

# Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers

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## Summary

1. Theory predicts that small grazers are regulated by the digestive quality of grass, while large grazers extract sufficient nutrients from low-quality forage and are regulated by its abundance instead. In addition, predation potentially affects populations of small grazers more than large grazers, because predators have difficulty capturing and handling large prey.

2. We analyse the spatial distribution of five grazer species of different body size in relation to gradients of food availability and predation risk. Specifically, we investigate how the quality of grass, the abundance of grass biomass and the associated risks of predation affect the habitat use of small, intermediate and large savanna grazers at a landscape level.

3. Resource selection functions of five mammalian grazer species surveyed over a 21-year period in Serengeti are calculated using logistic regressions. Variables included in the analyses are grass nitrogen, rainfall, topographic wetness index, woody cover, drainage lines, landscape curvature, water and human habitation. Structural equation modelling (SEM) is used to aggregate predictor variables into 'composites' representing food quality, food abundance and predation risk. Subsequently, SEM is used to investigate species' habitat use, defined as their recurrence in 5 × 5 km cells across repeated censuses.

4. The distribution of small grazers is constrained by predation and food quality, whereas the distribution of large grazers is relatively unconstrained. The distribution of the largest grazer (African buffalo) is primarily associated with forage abundance but not predation risk, while the distributions of the smallest grazers (Thomson's gazelle and Grant's gazelle) are associated with high grass quality and negatively with the risk of predation. The distributions of intermediate sized grazers (Coke's hartebeest and topi) suggest they optimize access to grass biomass of sufficient quality in relatively predator-safe areas.

5. The results illustrate how top-down (vegetation-mediated predation risk) and bottom-up factors (biomass and nutrient content of vegetation) predictably contribute to the division of niche space for herbivores that vary in body size. Furthermore, diverse grazing assemblages are composed of herbivores of many body sizes (rather than similar body sizes), because these herbivores best exploit the resources of different habitat types.

**Key-words:** allometry, consumer resource interaction, herbivore distribution, predator–prey, predator-safe refugia, resource selection, risk-forage trade-off, ruminant, trophic structure, ungulate

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## Introduction

Populations of herbivores are regulated by the availability of food and by predation which limits the total number of animals an area can support at any given time (Fritz & Duncan 1994; Hopcraft, Olf & Sinclair 2010; Sinclair, Mduma & Brashares 2003). Individuals must acquire sufficient food while avoid being killed (Lawton & McNeill 1979; Sinclair & Arcese 1995), and therefore, the overriding limitations of food availability and the risk of predation also affect which habitats individuals choose to occupy (Valeix *et al.* 2009b). Theory suggests that a herbivore's choice of habitat might be dependent on its body size because the net effect of predation and food supply differs between small and large herbivores (Hopcraft, Olf & Sinclair 2010). For instance, the size of a herbivore determines the number of predators to which it is susceptible (Sinclair, Mduma & Brashares 2003) but also determines the quality of forage it is capable of processing (Owen-Smith 1988). As a result, body size might constrain certain herbivore species to occupying specific habitats based on its safety, or its forage quality, or its forage abundance, and this could explain the differences in the spatial distribution of herbivores over a landscape (Bell 1982; Botkin, Mellilo & Wu 1981; Jarman 1974).

A ruminant's gastrointestinal tract scales isometrically with body size (Clauss *et al.* 2003; van Soest 1996). In other words, small ruminants have small rumens which means they can only retain ingesta for short periods of time (Demment & Soest 1985; Wilmshurst, Fryxell & Bergman 2000). Large ruminants tend to have wide mouths enabling them to ingest large amounts of food and a capacious rumen resulting in slow passage rates. By extending the ingesta retention time, large ruminants allow for additional fermentation and therefore extract more energy from coarse forage than small ruminants can (Gordon, Illius & Milne 1996b; Murray & Brown 1993; Owen-Smith 1988; Shipley *et al.* 1994). Other grazers, such as megaherbivores (elephant and rhino) and hind-gut fermenters (zebra), are an exception to this trend (Clauss & Hummel 2005). These species tend to mix their diet of coarse vegetation with high-quality vegetation (Foose 1982). In addition to the size-related limitations of digestive efficiency, small ruminants require proportionately more energy per unit body mass than large ruminants because a mammal's metabolic rate scales approximately three-fourths with body size. The high metabolic rate and the fast passage of ingesta in small ruminants means the only way these animals can extract sufficient nutrients from the grass is to select the most digestible components of the plant (e.g. their narrow mouths allow them to choose the highest-quality shoots and leaves), while avoiding coarse materials such as stems, sheaths and awns (Demment & Soest, 1985; Gordon & Illius 1996a; Illius & Gordon 1992). In contrast, the more complete fermentation process and the slow metabolic rate of large endotherms means that large ruminants can consume low-quality forage provided there is sufficient quantity.

Grasslands are composed of a diverse mixture of species that vary in their nutritional quality and their vegetative

architecture. The spatial distribution of grasses over a landscape is determined by the interplay between biotic and abiotic processes, such as soil quality, water, fire, grazing pressure and seed dispersal (Anderson *et al.* 2007a; Anderson, Ritchie & McNaughton 2007b; Blair 1997; Bond & Keeley 2005). For instance, grasses growing in moist areas tend to invest more resources into developing silica-rich structural supports than those growing in arid areas (McNaughton *et al.* 1985; Olf, Ritchie & Prins 2002). Furthermore, there is a compositional shift in wet areas towards tall grass species with high carbon-to-nitrogen ratios, which lowers the concentration of nitrogen and phosphorous available to herbivores (Anderson *et al.* 2007a). Hence, grasses in wet areas tend to have less nutrition per unit mass than the grasses in dry areas because the concentrations of key elements (i.e. N, P, Ca, Na, Mg, etc.) are diluted by the carboniferous support structures. As a result, we might expect attributes of the landscape that affect grass quality and quantity to shape the distribution of different-sized grazers.

The size of a herbivore also affects the rates at which it is predated (Cohen *et al.* 1993; Sinclair, Mduma & Brashares 2003). Large adult herbivores are difficult for predators to capture and handle and, as a result, they tend to escape predation (Sinclair, Mduma & Brashares 2003). The evolution of megaherbivores, like rhino and elephant which effectively escape predation altogether, is probably the result of this arms race (Owen-Smith 1988). Small herbivores and juveniles are exposed to greater rates of predation because large predators, in addition to eating large prey, also tend to supplement their diet with small prey (Cohen *et al.* 1993). However, evidence that the prey base of small carnivores is nested within that of large carnivores is conflicting; it has also been shown that carnivore diet can be partitioned such that large carnivores specialize on large prey and small carnivores specialize on small prey (Owen-Smith & Mills 2008). Therefore, the degree to which a herbivore population is predator-regulated depends on both the relative size of the predators and their prey, as well as how the prey base is partitioned by carnivores of different sizes (Hopcraft, Olf & Sinclair 2010).

The success rate of many predators is correlated with features in the landscape that facilitate the capture or detection of prey. For instance, ambush predators such as lion are most successful near water and in thick vegetation, which provide predictable locations where prey are encountered while still concealing the predator (Hopcraft, Sinclair & Packer 2005; Valeix *et al.* 2009a). Additionally, rivers, roads and open glades have been shown to be important features that contribute to the hunting success of cursorial predators such as wolves in other ecosystems (Hebblewhite, Merrill & McDonald 2005; Kauffman *et al.* 2007). Therefore, landscape features might influence predation risks, and this could also affect the distribution of different-sized grazers.

In this study, we investigate the relative importance of food quality, food quantity and predation risk in shaping the distribution of five different-sized grazing ruminants in the Serengeti ecosystem. Previous work suggests food quality, forage abundance and predation risk are important factors

that shape localized herbivore hot-spots (Anderson *et al.* 2010); however, the role of these factors in determining the distribution of multiple herbivores over an entire landscape has never been tested. We address this by testing whether theoretical expectations of herbivore distributions based on known body size–risk–resource relationships (see review by Hopcraft, Olf & Sinclair 2010) are consistent with empirical data on grazer distributions in a landscape that varies in both the available nutrients and vulnerability to predation. We predict that the smallest grazers such as Thomson's gazelle (*Eudorcas thomsoni*; 20 kg) and Grant's gazelle (*Nanger granti*; 55 kg) should be confined to the areas with the highest grass quality with the least risk of predation, because evidence suggests that small herbivores are predator-regulated (Sinclair 1985) and depend on high-quality food. Intermediate sized grazers such as topi (*Damaliscus korrigum*; 120 kg) and Coke's hartebeest (*Alcelaphus buselaphus*; 135 kg) should occur in areas where they can consume enough grass biomass of sufficient quality while remaining in the safest patches (i.e. a mixed strategy) (Cromsigt 2006; Wilmshurst, Fryxell & Bergman 2000). The largest grazers, African buffalo (*Syncerus caffer*; 630 kg), are relatively free from predation pressure and are bulk grazers (Fritz *et al.* 2002); their distribution is expected to be constrained only by the amount of food that is accessible.

## Materials and methods

The study was conducted in the Serengeti ecosystem in East Africa between 1°30' to 3°30' south and 34°00' and 35°45' east (Fig. 1). Semi-arid savannas and grasslands dominate the south, with mixed *Acacia* and *Commiphora* woodlands spread over the central and northern areas which are interspersed with large treeless glades (Reed *et al.* 2008; Sinclair *et al.* 2008). The average annual rainfall increases from *c.* 500 mm in the south-east to

over 1200 mm in the north-west and falls primarily in the wet season (November–May).

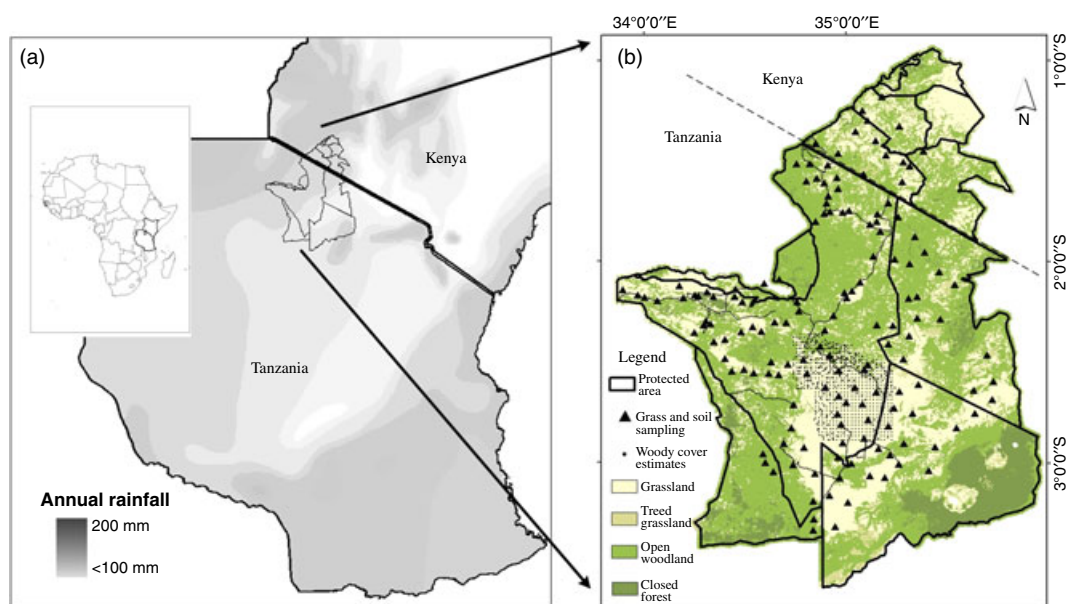
## HERBIVORE DISTRIBUTIONS

Data on the distribution of different-sized herbivores were collected from systematic aerial censuses conducted by the Tanzania Wildlife Research Institute and the Frankfurt Zoological Society over a 21-year period. The censuses were conducted in both the wet and the dry seasons giving a series of census 'snapshots' from which we compiled generalized large-scale distribution maps for each species. We used density measures of buffalo, topi, Coke's hartebeest, Grant's gazelle and Thomson's gazelle in 5 × 5 km blocks from systematic reconnaissance flight (SRF) censuses from 1985 to 2006. There were a total of 11 SRF censuses that included both Thomson's and Grant's gazelle, while buffalo, topi and Coke's hartebeest were included in a total of nine SRF censuses.

We estimated the relative degree at which grazers select or avoid resources from the SRF aerial census data by simultaneously accounting for the density of animals observed in a 5 × 5 km cell and how consistently the species occurred in that cell (i.e. the number of censuses which detected the species in the cell). The recurrence index for each species across years is calculated as follows:

$$\text{Log}\left(\frac{(\text{Sum of densities across all years by cell})^2}{(\text{SD of cell across all censuses} + 1)}\right)$$

such that cells with high densities of animals observed consistently across all censuses have the highest scores and cells with low densities of animals observed infrequently have the lowest scores. Because the recurrence index includes censuses conducted in both the wet and dry season over a 21-year period, the index averages out the interannual and seasonal variation and serves as a generalized large-scale metric of animal distributions despite local seasonal movement. Specifically, large indices imply that the cell is consistently used by many individuals in either the wet or dry seasons (or both) and over long periods of time (i.e. 21 years), which would indicate the cell has habitat features that can support the species for extended periods.



**Fig. 1.** Sampling points were distributed across (a) the rainfall gradient and (b) in every major vegetation type occurring in the greater Serengeti-Mara ecosystem, East Africa.

## FOOD QUALITY ESTIMATES

The quality of forage was estimated from field measures of grass nitrogen at 148 sites across the ecosystem (Fig. 1) collected between January and May (wet season) from 2006 to 2008. Wet season measures provide an estimate of the maximum available nutrients in the grass that is available to grazers (Anderson *et al.* 2007a). The sampling sites were chosen to maximize the variation in soil and vegetation types across the rainfall gradient. The above-ground grass nitrogen concentration from five 25 × 25 cm clippings was averaged at each of the 148 sites (pooling all grass species and grazing histories for an average grass nitrogen measure per site). Dried grass samples were ground using a Foss Cyclotec 1093 cyclonic grinder (Foss, Hillerød, Denmark) with a sieve size of 2 mm. Grass samples were then oven dried for 48 h at 72 °C, and nitrogen concentrations were measured using a near infra-red (NIR) spectrophotometer (Bruker Optik GmbH, Ettlingen, Germany). The multivariate calibration of the NIR used 'true' nitrogen concentrations of African savanna grasses measured on a CHNS EA1110 elemental analyzer (Carlo-Erba Instruments, Milan, Italy). Correlation between observed nitrogen concentrations from the CHNS elemental analyzer and the predicted NIR nitrogen concentrations suggest a high accuracy in the NIR technique ( $r^2 = 0.97$ ,  $n = 76$ ).

The spatial distribution of grass nitrogen was interpolated by regression kriging using a 9-year mean NDVI index as a covariate (raw data were 16-day NDVI composites from the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra satellite for the period from 2000 to 2009). Regression kriging (Hengl, Heuvelink & Rossiter 2007) is an interpolation technique that takes into account the spatial autocorrelation between sampling points (as per ordinary kriging), while simultaneously accounting for the correlation between samples and an underlying predictor variable. In this case, grass nitrogen samples are inversely correlated with the cell's mean NDVI ( $r^2 = 0.10$ , slope =  $-0.0001$ ,  $P < 0.001$ ,  $n = 148$ ; see Fig. S1). NDVI is commonly used as a measure of the vegetation greenness; large NDVI measures indicate live green vegetation while low measures suggest dry or dead vegetation. As a separate internal accuracy check, 30 samples were selected randomly and used to test the accuracy of a second regression kriged grass nitrogen map created from the remaining 118 samples. The predicted grass nitrogen values from the second map correlated well with the 30 random samples ( $r^2 = 0.25$ , slope =  $0.48$ ,  $P < 0.01$ ,  $n = 30$ ), which verifies this technique as having an acceptable level of accuracy.

It is possible that some herbivores might only require infrequent or seasonal access to patches of high food quality, rather than being constrained by a minimum daily requirement. A separate variable, distance to grass nitrogen, was estimated by calculating the Euclidean distance to cells with the greatest concentrations of grass nitrogen (i.e. any cell within the upper 25th percentile of grass nitrogen).

## FOOD ABUNDANCE ESTIMATES

The abundance of grass biomass is positively correlated with rainfall such that the largest quantity grows on moist sites. Conversely, rainfall tends to decrease the forage quality (i.e. the digestibility of vegetation) because under moist conditions vegetation tends to become more lignified (Breman & De Wit 1983; McNaughton *et al.* 1985; Olf, Ritchie & Prins 2002) (see Fig. S2). In addition, the species composition of a community shifts in areas with more rainfall and becomes dominated by grass species with lower leaf nitrogen and phosphorous concentrations (Anderson *et al.* 2007a). Therefore, we

used rainfall and the topographic wetness index (TWI) as a proxy for grass biomass rather than grass quality.

The mean annual rainfall was calculated from long-term monthly rainfall records collected by the Serengeti Ecology Department from 58 rain gauges for 46 years (1960–2006). Rain gauges with < 3 years of data were omitted. These data were regression kriged across a known south-east to north-west diagonal rainfall gradient to generate a smoothed rainfall map for the ecosystem. The correlation between average grass biomass with rainfall suggests a positive relationship ( $r^2 = 0.51$ , slope =  $0.28$ ,  $P < 0.01$ ; see Fig. S3).

The TWI is a measure of the landscape's capacity to retain water. TWI is calculated by combining the total water catchment area and the slope of a cell to estimate its relative capacity to retain water. Cells with higher TWI values tend to be flat or concave and have large catchment areas. A test of accuracy for TWI and average grass biomass suggests an acceptable correlation; however, the linear regression is not significant most likely because soil quality, rainfall, fire and herbivory also alter the total grass biomass at a site ( $r^2 = 0.25$ , slope =  $37.24$ ,  $P = 0.17$ ; see Fig. S4).

## PREDATION RISK ESTIMATES

Predation of herbivores is associated with certain landscape features such as dense woodland, embankments, water sources, predator viewsheds and slope which facilitate the capture of prey or conceal hunting predators (Balme, Hunter & Slotow 2007; Hebblewhite, Merrill & McDonald 2005; Hopcraft, Sinclair & Packer 2005; Kauffman *et al.* 2007). We used metrics of woody cover, distance to drainage beds and landscape curvature to estimate the exposure to predation risk for herbivores (Anderson *et al.* 2010; Valeix *et al.* 2009b). A re-analysis of historic data (Hopcraft, Sinclair & Packer 2005) shows that these parameters increase the probability of lions making a kill (see on-line supplementary material Fig. S5 and Table S1).

The average amount of woody cover available for an ambush predator was calculated for each of the 27 land cover classes identified by Reed (Reed *et al.* 2008). A total of 1882 points were sampled along transects (Fig. 1) and assigned to one of Reed's land cover classes. At each point, the mean per cent woody cover > 0.4 m high from four equidistant measurements at a radius of 15 m away was calculated (based on minimum cover requirements for lions (Elliott, Cowan & Holling 1977; Scheel 1993)). The sampling points were distributed across the ecosystem, providing estimates of horizontal cover capable of concealing predators for each class of land cover for the entire ecosystem.

The distance to any drainage bed with clearly defined embankments was calculated in ArcGIS 9.3 (classes 1–3 of the RiversV3 shapefile in the Serengeti Database <http://www.serengetidata.org>). Most drainage beds in Serengeti remain dry for the majority of the year but are often associated with other landscape features such as erosion embankments, thicker vegetation and confluences. We do not use drainages to imply access to water but as a description of a geographical landscape feature that is associated with ungulate risk.

An absolute value of landscape curvature (i.e. the degree of concavity or convexity for the landscape) was calculated in ArcGIS 9.3 using a digital elevation model (90-m resolution) derived from the SRTM data for East Africa (available through the NASA Jet Propulsion Laboratory <http://www.jpl.nasa.gov>).

## WATER

Access to free water was estimated by calculating the distance to any river that either flows continually or contains permanent pools

through the dry season (classes 1 and 2 of RiversV3 in the Serengeti Database). The majority of drainages in the Serengeti are ephemeral freshets and contain water only for a few weeks during the wet season (classes 3 and 4) and were not considered.

#### HUMAN-INDUCED RISK

The exposure to human-induced risks, such as poaching, was estimated by calculating the distance to villages inversely weighted by the estimated density of the human population:

$$(\text{Log}[\text{Human Population Density} + 1]) / (\text{Distance to Village (km)})$$

such that areas near densely populated villages have the highest values and lowest values correspond to areas furthest from small villages. Human density maps for the year 2000 (the most recent data available) were acquired for the region from the FAO AfriCover project (<http://www.africover.org>). Human density was log transformed as values were log-normally distributed; most cells had low-density estimates but a few had very high-density estimates.

#### STATISTICAL ANALYSES

The data were analysed at two levels of precision. The crudest response was presence/absence, where we ask what variables predict the occurrence of a species in a cell using logistic regressions (where 1 indicates the species has been detected in the cell at least once during any census). At the more refined level, we use structural equation models (SEM) to ask what variables predict the recurrence index of a species in a cell, given the species has been detected in the cell at least once during any census (i.e. a subset of only the nonzero cells from the entire data set). This scaled approach enabled us to determine whether the variables responsible for predicting the presence of a species in a cell were different to those that predicted their recurrence index, as well as accounting for nonlinear relationships that might exist between exogenous predictor variables in the logistic regression analysis.

The probability of a species occurring in a cell was predicted using resource selection probability functions (Boyce & McDonald 1999; Manly *et al.* 2002); specifically, we used binary logistic regressions with both backward and forward elimination processes. The models with the fewest number of parameters were selected based on the lowest AIC values (see on-line supplementary material Table S2). We tested for nonlinear relationships in the logistic regressions by including quadratic terms. If continuous variables behave quadratically, we expect the coefficient to be negative, meaning animals might select a resource but avoid areas where it is overabundant. If the coefficient of the quadratic was positive (i.e. a u-shaped response), we excluded the quadratic function if it was not ecologically meaningful. We did not include interaction terms in the logistic regression models because our intent was to test whether grazers of different body size reacted differently to the quality of food, the abundance of food and predation risk specifically. (We did not intend use the logistic regressions to build accurate predictive models of resource selection for each species, in which case interaction terms should be included.) We tested the sensitivity of the logistic regression models with an area under the curve (AUC) analysis and by cross-validation (CV). The AUC estimates the probability that a positive response (i.e. presence) is actually correctly classified as being positive by the model. The CV estimates the generalization error through bootstrapping, such that small values correspond to a small prediction error in the model.

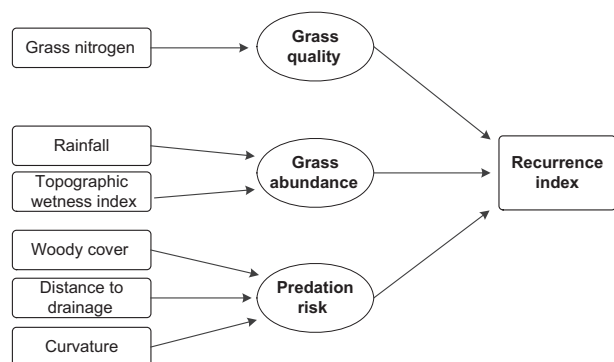
A principal component analysis of the exogenous predictor variables (shown in the supplementary on-line material Fig. S6 and

Table S3) illustrates that the landscape is divided into relatively mesic high-biomass sites with low-quality grass as opposed to arid low-biomass sites with high-quality grass. The second component describes the topographic relief that varies from hill tops to valley swales (i.e. catenas as first described by Bell 1970). The first two components account for 47.2% of the variation in the data. This supports our assertions as to how the landscape varies in forage quality and forage abundance, which might determine how different-sized grazers select specific areas of the landscape while avoiding others.

The recurrence index of different-sized grazers in response to food quality, food abundance and predation risk was assessed using SEM (Grace 2006). We specifically wanted to test the hypotheses that the effects of food resources and predation risk differ between different-sized species and so did not consider the effects of humans nor access to free water in the SEMs. (Proximity to humans and access to free water were used to predict a species presence or absence in a cell rather than their recurrence.) We used only the cells where the species had been detected for the SEM analysis (i.e. a subset composed of only the nonzero cells).

The *a priori* structural equation model describing the expected relationships between variables is illustrated in Figure 2 and was used to test hypotheses regarding the causes of herbivore recurrence based on body size. SEM analysis estimates the effect of variation in one entity on another based on a third (termed mediation), while simultaneously accounting for the correlation between predictor variables, which is one of its strengths. A direct path implies a causal relationship where one variable is directly responsible for variation in the other. Composite variables (shown by circles) aggregate several predictor variables into a single conceptual factor (such as risk) that is often not directly measurable itself (Grace *et al.* 2010; Grace & Bollen 2008), making it a good technique for the analysis of this data set. For instance, the combined effect of woody cover with distance to drainages and landscape curvature might determine the predation risk to which herbivores are exposed, and this might explain the variation in a species' recurrence index. The *a priori* model is tested against the data for each species and assessed for support using a chi-square statistic. ( $P > 0.05$  suggests there is no difference between the *a priori* model and the real relationships occurring in the data.)

We allowed all exogenous predictor variables (i.e. grass nitrogen, rainfall, TWI, woody cover, distance to drainage and curvature) to correlate with each other and report only the significant relationships ( $P < 0.05$ ). Sequential inclusion of correlations between exogenous



**Fig. 2.** The *a priori* structural equation model used to assess the recurrence index of savanna grazers. Exogenous environmental predictor variables (boxes on left) are combined into composite variables (circles) and used to predict the variation in the response variable (boxes on right).

predictor variables as recommended by the modification index was used to construct the SEM for each species. We used maximum likelihood to evaluate a model's overall goodness-of-fit in AMOS 17.0 (SPSS, IBM Corporation, Armonk, New York, USA).

## Results

The spatial distribution of grass nitrogen, rainfall, TWI, woody cover, drainages, curvature, water and humans shows strong differences across the ecosystem (Fig. 3). The short-grass plains in the south-eastern extent of the ecosystem tend to have high grass nitrogen, low rainfall but large water catchment areas (TWI), no woody cover to conceal ambush predators and few drainage beds because it is relatively flat, and tend to be far from permanent water and humans. In direct contrast, the western corridor and the north have low grass nitrogen, high rainfall, plenty of woody cover concealing predators, extensive topographic relief dissected by drainage beds which often contain permanent water pools, and are close to human boundaries. Grazers become more aggregated over the landscape as their body size decreases (Fig. 4).

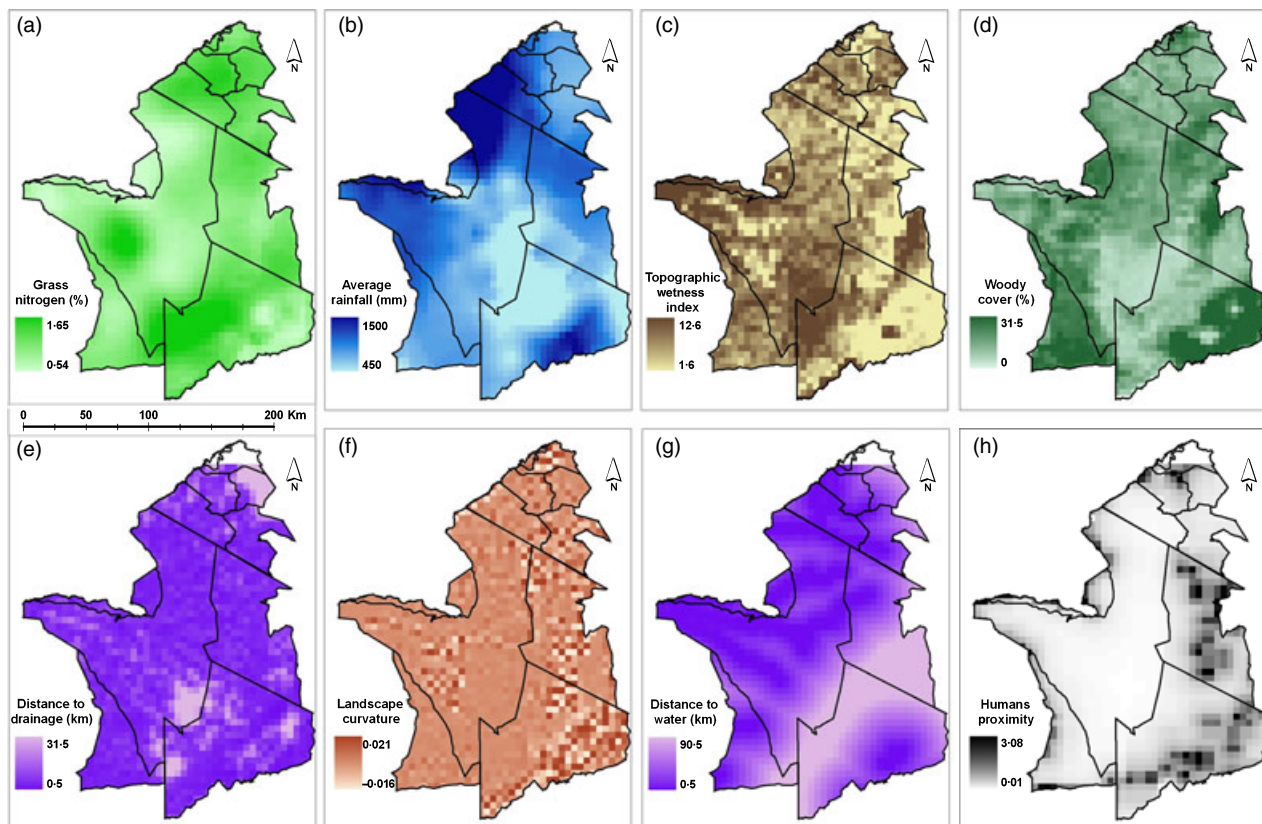
### LOGISTIC REGRESSIONS PREDICTING SPECIES PRESENCE/ABSENCE

Results from the logistic regression (Table 1) suggest that small grazers tend to be positively associated with some

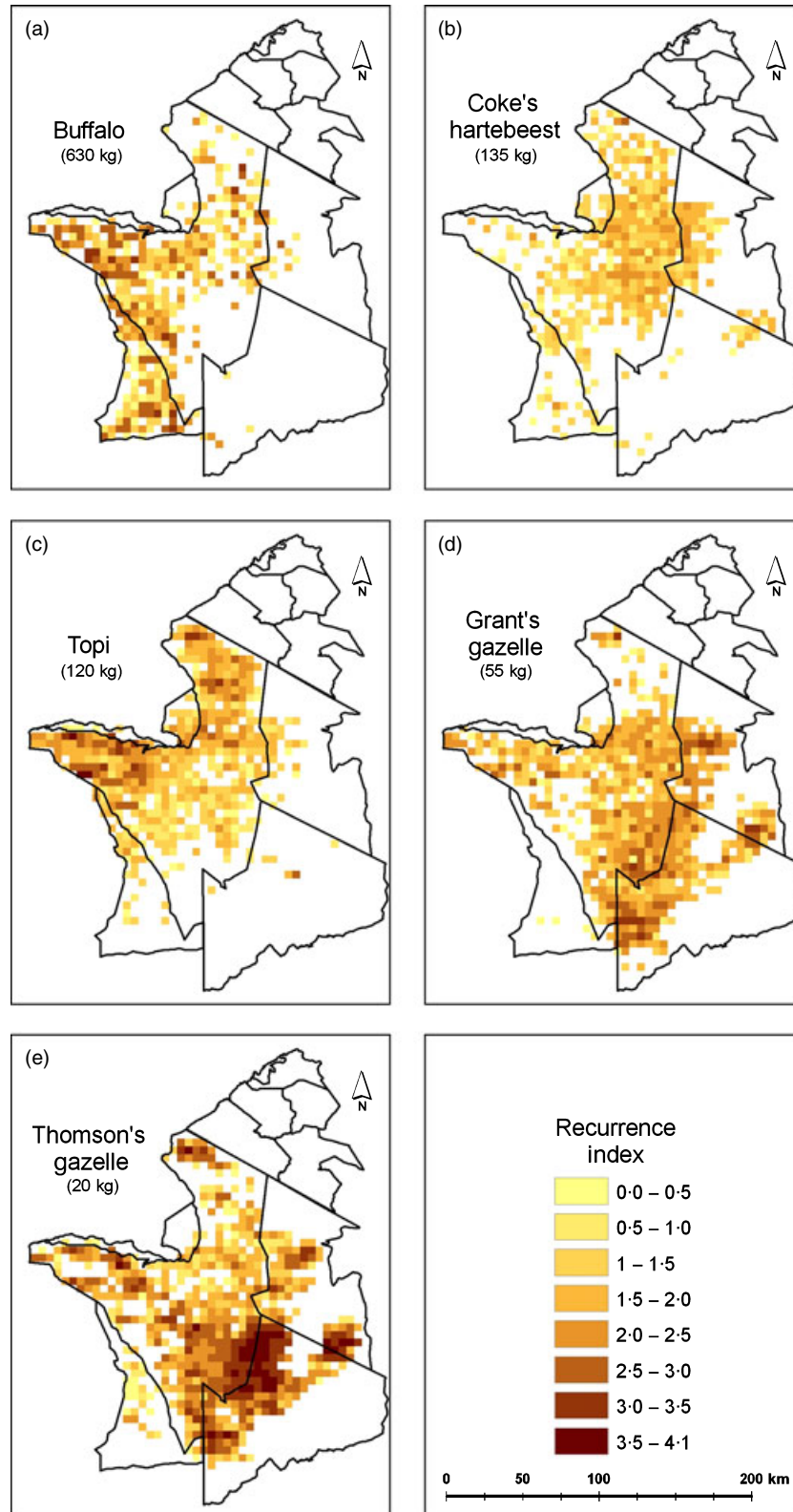
landscape features and negatively associated with other landscape features (suggesting they avoid some of the features we measured), whereas large grazers tend to only be positively associated (suggesting they do not avoid any of the features we measured). An area under the curve sensitivity analysis (AUC) and an estimate of the cross-validation prediction error (CV) suggest the models accurately predict herbivore occurrence (buffalo AUC = 0.833, CV = 0.164; Coke's hartebeest AUC = 0.861, CV = 0.143; topi AUC = 0.871, CV = 0.146; Grant's gazelle AUC = 0.850, CV = 0.155; Thomson's gazelle AUC = 0.829, CV = 0.163) (see Table S4 for details of the logistic regression models).

Forage quality, as estimated by grass nitrogen concentrations, is positively associated only with the presence of Thomson's gazelle, the smallest grazer (Table 1). Grass nitrogen does not increase the probability of large herbivores occurring in a cell and has a negative relationship with topi and Coke's hartebeest. The positive association between Thomson's gazelle and proximity to areas with high grass nitrogen is nonlinear (as indicated by the negative coefficient of the quadratic term), suggesting that gazelle switch to areas with intermediate grass nitrogen when high grass nitrogen patches are inaccessible.

The presence of buffalo, topi and Grant's gazelle is positively associated with high abundance of grass, as estimated



**Fig. 3.** The spatial distribution of variables predicting grass quality, grass abundance and predation risk. The quality of grazing is estimated by (a) the grass nitrogen content (%). Grass abundance is estimated by (b) mean rainfall (mm) and the (c) topographic wetness index. Exposure to predators is estimated from (d) woody cover (%), (e) distance to drainage beds (km) and (f) landscape curvature. Access to (g) free water and (h) proximity to humans also affect the distribution of grazers. GIS layers are posted at <http://www.serengetidata.org>.



**Fig. 4.** The spatial distribution of recurrence for (a) African buffalo (630 kg), (b) Coke's hartebeest (135 kg), (c) topi (120 kg), (d) Grant's gazelle (55 kg) and (e) Thomson's gazelle (20 kg) from repeated censuses in the Serengeti between 1985 and 2006.

by the mean annual rainfall and the TWI (Table 1). Thomson's gazelles are negatively associated with high rainfall areas (such as the north) which tend to be dominated by low-

quality high-biomass vegetation (as per Fig. S6 and Table S3); however, they are positively associated with greater topographic wetness.

**Table 1.** Summary results of the logistic regression analyses predicting species' presence in 5 × 5 km grid cells

	Buffalo (630 kg)	Coke's Hartebeest (135 kg)	Topi (120 kg)	Grant's gazelle (55 kg)	Thomson's gazelle (20 kg)
Food quality					
Grass <i>N</i>		−***	−***		+***
(Grass <i>N</i> ) <sup>2</sup>					+***
Distance to <i>N</i>					+***
(Distance to <i>N</i> ) <sup>2</sup>					−***
Food abundance					
Rain	+***		+**	+*	−***
(Rain) <sup>2</sup>	−***			−**	
Topographic wetness	+*	−*		+**	+**
(Topographic wetness) <sup>2</sup>				−**	
Predation risk					
Woody cover	+***	+***	+*	−***	−***
(Woody cover) <sup>2</sup>	−	−***	−*		
Distance to drainage	+		+***	+***	+**
(Distance to drainage) <sup>2</sup>	−*				
Curvature					
Water					
Distance to water	+*	+	+***	−***	−**
(Distance to water) <sup>2</sup>	−***	−***	−***		
Anthropogenic					
Proximity to human	−***	−***	−***	−**	−***

Signs indicate the variable either promotes (+) or reduces (−) the probability of occurrence (i.e. the  $e^{\beta}$  odds ratio is greater or less than 1). Blanks indicate the best models (based on AIC) did not include the variables. \*\*\* $P < 0.001$ , \*\* $P < 0.01$  and \* $P < 0.05$ . (For the details of the logistic regression parameters, see Table S4.)

There is a positive nonlinear relationship between the amount of cover available for ambush predators and the presence of buffalo, hartebeest and topi as indicated by a negative quadratic term for woody cover (Table 1). Smaller species (Grant's gazelle and Thomson's gazelle) are negatively associated with woody cover. Buffalo are more likely to occur at intermediate distances from drainages as indicated by the negative quadratic term. Grazers smaller than Coke's hartebeest (i.e. topi, Grant's gazelle and Thomson's gazelle) are positively associated with areas further away from drainages. Curvature is not significant in predicting the presence of any species at this scale, although it is significant at a finer scale of analysis (Anderson *et al.* 2010).

The largest grazers occur in areas that are in relative proximity to permanent water, but not immediately adjacent (as indicated by the negative coefficient of the quadratic term). Both Grant's gazelle and Thomson's gazelle are less likely to occur in areas that are far from access to permanent water (Table 1).

All species, regardless of body size, are negatively associated with areas close to high human densities, and this result is ubiquitous (Table 1). This is the strongest and most consistent variable predicting the presence or absence of grazers.

#### SEM PREDICTING SPECIES RECURRENCE INDEX

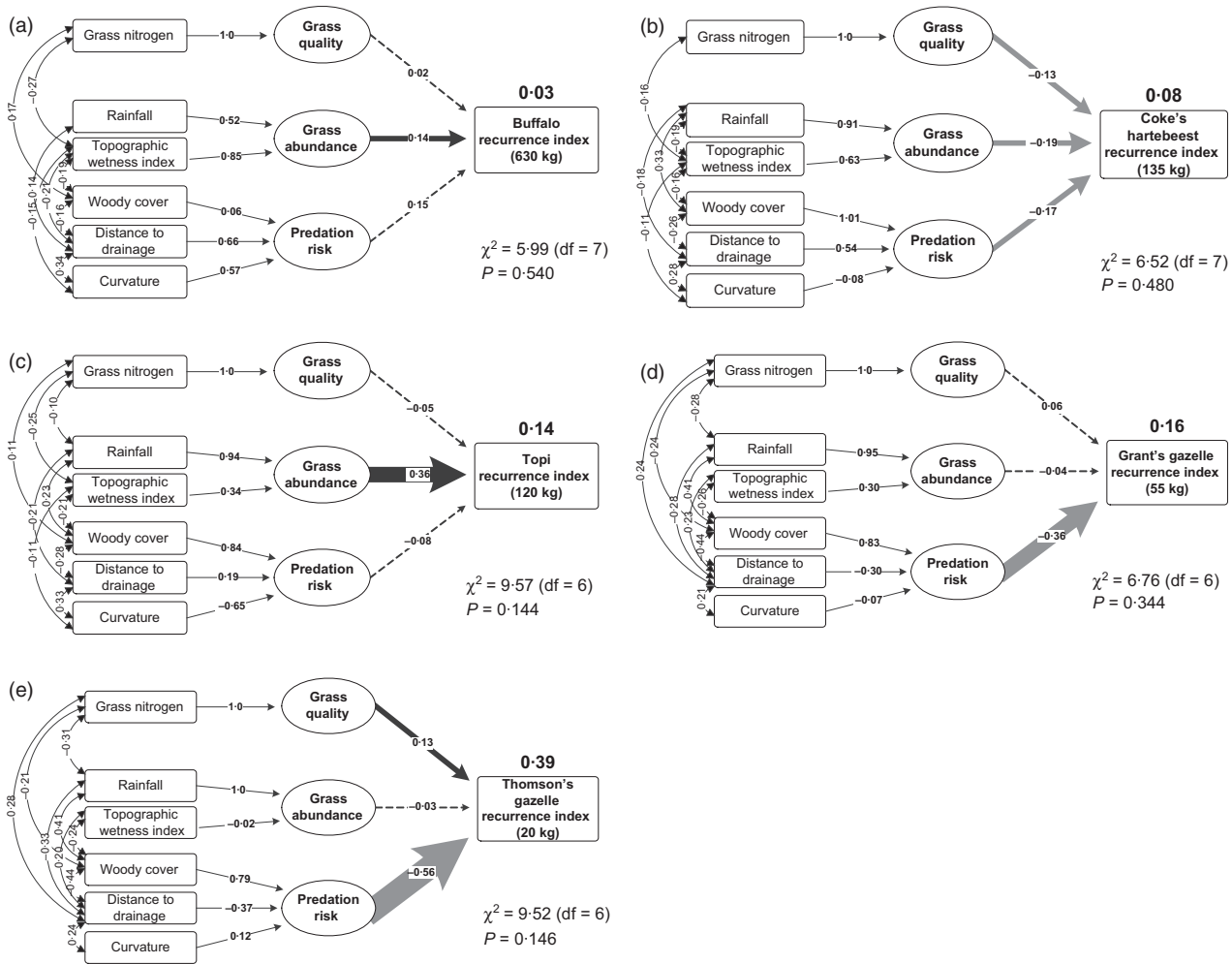
Structural equation models were used to predict the recurrence index for each species. The recurrence index is a continuous response variable that measures both how many times a

species was observed in a cell, as well as the abundance of the species in that cell. In general, the SEMs explain more of the observed variation in the spatial distribution of small grazers than large grazers (Fig. 5). The SEM for Thomson's gazelle explains 39% of the overall observed variance in their recurrence index, whereas the SEM for buffalo explains only 3%.

The correlations between exogenous environmental variables (i.e. variables on the far left of Fig. 5) are <0.35 for all SEMs, with the exception of rainfall, woody cover and distance to drainage beds for the Thomson's gazelle SEM and the Grant's gazelle SEM only. The small correlation between the exogenous variables (i.e. grass nitrogen, rainfall, TWI, woody cover, distance to drainages and curvature) suggests that the unique variation of these variables is high, and therefore, the conceptual nature of the composite variables (grass quality, grass abundance and predation risk) are not confounded by these correlations (Grace & Bolen, 2008; Kline 2005). The correlations between exogenous variables change between the SEMs for each species because they occupy different areas. The SEM reflects real correlations among the variables in the habitats the species occupy.

The chi-square associated with the SEM describing the buffalo recurrence index suggests the data support our *a priori* interpretation ( $\chi^2 = 5.99$ , d.f. = 7,  $P = 0.540$ ); however, the model explains very little of the overall observed variance (3%) (Fig. 5a). Only the abundance of food (as estimated by rainfall and the TWI) is significant in explaining the variation in the buffalo recurrence index (standardized path





**Fig. 5.** The results of the structural equation models assessing the recurrence index of savanna grazers of decreasing body size: (a) buffalo, (b) Coke's hartebeest, (c) topi, (d) Grant's gazelle, and (e) Thomson's gazelle. Solid lines indicate significant paths ( $P < 0.05$ ) and are weighted according to their standardized path strength (i.e. the value associated with each straight line). Black lines are positive path strengths which increase the probability of recurrence. Grey lines are negative path strengths and decrease the probability of recurrence. Dashed lines indicate nonsignificant paths. Curved double-headed arrows represent the correlation between the exogenous predictor variables (with  $r^2$  values). The overall amount of variation explained by the model is the bold number presented above the recurrence index box.

strength = 0.14). The exposure to predation risk (as estimated by the amount of woody cover available to ambush predators, the distance to riverbeds and the landscape curvature) is not significant in explaining the buffalo recurrence index. The amount of nitrogen available in the grass (i.e. forage quality) only explains 0.02 of the variation in the buffalo recurrence index and was not significant.

The data on the recurrence of Coke's hartebeest support the SEM ( $\chi^2 = 6.52$ , d.f. = 7,  $P = 0.480$ ). The SEM describes 8% of the variation in the Coke's hartebeest recurrence index, which is negatively related to food quality (standardized path strength = -0.13), food abundance (-0.19) and risk of predation (-0.17) approximately equally (Fig. 5b).

The recurrence index of topi is positively related to the abundance of food (0.36), while the risk of predation and food quality had nonsignificant negative trends. The SEM describing the topi recurrence index is supported by the data

( $\chi^2 = 9.57$ , d.f. = 6,  $P = 0.144$ ) and accounts for 14% of the overall observed variance (Fig. 5c).

The risk of predation has a strong negative relationship with the recurrence index of Grant's gazelle (-0.36). Food quality and the abundance of food do not have significant effects on the recurrence index of Grant's gazelle. The SEM model for Grant's gazelle is supported by the data ( $\chi^2 = 6.76$ , d.f. = 6,  $P = 0.344$ ) and accounts for 16% of the observed variation in recurrence index (Fig. 5d).

The Thomson's gazelle SEM accounts for the greatest amount of variation in the recurrence index (39%) out of all the species we analysed (Fig. 5e). The data on the recurrence of Thomson's gazelle support the SEM ( $\chi^2 = 9.52$ , d.f. = 6,  $P = 0.146$ ). The risk of predation has the largest negative effect on the Thomson's gazelle recurrence index (standardized path strength = -0.56). Grass nitrogen concentration (food quality) is positively associated with recurrence (0.13), while the abundance of grass is not significant.

## Discussion

Evolutionary theory suggests that herbivores should maximize their access to essential resources while minimizing their exposure to risk (Jarman 1974; Lawton & McNeill, 1979; Sinclair & Arcese, 1995). There are multiple solutions to this trade-off that has led to a wide diversity of mammalian grazers. For instance, grazers might become very large thereby reducing their exposure to small predators (Sinclair, Mduma & Brashares 2003). Alternatively, grazers might avoid predators by selecting relatively predator-free areas which tend to have low grass biomass (Oksanen *et al.* 1981). Evidence suggests that small grazers manage to extract sufficient energy from low-biomass patches by selecting high-quality components of the grass, while large grazers extract more energy from low-quality forage by retaining their ingesta for long periods (Gordon, Illius & Milne 1996b; Murray 1993; Owen-Smith 1988; Shipley *et al.* 1994). We test whether this size-dependent exposure to risks and resources explains the spatial distribution of grazers over a landscape that varies in forage quality and predation risk.

### BODY SIZE AND THE DIVISION OF NICHE SPACE

The most important finding of this study is that food and predation impose greater constraints on the distribution of small grazers than they do for large ones. Empirical data show that small savanna grazers are constrained primarily by food quality and predation, while large grazers tend to occur in patches with high food abundance regardless of the associated predation risks. Intermediate size herbivores balance the risks associated with high-biomass patches with the quality of food. This finding is consistently supported by several lines of analyses: (i) SEM results explain more overall variance in the recurrence index of small grazers and less variance of large grazers (Fig. 5). (ii) There is a clear shift in the role of food quality vs. predation risk in the SEMs from large to small grazers (Fig. 5) which supports our interpretation. (iii) Rainfall, woody cover and access to water are consistently selected by large grazers; however, they do not avoid any of the landscape or environmental features we measured (with the exception of humans, see Table 1). Conversely, small grazers avoid several of the features we measured (namely, high rainfall, woody cover and proximity to drainage beds) while displaying a strong selection for high grass nitrogen patches. This result suggests the distribution of small grazers is more constrained by food and predation pressure than large grazers.

The ecosystem-wide analyses of the spatial distribution of five co-occurring grazer species confirm the predictions based on theory and concur with previous studies of single species or at small spatial scales (Anderson *et al.* 2010; Cromsigt & Olf 2006; Murray & Brown 1993; Olf & Hopcraft 2008). First, the results show that small grazers, such as Thomson's and Grant's gazelles, (i) avoid areas that are risky (Fig 5) and (ii) are the only ones to select areas with high-quality grass in low-rainfall low-biomass areas (witness Thomson's gazelle in

Table 1 and Fig 5e). Topi and Coke's hartebeest rarely occur in the south-east portion of the Serengeti that has the lowest rainfall and is dominated by prostrate grasses with low biomass (Fig. 3b). The largest grazer (buffalo) never occurs on the short-grass plains (Fig. 4). The absence of large grazers from the short-grass plains suggests there is not enough grass biomass or enough free water to sustain viable populations in these areas (Sinclair 1977). It is only the smallest herbivores that can pick the greenest leaves from the low-lying grass sward that consistently occur on the short-grass plains (Fryxell *et al.* 2005). Previous findings show that small grazers can forage in low-biomass patches because their specialized mouth morphology and digestive physiology are adapted to selecting high-quality components of the grass (Wilmshurst, Fryxell & Colucci 1999).

Second, intermediate size grazers, such as topi and Coke's hartebeest, tend to optimize their grazing opportunities against the risk of predation, which suggests they do not entirely conform to the expectations based on predation or those based on food (i.e. a mixed strategy; Sinclair 1985). For instance, topi select areas with high rainfall and high grass biomass (Fig. 5c), but avoid the riskiest areas near rivers or dense thickets (Table 1). And the SEM of Coke's hartebeest (Fig. 5b) shows they avoid patches with high food quality and patches with high food abundance in roughly similar proportions, meaning they might select low food quality patches in low risk areas that have sufficient but not high biomass. This interpretation suggests hartebeest might select areas where they can balance the quality of forage and its abundance in nonlinear ways. Alternatively, the distribution of hartebeest might be better explained by a feature that we did not measure. Figures 4b,c illustrate a clear difference in the distribution of Coke's hartebeest and topi. Specifically, the results show that Coke's hartebeest are associated with intermediate rainfall areas in the central woodlands, while topi occur more often in wet areas especially in the western corridor (Fig. 3b). Previous research has shown that Coke's hartebeest offset their low intake rates with greater digestive efficiency over topi (Murray 1993), which might explain why the slightly larger of the two species occupies the drier lower-biomass patches.

Third, large grazers tend to be positively associated with rainfall (Table 1) and do not avoid areas with high risk of predation (Fig. 5). Species such as buffalo have essentially outgrown most predators (Sinclair, Mduma & Brashares 2003) and are difficult for carnivores to capture and handle (Scheel & Packer 1991). The strong herding instinct in buffalo also reduces an individual's risk of being killed by a predator (Fryxell *et al.* 2007; Hay, Cross & Funston 2008). Because large-bodied animals also face problems dissipating heat (Kinahan, Pimm & van Aarde 2007), they might select shady or cooler habitats such as woodlands which would confound our results. We were unable to control for thermal stress because we do not have data on ambient temperatures. From the data currently available, the best explanation why buffalo select risky patches (Table 1) and why large grazers tend to have the least restricted distributions in Serengeti

(Fig. 5) is because (i) they have outgrown all predators except the biggest, (ii) the anti-predator herding instinct allows these large-bodied animals to access grass resources in risky areas that would otherwise be inaccessible and (iii) their digestive strategy enables them to extract sufficient nutrients from coarse grass. These results indicate that large and small grazers are selecting opposite attributes of the grass (quantity vs. quality, respectively).

#### OTHER LARGE-SCALE FACTORS AFFECTING GRAZER DISTRIBUTIONS

Of the five species we analysed, only gazelles move seasonally to the short-grass plains. The results suggest that regardless of season and despite their local movement, gazelles consistently select specific areas in the Serengeti that have high-quality grass and low exposure to predation (data on grazer distributions combined wet and dry season censuses over a 21-year period). Animals that migrate very long distances between the best available food patches, such as wildebeest and zebra, gain additional anti-predator advantages and do not conform to our expectations based on body size (Fryxell 1995; Hebblewhite & Merrill 2009; Hopcraft, Olf & Sinclair 2010; Wilmshurst, Fryxell & Bergman 2000).

The probability of any grazer occurring in a cell declines sharply and consistently in areas approaching human habitation, irrespective of body size and regardless of the available forage or predator safety. The boundaries of the Serengeti are not fenced, which implies animals perceive a threat and create a soft boundary between themselves and human habitation which is an unexpected, yet interesting avenue for further research. Understanding how animals respond to human risk is important for conservation because it links management practices with ecological function and justifies the protection of critical areas. Furthermore, the strong avoidance by all grazers for human-dominated areas suggests that if the planned national highway through the Serengeti is built (Dobson *et al.* 2010), this could disrupt how animals use the area and would fragment otherwise contiguous populations.

An alternative explanation of our results is that the unit at which herbivores perceive the landscape might scale with body size, and might not be the unit at which we measured ( $5 \times 5$  km) and this could account for the differences we detected (Laca *et al.* 2010; Ritchie & Olf 1999). A reanalysis of the buffalo recurrence index at a  $10 \times 10$  km scale slightly improved the logistic regression results; the same variables increased the area under the curve sensitivity analysis (AUC) and decreased the estimate of the cross-validation prediction error (CV) from 0.833 and 0.164 (see Table S4) to 0.879 and 0.155, which is statistically expected when measuring at coarser resolutions (Fortin & Dale 2005). However, the overall variance in the buffalo recurrence index explained by the  $10 \times 10$  km SEM decreased and none of the paths were significant. Therefore, it is unlikely that gross vs. fine-scale habitat perception by larger herbivores explains these results. Ecosystem-wide data on herbivore abundance at a resolution

$< 5 \times 5$  km are not available so we could not test for fine-scale selection.

## Conclusions

Empirical evidence suggests that small grazers in the Serengeti are constrained by food nutrients and the risk of predation, while the distribution of large grazers is relatively less constrained and determined only by the abundance of forage and not by predation risk. This general conclusion supports the theoretical expectations as to how grazers of different sizes are distributed based on known body size–risk–resource relationships and might also hold for other grazing ecosystems. Similar results showing the distribution of grazers is constrained by the relative availability of food and the exposure to predation risks have been reported previously (Anderson *et al.* 2010; Cromsigt & Olf, 2006; Murray & Brown, 1993), but this conclusion has never before been shown across multiple species at an ecosystem-wide scale. These results suggest that diverse grazing assemblages (i.e. many species co-existing in the same area) should be composed of herbivores of varying body size because these herbivores will be able to exploit many different habitats. Furthermore, if body size determines how grazing niches are partitioned, then we might expect ecosystems with similar-sized grazers to be regulated more by competition for food resources than by predation (Sinclair 1985) because all similar-sized individuals would be searching for the same food simultaneously. Our results indicate that strong interdependencies between resources and risks occur through common underlying environmental gradients such as rainfall, which simultaneously drives top-down and bottom-up forces (Hopcraft, Olf & Sinclair 2010) and determines the spatial distribution of animals over a diverse landscape. The primary implication of these results is that they allude to the processes shaping the spatial structure of ecological communities which is important for understanding biodiversity and ecosystem function at a global level especially in the light of climate change.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article

**Fig. S1.** NDVI and grass nitrogen correlation.

**Fig. S2.** Rainfall and grass quality (C : N ratio) correlation.

**Fig. S3.** Rainfall and grass biomass correlation.

**Fig. S4.** Topographic wetness index and grass biomass correlation.

**Fig. S5.** Habitat use by hunting lions in relation to its availability.

**Fig. S6.** PCA of exogenous variables.

**Table S1.** Logistic regression results for lion resource selection.

**Table S2.** Comparison of AIC values for sequential models.

**Table S3.** Axis loading of principle components analysis.

**Table S4.** Detailed results of the logistic regression analyses predicting the presence of different-sized grazer species in Serengeti.

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