CHAPTER 1

INTRODUCTION ON RESOURCE ECOLOGY

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> "The question is often raised: why not stay with the real world and generalize our experiences in some succinctly descriptive form? The only answer is that such an approach never proves adequate. In evolutionary biology, it produces *inductive* generalizations that are encapsulated in tendencies or 'rules' (e.g. Bergmann's rule). Causal explanations, the heart of any science, are hard to reach and often impossible to prove by means of such concepts. The descriptive, natural-history stage of science is eventually replaced by a *deductive* theoretical stage, basically mathematical in nature, which creates the abstractions and measurements necessary to deepen causal analysis. (…) The purpose of mathematical theory is to deal with "all possible worlds". The purpose of experiments and field [work] is to deal with the real world: To measure the parameters, to search for new parameters, and to improve the theory which is ultimately our most effective way of viewing the real world." (Wilson and Bossert 1971, pp. 40 – 41)

Resource ecology, the ecology of trophic interactions between consumers and their resources, is central in ecology. It addresses fundamental aspects of the interactions between consumers and resources, and includes competition, plant–nutrient relationships, and predator–prey relationships such as herbivory, parasitism and carnivory. Resource ecology also provides the basis for understanding the diversity, structure and dynamics of multi-species assemblages. From the consumer's perspective, resources, such as energy, nutrients and water, are prerequisites of life that have to be acquired. Therefore, in resource ecology, foraging is the central process because it leads to growth, survival and reproduction of the animal. Resource ecology thus deals with foraging and ultimately with fitness of the consumer.

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Since a consumer's resources are often heterogeneously distributed and exposed to changing conditions, the search for food by animals is unavoidably uneven in space and time. Foraging theory has a long tradition that addresses questions how animals search and forage and what they should do so as to maximise their fitness, based on (i) how different possible behaviours affect fitness; and (ii) what the decision variables are to maximise fitness. Foraging theory has considerable success in explaining observations of foraging behaviour. As foraging behaviour is largely determined by the spatial distribution and variability in time of the resources, many studies recently have been done to investigate movements and spatial decisions in foraging at various spatial scales and under variability in time. Accordingly, resource ecology forms a bridge between the well-developed foraging theory and the emerging field of spatial ecology.

Resource ecology as link between foraging theory and spatial ecology

Spatial ecology addresses the effect of space on the dynamics of individual species and on the structure, dynamics, diversity and stability of multi-species assemblages. Although it is an emerging field, numerous theoretical and empirical studies showed the importance of considering the spatial structure of resources on the population dynamics and assemblage structure of consumers. The link between foraging theory and spatial ecology sets resource ecology in a new context from which new theory can emerge. We believe that new theory is needed because existing theories and models appear to be insufficient to explain the co-existence of species or the numerical abundance of assorted animal species in various assemblages. In this book, we will contribute to the advancement of such new theory.

LARGE HERBIVORES AS MODEL SPECIES TO DEVELOP THEORY ON RESOURCE ECOLOGY

The theme of the book is the relationship between foraging behaviour, population dynamics and assemblage structure of animals on the one hand, and the spatial heterogeneity and variability in time of their resources on the other. Even though there are many trophic interactions, we focus on herbivory, in particular on the interactions between large mammalian herbivores and the vegetation. What is a 'large herbivore'? We, as other researchers have done, defined a 'large herbivore' as a terrestrial mammal heavier than 5 kg in weight, which obtains most of its diet from vegetative plant parts. This definition includes most antelopes, deer and bovids, for instance, but excludes most rodents, geese and hares. The interactions between large herbivores and the vegetation are appealing because foragers, especially, large herbivores:

Relation between foraging behaviour of animals, their population dynamics and the structure of the assemblage

- have a large impact on the availability and quality of their resources and therefore affect the spatial resource heterogeneity
- use or can use quite accurate spatial memory in their searching for resources so that they can anticipate to the spatial heterogeneity and variability in time of their resources
- spend the majority of the day searching and foraging
- are highly mobile and have the ability to actively select locations to forage high-quality food or avoid depletion of food or lack of other resources such as water.

Moreover, large herbivores often occur in high diversity, for example on African savannas, and this group receives much attention from the point of view of conservation. Last but not least, the behaviour and requirements of large herbivores are relatively well studied (see the numerous references in this book), which makes them useful model organisms to study the relationship between foraging behaviour, population dynamics and assemblage structure of animals and the spatial heterogeneity and variability in time of their resources.

In the book, we deal with these issues in different subjects to quantify and synthesise resource ecology: from the dynamics in the spatial ecology of large herbivores, their foraging behaviour and their large-scale movements, through their population dynamics, to the structure of the assemblages in which these large herbivores occur. Although we focus on large herbivores in a spatially heterogeneous environment where the grazing resources follow environmental change in time as a particular trophic interaction, we are sure that many mechanisms and principles as discussed in this book are of relevance for understanding other trophic interactions.

Many consumers experience patchy distribution of their resources with certain distances between these patches. Patches are defined as localities (areas) that are more or less homogeneous with respect to a measured variable; in this case the variable is 'food' or 'grazing resource'. These patches can be distinguished at different spatial scales: from vegetated patches at fine scale (e.g., tufts of grass) to disjoint grazing areas at coarse scale (e.g., meadows in an otherwise closed forest). The herbivores may have incomplete knowledge about the spatial distribution of their resources and how this changes over time. In the case of this imperfect knowledge, it is impossible for them to predict accurately where to find sufficient food of sufficient quality. Herbivores have, however, adopted search strategies and have spatial memory to reduce this gap between the true distribution of food (and its quality) and their (imperfect) knowledge about this distribution. This book reviews the current state of knowledge on foraging animals and their strategies to cope with spatial heterogeneity and variability in time of their resources.

Focus of the book is large herbivores in spatially heterogeneous environments where grazing resources follow changes in time

Because of the similarity in the response to spatial heterogeneity and change in time of the grazing resources, the book includes wildlife, free-ranging livestock, and livestock of pastoralists. Traditionally, also pastoralists adopted large-scale movement to secure the availability and quality of the resources for their stock. In both wildlife and pastoral systems, the effects of spatial constraints on migratory movements are well studied. The book enables us to integrate this knowledge. Especially under arid and semi-arid conditions, environmental changeability in time is the rule rather than exception. The book, however, does not exclusively focus on these regions. Also in other regions, such as in temperate regions, there is seasonal variation in growth of the grazing resources due to, for example, changes in temperature and snow cover. In many regions of the world, such large-scale climatic oscillations have an effect on large herbivores and have therefore been included in the book.

Large herbivores adopted a range of strategies to deal with spatially heterogeneous resources that experience change over time, such as trait plasticity in physiology, behaviour, morphology and life history. There are, however, both advantages and disadvantages to such strategies. The disadvantages are costs for the individuals, often expressed in energy, that ultimately reduce the lifetime reproductive success. These strategies are trade-offs between costs and benefits subject to natural selection. At present, the relative costs and benefits associated with different strategies of herbivores that deal with spatial heterogeneity and variability in time of the grazing resources are poorly understood. For example, it is hypothesised that by grazing selectively, animals can achieve nutrient intake rates higher than the average from the environment as a whole. This, however, requires searching of the animal which increases the costs of foraging. At present, it is unsolved how this increased nutrient intake should be set off against the increased energy expenditure. Another issue that needs more thought is whether consumers are selected for maximisation of energy intake or whether they strive to minimise foraging time, or, perhaps to maximise instantaneous or daily intake. These and other hypotheses about the foraging behaviour of large herbivores in spatially heterogeneous environments affected by change in time are discussed in the various chapters.

LAY OUT OF THE BOOK

Each chapter reviews recent developments in resource ecology. At the end of each chapter several testable hypotheses are presented that mark out the current frontiers of this science. The chapters are followed by a comment that discusses the chapter. The commentaries are written to stimulate scientific debate about the issues raised in the chapters.

The first three chapters deal with the distribution of animals and their resources. ***Chapter 2*** discusses several mechanisms that determine the distribution of large herbivores at different spatial and temporal scales. The authors propose a new hypothesis to explain observed foraging behaviour, namely the satiety hypothesis. The satiety hypothesis has been used to explain the avoidance of toxins and the acquisition of nutrients in diet selection. The authors suggest that the satiety hypothesis can be used to better account for the variability in feeding site selection, and thus to better explain the distribution of large herbivores. ***Chapter 3*** further expands on the distribution of animals and provides statistical techniques to describe more accurately patterns in animal distribution. The authors argue that the techniques they propose (F-, G- and J-functions) can be used to better explain the spatial distribution of animals. They analyse the spatial distribution of herds of large herbivores in Laikipia, central Kenya, and discuss possible causes of this pattern. ***Chapter 4*** focuses on the description of the resource distribution and dynamics. The authors present examples where remote sensing is used as tool for producing high-spatial-resolution impressions of the variability of the landscape, and in particular land cover. The authors illustrate this use by mapping nitrogen concentration and phenolic-compound levels in grass and trees in the Kruger National Park, with a spatial resolution of 4 meters. These techniques open doors for new lines of research, where the distribution of herbivores can be linked to the actual resource distribution.

The next set of chapters focus on foraging behaviour of individuals and make predictions about their population dynamics. ***Chapter 5*** deals with intake and diet choice of animals. The author argues that heterogeneity and average herbage mass are frequently related, so that measured effects on intake cannot be unequivocally attributed to total herbage mass. The author concludes that coarser resolution of heterogeneity allows a greater selectivity, and he illustrates this with several examples. ***Chapter 6*** proceeds with the selection of patches of resources. The author shows that trade-offs between resource quality and abundance can change traditional models of patch use. Two aspects of patch use decisions are analysed in this chapter: which patches to visit and how long to stay in a patch, once visited? Empirical data for large herbivores often suggest that optimality principles are often useful in explaining which patches are used in a landscape, but are less successful at explaining how long herbivores choose to stay in a particular patch. ***Chapter 7*** continues with the selection of patches, but includes the intake of different resource types. These resources are unequally distributed over the landscapes, and it is only seldom that food of a herbivore at a given spot exactly matches its requirements. The authors introduce a modelling approach to consider the different satisficing requirements of herbivores. This yields new insights into the causality of the differential way that these animals use the same landscape. ***Chapter 8*** includes temporal variability in explaining foraging behaviour of large herbivores. The author considers how large herbivores adjust their foraging behaviour to cope with variability over different temporal frames. He outlines the conceptual foundation for 'adaptive resource ecology', covering changes in diet composition, daily time allocation, foraging movements, metabolic rate, digestive capacity and fat stores.

The next two chapters link large-scale movement of animals with their population dynamics. ***Chapter 9*** starts with looking at large-scale movements of large herbivores and focus on livestock herded by transhumant pastoralists. The authors analyse changes in the mobility of three pastoral groups, the Aymara of the South-American highlands, Mongolians, and the Maasai of Kenya and Tanzania. They show that pastoralists have successfully evolved methods of herding livestock to access adequate forage in areas of variable climate. ***Chapter 10*** continues with analysing large-scale movements of livestock and make a link between movements and so-called key resource areas. The authors discuss the various assumptions and conclusions regarding key resources and key resource areas, using the floodplains of the Sahel, especially those of Waza-Logone in Cameroon, as examples. They conclude by challenging the relevance of key resources and key resource areas for large-scale movements of livestock.

Chapter 11 illustrates that the mechanisms as discussed in the previous chapter have implications for explaining species diversity. This chapter address the question "Why are there so many species?" with a focus on the diversity of the ungulate community in Kruger National Park. The authors review several mechanisms of resource specialisation between herbivore species that allow coexistence, ranging from diet specialisation and habitat selection to spatial heterogeneity in resources. The authors argue that the focus on the constraints on species' exclusive resources governed by spatial heterogeneity is a useful tool for understanding how competitive interactions structure communities and limit species diversity.

Chapter 12 ends with providing prospects for further development of resource ecology. This chapter proposes six new directions for future research in the field of resource ecology based on the chapters, the hypotheses proposed in these chapters and the comments on the chapters.