ECOLOGY

A Different Approach to Modeling

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Large herbivores play a key role in many ecosystems in a variety of biomes around the world. They are often the focus of harvesting, poaching, or conservation efforts. Their proper management is therefore of the utmost importance, and it requires accurate understanding of their population dynamics. This is especially the case today, with the threats of climate change and an increasing human population. In this context, South African ecologist Norman Owen-Smith's *Adaptive Herbivore Ecology* is important because it aims at providing a platform for modeling the dynamics of herbivore populations through an explicit link to their foraging behavior.

Adaptive Herbivore Ecology
From Resources to Populations in Variable Environments
by Norman Owen-Smith
Cambridge University Press, Cambridge, 2002. 390 pp. $90, £65. ISBN 0-521-81061-2.

Adaptive Herbivore Ecology deals with phenotypic plasticity in herbivore behavior, physiology, morphology, and life history traits within a framework of population and community ecology. The "adaptive" in the book's title may, incorrectly, suggest adaptation in an evolutionary sense. The term is primarily used, though, to avoid the somewhat more emotion-laden "optimal." Rather than serving as a general overview of herbivore ecology, the book emphasizes conceptual issues; it provides ideas but presents little data.

Through the course of the book, Owen-Smith works up a hierarchy from considerations of foraging behavior toward processes that occur at higher levels of integration in populations and communities. He begins by presenting the conceptual basis of the bioenergetics-based growth, metabolism, and mortality (GMM) model that forms the foundation of his account. It resembles the modeling approach often taken in the 1970s, during the period of the International Biological Programme. However, at that time, the modelers lacked in-depth, field-based knowledge about the systems they modeled—knowledge Owen-Smith possesses. And the author, as he points out, avoids the ambition of modeling an entire ecosystem. Instead, he develops an integrated set of process-based models that represent the various components of the herbivores' ecology, with a focus on how herbivores relate to the living and nonliving parts of their environment.

Four chapters cover the ecology of resource use of individual herbivores. These examine the functional response (the relation between food intake rate and resource abundance), resource patchiness and depletion, heterogeneity in plant quality and abundance, and physiological processes such as digestion. This section is well balanced—almost unexpectedly so, given how involved Owen-Smith was in the back-and-forth debate over the linear programming model. (He was the principal critic of this much-used approach to predicting foraging behavior in ungulates.) His coverage of ungulate foraging behavior provides an excellent, though not exhaustive, treatment of the topic; quite properly, it is written with great authority.

In the next several chapters, Owen-Smith considers the links between resource acquisition and metabolism on the one hand, and between resource acquisition and population dynamics on the other. He guides the reader through topics such as the dynamic allocation of resources to growth, storage, and reproduction; the regenerative responses of vegetation resources to herbivory in seasonally varying environments; the generation of density dependence over the seasonal cycle by within-population competition; and the dependence of mortality on resource gains.

Well-regulated populations. Despite variations in population density, greater kudu (*Tragelaphus strepsiceros*) are neither rare nor overabundant in South Africa's Kruger National Park.

Owen-Smith comments, "Equilibrium thinking—the 'balance of nature' paradigm—still permeates much of ecological theory. I see too many formal models occupying the pages of journals like *The American Naturalist* that seek analytic solutions around near-equilibrium states. As a former physical scientist (in my early student days!), I perceive such modeling attempts as little more than physics masquerading as biology." That view may irritate many theoretical ecologists, but the Lotka-Volterra approach (which incorporates coefficients for the interactions between species into the population growth equations) certainly has clear limitations even though it has guided much of modern ecology. Owen-Smith has based the cornerstone of his metaphysiological modeling on Australian ecologist Graeme Caughley's modification of these famous equations to apply specifically to herbivore-vegetation systems (*1*). The author further develops Caughley's original model by defining mortality as a nonlinear function of nutritional gain and by allowing for physiological expenditures. After describing the GMM model, Owen-Smith uses it to explore various problems faced by an adaptive herbivore. He considers such questions as: How important is seasonality? How does access to food of variable quality affect population stability? And how does this relationship depend upon the size of the herbivore species?

The book's population-dynamic modeling is novel and thought-provoking. It provides a good basis for further work, prospects that Owen-Smith discusses in the final chapter. We are unsure, however, whether the GMM approach—using biomass rather than number of individuals—will convince many population biologists to change track. Even though in considering the Soay sheep population of the Hebrides island of Hirta Owen-Smith does extend his GMM model to include a simple age- and sex-structure, biomass will only be a poor proxy for the number of individuals.

The author's background lies in the ecology of African ungulates. His doctoral research on the behavioral ecology of white rhinoceros (*Ceratotherium simum*) included 3.5 years of following individuals on their daily activities in South Africa's Hluhluwe-Umfolozi Park. Later, he carried out similar studies on the greater kudu (*Tragelaphus strepsiceros*) in Kruger National Park. The book clearly reflects this African foundation. Though quite good, Owen-Smith's overview of ungulates living in the highly seasonally changing environments at northern latitudes is weaker than his treatment of other topics.

It is nearly unique and rather important that a field ecologist with such a solid empirical background should write a book on modeling. Indeed, Owen-Smith qualifies as an adaptive herbivore ecologist. He clearly has grasped the tremendous advantages of modeling while still remembering the importance of in-depth knowledge about the systems being modeled. We found *Adaptive Herbivore Ecology* an enjoyable and informative addition to the ecological literature. Above all, it forced us to reassess the more standard approaches we typically take in the modeling of ecological dynamics and processes. We are convinced others will find the book equally stimulating and useful.

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Reference

1. G. Caughley, in *Theoretical Ecology*, R. May, Ed. (Blackwell, Oxford, 1976) pp. 94–113.