General Summary

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SECTION IV: Synthesis.

SUMMARY

In this thesis I ask how grazers of different body sizes distribute themselves spatially with respect to food abundance, food quality and predation risk, and how these factors might influence the migration patterns of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in the Serengeti ecosystem. The analysis of long-term aerial wildlife counts from the Serengeti, data from GPS radio collars, and ground and satellite measurements of vegetation and soils illustrate how forage quality, forage abundance and predation risk affect the choices grazers make about the habitats they occupy. Specifically, the areas in which different species occur and the choices they make while moving between these areas depend on both the size of the species and their digestive physiology. Body size and physiology affect the resource use and predation rates of savanna grazers because they simultaneously influence how grazers extract energy from plant material and which predators are capable of killing them. I conclude that if global climate change leads to shifts in vegetation patterns in sub-Sahara Africa (due to shifts in rainfall patterns), then the regulation of different sized herbivores by food or predation might switch. Under low rainfall conditions, the abundance of vegetation will be reduced but its quality would increase, meaning that smaller savanna grazers will be favored over larger grazers (and visa versa). Regulation by food or predation will be even more acute if animals are unable to move along the rainfall gradient beyond protected area boundaries.

WHY ARE WILDEBEEST SUPER-ABUNDANT IN THE SERENGETI?

There are specific aspects of wildebeest biology which are unique and give them a competitive advantage over other species, and which partially explains their abundance in Serengeti. In Chapter 2 we review these biological attributes which include; synchronous birth of precocial calves which coincides with seasonal abundance of food and swamps the predator community, and a strong selection for high quality matt-forming grasses on which they have the highest intake rates. However, these factors alone do not explain wildebeest abundance because there should be similar densities of wildebeest in other ecosystems which is not the case. The Serengeti ecosystem has a unique counter-gradient of soil fertility and rainfall which creates exceptionally large areas of high quality grasses (more than 3,500km$^2$). Furthermore, this nutritional gradient in the grass occurs at a scale which is accessible to migratory wildebeest. Therefore, specific aspects of wildebeest diet and reproduction, combined with their capacity to move long distances in an ecosystem with a predictable nutrient gradient enables migrant wildebeest to escape regulation by predation or food quality, and this combination enables wildebeest to dominate the ecosystem beyond the capacity of any other competitor species. In addition, the large densities of wildebeest in Serengeti might facilitate themselves in a positive feed-back loop by keeping large areas heavily grazed which further stimulates increased production and protein concentration in the grass. Therefore, wildebeest are super-abundant in Serengeti because the ecosystem closely matches their requirements which is not the case for impala or topi which dominate other ecosystems.

HOW COULD TWO SAVANNAS WITH THE SAME SPECIES LOOK SO DIFFERENT FROM EACH OTHER?

In the review paper which sets the theme for the thesis (Chapter 3) we find that herbivores are regulated by predation under certain environmental conditions, whereas in other situations they are limited by forage abundance and nutritional quality. Whether a herbivores in an ecosystem are top-down regulated (i.e. predator mediated) or bottom-up regulated (i.e. food mediated) depends both on the abiotic constraints on forage availability and body size, because size simultaneously affects herbivores’ risk of predation and their nutritional demands. Consequently, ecosystems composed of similar species can have different dynamics if they
differ in resource supply, which explains why two savannas can have very different amounts of vegetation, herbivores and their predators. The interplay between: (i) the availability of limited abiotic resources (such as nutrients and rainfall) that determine the quality and quantity of primary production; (ii) the evolutionary tradeoffs related to body size (including predation sensitivity, digestive capacity and metabolic requirements); (iii) adaptive behaviors (such as migration or group vigilance), which enable primary consumers to escape regulation; and (iv) the extent and frequency of disturbances (such as fires, storms, extreme temperatures, salinity shifts, scouring, etc.) are processes affecting how predation and competition collectively structure communities. In general, abiotic factors determine the importance of predation, forage quality and forage abundance in regulating herbivores of different sizes and this alters the relative strength of the connections between biotic and abiotic components in ecosystems. This framework captures how top-down and bottom-up mechanisms are dependent on common underlying environmental gradients and how environmental gradients can switch top-down and bottom-up processes that regulate animal abundance. The framework also provides testable hypotheses as to how we expect herbivores of different sizes to be distributed across the landscape. Smallest herbivores should be constrained to the areas with the highest food quality and the least risk of predation, while large herbivores should be constrained by the biomass of grass.

**DOES PREDATION VARY ACROSS LANDSCAPES?**

A comprehensive analysis of 16 years of radio-telemetry data from Serengeti lions (Panthera leo) was used to study how lions distribute themselves with respect to hunting opportunities in order to understand landscape level gradients of predation (Chapter 4). Specifically, we investigated whether lions hunt in areas where prey are easy to capture or where prey are locally abundant. The results of resource selection analyses illustrate that on a broad-scale lions shifted their ranges according to the seasonal movement of prey, but at a finer scale (< 100 m) lions fed in areas with high prey 'catchability' rather than high prey density. Specifically, plains lions selected landscape features such as erosion embankments, view-sheds from rocky outcrops, and access to free water. Lions living in woodlands tended to select areas with erosion embankments, and woody vegetation. As expected for an ambush predator, resting lions spent more time in areas with good cover. The results emphasize that fine-scale landscape and habitat features are critically important for predators’ hunting success and that these landscape features pose areas of greatest risk for herbivores.

**DOES FOOD AND PREDATION ACCOUNT FOR THE SPATIAL DISTRIBUTION OF SAVANNA GRAZERS?**

The spatial distribution of different sized savanna grazers was analyzed in relation to gradients food quality, food abundance and predation risk in the Serengeti ecosystem (Chapter 5). Food quality (measured as grass nitrogen) and food abundance (grass biomass correlated with rainfall and topographic wetness index) were measured at 148 points across the ecosystem. The risk of predation was estimated from woody cover, proximity to drainage lines, water, and landscape curvature at 1882 points. The data from 11 aerial surveys conducted over a period of 21 years clearly shows that 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 determining food quality and predation risk than for large grazers. Furthermore, the results show 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.

**IS THE RECURRENCE OF HERBIVORES IN HOTSPOT AREAS DETERMINED BY FOOD OR PREDATION?**

The location of long-term herbivore hotspots (i.e. areas where mixed herds of resident grazers continually occur for many years regardless of season) were analyzed in relation to their food quality, food abundance and predation risk (Chapter 6). Hotspots were identified from long-term areal censuses and ground transects. The attributes of herbivore hotspots were compared to random sites. Hotspots in Serengeti occur in areas that are relatively flat and located away from rivers where ungulates are less susceptible to predation. Specifically, herbivore hotspots tend to occur in areas where hydrology and rainfall create conditions of relatively low-standing plant biomass, which, coupled with grazing, increases forage quality while decreasing predation risk. Low-standing biomass and higher leaf concentrations of nitrogen, sodium, and magnesium were strong direct predictors of hotspot occurrence. Soil fertility promoted leaf sodium and magnesium and had indirect effects on hotspot occurrence. Therefore landscape features contribute in direct and indirect ways to influence the spatial distribution of herbivore hotspots. Attributes of hotspots incorporated both food benefits and predation refuges which were absent in other locations. The results highlight the simultaneous role of bottom-up and top-down factors in determining herbivore spatial distributions.

**HOW DO MIGRATING HERBIVORES MOVE ACROSS LANDSCAPES THAT VARY IN FOOD AND PREDATION RISK?**

Long distance migrations by terrestrial herbivores occur across predictable gradients such as rainfall or latitude, however the quality and quantity of food sought by migrants occurs at multiple spatial scales and is often ephemeral. Acquiring sufficient resources while minimizing the risks of being killed by a predator means herbivores must adopt search strategies that vary with season and landscape heterogeneity. In Chapter 7 we assess if food quality, food abundance and predation affects the routes migrants choose. Data from 30 GPS radio collared wildebeest and zebra migrating seasonally in the Serengeti-Mara ecosystem illustrate that food and predation differentially affect the movement patterns of these co-occurring species. The daily step lengths and turn angles of wildebeest is determined primarily by the quality of grass rather than its abundance or the risk of predation. Conversely, zebra movement is best explained as accessing the most food of sufficient quality while avoiding predation. Both species are influenced by drying and greening processes and tend to move directionally without lingering when near water because the thick woody vegetation associated with these areas are frequented by predators. Furthermore, both species consistently move further each day when close to human habitation. In general, these results suggest zebra movements are more determined by landscape predictors of predation risk, than by forage availability which is opposite to wildebeest. The findings indicate wildebeest and zebra select different attributes of the same landscape, which increases our understanding of migratory behavior and highlights the importance of maintaining landscape heterogeneity and connectivity for the long-term conservation of migratory herbivores.

**WHAT IS THE BASIS OF HUMAN WILDLIFE INTERACTIONS?**

The previous chapters conclude that savanna grazers are distributed and move across diverse landscapes so as to balance their nutritional requirements while minimizing the risk of predation, and this balance is affected by the grazers’ body size as well as by common underlying environmental gradients such as rainfall and soil fertility in the ecosystem. However,
rainfall, soil fertility, and wildlife are also sought by human populations for agriculture and wild meat. In Chapter 8 we conduct a comprehensive analysis of Serengeti herbivore populations in relation to human growth. The results illustrate that long-term economic forces favor more profitable land-use strategies which push older forms of land-use down the rainfall gradient. The trend will continue to lead to serious deterioration in the livelihoods of subsistence farmers and has large implications for the majority of people living in rural Tanzania and Kenya. Furthermore, the change in land-use usually implies more intensive use of the natural resources by larger human populations at the expense of biodiversity. The largest impacts on natural savanna ecosystems occur first in the wettest areas, which experience the most drastic declines in large wild grazers. Without further measures such as land-use planning and zoning, such changes will lead to greater rural poverty as well as accelerate biodiversity loss, especially in the high rainfall, high soil-fertility areas. Increasing conflicts along protected area boundaries should be expected.

**What is the most effective strategy for ensuring the long-term conservation of ecosystems?**

Much of the data in this thesis is a result of long-term monitoring. In Chapter 9 we review why compiling and routinely using information about protected areas is critical to conservation. Primarily information (a) provides institutional memory, which (b) enables a protected area to critically answer management questions. Furthermore, routine collection of information about a protected area (c) highlights priorities and facilitates the wise use of resources. In addition, information collected by parks (d) contributes to understanding regional processes and (e) ultimately supports conservation efforts in the political arena by providing a factual backbone on which assertions and decisions are made. Ideally, a monitoring program for a protected area should reflect the objectives established in the General Management Plan (which also documents the threats the protected area faces). The costs and effort involved in collecting data should be carefully balanced against its relevance. The data collected as part of a monitoring program should endeavor to link with other databases as this avoids the expense of duplication and strengthens the database’s utility through information sharing. Furthermore, devising ways to include historical data makes new databases immediately useful and additionally strengthens a database. Cataloguing information sources (i.e. metadata) saves time when editing data and provides an index of data quality. Most importantly, maintaining the flow of information between field staff, managers, and funding agencies boosts the morale of those involved, provides solidarity, and assists in raising additional funds. Unfortunately there is a tendency for monitoring projects to be over ambitious which leads to failure because they become unmanageable. For a monitoring database to work it must start very simply and develop with the park, growing to fill the niche as it is required.