

CHAPTER 12

PROSPECTS FOR FURTHER DEVELOPMENT OF RESOURCE ECOLOGY

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This book is about ‘resource ecology’, which we defined in our introductory chapter as “the ecology of trophic interactions between consumers and their resources”. We have chosen to focus on a particular class of consumers, namely, large mammalian placental herbivores. All chapters in this book deal actually with ungulates (in the broad sense, thus including elephant), whether free-ranging or domestic, but we are certain that every chapter is of much use to understand other classes of herbivores, such as marsupials, herbivorous birds or even herbivorous reptiles. In the comment on Chapter 4, the definition of ‘resource’ is given as “usable energy or any biotic or abiotic substance directly exploited by an organism, which includes food, nutrients, water, atmospheric gas compounds, as well as light, and the use of which can lead to the (temporary) exhaustion of that resource”. The essence of the concept of ‘resource’ is that organisms can compete for a resource and that it can be limiting the growth of individual organisms or of populations. In herbivores, the resource that is most interesting from a conceptual point of view, is herbage, because the feedback relations that exist between consumers and this type of resource (see for instance Van de Koppel et al. 2002; Rietkerk et al. 2002a; Van Langevelde et al. 2003). This of course does not deny the fact that other resources, such as water, or environmental conditions, such as temperature, can be very important factors to understand the distribution of herbivores (Bailey and Provenza, Chapter 2; Stein and Georgiadis, Chapter 3). From the consumer’s perspective, acquiring sufficient resources, such as energy, nutrients and water, are conditions for life and reproduction. In resource ecology, foraging is the central process because it leads to growth, survival and reproduction of the animal. This book deals with foraging, and it ignores predation or disease and highlights only a restricted set of fitness parameters of the consumer.



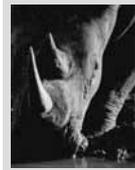
New technologies allow a much better description of both resource distribution and animals across the landscape

In nature, resources are always heterogeneously distributed and exposed to changing conditions (Skidmore and Ferwerda, Chapter 4). Seeking out food by animals is thus inevitably uneven in space and over time. For many years, foraging theory concentrates on issues how animals search and forage and what they should do so as to maximise their fitness, based on problems (i) how different possible behaviours affect fitness and (ii) what the decision variables are to maximise fitness. Foraging theory has made substantial achievements explicating observations of foraging behaviour. As foraging behaviour is largely determined by the spatial distribution and variability in time of the resources, many studies have recently 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.

From the contributions in this book a number of issues arise. The *first* is that new technologies, including new algorithms, allow a much better description of both resource distribution and of animals across the landscape. Bailey and Provenza (Chapter 2) show how GPS technology allows tracking of individual animals over a landscape. Different types of transponders are now so good that even information about physiological states of free-ranging individuals can be followed real-time. The accuracy is now so great that this can be done with a precision of metres while the time frames are down to minutes and even seconds. Stein and Georgiadis (Chapter 3) highlight new statistical techniques to describe aggregation patterns of animals. During the last few years, the development of new and better/faster algorithms even outstrips the speed of development of electronic hardware. The combination of new algorithms with faster and more precise hardware allows for the first time data collection and data handling surpassing theoretical insights. Skidmore and Ferwerda (Chapter 4) show how hyperspectral remote sensing allows an incredibly precise spatial description of the amounts of food, and even the quality of that food or the different plant species. We as scientists can now make accurate maps with every individual plant or clump of vegetation with a precision of centimetres and an extent of tens of kilometres within a brief span of time. It further develops theory by formulating new hypotheses to be tested. As the comment on Chapter 4 brings to the fore, it is now the task of students of animal behaviour to harness this new way of looking at resources or animals, and to use this plethora of data for testing ecological theories and for yielding a better understanding of resource ecology. Data now can become an embarrassment of riches in ecology.

Linked to this is the *second* conclusion to be drawn from the first three chapters: we can now describe both the distribution of resources and animals in such a more detailed and repeatable way that simple optimal foraging theory is insufficient to deal with the richness of the spatial data. Prior to the explosion of detailed knowledge of resource distribution over time and in space, optimal foraging theory provided a very useful 'harness' for the analysis of foraging between a few different

patches containing food, but now it only does so in simple experimental set-ups. In that context it can still provide very useful insights, just as basic insights in economy are still very useful in understanding some behaviour of consumers. Indeed, optimal

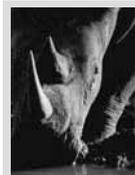


Simple optimal-foraging theory is insufficient to deal with the richness of the spatial data

foraging theory is not dead or outdated. In Chapters 2 and 6, the authors show how new insights can be gained to understand the giving-up time for patches that are visited by herbivores. It is important perhaps here to give a definition of what a 'patch' is, since it is such a central concept in this book and in resource

ecology in general. Patches are defined as regions that are more or less homogeneous with respect to a measured variable. There are four general approaches to defining patches, namely, simple aggregation of like-valued regions, moving- or split-window methods, global zonation and finally spatially constrained clustering (see, e.g., Pielou 1984; Legendre and Fortin 1989; Fortin 1994; Fortin and Drapeau 1995). Understanding giving-up times is an essential part of the development of optimal foraging theory. Bailey and Provenza (Chapter 2) point out that giving-up rules are not very robust when food in patches is plentiful. This clearly needs more attention in future. Yet, spatial ecology now can become a mature science since it is realised that scale issues become of overriding importance in ecology (see Rietkerk et al. 2002b). Indeed, numerous studies demonstrate the significance of taking into account the spatial structure of resources, including scale, both on the population dynamics of individual species as on 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.

The *third* conclusion we can draw is brought to the fore in Chapter 5 by Laca, namely, that large herbivores, like all other consumers, interact with their resources through a series of nested processes such as ingestion, searching, digestion and resting, which define relevant scales (see also Chapter 2, where definitions are



Animals interact with their resources through a series of nested processes, which define relevant scales for research but also for understanding what herbivores do

given) for research but also for understanding what herbivores do. Classical optimal-foraging theory does not address the issue of scale. In the comment on Laca's Chapter 5, the potential consequence of size and mobility on the perception of heterogeneity, diet choice and patch choice in large herbivores is discussed. In that comment reference is made to relevant

experiments (Drescher 2003). The point is that because resource distribution has to be understood at a nested series of scales, new theory is needed to cope with that. Murwira's (2003) work on using wavelets to describe resource heterogeneity, referred to in Chapter 4, is a possible way to use new mathematical techniques to understand the resource heterogeneity better. Not only spatial scale is relevant to understand animal foraging, Owen-Smith (Chapter 8) clearly demonstrates that temporal change in food quality and availability largely explains foraging. Different time scales may simultaneously interact: resource depletion and regrowth, day-night variation, even up to seasonal variation (see also Boone et al., Chapter 9).

The *fourth* generalization is that we begin to understand upscaling of foraging decisions much better than a few years ago. Several chapters (for instance, Chapters 5, 6, 7, 8 and 9) deal with this. In Chapter 9, Boone et al. point out that even the functional-response curve describing the relation between intake and biomass on



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offer is scale-dependent. In an elegant application of the SAVANNA-model, they show that subdivision of land leads to a lower total herbivore biomass offtake. Similar results were found by Kramer et al. (2006) when they investigated the interaction between resources and a set of temperate herbivores using the FORSPACE-model (see also Groot-Bruinderink et

al. 1999). Linked to these issues of nestedness and upscaling is the *fifth* important theme emerging from this book, which is non-linearity. Chapter 5 addresses this issue, but it is really emphasized in Chapter 9. Perhaps we can safely draw the conclusion that neither resource utilization nor feedback between herbivores and resources can be linearly upscaled. Chapters 7, 9 and 10 deal with animal movements. Mobility is the important differentiating factor between plants and sedentary organisms on the one hand and most animals on the other. These chapters lead to the *sixth* general conclusion, namely that mobility can counteract resource heterogeneity. These chapters offer the building blocks for new theory. This novel theory has not crystallised yet but we are sure that it will entail the following hypothesis, namely “the relative abundance of large animals (in contrast to small ones) in assemblages increases with spatial variation and sudden fluctuations in resource availability that result in longer time periods between foraging events”. The rationale behind this hypothesis is that larger animals are better in dealing with increased spatial variation in resource availability (Prins and Van Langevelde, Chapter 7; Morse et al. 1985; Ritchie and Olff 1999) and in buffering drops in resource availability of longer duration than are smaller ones (Owen-Smith, Chapter 8; Biddanda et al. 2001; Li 2002; Li et al. 2004), as their metabolic energy use per unit of mass and per unit of time is lower than for smaller animals. Increased spatial variation may lead to larger distances between food patches, resulting in decreased food intake (Laca, Chapter 5; Fryxell, Chapter 6; Prins and Van Langevelde, Chapter 7). Food intake also decreases with more fluctuations in resource



Animal's mobility can counteract resource heterogeneity

availability (Owen-Smith, Chapter 8). Both increased spatial variation and more fluctuations lead to longer time periods between foraging events, and could even lead to starvation. Larger animals can move larger distances between spatially distributed resources (have larger home ranges, Haskell et al. 2002; Jetz et al. 2004, and higher movement speed, Prins and

Van Langevelde, Chapter 7; Jetz et al. 2004), and buffer sudden drops in resources over a longer time than smaller species (Owen-Smith, Chapter 8; Dunbrack and Ramsay 1993) as they have more fat reserves per unit mass, hence higher starvation

resistance. Although there are many strategies that animals can adopt to cushion the stress of seasonality (e.g., migration and hibernation), these strategies fail when resource availability becomes increasingly irregular.

By applying the allometric scaling laws for mobility and starvation resistance from Chapter 7 of Prins and Van Langevelde, one could model food intake as a function of spatial variation and variation over time in resource availability. By including this intake model into population models one could then make predictions about abundances as function of body mass and spatial and temporal variation in resource availability (Prins and Van Langevelde, Chapter 7; Van Langevelde et al. submitted), which will perhaps be the breakthrough needed. Science is in progress, and if we were certain then it would have been published already.

Perhaps the two most important elements in the present volume are the commentaries and the hypotheses. All contributors to the present volume sincerely hope that the commentaries will stimulate discussions or provoke new insights. The commentaries were not written to please the authors but they were put in writing so as to put on view disparities in opinion. Indeed, in science the age-old method of dialectics with its formulation of thesis and antithesis is still valid, and we hope that readers will further contribute to this dialectic discourse so as to arrive at new insights. The second important element is comprised of the sets of hypotheses. We are acutely aware that the purpose of mathematical theory is to deal with 'all possible worlds' and the purpose of experiments and fieldwork is to deal with the real world. We believe with Wilson and Bossert (1971) that to measure the parameters, to search for new parameters and to improve theory is ultimately the most effective way of viewing the real world. Well-formulated hypotheses can be a sure way of organising one's research, and can help searching for new parameters and measuring them well. All in all, the authors have formulated some 30-odd hypotheses to further develop theory on resource ecology. Some of them can be tested quite straightforward from observational data. Other hypotheses need careful experimentation. We believe, however, that these hypotheses and propositions have been formulated in such a way that they can and must be tested.