm$ 180	0.313	0.576	1.106	0.777–1.573
Distance to water	0.000 $\pm$ 000	2.870	0.090	1.000	1.000–1.000
Constant	9.804 $\pm$ 10.274	0.911	0.340	18098.348	

\*\* $P < 0.01$ ; Nagelkerke  $R^2 = 0.072$ .

had a good fit (Hosmer & Lemeshow;  $\chi^2_8 = 3.51$ ,  $P = 0.898$ ) but was non-significant overall ( $\chi^2_7 = 12.25$ ,  $P = 0.093$ ), despite the significance of biomass in the model. However, both the Cox & Snell  $R^2$  and Nagelkerke  $R^2$  values were very low (0.041 and 0.072, respectively), indicating that the model is only able to account for <10% of the variation seen.

## Discussion

Ecological theory emphasizes the logic of spatially extensive movements across a heterogeneous environment so that wildlife can make best use of spatially separated key resources (see Burnsilver, Boone & Galvin, 2003). Theoretically, herbivores should locate themselves in areas where they can maximize their energy gains (Bailey *et al.*, 1996) within the natural constraints imposed by abiotic factors such as slope and distance to water.

On Mbirikani, during the wet season grazers were positively associated with areas of higher grass biomass and greener grass, whereas a higher percentage of digestible organic matter (%DOM) in the grass significantly decreased the odds of grazer presence. Grass greenness can be considered a proxy for grass quality, and may be a better predictor than percentage crude protein (%CP), since greenness data were collected at a much finer resolution than %CP. Thus in the wet season, wild grazers on Mbirikani were selecting areas which had both high quantity and quality of grass, and grass characteristics were more important than abiotic or human-related variables in explaining the observed distribution of wild grazers.

The negative relationship between wild grazer density and the organic matter digestibility of grass is not easily explained, and merits further investigation. It is possible that, because the majority of grazers were zebras, that is, bulk feeders for which quantity is more important than quality (Bell, 1971), selecting for more digestible grass was less of a priority than selecting for biomass and greenness.

In the other three scenarios (Mbirikani dry season, Merueshi wet and dry seasons), only grass biomass was positively related to the presence of wild grazers. This might appear contrary to much of the literature, which suggests that many species of wildlife (especially wildebeest and Thomson's gazelles) prefer areas of lower biomass (Maddock, 1979; Sinclair, 1985; Fryxell & Sinclair, 1988; Estes, 1997), since this often indicates better food quality (Bergstrom & Skarpe, 1999; Wallisdevries, Laca & Demment, 1999). However, there was a fairly low biomass

on both Mbirikani and Merueshi, and so selecting areas of higher biomass simply equated to choosing areas where there actually was some grass. This may also help explain why grazers did not actively select areas of better quality grass; it is likely that there was so little grass available that they went wherever they could find grazing, irrespective of its quality. This is supported by other studies: Sinclair (1974) for example found that, in the dry season in the Serengeti, buffalo had to expand their diets to include lower quality grass components since they could not maintain their minimum nutritional intake rate by only selecting rare high quality grass. In addition, zebra need to eat considerable quantities of grass to fulfil their nutrient requirements (Bell, 1971; Estes, 1997) and, since zebras constituted 73% of the grazers on Merueshi, this probably explains why grass biomass rather than quality was consistently positively associated with the presence of wild grazers. Indeed Sinclair (1985) found that in the dry season in the Serengeti, zebra preferred areas with the tallest grass.

Redfern *et al.* (2003) predicted that herbivores in African savannah ecosystems must meet their nutritional requirements within the constraints of water availability, and found this to be the case for all water-dependent or semi water-dependent species in the Kruger National Park, South Africa. However, even though 99% of the overall grazer density in this study consisted of water-dependent species, we found no evidence that distance to water constrained the distributions of wild herbivores, even in dry seasons. There are several possible explanations for the absence of a significant relationship with water availability. These include the lower forage availability close to water, the influence of livestock and human activities close to water and the actual distances involved. Irregular water availability in semi-arid savannahs can affect the distribution, quality and quantity of food available for large herbivores (Mcnaughton & Georgiadis, 1986; Bergstrom & Skarpe, 1999), with forage availability depleted more rapidly near water sources (Ibrahim, 1993; Johnson, 1993). It may be, therefore, that in this arid/semi-arid landscape grazers were compromising closeness to water for forage availability (e.g. see Bergstrom & Skarpe, 1999).

Such a compromise is made possible by a degree of elasticity of their intrinsic constraints (Owen-Smith, 1993), which allow grazers to increase their foraging distances when the benefits provided by distant forage outweigh the costs of travel (Brooks & Harris, 2008). This would only be possible, however, if the animals could walk to water when necessary. Western (1975) shows that

wildebeest can be found 10–15 km from water but that the highest densities are found within 5 km of water. His results suggest that Thompson's gazelles are rarely found more than 6 km from water, whereas Estes (1997) reports that these gazelle can walk up to 16 km to water. In this study, dry season concentrations of grazers on Mbirikani were located between 20 and 26 km from most available surface water, but much closer to a safari lodge water hole, which may have supplemented their water requirements between long treks to the rivers. However, these species were rarely observed at the lodge waterhole, probably because of the intensive use of the water by elephants (RG's pers. obs.). Zebra can forage at much greater distances from water, up to 34.5 km (Brooks & Harris, 2008), and were frequently observed moving to and from the river, from distances up to 30 km.

Because of the highly intensive use of all available permanent water in the study area by livestock and people, herders may have intentionally or unintentionally scared wildlife away from the vicinity of water (De Leeuw *et al.*, 2001). In Australia, for example, Andrew & Lange (1986) found that kangaroos avoided areas close to water points used intensively by sheep, and in northern Kenya wildlife was found much further away from water than livestock, and wildlife assemblages were more diverse further from water (De Leeuw *et al.*, 2001).

The scarcity of significant predictors emerging from the models suggests that other factors may be influencing the distribution of wildlife on these two ranches. Indeed, even in the best model (Mbirikani dry season), less than 50% of the variation in wild grazer distribution was accounted for by the single significant predictor, grass biomass ( $R^2 = 0.445$ ). For Merueshi in the dry season, less than 10% of the variation was explained by grass biomass, which was also the only significant predictor ( $R^2 = 0.072$ ). A further stage of analysis was carried out using multiple linear regressions on the same data, once all transects with an observation of zero wild grazers had been removed, but this provided little additional information (Groom, 2007).

Other factors which could be influencing the presence of wild grazers include predation, and the distribution of salt licks, shade and temperature (Kennedy & Gray, 1993). Predation was found to be important in structuring the community of herbivores in the Serengeti-Mara ecosystem in East Africa (Sinclair, 1985). In this study, however, data on carnivore densities were scarce for Mbirikani and absent from Merueshi, so an indicator of predation could not be included in the model. Salt licks are an important

determinant of wildlife distribution patterns, and the provision of salt has been used to manage the distribution of wildlife (e.g. Case, 1938). In this study, the lack of data on the location of salt licks and concentrations of minerals precluded investigation of their influence on the observed distribution patterns of wild grazers.

Another limitation of the study was the measurement of grass quality. Cattle faecal analysis provides a good indicator of the quality of the grass selected by cattle, which may not be representative of the general habitat quality, but rather indicate the best forage available (to cattle). Moreover, cattle browse when nutritionally stressed (Barnes, 1978; Bayer, 1990) and browse material would significantly affect the CP content in faeces (e.g. Gwynne & Bell, 1968; Bayer, 1990). However, personal observations by RG indicated that the vast majority of the cattle foraging was grazing because there was little suitable browse available in most habitats. Thus, the cattle faecal analysis gave a measure of the relative quality of the grazing between areas, which was the important point in this analysis, although collecting forage quality data at a finer resolution may have been beneficial.

Nonetheless, these results suggest that where forage quantity is limited, grazers may have no choice but to select the areas of highest grass biomass to get sufficient forage, suggesting that forage quantity is more important than quality in a resource-stressed environment. Where maximum distances to water are less than 26 km, the distribution of surface water does not seem to have a significant effect on grazer distributions.

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