Chapter 5

Food and predation differentially shape the spatial distribution of savanna grazers.

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Section II: Balancing Resources and Risks.

**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 instead by its abundance. In addition, predation potentially affects populations of small grazers more than large grazers, because predators have difficulty capturing and handling large prey.

2) We test how different body-sized grazers are distributed along gradients of food availability and predation risk by using long-term aerial wildlife counts from the Serengeti in combination with detailed vegetation analysis. Specifically, we investigate how the quality of grass, the abundance of grass biomass, and the associated risks of predation affects the presence/absence and habitat use of small, intermediate and large savanna grazers.

3) Logistic regressions are used to analyze the presence/absence of five mammalian grazer species with respect to grass nitrogen, rainfall, topographic wetness index, woody cover, drainage lines, landscape curvature, water, and human habitation. Structural equation modeling (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 5x5km cells across repeated censuses.

4) 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 grass quality and negatively with the risk of predation. The distributions of intermediate sized grazers (Coke’s hartebeest and topi) are best predicted by grass biomass of sufficient quality in relatively predator safe areas. The results illustrate that the distribution of smaller grazers is more constrained by landscape and environmental factors than large grazers.

5) The results highlight the importance of habitat heterogeneity in maintaining multi-species grazer assemblages, and 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.
INTRODUCTION

Herbivores face the dilemma of acquiring sufficient resources while simultaneously avoiding predators (Lawton & McNeil, 1979). Areas with abundant resources can also be very risky since predators might concentrate in these patches so as to maximize their chances of encountering prey, while herbivores in safer places might suffer from insufficient quantity or quality of food (Hebblewhite & Merrill, 2009; Hopcraft, Olff & Sinclair, 2010).

The size of a mammalian herbivore imposes restrictions on its diet (Demment & Soest, 1985; Wilmshurst, Fryxell & Bergman, 2000) because a ruminant’s gastro-intestinal tract scales isometrically with body size (Clauss et al., 2003; van Soest, 1996). Small grazers have small rumens and can only retain ingesta in the rumen for short periods of time. Therefore, in order to extract sufficient nutrients from the grass, small ruminants select the most easily digestible plant matter (i.e. highest quality shoots or leaves), while avoiding coarse material such as stems, sheaths and awns (Demment et al., 1985; Gordon & Illius, 1996a; Illius & Gordon, 1992). Additionally, small endotherms have a higher per mass metabolic rate and must select high energy forage to maintain homeostasis.

In contrast, theory predicts that large grazers should be relatively unconstrained by the quality of forage because their large capacious rumens result in slower passage rates. By extending the ingesta retention time, large ruminants allow for additional fermentation and therefore extract sufficient energy from coarse forage (Owen-Smith, 1988), except for megaherbivores such as elephants which mix coarse and high quality vegetation (Clauss & Hummel, 2005). The more complete fermentation process and the lower per mass metabolic rate of large endotherms, mean that larger grazers can consume low quality forage provided there is sufficient quantity.

The size of a herbivore has also been suggested to have important implications for the predation risk it encounters (Hopcraft et al., 2010). From a predator standpoint, large adult herbivores are difficult to capture and handle, and as a result, they tend to escape predation (Sinclair, Mduma & Brashares, 2003). The evolution of megaherbivores such as rhino and elephant which effectively escape predation altogether, is probably the result of this arms race (Owen-Smith, 1988). Small herbivores and juveniles tend to be 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 predators and their prey as well as how the prey base is partitioned by carnivores of different sizes (Hopcraft et al., 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 more successful closer to water in thicker vegetation, which provides predictable locations where prey can be encountered while concealing predators (Hopcraft, Sinclair & Packer, 2005; Valeix et al., 2009a). Additionally, rivers, roads and open glades have been shown as important features that contribute to the hunting success of cursorial predators such as wolves (Hebblewhite, Merrill & McDonald, 2005; Kauffman et al., 2007).

In summary, the resulting frame-work suggests the extent to which a population is regulated by either food quality, food abundance, or predation is dependent on body size and varies between landscapes that have different environmental gradients (Fritz & Duncan, 1994; Hopcraft et al., 2010; Sinclair et al., 2003; Valeix et al., 2009b). Consequently, we can expect food quality, food abundance and predation to influence the behavioral decisions herbivores make while selecting resources and which might determine their spatial distribution (Bell,
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1982; Botkin, Mellilo & Wu, 1981; Jarman, 1974). Previous work suggests food quality, forage abundance, and predation risk are important factors that shape localized herbivore hot-spots (Anderson et al., in press), however the role of these factors in determining the distribution of herbivores over the landscape has never been tested.

We analyzed the spatial distribution of species occurrence in a landscape that varies in both available nutrients and vulnerability to predation in comparison to the theoretical expectations based on known body size–risk–resource relationships (see review by Hopcraft et al. 2010). Since evidence suggests that small herbivores are predator regulated and depend on high quality food, we predict that smallest most selective grazers, Thomson’s gazelle (*Eudorcas thomsoni*; 20kg) and Grant’s gazelle (*Nanger granti*; 55kg) should be confined to the areas with the highest grass quality and the least predation risk (Sinclair, 1985). The habitat affinity of intermediate sized grazers such as topi (*Damaliscus korrigum*; 120kg) and Coke’s hartebeest (*Alcelaphus buselaphus*; 135kg) should optimally balance grass biomass of sufficient quality in the safest patches (Cromsigt, 2006; Wilmshurst et al., 2000). The largest grazers, African buffalo (*Syncerus caffer*; 630 kg) are relatively free from predation pressure and tend to be bulk grazers (Fritz et al., 2002); their distribution is expected to be constrained only by the amount of food 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 approximately 500mm in the south-east to over 1200mm in the north-west, and falls primarily in the wet season (November to May).

Data on the distribution of different sized herbivores was collected from systematic aerial censuses conducted by the Tanzania Wildlife Research Institute and the Frankfurt Zoological Society over a 21 year period. We used density measures of buffalo, topi, Coke’s hartebeest, Grant’s gazelle and Thomson’s gazelle in 5 x 5 km blocks from systematic reconnaissance flight (SRF) censuses from 1985 to 2006. There were a total of 11 SRF censuses which included gazelle, while buffalo, topi and Coke’s hartebeest were included in a total of 9 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 5x5km 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:

\[
\log((\text{Sum of densities across all years by cell})^2 / (\text{st dev of cell across all censuses})+1))
\]

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. The recurrence-index averages out the interannual and seasonal variation and provides a gross estimate of how consistently a species occurs in a cell over the 21 year period.

**Food Quality Estimates**

The quality of forage was estimated from field measures of grass nitrogen at 148 sites across the ecosystem (Fig. 1). The sampling sites were chosen to maximize the variation in soil and vegetation types across the rainfall gradient. The aboveground grass nitrogen concentration from five 25cm x 25cm clippings were averaged at each of the 148 sites (pooling all grass species). Dried grass samples were ground using a cyclonic grinder (Foss Cyclotec 1093) with a
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Sieve size of 2mm. Grass samples were then oven dried for 48 hours at 72°C and nitrogen concentrations were measured using a Near Infra-Red (NIR) spectrophotometer (Bruker MPA NIR). The multivariate calibration of the NIR was done using ‘true’ nitrogen concentrations of African savanna grasses measured on a CHNS elemental analyzer (Carlo-Erba Instruments EA1110 CHNS). 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 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 supporting on-line information 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, $p < 0.01$, $n = 30$), and verify 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).

Figure 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.
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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; Olff, Ritchie & Prins, 2002) (see supporting on-line information 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., 2007). Therefore, we used rainfall and the topographic wetness index (TWI) as a proxy for grass biomass and not 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 to 2006). Rain gauges with less than three years of data were omitted. These data were regression kriged across a known southeast to northwest 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 supporting on-line information Fig. S3).

The topographic wetness index (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 supporting on-line information 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 et al., 2005; Hopcraft et al., 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., in press; Valeix et al., 2009b).

The average amount of woody cover available for an ambush predator was calculated for each of the 27 physiognomic land-cover class identified by Reed (Reed et al., 2008). A total of 1,882 points were sampled along transects (Fig. 1) and assigned to one of Reed’s land-cover classes. At each point the mean percent woody cover greater than 0.4m high from four equidistant measurements at a radius of 15 meters 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 to 3 of the RiversV3 shapefile in the Serengeti Database 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 (see below) 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 (90m resolution)
derived from the SRTM data for East Africa (available through the NASA Jet Propulsion Laboratory [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 (class 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:

\[
\frac{(\log(\text{Human Population Density} + 1))}{(\text{Distance to Village (km)})}
\]

such that highest values are assigned to locations near densely populated villages and lowest values correspond to areas furthest from small villages. Human density maps for the year 2000 for the region were acquired from the FAO AfriCover project ([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 Analysis**

The data were analyzed 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. only non-zero cells). This scaled approach enabled us to determine if the variables responsible for predicting the presence of a species in a cell were different to those that predicted their recurrence-index.

The probability of a species occurring in a cell was predicted using binary logistic regressions with a stepwise backward elimination process based on the Wald statistic. Variables were kept in the model if the p-value was less than 0.2 (as opposed to 0.05) to prevent potentially important (but co-varying) variables from being omitted (Tabachnick & Fidell, 1996). We tested for non-linear relationships 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 variable if it was not ecologically meaningful.

The recurrence-index of different sized grazers in response to food quality, food abundance and predation risk was assessed using structural equation modeling (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 SEM’s. Proximity to humans and access to free water better predict a species presence or absence in a cell, and there is no evidence to suggest they are affected by the grazer’s body size. We used only the cells where the species had been detected for the SEM analysis (i.e. only non-zero 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. 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 that is often not
directly measurable itself (Grace et al., in press; Grace & Bollen, 2008). For instance the
combined effect of woody cover in combination 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 prior 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 model and the observed data).

We allowed all exogenous predictor variables to correlate with each other and report
only the significant relationships (p < 0.05). Sequential inclusion of correlations between
exogenous 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 2009).

RESULTS

The spatial distribution of the exogenous predictor variables illustrates strong
landscape differences across the ecosystem (Fig. 3). The short-grass plains in southeastern
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, few drainage beds because it is rela-

Figure 3. The spatial distribution of variables predicting grass quality, grass
abundance, and predation risk. The quality of grazing is estimated by (a) the
glass nitrogen content (%). Grass abundance is estimated by (b) mean rainfall
(mm) and the (c) topographic wetting 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
www.serengetidata.org.
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tively flat, and tend to be far from permanent water and humans. In direct contrast, the western corridor and the north have lower 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 closer human boundaries.

The distribution of grazers over the landscape becomes more aggregated as their body-size decreases (Fig. 4). Buffalo, the largest grazer, are scattered across the north and west and do not occur in the southeast portion of the ecosystem at all. Coke's hartebeest tend to occur in the central part of the ecosystem, while topi are more prevalent in the west and north. The recurrence of Grant's gazelle is more aggregated in the east and south. The distribution of the smallest grazers, Thomson's gazelle, is the most aggregated. Thomson's gazelle tend to occur in the southeast and their spatial distribution is almost opposite to that of buffalo.

**Logistic Regressions Predicting Species Presence/Absence**

Results from the logistic regression (Table 1) suggest that the environmental predictor variables better explain the presence or absence of small grazers; large grazers have fewer significant trends than small grazers. Furthermore, small grazers tend to be positively associated with some landscape features and negatively associated with other landscape features, where as large grazers tend to be positively associated only. Results of the Hosmer-Lemeshow goodness-of-fit test support the logistic regression models for all species, with the exception of Coke's hartebeest which should be interpreted with caution (buffalo, p =0.159; Coke's hartebeest, p=0.033; topi, p=0.872; Grant's gazelle, p=0.645; Thomson's gazelle, p=0.597) (see supporting on-line information Table S1 for details of the logistic regression models).

Forage quality, as estimated by grass nitrogen concentrations, is selected only by Thomson's gazelle, the smallest grazer (Table 1). Grass nitrogen does not increase the probability of large herbivores occurring in a cell, and is actually avoided by topi. The selection by Coke's hartebeest for areas close to high grass nitrogen concentrations is non-linear (as indicated by the negative coefficient of the quadratic term), perhaps suggesting a selection for intermediate grass nitrogen concentrations at some optimum. However, the logistic regression model for Coke's hartebeest did not fit the data well and their selection should be interpreted cautiously.

High abundance of grass, as estimated by the mean annual rainfall and the topographic wetting index, is selected by buffalo, topi, and Grant's gazelle. Thomson's gazelles avoid high rainfall areas, but tend to be non-linearly associated with greater topographic wetness, perhaps as a means of trading-off high grass biomass with acquiring moisture through their forage (Maloiy *et al.*, 2008).

There is a positive relationship between the amount of cover available for ambush predators and the presence of buffalo, whereas there is a positive non-linear relationship for hartebeest and topi as indicated by a negative quadratic term for woody cover. Smaller species (Grant's gazelle and Thomson's gazelle) strictly avoid woody cover, and occur in areas further away from drainage beds. Proximity to drainage beds is not significant for buffalo, while Coke's hartebeest tend to occur closer to drainages in general (however the logistic regression model did not fit the data well). The grazers smaller than Coke's hartebeest (i.e. topi, Grant's gazelle and Thomson's gazelle) all select areas further away from riverbeds. Curvature is not significant in predicting the presence of any species at this scale.

The largest grazers select 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 avoid areas that are far from access to permanent water.

All species, regardless of body size, ubiquitously avoid areas close to high human densities. This is the strongest and most consistent variable predicting the presence or absence of grazers.
Figure 4. The spatial distribution of recurrence for (a) African buffalo (630kg), (b) Coke’s hartebeest (135kg), (c) topi (120kg), (d) Grant’s gazelle (55kg), and (e) Thomson’s gazelle (20kg) from repeated censuses in the Serengeti between 1985 and 2006.
Table 1. Summary results of the logistic regression analyses predicting species’ presence in 5x5km grid cells. 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 variable was not a significant predictor. *** $p<0.001$, ** $p<0.01$, and * $p<0.05$. (For the details of the logistic regression parameters see supporting on-line information Table S5)

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Structural Equation Models (SEM) Predicting Species Recurrence-index

SEMs were used to predict each species’ recurrence-index, a continuous response variable that measures how many times a species was observed in an occupied cell and a measure of its abundance in the cell. In general, the SEMs explain more of the observed variation in the spatial distribution of smaller grazers than larger 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 less than 0.35 for all SEM’s, 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 suggests that the unique variation of the variables is high and therefore the conceptual nature of the composite variable is not confounded by other variables. The correlations between exogenous variables change between the SEM’s for each species because they occupy different areas. The SEM reflects the real correlation among the variables in the habitats the species occupies.

Previous SEM’s included proximity to humans and water as additional variables accounting for the variation in the recurrence-index, however these models were not supported by the data. This suggests that the factors that predict a species recurrence-index are a subset of those predicting presence/absence.

The chi-square associated with the SEM describing the buffalo recurrence-index suggests the data supports our a priori interpretation ($\chi^2=5.99$, df=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 topographic wetting index) is significant in explaining the variation in the buffalo recurrence-index (standardized path 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 also not significant.

The data on the recurrence of Coke’s hartebeest support the structural equation model ($\chi^2=6.52$, df=7, p=0.480). The SEM describes 8% of the variation in 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 non-significant negative trends. The SEM describing the topi recurrence-index is supported by the data ($\chi^2=9.57$, df=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), suggesting a distinct aversion. 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 ($\chi^2=6.76$, df=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 any of the species we analyzed (Fig. 5e). The data on the recurrence of Thomson’s gazelle support the SEM ($\chi^2=9.52$, df=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.
Section II: Balancing Resources and Risks.

**Buffalo Recurrence Index** (630 kg)

- Grass Nitrogen: 1.0
- Rainfall: 0.52
- Topographic Wetting Index: 0.085
- Woody Cover: 0.06
- Distance to Drainage: 0.66
- Curvature: 0.57

**Coke's Hartebeest Recurrence Index** (135 kg)

- Grass Nitrogen: 1.0
- Rainfall: 0.91
- Topographic Wetting Index: 0.63
- Woody Cover: 1.01
- Distance to Drainage: 0.54
- Curvature: -0.08

**Topi Recurrence Index** (120 kg)

- Grass Nitrogen: 1.0
- Rainfall: 0.94
- Topographic Wetting Index: 0.34
- Woody Cover: 0.84
- Distance to Drainage: 0.19
- Curvature: -0.65

\[ \chi^2 = 5.99 \text{ (df= 7)} \]
\[ p = 0.540 \]

\[ \chi^2 = 6.52 \text{ (df= 7)} \]
\[ p = 0.480 \]

\[ \chi^2 = 9.57 \text{ (df= 6)} \]
\[ p = 0.144 \]
Figure 5. The results of the structural equation models assessing the recurrence-index of savanna grazers of decreasing body size. 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 non-significant 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.
DISCUSSION

Evolutionary theory suggests that herbivores should maximize their access to essential resources while minimizing their exposure to risk. There are multiple solutions to this trade-off which has led to a wide diversity of mammalian grazers. For instance, grazers might become very large thereby reducing their exposure to smaller predators (Sinclair et al., 2003). Alternatively, grazers might avoid predators by selecting relatively predator-free areas which tend to have lower grass biomass (Oksanen et al., 1981). Small grazers manage to extract sufficient energy from low-biomass patches by selecting highest quality components of the grass, while large grazers extract more energy from low-quality forage by retaining their ingesta for longer periods (Owen-Smith, 1988). We test if 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.

The most important finding of this study is that the distribution of small savanna grazers is constrained primarily by food quality and predation, while large grazers are less restricted in general but tend to occur in patches with high food abundance regardless of the associated predation risks. Intermediate size herbivores balance the risks associated with high grass biomass patches with the quality of food. Although this has been found in previous studies for individual species or in smaller areas (Anderson et al., in press; Cromsigt & Olff, 2006; Murray & Brown, 1993), this generalization has never been confirmed with many species on an ecosystem-wide scale. We suggest this general conclusion might also hold for other grazing ecosystems.

The food and predation constraints imposed on small grazers are consistently supported by several lines of analyses: (1) the SEM results explain more overall variance in the recurrence-index of small grazers and less variance of large grazers (Fig. 5). (2) There is a clear shift in the role of food quality versus predation risk in the SEMs from large to small grazers (Fig. 5) and supports our interpretation. (3) The variables describing the distribution of small herbivores are all strongly significant (p<.01), whereas the results for large herbivores tend to be less definitive (Table 1); a result also supported by previous investigations (Olff & Hopcraft, 2008). (4) Rainfall, woody cover, and access to water are selected by large grazers however they do not avoid any landscape or environmental features (with the exception of humans, see Table 1). Conversely, small grazers both select and avoid attributes of the landscape (namely, a strong selection for high grass nitrogen patches while avoiding high rainfall, woody cover and proximity to drainage beds), further suggesting the distribution of small grazers is more constrained by food and predation pressure than large grazers.

Grasses tend to invest more resources into developing silica-rich structural supports in moister areas (McNaughton et al., 1985; Olff et al., 2002). Furthermore there is a compositional shift in wetter areas towards taller grass species with higher carbon to nitrogen ratios which lowers the concentration of nitrogen and phosphorous available to herbivores (Anderson et al., 2007). Therefore grasses in wetter areas tend to be more difficult to digest than in drier areas. As such, we expect the smallest grazers to avoid tall lignified grasses associated with high rainfall and topographically wetter areas (Gordon et al., 1996a). The logistic regression results (Table 1) show that the occurrence of buffalo, Coke’s hartebeest, topi and Grant’s gazelle are positively related with rainfall, while the occurrence of the smallest grazer, Thomson’s gazelle, is negatively associated with rainfall. This supports our expectations based on food abundance and suggests that large and small grazers are selecting opposite attributes of the grasses.

The capacious rumen and wide mouth structure of large herbivores are adapted to ingest large amounts of grass biomass (Gordon, Illius & Milne, 1996b; Murray et al., 1993; Owen-Smith, 1988; Shipley et al., 1994). Therefore, we expect the largest grazers to be precluded from the areas with the insufficient biomass. The southeast portion of the Serengeti is dominated by prostrate grasses with low biomass because of the low average rainfall (Fig.
Determinants of the spatial distribution of savanna grazers.

3b) and shallow soils. Topi and Coke’s hartebeest rarely occur in these areas and buffalo, the largest grazer, never occur on the short-grass plains (Fig. 4) most likely because they cannot access sufficient quantities of the grass sward and their high water requirements. It is only the smallest herbivores that can pick the greenest leaves from the low-lying grass sward in these areas (Fryxell et al., 2005). This is supported by previous findings that show small grazers can forage in low biomass patches because of their specialized mouth morphology and digestive processes which are adapted to selecting specific high-quality components of the grass (Wilmshurst, Fryxell & Colucci, 1999).

High grass biomass patches are inherently risky because the tall grass provides cover for ambush predators (note the correlations between exogenous variables illustrated in Fig. 5). Herbivores accessing these patches must balance the benefits of the grazing resources against the associated risk of predation (Lawton et al., 1979; Sinclair & Arcese, 1995). Our results show that small grazers such as Thomson’s and Grant’s gazelles which are susceptible to predation avoid these areas, however large grazers which generally employ mixed strategies do not (Sinclair, 1985). Species such as buffalo, have essentially outgrown most predators (Sinclair et al., 2003) and become difficult for carnivores to capture and handle (Scheel & Packer, 1991). The strong herding instinct in buffalo also reduces an individuals risk of being killed by a predator (Fryxell et al., 2007; Hay, Cross & Funston, 2008). The combination of predator evasion and digestive strategy is the best explanation why buffalo select risky patches (Table 1) and why larger grazers tend to have the least restricted distributions in the Serengeti.

We found that intermediate size grazers, such as topi and Coke’s hartebeest, tend to optimize the grazing opportunities in moderate to high grass biomass patches against the risk of predation and the forage quality. For instance, topi select areas with higher rainfall and more grass biomass (Fig. 5c), but avoid the riskiest areas near rivers or dense thickets (Table 1). The SEM of Coke’s hartebeest (Fig. 5b) suggests they avoid food quality and abundance in roughly similar proportions, meaning that they might be balancing the variables approximately equally but in a non-linear way; selecting lower food quality patches in less risky areas that have sufficient, but not high biomass. It is also possible we are missing a key environmental variable which better describes the Coke’s hartebeest distribution and would improve the logistic regression. Figures 4b and 4c 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 wetter areas especially in the western corridor (Fig. 3b). Previous research has shown that Coke’s hartebeest offset lower intake rates with greater digestive efficiency over topi or wildebeest (Murray, 1993), which might explain why the slightly larger of the two species occupies the drier lower-biomass patches.

Some grazers escape predation by forming vigilant herds or migrating (Hebblewhite et al., 2009). We chose not to include wildebeest in this analysis because the large migratory herds have been shown to reduce an individual wildebeest’s exposure to predators (Fryxell, 1995), and because the wildebeest population is regulated by the abundance of dry season forage (Mduma, Sinclair & Hilborn, 1999) and not by the quality of grass. The advantages gained by migrating mean that wildebeest do not conform to our expectations based only on the body size of resident grazers (Hopcraft et al., 2010; Wilmshurst et al., 2000). Other migrants, such as zebra, are hind-gut fermenters and can extract sufficient nutrients from coarser grasses than an equivalent sized ruminant. Individual zebra therefore tend to be less constrained by food quality than wildebeest (Grange & Duncan, 2006). Our results show that the degree of predation, forage quality, and forage abundance varies across the Serengeti, and this poses some interesting questions as to how and when migrants might trade-off these potentially limiting factors (Hebblewhite et al., 2009). It is possible that wildebeest migrate so as to maximize their access to high quality grass (Boone, Thirgood & Hopcraft, 2006; Holdo, Holt & Fryxell, 2009; Thirgood et al., 2004), where as zebra might migrate partially to reduce their exposure to predators (Grange et al., 2004; Sinclair, 1985).
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 (5x5km) which might account for the differences we detected (Laca et al., 2010; Ritchie & Olff, 1999). A reanalysis of the buffalo recurrence-index at a 10x10km scale slightly improved the logistic regression results; the same variables increased the model sensitivity from 68.7% to 87.6%, which is statistically expected when measuring at coarser resolutions (Fortin & Dale, 2005). However the overall variance in the buffalo recurrence-index explained by the 10x10km SEM decreased and none of the paths were significant. Therefore, it is unlikely that gross versus fine scale habitat perception by larger herbivores explains the results.

Additionally, it is possible that the scale at which herbivore abundance was measured is not necessarily the scale at which the resources vary. For instance, the long-term average rainfall for a cell is probably accurate, but the degree of curvature might vary at a finer scale along local catenas (Bell, 1970), suggesting that an average curvature for a 5x5km block does not capture the true quality of the attribute. The coarse scale at which we measure might explain why curvature is not significant in our analysis (Table 1) but is a significant predictor of herbivore occurrence at finer resolutions (Anderson et al., in press). Ecosystem wide data on herbivore abundance at a resolution less than 5x5km is not available so we could not test for fine scale selection.

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.

In conclusion, we find that small grazers are more constrained by food nutrients and risk. Forage abundance influences only the larger animals and the risk of predation has little impact on their recurrence. It is clear 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 determining the spatial distribution of animals over a diverse landscape (Hopcraft et al., 2010). 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.

Shifts in global climate could result in a mismatch between the location of protected areas and a species’ preferred niche. In sub-sahara Africa, the primary response to global climate change is precipitation which affects the nutritional quality and abundance of grass, as well as the vegetative cover that conceals predators. If global warming leads to less rainfall, our results suggest smaller savanna grazers will be favored over larger grazers (and visa versa). We conclude that regulation of different sized herbivores by food or predation might switch if global warming leads to changes in the rainfall patterns across Africa, particularly if animals are unable to move beyond protected area boundaries.

ACKNOWLEDGEMENTS

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REFERENCES


Section II: Balancing Resources and Risks.


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**Supporting Information**

The following information is intended to be on-line supporting information:

Figure S 1. The nitrogen concentration of grass decreases with mean NDVI (n=148).

Figure S 2. The ratio of carbon : nitrogen in the grass tends to increase with rainfall, meaning the highest quality patches tend to be in low rainfall areas (n=148).
Section II: Balancing Resources and Risks.

Figure S 3. Grass biomass tends to be greatest in high rainfall areas (n=148).

Figure S 4. Grass biomass tends to increase in areas with greater topographic wetness (data from 36 sites in the Western Corridor of Serengeti).
Table S1. Results of the logistic regression analyses predicting the presence of different sized grazer species in Serengeti. The model sensitivity is the percentage of cells classified as positive that are truly positive.

<table>
<thead>
<tr>
<th></th>
<th>Buffalo (630 kg)</th>
<th>Coke’s Hrtbst (135 kg)</th>
<th>Topi (120 kg)</th>
<th>Grant’s Gazelle (55 kg)</th>
<th>Thomson’s Gazelle (20 kg)</th>
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<td>eB odds</td>
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<td>(Ln (% Grass N))^2</td>
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<td>Distance to N km</td>
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